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SOME ASPECTS OF MARIANA ISLANDS PARTULIDAE (Mollusca, Pulmonata)

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IN THIS PAPER a new species of *Partula,* living in sympatric association with *Partula gibba* on Agiguan, is dedicated to the late Daniel B. Langford; the sinistral form of *P. gibba* on Saipan is discussed; the northward distribution of *P. gibba* to Pagan and Alamagan is recorded; and the 1959 discovery of *Samoana fragilis* on Rota by Robert P. Owen is documented.

The 126 known species of Partulidae are distributed (Fig. 1) on most of the high islands of the Pacific, from Palau to the Marquesas, a range of 5,300 miles. They are absent from a few high islands, including Yap, Truk, Hawaii, Mangareva, Pitcairn, and Juan Fernandez. Precise differences in genital anatomy divide Partulidae into 3 clearly defined genera, namely, *Eua* with 4 species, *Samoana* with 22, and *Partula* with about 100 species. The oldest genus, *Eua,* is narrowly confined to Tonga and Samoa. *Samoana,* the intermediate genus, is distributed from the Mariana to the Marquesas Islands. The youngest genus, *Partula,* is distributed from Palau to the Society Islands. Genitalia of the 3 genera are described by Pilsbry and Cooke (1934).

* Volume XXIV of the Occasional Papers is published in honor of Edwin H. Bryan, Jr., whose service to Bishop Museum began in 1919. He was for many years Curator of Collections, and at present is Manager of the Museum's Pacific Scientific Information Center. A Symposium, at which several of the papers in this volume were read, was held at the Museum on April 13, 1968, honoring Mr. Bryan on the occasion of his 70th birthday.

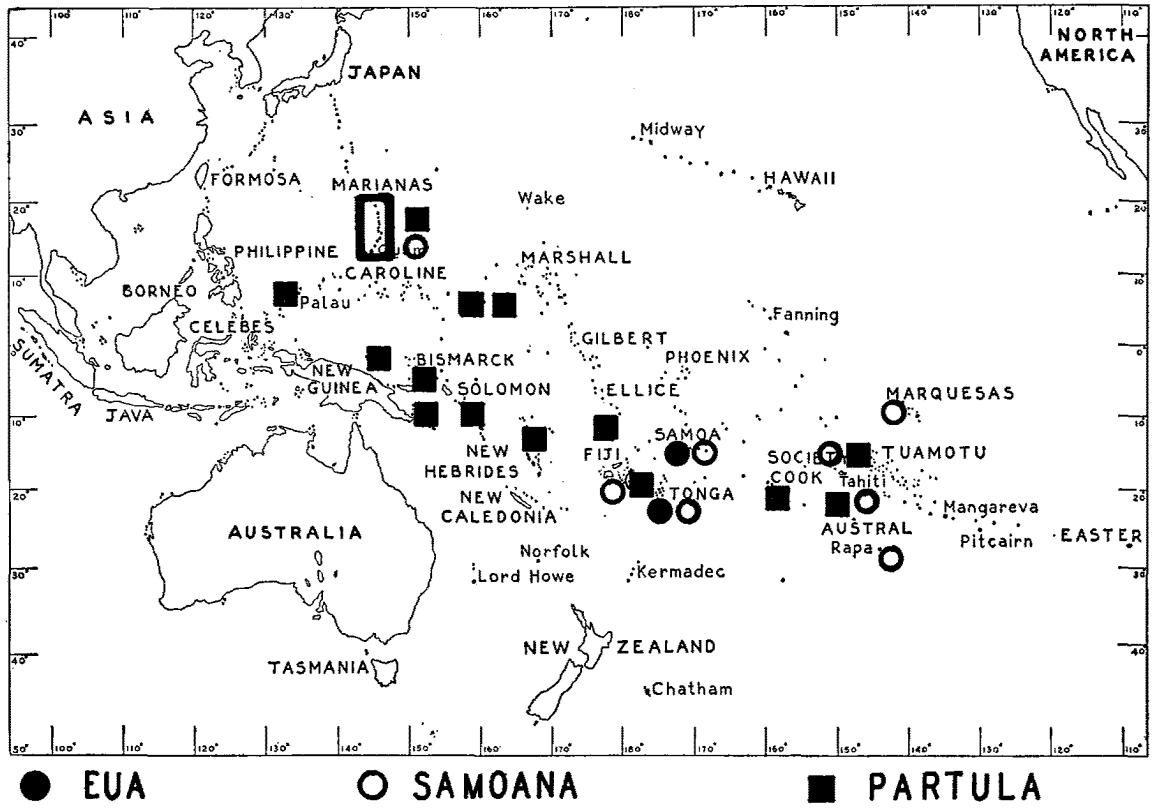
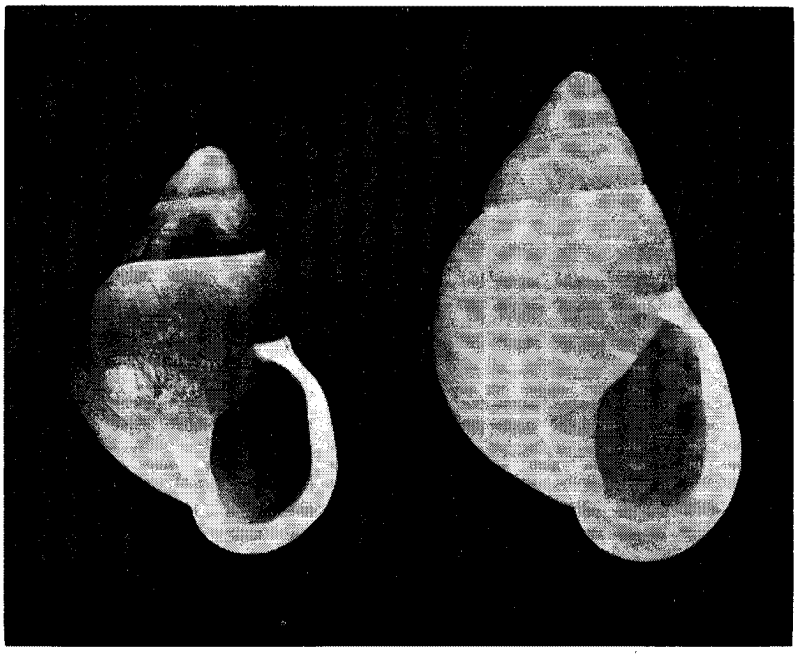


