

PARTULIDAE OF TONGA AND RELATED  
FORMS

By

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## INTRODUCTION

Tree snails of the family Partulidae are distributed so widely in Polynesia and Melanesia that they offer excellent clues for tracing the affinities and lineage of the insular faunas. The receipt of two species of this family from the island of Eua has given an opportunity for consideration of the filiations of the Tongan Partulidae. None were previously known from these islands.

Relationships in the Partulidae can only be determined approximately at present for the reason that the family has been classified upon the basis of shell characters, which are not fundamental as guides to phylogeny. Hitherto the anatomy has been worked out only in a few Society Islands species referable to the subgenus of *Partula*. By utilizing abundant material recently received at Bernice P. Bishop Museum it has been possible to overcome this handicap, so far as Tongan species are concerned, by studies of the anatomy of species of the neighboring Samoan and Fijian islands, together with some further information of the Society Islands species.

The chief anatomic differentiation of the family appears to be in the structure of the penis, which is remarkably varied in the several groups which we are now recognizing as genera.

In the pallial complex we have not found any constant differences between the genera. The shape and length of the kidney vary among the Partulidae, but the variations do not appear to have more than specific significance in the material we have gone over. The lung may be either maculate or plain in some groups; *Samoana canalis* has it profusely marbled with black, and *Samoana conica* has no maculation.

The jaw and teeth seem to be very conservative throughout the family. No significant differentiation has been observed among the species belonging to *Partula* sensu stricto, *Thakombaua*, *Melanesica*, *Samoana*, *Eua*, and *Marianella* investigated by Binney, Heynemann, Semper, Thiele, and Pilsbry and Cooke.

## DESCRIPTION OF TONGAN SPECIES

Genus *EUA*, new genus

*Eua* is pronounced in three syllables, the stress on the penultimate.

The shell is globose-conic or oblong-conic, of a few ( $4\frac{1}{2}$ ) whorls, moderately to very widely umbilicate, spirally striate, not glossy; all the known species are dextral. The short penis contains a fleshy ridge as long as the cavity, adnate along one side, its free edge folded over. The retractor muscle and the *vas deferens* are terminal, the *vas deferens* passing directly forward to the base of the penis. The spermatheca is of medium length. The posterior prostate gland, the lung, teeth, and jaw are as in *Partula*. Type, *Eua globosa*, new species. Distribution, Tonga and Samoa.

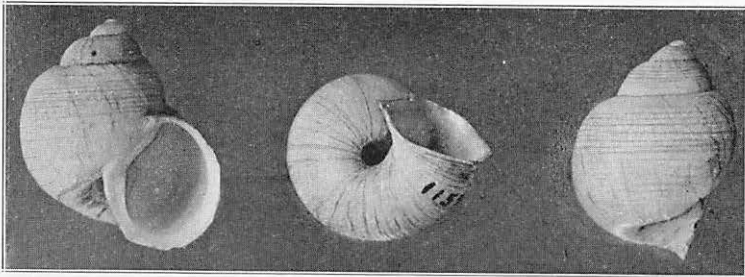


FIGURE 1.—*Eua globosa*, new species, enlarged.

The typical subgenus of *Eua* is characterized by the globosely conic, widely umbilicate shell, which is strongly striate spirally and is unicolorous.

***Eua globosa***, new species (figs. 1, 2, 3, a-c).

The shell is globose-conic, broadly umbilicate, moderately thin, uniform pale buff (between cream and cartridge-buff), nearly lusterless. The spire of  $4\frac{1}{2}$  whorls is short, terminating in an obtuse apex with a rather deep dimple. The whorls are strongly convex, the last ample, globose. The umbilicus opens broadly in the last whorl but is quite narrow in those preceding. Sculpture of close spiral lines weak on the first whorl (where they are generally worn and faint in adult shells), very deeply engraved on the rest of the embryonic shells of  $2\frac{1}{2}$  whorls. They become coarser on the post-embryonic whorls, and on the upper half of the last whorl have the appearance of coarse but very weak spiral cords; below the periphery they are irregular, smaller, subobsolete or often scarcely discernible. These spirals are crossed by very fine, irregular, crowded axial striae on the spire and low wrinkles on the last whorl. The aperture is

broad, shortly ovate, white. The white peristome is expanded, slightly thickened within. The columellar margin is built forward, and joined to the outer margin by a short, white parietal callus.

Length	Diameter	Length, aperture
22.3 mm	20.0 mm	13.5 mm
22.0 mm	19.5 mm	13.3 mm
21.6 mm	19.8 mm	13.2 mm

Bugai, Eua, altitude 300 feet, cotypes no. 115426 (B. P. Bishop Mus.) and no. 162130 (Acad. Nat. Sci. Phila.), A. Powell. Eua, the island at the southernmost end of Tonga, is  $12\frac{1}{4}$  miles long,  $4\frac{1}{2}$  miles wide, and attains a maximum elevation of 960 feet. As described by J. Edward Hoffmeister (B. P. Bishop Mus., Bull. 96, 1932), it is composed of a nucleus of volcanic material on which late Tertiary limestone has been deposited, but there are considerable areas of Eocene limestone and of volcanic rocks.

The foot (in alcohol) of *E. globosa* is a uniform gray color. Sole undivided. Upper surface is rather coarsely and deeply reticulate, the warts polygonal to oval, those along the foot edge lengthened. The tail is depressed.

The mantle is wide, broadly reflected all around. There is a very small body lobe behind the pneumostome, and the weak trace of another before it. Within the shell the mantle lining the upper whorls is largely white.

The lung (fig. 2, *c*) is rather short and wide, the transparent outer wall more or less profusely maculate with black and having many opaque silvery spots or ragged patches of minute white dots (outlined in the figure). No venation is visible except the vein leading to the heart, which is faintly seen. The kidney is triangular posteriorly, with an equally long extension forward, simulating a ureter, with lateral orifice at the end. There is no ridge or thread running backward from the orifice. The pericardium is equal in length to the triangular portion of the kidney.

