THE GENUS TUBUAIA PULMONATA, ACHATINELLIDAE

BY

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The Genus Tubuaia (Pulmonata, Achatinellidae)

By YOSHIO KONDO

BERNICE P. BISHOP MUSEUM

INTRODUCTION

This paper deals with 18 species of *Tubuaia*. Of these, 10 species, 11 subspecies, and one variety are new. The order of treatment of the species is from the complex group of shells to the simplified group, thereby indicating a loose relationship.

The species and lesser forms of the genus Tubuaia are divisible into three primary groups of species: *perplexa*, *cylindrata*, and *hygrobia* (table 1). These groups can well be given subgeneric positions, for the boundaries which separate one group from the other are fairly clear cut. The separation of the three groups depends primarily upon the peculiarities of the palatal armature and upon characteristics peculiar to the parietal lamella. The three groups are further divisible into eight subgroups, seven of which are encompassed by fairly well-defined combinations of variations of the parietal folds. The eighth subgroup, T. voyana, with its subspecies, is difficult to define.

Members of the *T. perplexa* group have two plicae on the palatal wall, the upper of which is either bifid (a single tooth split to form two peaks, as in figure 2, *d*, *T. garrettiana*) or twin (two identical denticles close to each other, as in figure 3, *b*, *T. bakerorum*).

In some species of the group, the palatal wall has or is devoid of the transverse rib on which the plicae are situated. The group is divided into three well-defined subgroups: those species with palatal wall ribbed, upper fold bifid; those with palatal wall ribbed, upper fold twin; and those with palatal wall not ribbed, upper fold twin.

The group of T. cylindrata is characterized by two beaded palatal plicae except in T. voyana and T. hendersoni. T. voyana has one, two, or no plicae; in T. hendersoni the upper plica is beaded, but the lower plica is typically continuous. Because of these differences the T. cylindrata group may be divided into three subgroups.

In both the *T. perplexa* and the *T. cylindrata* groups of species the parietal lamellae are well developed and are preponderately sinuous.

In the third, and last, group of species (T. hygrobia) the characteristic absence of the palatal folds occurs, in general, in conjunction with a diminution of the parietal teeth. The single exception, T. saproderma, should be relegated to its own subgroup, since it has a well-developed parietal lamella and some specimens have a palatal tubercle.

The great range of T. voyana argues in favor of its being the senior member of the genus. Its fluxional, inconstant, and unstable apertural dentitional characters seem to indicate that its potentialities are not exhausted. The proof of this is in the number of subspecies in the species. T. voyana appears to be the representative of the ancestral form of *Tubuaia*, if not actually that form; though the possibility that its wide dissemination is the result of accidental transportation by the Polynesians or their predecessors cannot be ignored. However, if this were true, T. voyana would be more or less limited to the lowland (near shore, on cultivated land, in coconut plantations, and in villages, with rare intrusions into the native forests); whereas it is almost invariably collected in the native forests and from 20 feet (Rurutu, Mato Naa) to 1,000 feet (Mangareva, Mount Mokoto).

The evolution of the other groups of species from the voyana stock can only be conjectured, but evidence at hand indicates that two independent lines diverged from the primitive: (a) the simple T. hygrobia group (including T. saproderma) and (b) the relatively complex T. cylindrata group (including T. hendersoni), which gave rise to the highly specialized T. perplexa group. It is probable that the intermediate form between the cylindrata and perplexa groups is T. amoebodonta or some form related to it, in which the incipient twinning of the upper palatal plica is evident. The course taken by the immediate ancestor of the T. hygrobia group to arrive at its present form remains unknown for lack of evidence. That this group once had palatal plicae is evidenced by the apparently adventitious palatal tubercle in T. saproderma.

Most of the material was collected by the Mangarevan Expedition, 1934, but specimens collected by Peter H. Buck (Cook Islands, Mangaia) and Andrew Garrett (Society Islands), as well as material from the Fulton collection are included. Unless otherwise specified, they were collected by the Mangarevan Expedition.

METHODS

I studied every shell carefully before selecting the typical form, or the one which was most common. I then measured a good series for length and established the average. The oblong-conic form was selected as typical. For example, in *Tubuaia voyana manurevae* the commonest form is oblong-conic but there are (a) shells which have a squarish body whorl (gerontic), (b) others with a very broad body whorl and a short spire, and (c) still others with whorls flatter than usual although typical in other ways. To arrive at the average length (3.3 mm.), about 30 measurements were made of all forms of

the subspecies. An oblong-conic shell 3.3 mm. long was selected as the holotype of T. v. manurevae. All measurements at the end of each description were taken from the figure of the shell, not from the shell itself. Lengths of juvenile specimens were taken by laying them on a ruler under a microscope; the fractions were estimated.