FIGURE 1.—Distribution of the genera of Partulidae: *Eua* in solid circle; *Samoana* in open circle; *Partula* in solid square. Map of Mariana Islands is enlarged in Figure 13.

Partulidae of Guam are: *Samoana fragilis* (Férussac), *Partula gibba* Férussac, *P. salifana* Crampton, and *P. radiolata* (Pfeiffer). These are colorfully illustrated in Crampton's Mariana volume on Partulidae (1925). Existence of *P. gibba* on Rota, Tinian, and Saipan was known previously. In 1949 *P. gibba* was discovered on Pagan and Alamagan; in 1952 it was discovered on Agiguan, living sympatrically with the new species described here.



FIGURES 2, 3.—Left (Fig. 2) *Partula langfordi,* a new species from Agiguan, living in sympatric association with *Partula gibba,* right (Fig. 3).

Partula langfordi, new species (Figs. 2, 4, 5, 8).

Shell dextral, ovate-conic, moderately thin, perforate (Fig. 2). Spire of 5 whorls, short, apex obtuse. Whorls slightly convex, the last subglobose and faintly gibbous, periphery weakly angled. Sculpture of closely spiral lines, weak in the embryonic, strengthening in postembryonic whorls to form a fine network on conjoining with fine growth striae. Aperture oblong-ovate, the white peristome thickened and expanded. Columella with a faint upswelling, margin of columella built forward over small umbilical perforation and joined to outer margin by a thinly laid callus. Background color buff, superimposed by

maroon; the maroon appearing as a band on whorls 2 and 3 on frontal view. Band begins at whorl 1½ as a faint brown suprasutural marking one-third the width of whorl and gradually widens to one-half width of whorl and deepens to maroon at whorl 3, thence expanding to three-fourths width of whorl 4 and finally dissipating into a vague blend of buff-maroon at the beginning of whorl 5 to the end of shell.