The reproductive organs (fig. 3, *a-c*). The spermooviduct is closely convoluted as usual. A talon appears to be wanting as in all Partulidæ. The prostate gland is short and posterior. The *vas deferens* adheres closely to the uterus, where it is wide but not glandular. The uterine part of the oviduct is, in the individual figured, much distended over two embryos, the walls there being as thin as tissue paper. The largest embryo has a shell 7 mm long, of  $2\frac{1}{2}$  whorls, with narrow umbilical perforation. The vagina has mus-

cular walls, ribbed within. The spermatheca is oblong, with a slender duct of medium length, the whole 13.5 mm long. The penis is short (5.3 mm), wide, with the *vas deferens* and the retractor muscle inserted together at one side of the blunt end. The retractor is inserted posteriorly on the lung floor and is 7 mm long. The thin-

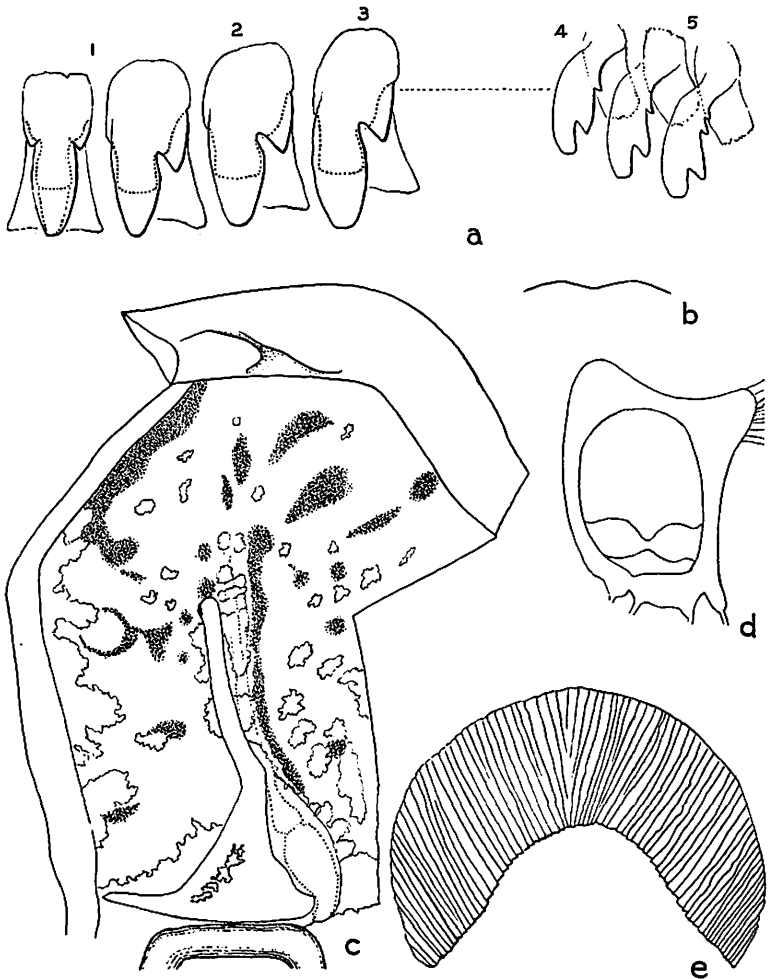


FIGURE 2.—*Eua globosa*, new species: *a*, central, lateral, and marginal teeth; *b*, contour of transverse row of teeth; *c*, pallial organs; *d*, outline of central nervous system; *e*, jaw.

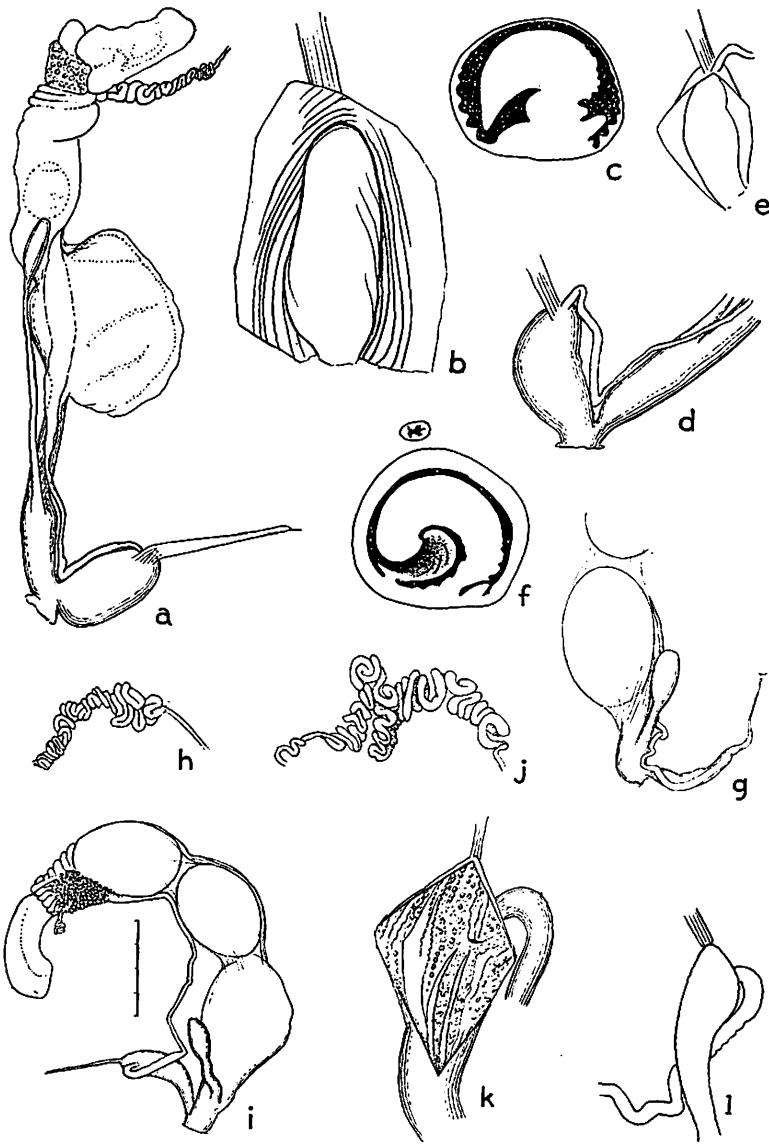


FIGURE 3.—Reproductive organs. *a-c*, *Eua globosa*, new species: *a*, organs of reproduction from above; *b*, penis opened; *c*, transverse section about midway of penis. *d-f*, *Eua zebrina* (Gould): *d*, terminal ducts of genitalia, lower side; *e*, penis opened (diagrammatic); *f*, section of penis. *g-h*, *Partula lanceolata* Cooke and Crampton: *g*, anterior ducts of genitalia; *h*, part of ovisperm duct. *i-l*, *Partula lirata* Mousson: *i*, organs of reproduction, lower side; *j*, part of ovisperm duct; *k*, penis opened near distal end, *vas deferens* on right; *l*, penis from above.