Juvenile characters in the apertual armature are at optimum development in or near the metaneanic substage. In the paraneanic substage there is a tendency toward the reduction or loss of some of the plicae, whereas in the ananeanic to younger substages some of the plicae are undeveloped, the subcolumellar lamella for instance.

Descriptions of the apertural armature of a species or of a lesser form are based on juveniles, usually in the metaneanic substage (whorls about 4.5 to 5.0). However, unless otherwise stated, the mature, or adult, shell is being described when the size, shape, color, number of whorls, and so forth are given.

The terminology used in descriptions of the substages of the neanic stage is proposed by Pilsbry in the Manual of Conchology (vol. 23, p. xi), wherein the ana-, meta-, and paraneanic substages are selected according to their relative lengths in relation to that of the adult and are correlated with the development of the apertural armature. The number of whorls is incidental.

The nomenclature used in descriptions of apertural lamellae and plicae is that proposed by Pilsbry (Man. Conch., vol. 24, p. vii), who designates the columellar lamellae as supracolumellar, columellar, and subcolumellar. The lamellae number two or three. In Tubuaia voyana a mixture of two-lamellate and three-lamellate individuals occurs, and the subcolumellar lamella is considered vestigial. The juvenile parietal lamella is characterized by undulations (except in most species in the T. hygrobia group). In T. voyana it ranges in degree from very strong to barely perceptible. The adult parietal lamella is generally strong, but in most of the T. hygrobia group it is degenerating. Palatal plicae are usually two in number and discontinuous or broken into a series of flattened beads (or tubercles) with substantial spaces between them or the beads may be oblong with small spaces between them. Rarely (in T. hendersoni), one of the lower plica is continuous. Occasionally, there is only one plica, a condition found in some of the races of T. voyana. In the T. perplexa group the upper plica is either bifid or twin. Where the upper palatal plica is bifid only (figure 2, d, T. garrettiana), a biplicate condition is indicated, whereas where twinning (T. bakerorum, figure 3, b) occurs, triplication is evident. However, these conditions are apparently merely variations of the biplicate state. Palatal ribs, running at right angles to the plicae, are characteristic of some members of the *perplexa* group.

Whorls are counted from the body whorl, ascending the spire. An imaginary line is projected from the juncture of the peristome with the body whorl to the apex of the shell. The first whorl is at this juncture, the second is above it,

Species	Island	No, Col. lam. ^b	Dev. Par. lam.°	Sinuosity Par. Lam.	Palatal armature Ribbed	Palatal armature Plicae
PERPLEXA						······································
T. gouldi T. gouldi nannodes T. garrettiana	Mangareva Mangareva Mangareva	2 2 3	strong strong strong	strong strong strong	X X X	2, upper bifid 2, upper bifid 2, upper bifid
T. perplexa	(Rurutu (Rimatara	} 3	strong	strong	х	2, upper twin
T. affinis	Rurutu	2 or 3	strong	strong	х	2, upper twin
T. bakerorum T. amoebodonta	Rurutu Rurutu	3 3	strong strong	strong strong		2, upper twin 2, upper twin
CYLINDRATA						
T. fosbergi	Pitcairn	2	strong	strong		2, beaded
T. cremnobates	Rapa	2	strong	strong		2, beaded
T. cylindrata	Rapa	3	strong	fairly		2, beaded
T. cylindrata philolichen.	Rapa	3	strong	fairly strong		2, beaded
T. myojinae + forms	Raivavae	3	strong	strong		2, beaded
T. raoulensis	Kermadec	3	strong	strong		2, beaded
T. voyana + races*	various	2 or 3	strong	very strong to faint		0, 1, 2, beaded
T. hendersoni	Henderson	2	strong	not sinuous		2, upper beaded; lower continuous or nearly so
HYGROBIA						
T. saproderma	Mangareva	2	strong	weak		none, rarely with tubercle
T. coprophora	Raivavae	2	weak	not sinuous		none
T. coprophora diminuta	Raivavae	2	weak	not		none
T. hygrobia	Raivavae	2	weak	not		none
T. saintjohni	Raivavae	2	weak	not		none
T. inconstans	Rapa	2	weak	not		none

Table 1.—Summary of apertural armature in Tubuaia^a

^a Heavy rules set off the major groups; broken rules, the subgroups.
^b No. Col. lam. = number of columellar lamellae.
^c Dev. Par. lam. = degree of development of parietal lamella.
* Summary of geographical races of *T. voyana* is given under the species.

and so on. If the final whorl is a fraction, it is estimated in halves, thirds, or quarters (0.5, 0.3, 0.25).