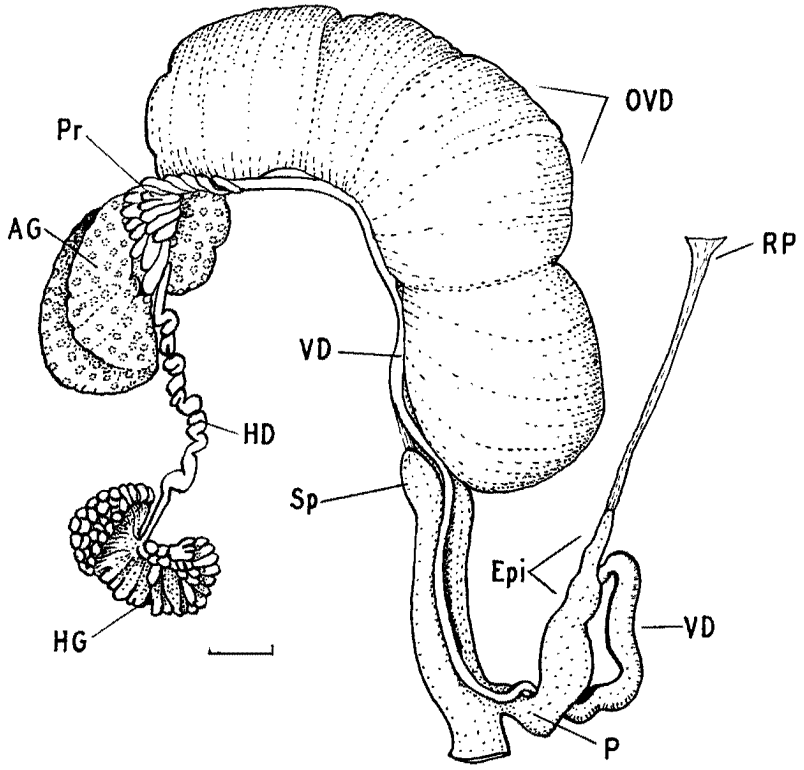


FIGURE 4.—Genitalia of *Partula langfordi*. AG, albumen gland; Epi, epiphallus; HD, hermaphrodite duct or duct of ovotestis; HG, hermaphrodite gland or ovotestis; OVD, oviduct; P, penis or phallus; Pr, prostate gland; RP, retractor of penis; Sp, spermatheca; VD, *vas deferens*. Scale is 1 mm.

Genitalia (Fig. 4) similar to that of *Partula gibba:* hermaphrodite gland or ovotestis (HG) 4- to 5-lobed, follicles numerous and distended; duct (HD) convoluted; albumen gland (AG) enlarged; prostate (Pr) diminished, follicles few, appearing depleted; *vas deferens* (VD) free from prostate to epiphallus (Epi), entering epiphallus at midpoint; oviduct (OVD) distended with four embryos, the two upper immature, the two lower mature; spermatheca short, tip bluntly pointed, joining oviduct just above juncture of penis with it. Penis

(Fig. 4, P) small, slightly contracted, narrower at base, enlarged at middle, constricted at the commencement of epiphallus; base of epiphallus forming a small bulb where *vas deferens* enters it, ending in a narrow tip to which retractor of penis (RP) is attached terminally; retractor attached to diaphragm.

The penis of a younger specimen (Fig. 5), lacking any embryo in the oviduct, is illustrated to demonstrate a phallus of *P. langfordi* in normal relaxed condition. The penis of a mature *P. gibba* with three embryos and living sympatrically with *P. langfordi* is illustrated to demonstrate that no morphological difference exists between these two species (Fig. 6). Further-

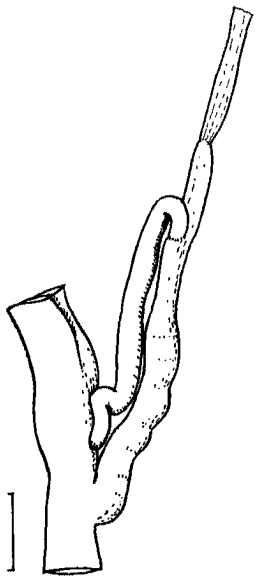


FIGURE 5.—Closeup of penis from another specimen of *P. langfordi* showing relaxed state. Scale is 1 mm.

more, no difference exists between the penis of these two species and those of *P. radiolata* (188924) and *P. salifana* (152877) of Guam.

Interior of penis of all four species of *Partula* is similar to that of *P. gibba* of Guam (Fig. 7), 190272. Epiphallus thin-walled, ornamented with vertically oriented soft ridges of flesh which divide into tubercles when spread out for examination. *Vas deferens* debouches into epiphallus at midpoint. Interior of phallus consists of vertically oriented cords of thick fleshy ridges, the principal cords bound laterally to each other by smaller interconnecting spurs.

Holotype of *P. langfordi,* 213183: length 14.0 mm., diameter 9.0 mm., length of aperture 8.0 mm.; range of measured specimens 213190 to 213199: 12.9 mm. × 9 mm. to 15 mm. × 11.4 mm.

Mariana Islands, Agiguan (Aguijan) near 14° 50'N., 145° 30'E., 1,000 yards northeast of Boat Landing (Army Map Service W843 of 1951) at station 1952-15, altitude 200 feet, in open forest, on native plants predominantly *Aglaia,* 26 May 1952, collectors Yoshio Kondo, Albert B. Bronson, Ramon Sannicolas, BBM 213189-200, total 95 adults (10 given to Dr. H. E. Crampton of The American Museum of Natural History on 11 December 1954), 7 juveniles. Same location 213171-173, 80 adult specimens, 1952-15A, 8 June, Yoshio Kondo. Specimens dissected from 213189-200.

Collected in sympatric association with *Partula gibba* (Fig. 3) in five nearby colonies. The specimen illustrated here is 17 mm. × 11 mm. in con-

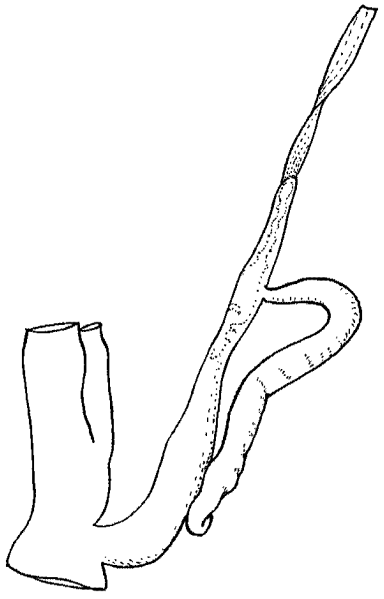


FIGURE 6.—Penis of *Partula gibba* from Agiguan.

trast to *P. langfordi* 14 mm. × 9 mm., and is whitish-yellow or straw-colored. Range of measured *P. gibba* is 15.6 mm. × 11.1 mm. to 17.6 mm. × 12.6 mm. Absence of intermediates in all these colonies provides firm evidence that reproductive isolation exists between these two forms of *Partula* on Agiguan. Dr. John Easley, formerly of the Hilo Campus, University of Hawaii, constructed a scattergram (Fig. 10), based on the measurements of 73 specimens of *P. langfordi* and 48 of *P. gibba,* which adds additional evidence that the two coexisting forms are separable as species. Dr. Easley's text is appended at the end of this paper.