walled penis sac is almost filled by a fleshy ridge extending from end to end, adnate to one side throughout, its edge recurved, as in figure 3, *b*. The cavity formed by the folded ridge receives the *vas deferens* at the apex of the penis. The outer wall of the penis is longitudinally plicate in the vicinity of the ridge, the folds extending somewhat upon the latter (fig. 3, *b, c*).

The jaw (fig. 2, *e*) is thin, strongly arched, composed of many (80-85) narrow plaits with slightly irregular free edges, the plaits converging downward, leaving in the middle several short ones, as in *Drymaeus*. It is somewhat asymmetrical, having 45 plaits on one side, 36 on the other in the jaw figured.

The radula has thrice-bent transverse rows (fig. 2, *b*), the lines of lateral teeth running forward, those of marginals backward. There are about 23, 16, 1, 16, 23 teeth. The centrals are slightly narrower than the laterals, tricuspid, the mesocone slightly surpassing the basal plate, the ectocones smaller than in the lateral teeth. The laterals have long, blunt mesocones and large ectocones. The marginal teeth are oblique, tricuspid, the third cusp small, rarely doubled (fig. 2, *a*).

The central nervous system is drawn in figure 2, *d*. The cerebral ganglia are united by a long commissure. The visceral ganglia are conrescent into one lobed mass.

The small white dots in the mantle, the neurilemma, etc., are oblong, about 50  $\mu$  long, and are evidently calcareous, as they effervesce with acid. They are much less profusely spread in some individuals than in others, the calcareous material stored in the granules possibly having been used in forming the shells of embryos. All Partulidae examined possess these calcareous granules.

#### Genus SAMOANA Pilsbry

***Samoana cramptoni***, new species (figs. 4, *a, b*; 5, *f*; 6, *a-c*; 8, *a*; 9, *g*).

The shell is narrowly umbilicate and rimate, oblong-conic, thin, isabella color fading to cream buff at the summit, with a chestnut band at the periphery and narrowly showing above the suture in its last two turns. Surface rather glossy, the first whorl worn, the next  $1\frac{1}{2}$  whorls having finely engraved spiral lines in the upper half; last 3 whorls with weak, fine wrinkles of growth but no spiral lines except on the base, where a few weak spirals are visible. The apex is rather obtuse. The whorls are rather strongly convex, the last very shortly ascending in front to the upper edge of the band. The small aperture is nearly vertical, shortly oval, slightly bluish and showing the band within. The peri-



stome is faintly flesh-tinted, narrowly expanded, subreflected, dilated at the columella, which, in an oblique view in the mouth, is slightly convex.

Length	Diameter	Aperture, length	Whorls
19.0 mm	10.5 mm	4.3 mm	5 1/3
18.5 mm	10.5 mm	4.0 mm	5 1/3

Eua, cotypes no. 118453 (B. P. Bishop Mus.) and no. 162332 (Acad. Nat. Sci. Phila.).

We take great pleasure in naming this species for Professor H. E. Crampton. It is not closely related to any of the known forms of *Samoana* but stands nearer to the Samoan species than to the Fijian *S. alabastrina*. It is the only *Samoana* having a band of any color markings. Under the microscope some traces of punctuation are seen in the engraved lines of the second and third whorls.

The lung (fig. 5, *f*) is 20 mm long, opaque, chalky white with some small, scattered, angular black spots, chiefly anteriorly. The triangular posterior part of the kidney is about one fourth of its length.

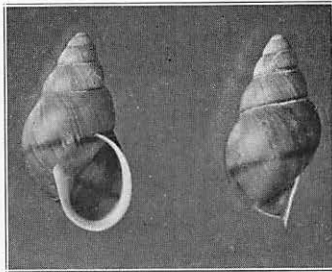


FIGURE 4.—*Samoana cramptoni*, new species, enlarged.

The reproductive system (fig. 6, *a-c*) has the usual short, stout penis of the genus, containing a large longitudinal ridge with folded-over edge (fig. 6, *b, c*). The epiphallus (figs. 6, *a*; 9, *g*) is longer than the penis, with a terminal retractor, which also continues weakly to the apex of the penis. The *vas deferens* enters a short distance below the end of the epiphallus. The duct of the spermatheca is longer than in any partulid snail examined, being nearly as long as the oviduct. The eggs (fig. 8, *a*) are oblong and flattened, measuring 4.2 by 3.4 by 2.8 mm.

The right ocular retractor passes between the branches of the genitalia as usual.