I have used Ridgway's "Color standards and color nomenclature" as a guide.

Drawings for this paper were made by me. The scales in each figure represent 1 mm.; and with certain exceptions, all adults in the same figure have the same scale and all juveniles in one figure are based on one scale.

GEOGRAPHIC DISTRIBUTION

Kermadec Islands: T. raoulensis

Cook Islands: Mauke, Mangaia (T. voyana voyana)

"Society Islands" (Garrett) : T. voyana peasei

Austral Islands: Rimatara (T. perplexa, T. voyana oromanaensis); Rurutu (T. affinis, T. amoebodonta, T. bakerorum, T. perplexa, T. voyana manurevae, T. voyana matonaaensis); Tubuai: T. voyana, new undescribed subspecies; Raivavae: T. coprophora, T. coprophora diminuta, T. hygrobia, T. myojinae, T. saintjohni, T. voyana turivaoensis, T. voyana vaiaunanae

Rapa: T. cremnobates, T. cylindrata, T. cylindrata philolichen, T. inconstans, T. voyana rapaensis, T. voyana teutuensis

Mangareva: T. garrettiana, T. gouldi, T. gouldi nannodes, T. saproderma, T. voyana anceyana, T. voyana enokai

Pitcairn : T. fosbergi, T. voyana christiani

Henderson: T. hendersoni

		•	A		Ì	В	1	D	
West to East	4	Endemi 3	c specie 2	s 1	ENI SUBS 2	DEMIC PECIES 1	SUBS OF VC 2	T. per- plexa	
Kermadec	il		1		1	1			
Cook	1	1			1	1		X	•
Society	1	1	1					X	
Austral Rimatara								x	x
Rurutu	X				·		X		X
Tubuai		Ì				-		X	
Raivavae	X					X	X		
Rapa		X				X	X		
Mangareva		X				X	X		il
Pitcairn		<u> </u>	1	X				X	
Henderson		1		X					

Table 2.—Tabular summary of distribution of endemic species of Tubuaia and subspecies of T. voyana

I published a simple distribution map of the genus Tubuaia in 1960 (Cooke and Kondo, B. P. Bishop Mus., Bull. 221, p. 144), but did not discuss distribution in detail because no close analysis of the several species of Tubuaia had been made at that time. The genus Tubuaia has an interesting but not a startling distribution pattern. Latitudinally, the genus is spread out over an area in which the extreme island limits, Kermadec to Henderson, are 3,400 miles apart (fig. 1). The longest distance between two species without intervening islands is 1,300 miles, from the Kermadecs to the Cook Islands. One of the shortest distances between species is 90 miles, from Rurutu to Rimatara, where T. perplexa, incidentally, has successfully island-hopped, probably from Rurutu to Rimatara.



FIGURE 1.—Distribution of *Tubuaia*: small solid circles indicate single species; large solid circles indicate three to four species.

The present over-all picture of the distribution of *Tubuaia* is shown in figure 1 and in table 2 of this report. Fourteen of the 18 species cluster around the 140th meridian, within a triangle formed by Rurutu, Rapa, and Mangareva. With Raivavae, these islands form the center of speciation and, apparently, even the center of dispersal.

Tentatively considering Kermadec as an anomaly and leaving it temporarily out of consideration, there is high endemism (table 2, column A) in the Austral Islands (Rurutu and Raivavae, eight species). Endemism apparently decreases eastward to six (Rapa, Mangareva), then drops to two (Pitcairn, Henderson). The eastward trend and the apparent concomitant funneling

effect is clear. However, evidence indicates that the real center of speciation and of dispersal may be Mangareva, not the Austral Islands. Mangareva is almost completely denuded of native forests, whereas sizable remnants of native forests could still be found in the Austral Islands in 1934. Subfossil remains of land shells associated with *Tubuaia* in the Mangarevan islands indicate that during the forested stage the islands supported a rich land-mollusk fauna, richer than that of any surrounding island except Rapa. At least three new forms of *Tubuaia*, considered numerically insufficient for effective study, still remain to be described from Mangareva. Should these new forms prove to be good species, a reconstructed table of distribution may show a modified radiating effect rather than the funneling effect it shows now.

Subspecies of the endemic species (table 2, column B) are not numerous; but the occurrence of one subspecies each on Raivavae, Rapa, and Mangareva, where high endemism has been shown, adds strength to the hypothesis that this area is the center of speciation.