The reproductive isolation which separates these two closely associated forms so distinctly is remarkable and requires an explanation. The first is

that they are the products of a double invasion: the one arriving on Agiguan in sufficient time to develop in its own line; the other arriving later, and both sufficiently divergent from each other to preclude interbreeding. The second is that they are widely separate segments of an allopatric species carried to Agiguan at the same or at separate times and incapable of interbreeding. Both hypotheses are from Ernst Mayr (1949).

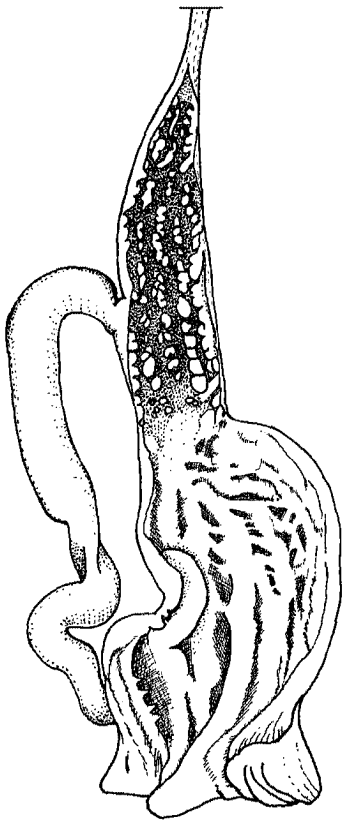
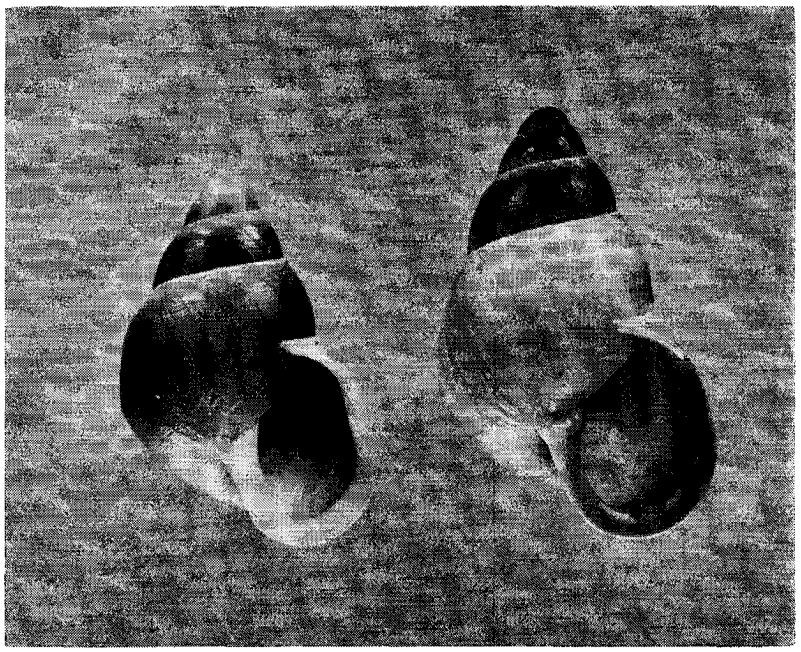


FIGURE 7.—Interior of penis, *Partula gibba* from Guam.

Comparison: it is evident that *P. langfordi* is a direct derivative of *P. gibba* of such a form as illustrated by Crampton (1925, Pl. 13, Figs. 15-19, color order phaea-purpurea) from Guam. *Partula langfordi* (Fig. 8) is here photographically compared with a color form of *P. gibba* from Rota (Fig. 9), BBM 213281. *P. langfordi* is much smaller; its spire is shorter and the convexity of whorls much less; the last whorl is proportionately more capacious and its gibbous outline emphatic, whereas the Rota specimen does not show this.