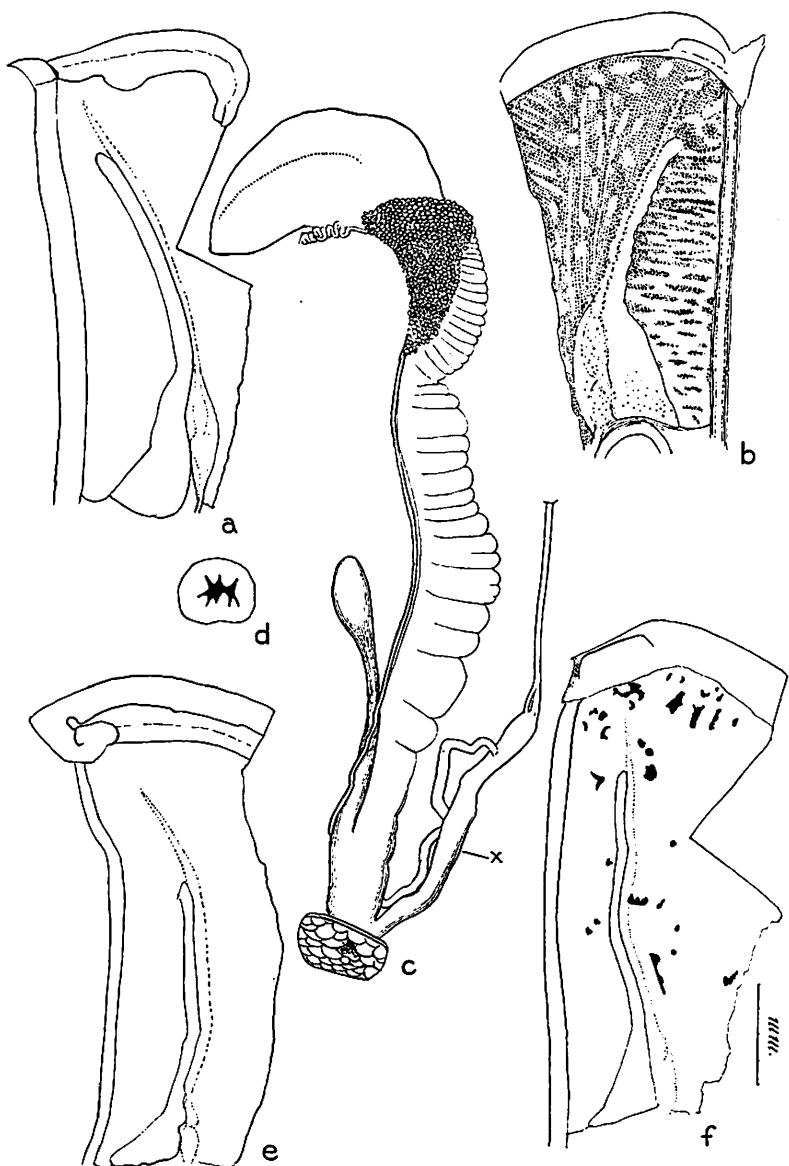


FIGURE 5.—Pallial and reproductive organs. *a*, *Partula lanceolata* Cooke and Crampton, pallial organs. *b*, *Samoana canalis* (Mousson), pallial organs. *c-d*, *Partula turneri perstrigata* Pilsbry: *c*, reproductive system from above; *d*, transverse section of penis at point marked *x* in figure 5, *c*; *e*, *Partula faba* (Gmelin), pallial organs. *f*, *Samoana cramptoni*, new species, pallial organs.

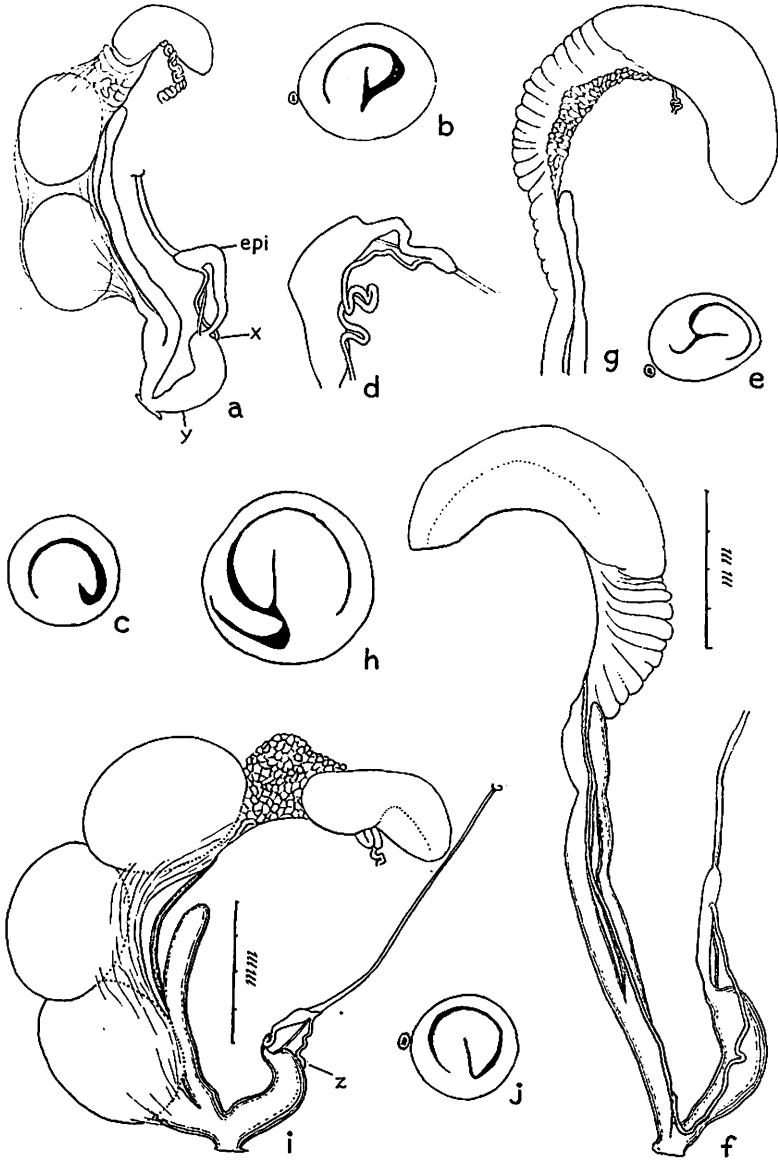


FIGURE 6.—Reproductive organs. *a-c*, *Samoana cramptoni*, new species: *a*, reproductive organs from above; *b, c*, transverse sections of penis at points *x* and *y* in figure 6, *a*. *d-e*, *Samoana canalis* (Mousson): *d*, penis, epiphallus, and part of *vas deferens*; *e*, transverse section of penis. *f-h*, *Samoana conica* (Gould): *f*, reproductive organs from above; *g*, posterior organs seen from below, showing prostate gland; *h*, transverse section of penis. *i-j*, *Samoana alabastrina* (Pfeiffer): *i*, reproductive organs from above; *j*, transverse section of penis at *s* in figure 6, *i*.

## NOTES ON ANATOMY

## Genus PARTULA Férussac

In *Partulae* of the Society Islands belonging to the typical subgenus the cavity of the penis is divided into upper and lower sections by a difference in the sculpture of its walls, the upper part possessing densely papillose, irregular ridges (fig. 7, *d, g-i*), the lower part with strong longitudinal folds (fig. 7, *e, h, j*). At the junction of these two patterns is a more or less conspicuous constriction of the sac externally, as in figure 7, *b*.

The genotype, *P. faba* (Gmelin), from Opua valley, Raiatea, no. 81723 (B. P. Bishop Mus.) (fig. 7, *a-e*), has some irregular folds in the densely papillose upper portion, as in figure 7, *e*, and there is a lateral sac or pocket where the *vas deferens* enters, shown in the two outlines of the penis (fig. 7, *b, c*). The large spermatheca and its duct are 14 mm long. The specimen drawn contained two eggs and one embryo of more than two whorls.

In *P. rosea* Broderip, from Huahine, no. 72012 (Acad. Nat. Sci. Phila.), one side of the upper section of the penis has greatly thickened fleshy ribs (fig. 7, *h, j*). In a species sent by Garrett without the shell (fig. 7, *f, g*) the same side has a chevron of oblique ridges. In both species the *vas deferens* enters the penis sac in a thin-walled side opposite these thickenings and at the distal third or fourth of the length of the penis, not at the end. The penial retractor muscle is terminal. The short duct of the spermatheca is swollen basally in these species.

This structure of the penis is entirely unlike what we found in *Eua*, where the penis is not divided into diverse upper and lower sections; no part has papillose walls, and the *vas deferens* enters terminally, near the penial retractor, and is received in the fold of the fleshy ridge which occupies the whole length of the penis sac. This differs so radically from *Partula* proper that we believe a different genus is indicated.

W. G. Binney (Acad. Nat. Sci. Phila., Proc., pl. 19, 1875) has figured the reproductive organs of *Partula bilineata*, *fusca*, *virginea*, *umbilicata*, and an undetermined species. The figures, made 60 years ago, are crude; but all agree in showing the penis constricted

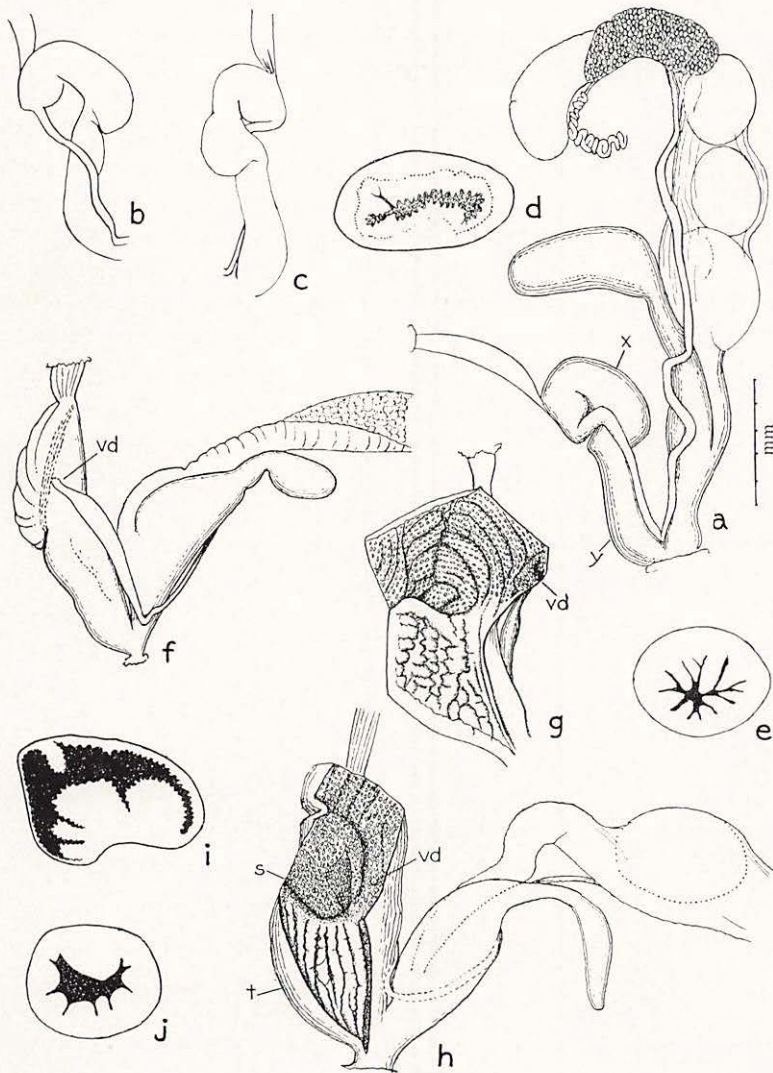


FIGURE 7.—Reproductive organs. *a-c*, *Partula faba* (Gmelin): *a*, reproductive system from below; *b*, *c*, two outlines of penis to show constriction; *d*, *e*, transverse sections of penis at *x* and *y*. *f-g*, *Partula*, undetermined species, anterior part of reproductive organs; *v.d.*, *vas deferens* where it enters the penis; *g*, penis opened, *vas deferens* on right. *h-j*, *Partula rosea* Broderip: *h*, anterior part of reproductive system; *v.d.*, pore where *vas deferens* enters penis; *i*, *j*, transverse sections of penis at points *s* and *t* in figure 7, *h*.

mesially, with the retractor muscle terminal and the *vas deferens* entering some distance before the end.