When first collected, these two forms were assumed to be two extreme variants of *P. gibba, P. langfordi* being diminutive and bluish, *P. gibba* being very much larger and whitish-yellow. This assumption was based on the fact that notable variability in size and coloration exists elsewhere and is particularly outstanding on Guam. But the absence of intermediates made a more detailed survey necessary for later analysis. The Pacific Science Board's *Gonaxis* Survey Expedition was then gathering evidence of the percentage of control *Gonaxis kib-*



FIGURES 8, 9.—Left (Fig. 8) *Partula langfordi* compared with *P. gibba* from Rota, right (Fig. 9).

weziensis (E. A. Smith) was exercising over *Achatina fulica* Bowdich. Robert P. Owen, Albert B. Bronson, and George D. Peterson volunteered to attempt a definition of the limits of this particular colony; the extent and density of the commingling of the "Blue" (*langfordi*) and the "Yellow" (*gibba*), as the two species were informally named, and the point at which they admixed. The three men spent 28 May in this survey, and constructed a crude map of

that population with station 1952-15 as reference point (point zero). The site is 1,000 yards northeast of the *Gonaxis* survey camp, near Boat Landing, along a trail 200 yards south of the northern sea cliffs rising 100 feet vertically from the ocean. Eight collections were made by Owen, Bronson, and Peterson (the first five and last three on the tabulation); these are tabulated (Table 1) with those of Kondo (55A) and with 15 and 15A (point zero). The directions west and east include those southwest and southeast. Only adults are enumerated.

TABLE 1

WEST	STATION	*Partula langfordi*	*Partula gibba*
400 yards	33	0	4
400	30	0	14
325	34	0	52
50	35	32	17
25	29	10	12
25	55A	11	19
0	15, 15A	168	46
EAST			
25	36	78	8
25	31	89	1
300	32	76	0

The mixed population occupied an area of 700 yards east-west and 400 yards north-south. The population was not uniformly distributed, but occurred in small colonies with large unoccupied spaces between colonies beyond point zero. The intermixture of *P. langfordi* and *P. gibba* occupied a space 75 yards east-west and 60 yards north-south. In the mixed colonies *P. langfordi* outnumbered *P. gibba,* except at 29, where the three men pinpointed a line of separation between the two which Kondo checked later (55A). The tabulated figures provide evidence that *P. gibba*'s domain is the western side of the population and *P. langfordi*'s the eastern.

Nine other colonies of *Partula* were collected on Agiguan, two on the north coast (*langfordi*), and seven on the west end (six *gibba,* one *langfordi*). No collections were possible at the east end and on the south coast.

Agiguan is an uplifted oblong limestone island, 3 miles long and 1 mile wide, composed of the same Cenozoic limestone and volcanic

material as nearby Saipan. Its highest point is a 168-meter peak near the west end; the top central plateau at 135-155 meters was cultivated for sugar and pineapple by the Japanese. Some of the native forest below the plateau remained in 1952, but was subjected to foraging by numerous bands of feral goats. The island was then uninhabited.

Partula langfordi is dedicated to the late Daniel B. Langford who, in company with his brother-in-law, Ditlev Thaanum, compiled the Thaanum-Langford Collection of Pacific marine shells between 1893 and 1952. This 160,000-specimen collection was given to Bishop Museum in 1963.

Data for the species described or figured in connection with *Partula langfordi* of Agiguan are as follows: *Partula gibba* figured shell Agiguan 213184, figured penis 213177; figured interior of penis Guam 190272, Dededo-Yigo, 23 February 1946, S. L. Kimball; figured shell Rota 213185, north coast, altitude 20 ft., 21 June 1952, Ignacio Benavente, Juan Dias, Y. Kondo. *Partula salifana* (not fig.) Guam 152877, Mt. Alifan, altitude 800 ft., 20 April 1936, Edwin H. Bryan, Jr.; *P. radiolata* (not fig.) Guam 188924, Tumon Bay, inland 100 ft., altitude 11 ft., 10 July 1946, D. F. Grether.

Partula gibba, measured by John Easley for scattergram, are from 213177, 213180, 213182, and 213010, Agiguan, 48 specimens; *P. langfordi,* measured for the same scattergram, are from 213190 to 213199, Agiguan, 73 specimens.

QUANTITATIVE ANALYSIS OF *Partula langfordi* AND *P. gibba* ON AGIGUAN

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THE INITIAL MEASUREMENTS serve to demonstrate the absence of intergrading between the blue *Partula langfordi* and the yellow *P. gibba* of Agiguan. No specimen of the 121 shells studied could be misclassified as to size. This is shown clearly by the data presented graphically in the scattergram (Fig. 10). The difference in the color distributions is even greater, and it was therefore not judged necessary to measure the color of the specimens and determine the distributions. From these facts we may infer that there is probably no gene flow between the two sympatric populations. Such gene flow would surely manifest itself in a noticeable intergradation of color as well as size, and much less is observable than that shown in length and width. The few blue individuals which are noticeably lighter than the average are still pronouncedly darker than the yellow, which show scarcely any noticeable variation in color at all.

There is a striking feature of the distributions of length and width of the two groups. Both distributions are pronouncedly skewed toward each other. Statistically, this implies that none of the usual tests of significance of the difference are applicable. Fortunately, none are needed to determine the fact that the two populations do not overlap in length or color. The chances are minute, indeed far less than calculated in any table, that a difference as great as that observed for these sample sizes could arise by chance fluctuations in the samples. The nonparametric Kolmogorov-Smirnov Test (Walker and Lev, 1953, p. 428) shows that an overlap as great as 60 percent would be significantly different at the .001 level for these sample sizes.