In *P. virginea* the constriction of the penis is represented as very long, with the upper portion slender, so that Binney questioned whether it might not be a modified part of the *vas deferens*. As figured, the structure appears to be very much like the epiphallus of *Samoana*, and a point requiring further investigation is whether what we are calling the epiphallus in *Samoana* is not homologous with the distal part of the penis in Society Islands *Partulae*. The question has taxonomic as well as morphologic interest, but it cannot be settled until the penis of *P. virginea* can be opened and a full comparison with that of the *Samoanae* made. A thorough study of the anatomy of the great and varied Society Islands series is much needed.

In the Melanesian *Partulae* the penis has no median constriction such as characterizes those of the Society Islands; but only three species have been dissected, and for the present we leave them in the genus *Partula*, subgenera *Thakombaua* and *Melanesica*.

***Partula (Thakombaua) lirata*** Mousson (fig. 3, *i-l*).

Fiji: Mango Island, Lau Archipelago, no. 78936 B. P. Bishop Mus.), E. H. Bryan, Jr.

The penis is club-shaped with terminal retractor, the *vas deferens* entering a short distance forward of the end. Internally it has irregular ridges and papillae in the posterior part, becoming somewhat more strongly plicate lengthwise anteriorly. The *vas deferens* is somewhat enlarged in the part lying along the penis. The oblong spermatheca is about as long as its duct, the whole being shorter in this species and *P. lanceolata* than in any other Partulidae examined. The ovisperm duct is remarkably knotted (fig. 3, *j*). The uterus contained three oblong eggs measuring 3 by 4.3 mm, the anterior one with a well-formed embryonic shell and only fragments of the egg shell.

The lung is very long, very densely and evenly peppered with white, the specks forming longitudinal rows in some places. There is a short, triangular kidney with an extremely long anterior extension reaching to the anterior fifth of the lung. The orifice is lateral at the end, as usual, with a weak ridge running a short distance backward.

**Partula** (*Thakombaua*) *lanceolata* Cooke and Crampton (fig. 3, *g, h*).

Fiji: Mango Island, Lau Archipelago, no. 78942 (B. P. Bishop Mus.) E. H. Bryan, Jr.

The reproductive organs are substantially as in *P. lirata* except that the penis is longer and of about equal diameter throughout. The *vas deferens* is rather thick. The ovisperm duct is less elaborately convoluted (fig. 3, *h*):

The lung (fig. 5, *a*) is peppered with white dots. The narrow part of the kidney is nearly twice as long as the triangular portion and reaches far forward, as in *P. lirata*.

Anatomically *Thakombaua* is characterized by the small penis without a constriction, and the very short spermatheca.

**Partula** (*Melanesica*) *turneri perstrigata* Pilsbry (fig. 5, *c, d*).

New Hebrides: Tanna Island, no. 81632 (B. P. Bishop Mus.), E. Robertson.

The reproductive organs (fig. 5, *c, d*) are much as in *P. lirata* except that the organs are longer. The penis and its retractor are long and slender, the *vas deferens* entering at about the posterior third of the penis. The ovisperm duct is simpler and the spermathecal duct longer than in *Thakombaua*, though it does not reach medium length. The specimens opened contained neither eggs nor embryos.

The lung is opaque, grayish brown within, seen under the microscope to be minutely peppered with white specks and with a loose network of deep brown or gray pigment in fine points and short lines. There is an appearance of longitudinal striae in places. The kidney has a small triangular expansion posteriorly, about one sixth of its total length, and a very long, narrow anterior extension, the whole more than two thirds the length of the lung.

*Partula turneri* is type of the subgenus *Melanesica*.

#### Genus SAMOANA Pilsbry

*Evadne* Hartman, Cat. Genus *Partula*, p. 12, 1881. Not *Evadne* S. Lovén (Crustacea), 1836.

*Samoana* Pilsbry, Man. Conch., vol. 20, pp. 165, 263, 1909. Type *Partula canalis* Mousson.

Penis short and stout, its cavity nearly filled by a fleshy longitudinal ridge with recurved edge and adnate along one side, exactly as in *Eua*. A club-shaped epiphallus (fig. 9, *g*) surmounts the penis, the penial retractor inserted at its apex, with a slender continuation to the apex of the penis. The *vas deferens* enters the epiphallus below its apex. The spermatheca is small, oblong, on a duct of medium length. Other organs as in Partulidae generally.

The essential character of *Samoana* is that there is a well-developed epiphallus with terminal retractor muscle. In other Partulidae examined the *vas deferens* is not continued beyond the apex of the penis, but proceeds directly to the anterior or basal end, either from an apical insertion, as in *Eua*, or from a point below the apex, as in *Partula* proper; and it has no connection with the penial retractor. The spermathecal duct is somewhat longer than in *Partula*.

In the sinistral species *S. canalis* and *S. conica* the direction of recurvature of the ridge in the penis is opposite to that in the dextral species.

We have elsewhere referred to the resemblance of the epiphallus of *Samoana* to the distal section of the penis in *Partula* sensu stricto, and the probability that they may be homologous structures.

The following species belong to *Samoana*. Those marked with an asterisk have been dissected.

#### SAMOA

- \**Samoana canalis* (Mousson), Upolu, Savaii
- Samoana canalis biconica* (Pilsbry)
- Samoana canalis semilineata* (Mousson), Tutuila
- \**Samoana conica* (Gould), Tutuila
- Samoana stevensoniana* (Pilsbry), Upolu
- Samoana thurstoni* (Cooke and Crampton), Ofu
- \**Samoana abbreviata* (Mousson), Tutuila

#### TONGA

- Samoana cramptoni* Pilsbry and Cooke, Eua

#### FIIJI

- \**Samoana alabastrina* (Pfeiffer), Moala

***Samoana conica*** (Gould) (fig. 6, *f-h*).

Samoa: foot of Tau Peak, Tutuila, no. 84454 (B. P. Bishop Mus.), C. M. Cooke, Jr.

Specimens dissected contained neither eggs nor embryos. The penis cavity has a small longitudinal ridge in addition to the large, folded one (fig. 6, *h*). The spermathecal duct is more than half as



long as the oviduct. The vagina is longer than usual in *Partulidae*, about as long as the penis. The left ocular retractor passes over the penis (between penis and vagina) as in all sinistral *Partulidae* examined.

The lung is densely and evenly peppered with white, the particles mainly arranged in longitudinal lines. Kidney triangular posteriorly, with the narrow anterior extension nearly twice as long, the whole occupying about two thirds the length of the lung.

***Samoana canalis*** (Mousson) (fig. 6, *d, e*).

Samoa: Safuni, Savaii, no. 75896 (B. P. Bishop Mus.), E. H. Bryan, Jr.

In the reproductive organs this species resembles *S. conica*, but it differs slightly by having the *vas deferens* more looped, and the secondary ridge within the penis is lower (fig. 6, *e*).

The lung (fig. 5, *b*) is 17 mm long, slaty black, streaked and mottled with white, the white predominating on the cardiac side. It is much shorter than the lung of *P. conica*. The kidney is 13 mm long.

In the dextral *S. abbreviata* (Mousson) the penis and *vas deferens* are as figured for *P. canalis*. The lung has no dark markings.

***Samoana cramptoni*** Pilsbry and Cooke (fig. 6, *a-c*).

Described under Tongan species. The main difference between this and the Samoan species is that the spermathecal duct is longer.

***Samoana alabastrina*** (Pfeiffer) (fig. 6, *i, j*).

Fiji: Moala, no. 77131 (B. P. Bishop Mus.), E. H. Bryan, Jr.

The penis and its appendages are about as in the typical Samoan species except that there is no accessory ridge in the penial cavity (fig. 6, *j*). The vagina is very short, and the spermatheca is much shorter than in other species of *Samoana* examined. The uterus contained three eggs which are nearly circular in one view, flattened in another, measuring 4.4 by 4.2 by 3.5 mm (fig. 8, *b*).

The shells from Moala correspond fully with *Partula nematoraphe* Pilsbry (Man. Conch., vol. 20, p. 279, 1909-10) said to come from "Fiji," obtained from the London dealer Geale; but this appears to be identical with *Partula alabastrina* Pfeiffer, supposed to be from the Solomon Islands; habitat was apparently incorrect.

The species has been placed in the subgenus *Melanesica*, but it proves to have all the anatomical characters of *Samoana*. A cord above the suture, such as appears in the description and figures of *P. nematoraphe*, is also to be seen in some examples of *S. canalis*.

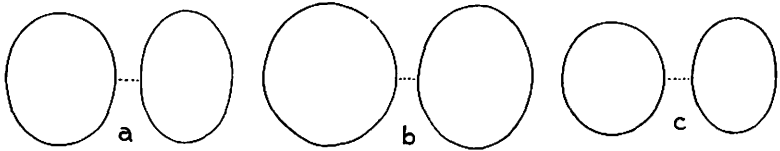


FIGURE 8.—Eggs of Partulidae: a, *Samoana cramptoni*; b, *Samoana alabastrina*; c, *Eua zebrina*.

### Genus *EUA* Pilsbry and Cooke

#### Subgenus *NESANASSA*, new subgenus

The subgenus is named from the Greek *Νησος* (island), *ανασσα* (princess).

The oblong or obliquely conic shell is moderately to widely umbilicate, opaque, more or less variegated, of few ( $4\frac{1}{2}$ ) whorls; peristome flatly reflected and thickened within. Soft anatomy as in *Eua*. Type, *Partula zebrina* Gould.

***Eua (Nesanassa) zebrina*** (Gould) (fig. 3, d-f).

Samoa: wooded slope behind Pagopago, Tutuila, no. 134746 (Acad. Nat. Sci. Phila.), H. A. Pilsbry.

This has essentially the penial structure of *Eua globosa*. The *vas deferens* and the retractor muscle are terminal on the short, stout penis, the cavity of which is occupied by a fleshy ridge adnate along one side, its free edge folded over. It extends the whole length of the penis sac (fig. 3, e, f). The uterus contained two or three eggs measuring 3.35 by 3.1 by 2.65 mm (fig. 8, c). These eggs are decidedly smaller than those of the *Samoanae*. Anteriorly there may be one embryo with a shell about 4.5 mm long, without an eggshell, this apparently being absorbed before birth.

The carnivorous habit of *E. zebrina*, which apparently swallows other snails for the lime of their shells, has been described (B. P. Bishop Mus., Bull. 47, pp. 5-12, 1928).

The following species belong to this subgenus: *Eua* (*Nesanassa*) *zebrina* (Gould), Tutuila; *Eua* (*Nesanassa*) *expansa* (Pease), Upolu; *Eua* (*Nesanassa*) *montana* (Cooke and Crampton), Upolu.

### Key to Genera and Subgenera

- a. Cavity of the penis with ribbed and papillose walls in the distal part, only ribbed anteriorly (fig. 9, *c, d*), the *vas deferens* entering some distance before the end.....Genus **Partula**
  - b. Penis with an external constriction between papillose and ribbed portions (fig. 9, *b*); Society Islands.....Subgenus **Partula**
  - bb. Penis not constricted (fig. 9, *a*).
    - c. Spermatheca and duct very short; shell with raised spiral striae, and a callous pad on the parietal wall contiguous to the columella; Fiji.....Subgenus **Thakombaua**
    - cc. Spermatheca of moderate length; no raised spirals and no callus on the parietal wall; New Hebrides.....Subgenus **Melanesica**
- aa. Cavity of the short, stout penis not papillose, occupied by a fleshy ridge with folded-over edge and adnate along one side (fig. 9, *f*)
  - b. A club-shaped epiphallus present, the penial retractor terminal on it, with a slender continuation to the apex of penis (fig. 9, *g*); shell glossy, spiral striae weak or wanting on later whorls; Samoa, Tonga, and Fiji.....Genus **Samoa**
  - bb. Penial retractor and *vas deferens* inserted at apex of penis, the *vas deferens* passing thence directly to base of penis (fig. 9, *e*), shell dull, with spiral sculpture.....Genus **Eua**
    - c. Shell globose-conic, with broad umbilicus, unicolorous; Tonga .....Subgenus **Eua**
    - cc. Shell oblong-conic or obliquely conic, variegated; Samoa .....Subgenus **Nesanassa**

This is by no means a general classification of the Partulidae, as nothing is known of the anatomy of species of the Marquesas and Micronesia, and of numerous isolated forms scattered over Polynesia; moreover, the information on Society Islands and Melanesian species is still quite inadequate.