However, the biological implications of the skewness require further study. Since the distinct gap between the two clusters implies a genetic separation, it is possible that the skewness represents the result of selective pressure operating against the genetic limits of size variability. A comparative study of the whole group of Partulidae is required to provide any basis for such a conclusion. The opportunity for investigating the process of speciation in this group is suggested by the distribution of the size of the two populations on Agiguan. The

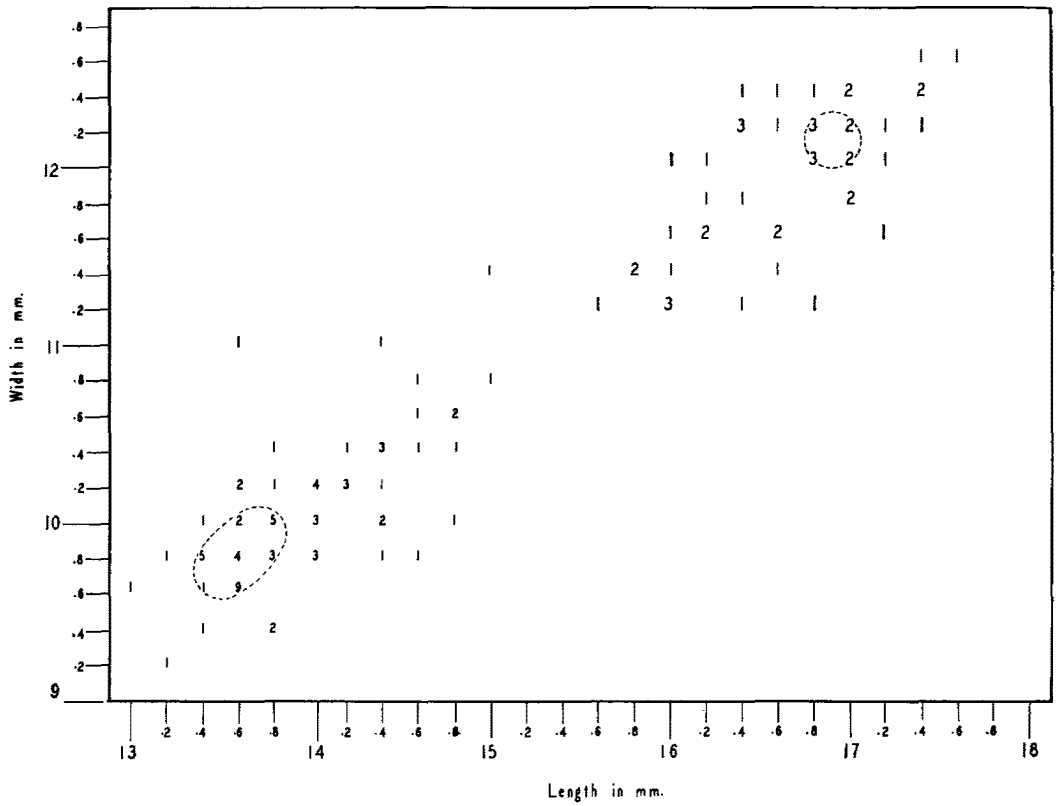


FIGURE 10.—Scattergram of the length and width of 73 specimens of *Partula langfordi* (left, lower) and 48 specimens of *P. gibba* (right, upper) from Agiguan. The number of specimens of *P. langfordi* in small print; those of *P. gibba* in large print. The maximum densities of 25 percent of each species are encircled. (By John Easley.)

parameters of the distributions of size of all Partulidae, if determined, could indicate the nature of the relationships and the direction of selective pressures involved in the process of differentiation and speciation in this group.

Measurements plotted in the scattergram were recorded to .2 mm. and made with calipers placed parallel to the axis of the shells for length (see Table 2). Width was similarly measured at right angles to the axis through the greatest thickness of the shell.

TABLE 2

	P. langfordi		*P. gibba*	
	L.	D.	L.	D.
Max.	15.0 mm.	11.4 mm.	17.6 mm.	12.6 mm.
Min.	12.9	9.1	15.6	11.1
Range	2.1	2.3	1.8	1.5

SINISTRAL *Partula gibba* ON SAIPAN (FIG. 11)