### ZOOGEOGRAPHIC RELATIONS

According to J. E. Hoffmeister (B. P. Bishop Mus., Bull. 95, p. 34, 1932), "it may be that the early history of *Eua* is related in some way to an old western Pacific continent." Harold L. Alling (B. P. Bishop Mus., Bull. 96, p. 47, 1932), who worked up the petrology of *Eua*, believes that "*Eua* and probably other Tongan islands

are the remnants of a continental series of volcanos, situated on the coast of a former continent; or perhaps I should say these islands represent a pre-Eocene continental shelf." Immediately to the east lies the Tonga Deep, a trough about six miles deep. Between the Tongan plateau and Fiji, depths seem to be 2,000 to 3,000 meters, and Samoa is separated by depths between 4,000 and 5,000 meters. It is not believed that soundings have been sufficiently thorough to determine the least depths between these archipelagos.

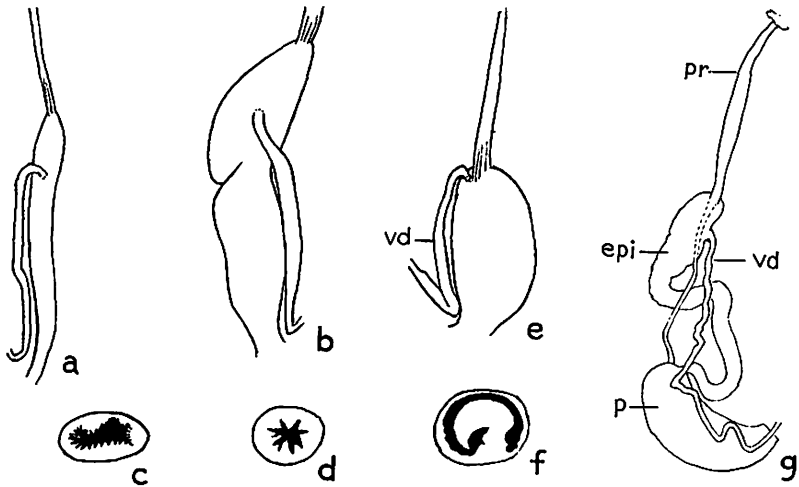


FIGURE 9.—Penes of Partulidae: a, *Melanesica*; b-d, *Partula*; e-f, *Eua*; g, *Samoana cramptoni*; Epi., epiphallus; p, penis; p.r., penis retractor; v.d., vas deferens.

This information prepared us to find the Tongan Partulidae most nearly related to the Fijian, but it turns out that they show much greater affinity to those of Samoa. Both of these island groups have only the two genera, *Eua* and *Samoana*. *Eua* has been found only in Samoa and Tonga, but one species of *Samoana* occurs on the Fijian island, Moala. Otherwise Fiji has only the very different partulid group *Thakombaua*, which is closely related to *Melanesica* of the New Hebrides.

It appears therefore that Tonga is as wholly Polynesian as Samoa in its *Partula* fauna, whereas Fiji is Melanesian but with one characteristic Samoa-Tonga genus represented by *Samoana alabastrina*.

Although the Samoan *Partulidae* are fairly well known, Tonga and the Lau Archipelago of Fiji have been so little worked that conclusions reached now are only tentative. They will have a certain value, however, if they direct attention to research in the Fiji-Tonga-Samoa region where the Melanesian and Polynesian faunas make their closest contacts.

#### SYSTEMATIC POSITION OF *PARTULA*

A few words on the position of *Partula* in the system of Stylommatophora may be in order. Eduard von Martens in 1860 placed the genus between *Buliminis* and *Achatinella*. This can only be regarded as a very lucky guess, as nothing was known of the anatomy of either of the Pacific genera. Fischer, 1885, knew the jaw and teeth; he ranked *Partula* as a subgenus of *Bulimulus*, which included *Amphidromus*, *Placostylus*, and others. Pilsbry, in 1900, recognized the affinity of *Partula* to Achatinellidae, Amastridae, Pupillidae, and the bulimoid snails by the possession of a kidney of the basommatophorus type and a lung without venation. It was segregated in a family *Partulidae*.

The classification adopted by Thiele (*Handbuch der Systematischen Weichtierkunde*, II, p. 658, 1931), by returning to the old idea that *Partula* is a genus of *Bulimulidae*, which he places between *Zaplagius* and *Bothriembryon*, seems distinctly reactionary. The teeth and the shape of the kidney, which he mentions as supporting that classification, are weak defenses of an untenable position. In those *Bulimulidae* having superficially similar tricuspid side teeth, the three cusps are endocone, mesocone, and ectocone. In *Partulidae* an endocone is not present, a mesocone and two ectocones being developed. The supposed similarity is one of analogy, not of homology. The triangular shape of the kidney is so common in land mollusks that it would have little value if it were alike in bulimulid and partulid snails. The resemblance claimed is merely superficial. *Bulimulidae* have a triangular kidney with the apical ureter reflected to the base of the lung, thence passing forward along the hindgut to an external opening. In *Partulidae* the kidney is dilated and triangular posteriorly, but becomes narrow and bandlike in the anterior moiety. There is no ureter, the kidney opening directly into the lung by a lateral pore at the apex of the long anterior extension and remote

from the hindgut. The texture of the veinless lung of *Partula* is so different from the copiously vascular lung of Bulimulidae that no malacologist who actually dissected a *Partula* could fail to notice their diversity. The classification of the land pulmonates in Thiele's "Handbuch" is for the most part excellent, as nearly all the groups had been well worked out by the authorities he followed; but his failure to recognize the value of the groups Orthurethra and Aulacopoda has led to occasional anachronisms, such as the inclusion of Clausiliidae in his stirps Vertiginacea, where it has no place, and his extraordinarily heterogeneous stirps Zonitacea.