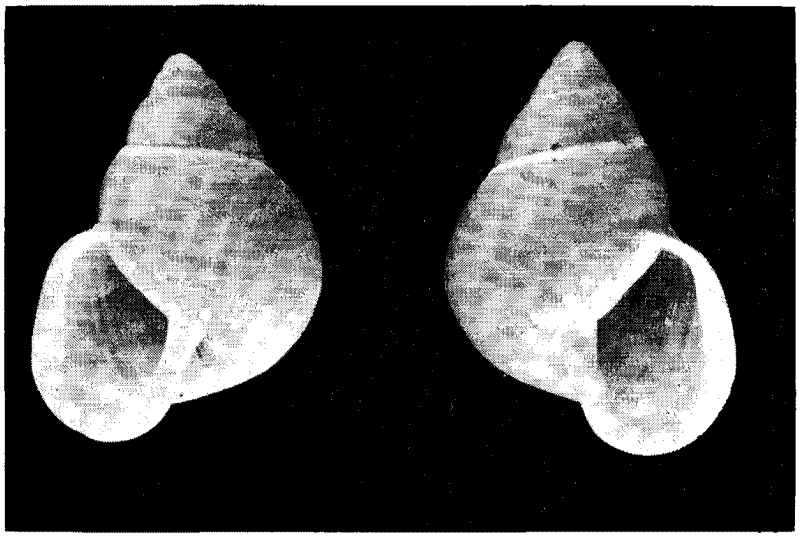
Haltenorth and Jaeckel (1941) reported sinistrality in *Partula gibba* from Saipan and figured a specimen with a dextral; of 91 specimens 10, or 10 percent, were noted to be sinistral. Since the end of World War II, further reports were made (personal communications) by R. T. Abbott and Daniel B. Langford. In 1949, R. K. Enders, A. R. Mead, and Y. Kondo made two collections of sinistral and dextral *P. gibba* on Saipan, on the centrally located Mt. Tapochau at 1,300 feet, and at its peak, 1,555 feet. In 1952, 13 collections were made in this location and its vicinity by I. Benavente, G. D. Peterson, and Y. Kondo as follows: 3 at Tapochau; 6 at subhill 1,299 feet, ¼ mile north; 4 at Canad-i-Eddot, 1½ miles south at 700 feet. These are tabulated in Table 3; only adults are enumerated.

TABLE 3

NORTH			TAPOCHAU			SOUTH		
STATION	DEXT.	SIN.	STATION	DEXT.	SIN.	STATION	DEXT.	SIN.
1952-5	77	11	1949-38	95	22	1952-91	153	3
-5A	58	11	-39	71	5	-92	283	24
-5B	53	14	1952-8	109	37	-93A	210	12
-6	30	16	-9	126	21	-93B	101	12
-6A	22	7	-8A	13	1			
-7	132	7						

The tabulation of the 15 collections provides the following information: the percentage of sinistrals is highly variable, and it tends to be higher at Tapochau and its close vicinity (north) as compared to a location farther south which is at a lower altitude.

The sinistral specimen Saipan 213187 is 18 mm. × 15 mm., whitish-yellow or straw-colored; the dextral specimen (Fig. 12) is 19 mm. × 13 mm., and similarly colored. Both specimens are from Canad-i-Eddot, 700 feet, 26 June 1952, I. Benavente and Y. Kondo.



FIGURES 11, 12.—Left (Fig. 11), *Partula gibba,* sinistral form from Saipan, illustrated with ordinary dextral form, right (Fig. 12).

Samoana fragilis ON ROTA

On 10 September 1959, Robert P. Owen collected 16 specimens of *Samoana fragilis* (see Crampton, 1925, Pl. 11, Figs. 12-19) on Rota, associated with *Partula gibba* on the plant *Hernandia.* This is the first record of *S. fragilis* being found beyond the island of Guam, where it is endemic. Hans G. Hornbostel collected on Rota for Bishop Museum in 1925-1926 and did not find it there. Ignacio Benavente and Yoshio Kondo collected within 400 yards of Owen's

locality in 1952 (1952-87), and other stations, but did not find this species. The form of *P. gibba* associated with Owen's *S. fragilis* is an exact counterpart of those from 1952-87: a dirty white background with a faint eroded maroon banding on the upper whorls, lip also tinged with faint maroon. Exact location is at grids 305 and 1564 (Army Map Service W843); thence east 250 yards and north 100 yards; in the middle of the western half of Rota, altitude 1,100 feet, at the end of Sabana Road where the trail to the open phosphate mine leads off, 213164-168.

Partula gibba FROM ALAMAGAN AND PAGAN

In 1949, during the Pacific Science Board's *Achatina* survey of the Bonin and Mariana Islands, Palau, and Truk, samples of *Partula gibba* were collected on Alamagan and Pagan, islands which are geologically younger than those of the Southern Marianas, and composed of active or recently active Quaternary volcanoes (Schmidt, 1957).

On Pagan Island, Donald Anderson and Yoshio Kondo collected a total of 28 adults and numerous juveniles in six locations between 50 and 500 feet altitude, from 21 to 29 September 1949. The largest collection of 17 specimens came from station 1949-103, in a grove of breadfruit mixed with *Aglaia,* 213947-952, 50 to 75 feet altitude, 28 September 1949. The six stations are on and below the 500-foot cliff leading east from Shomushon, central Pagan. Coloration of Pagan shells is yellowish-white or straw, and they are about the size of the Agiguan and Saipan shells figured in this paper. The forest was very poor in this part of Pagan because of cultivation.

On Alamagan in 1949, 339 adults and numerous juveniles of *Partula gibba* were collected by Donald Anderson, Yoshio Kondo, and Navy electrician Ben Harrison, in five locations on the western and southern parts of the island in three days, from altitudes 600 to 800 feet. Station 1949-109 is selected as typical, eight gulches south of Pattido, dense forest, 700-800 feet, 49 specimens from 214041-042, 2 October 1949. The shells are either straw-colored or light gray, or an intermediate color between the two, and about the same size as those from Pagan, Saipan, and Agiguan. In contrast to Pagan, the forest was dense, wet, and lush, and the snail fauna rich.

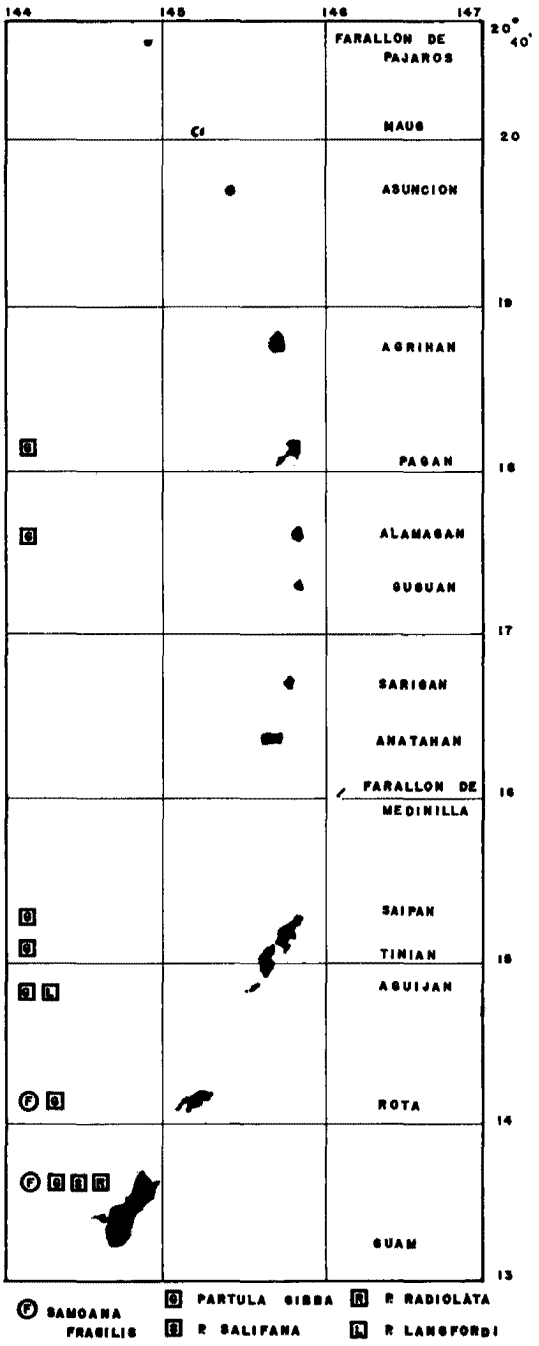


FIGURE 13.—Map of Mariana Islands illustrating the distribution of *Partula gibba, salifana, radiolata, langfordi,* and *Samoana fragilis.*

DISTRIBUTION OF PARTULIDAE IN THE MARIANA ISLANDS (FIG. 13)

Four species of Partulidae exist on Guam, namely, *Partula gibba* Férussac, *P. radiolata* (Pfeiffer), *P. salifana* Crampton, and *Samoana fragilis* (Férussac). *Partula gibba* occupies low, middle, and high altitudes universally; *P. radiolata* occupies low and middle altitudes but not the high, and to a lesser extent than *P. gibba; P. salifana* is a high-altitude species, and sparsely distributed. *Samoana fragilis* occupies middle and high altitudes, and is distributed universally, but in a spotty manner. Highest altitude on Guam is 1,334 feet at Mt. Lamlam.

Partula gibba appears to be endowed with certain characteristics which indicate a species about to undergo diversification in several directions: universal distribution over Guam and its neighbor islands; dense populations in most places, indicating high fertility; great diversity in coloration; and diversity in size from place to place. One of its foremost characteristics is its ability to survive migratory voyages and to propagate its kind. This has led to the dispersal of *P. gibba* to Rota, Agiguan, Tinian, and Saipan in the Southern Marianas and to Pagan and Alamagan in the Northern Marianas (Fig. 13). A close search of the other Northern Marianas should reveal other islands on which *P. gibba* has arrived.

The mechanism providing power and motility for the northward migration of *Partula gibba* must be credited to the annual typhoons, which have a generally northerly direction in this region.

To summarize: *Partula gibba* (G in Fig. 13) has been distributed northward from Guam to Rota, Agiguan, Tinian, Saipan, Alamagan, and Pagan. *Partula langfordi* (L in Fig. 13), a species evolving from *P. gibba* elsewhere, lives in sympatric association with *P. gibba* on that island. *Samoana fragilis* (F in Fig. 13) appears to be a recent migrant from Guam to Rota.

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