Subspecies of the widespread cosmopolitan species Tubuaia voyana (table 2, column C) show that subspeciation is richer in the central speciation area mentioned above, namely, the Rurutu-Rapa-Mangareva triangle, and that its trend of dispersal is apparently westward. If this apparent westward trend is genuine, it points to an eastern point of origin, probably Mangareva, for the reasons noted above. The biological *Tubuaia voyana voyana* must, therefore, be sought on Mangareva rather than in the Cook Islands, where the nominate taxonomic *T. v. voyana* is now located. The presence of *T. voyana* in the Society Islands remains in doubt. The Mangarevan Expedition failed to find it in 1934, although Garrett had reported it from there. However, it is possible that the species is a relatively recent introduction there and is confined to a few limited, circumscribed localities which we missed.

Tubuaia perplexa (table 2, column D) is the only endemic species out of 18 that has crossed from one island to another. It is found on both Rurutu and Rimatara. Its place of origin is undoubtedly Rurutu, an island characterized by high endemism, rather than Rimatara, which has a low index of endemism.

The single species (*Tubuaia raoulensis*) on Kermadec is an anomaly. The 1,300 miles distance over water from its nearest neighbor (*T. voyana*) in the Cook Islands leads one to wonder how it ever made such a long jump. Furthermore, if it reached the Kermadecs, why not Fiji, Tonga, Samoa, and the Tuamotu Islands?

Species of *Tubuaia* collected on the high islands of Mangareva and Raivavae in 1934 (Cooke and Kondo, B. P. Bishop Mus., Bull. 221, pp. 143, 145, 1960) but never found on their satellite coral islets tend to show that the species of *Tubuaia* may not be adaptable to impoverished atoll conditions like those of the Tuamotus, whereas some species of *Lamellidea* and *Tornatellinops* are able to adapt themselves. As to why Fiji, Tonga, and Samoa have not been invaded by forms of *Tubuaia*, only a hypothetical answer is possible. If waifs did arrive there from time to time, they were incapable of obtaining a foothold in lands already occupied by a well-established molluscan fauna.

MEANS OF DISPERSAL

Gales and hurricanes, which occur with annual regularity in this part of the Pacific, probably provide the most effective means of scattering land snails. Two transportation mediums are involved: (1) leaves, both green leaves from trees and dead ones from the forest floor, to which active snails may adhere by means of their sticky feet or to which aestivating snails may adhere by means of the tight adhesive usual around the aperture; (2) sea or land birds, which can harbor a gravid snail or two and which can be blown to a neighboring island or voluntarily flee to another island, seeking temporary shelter from a storm.

Baker assumes that migratory birds such as plovers are rare and fortuitous carriers of some zonitids distributed in a north and south direction (B. P. Bishop Mus., Bull. 166, pp. 351-352, 1941). Such accidental transport may explain the presence of T. raoulensis in Kermadec.

It was my good fortune to observe land snails on a sea bird's feathers and to collect them (October 3, 1949) on the island of Alamagan, about 250 miles north of Guam. A colony of noddy terns (*Anous stolidus*) was nesting in a lush, moist native forest 800 feet above sea level, where the dominant plant was the birdsnest fern (*Asplenium nidus*), canopied by tall trees. This fern and other low plants were heavily populated by small, crawling snails. When Donald Anderson and I accidentally flushed many juvenile terns, which were close to the flying stage, I caught one which partly flew, partly ran through the jungle. On it was a species of *Succinea* and a species of *Elasmias*. As a matter of interest, the northward dispersal of land snails in the Marianas apparently occurred primarily by means of violent winds and mechanisms attendant to them, as evidenced by the distribution picture in the Marianas Islands.

In any case, while we attempt to find a pattern of distribution by mapping and by making tabular analyses, it is well to remember that random, sporadic, and adventitious dissemination of land snails is probably the rule in the inner Pacific. Any apparent directional movement must be viewed with the several modifying factors which may have influenced the picture. The prime factor is the distributional pattern of the islands themselves. For instance, the position of the high islands evidently shapes the directional picture for *Tubuaia*. If the southeast Pacific were sprinkled with many more islands west, south, east, and north of Henderson, a distributional pattern different from the present might emerge.

PULMONATA

FAMILY ACHATINELLIDAE

SUBFAMILY PITYSINAE

Tribe TUBUAIINI

Genus Tubuaia Cooke and Kondo

Key to Tubuaia Groups

A. Upper palatal fold always present, bifid or twin......perplexa

AA. Upper palatal fold, when present, not bifid or twin

- B. Palatal folds always absent within a series; parietal lamella weak in both adults and juveniles.....hygrobia
- BB. Palatal folds present or absent within a series; parietal lamella strong in adults and juveniles
 - C. Palatal folds usually absent; when present, represented by a tuber-
 - CC. Palatal folds present or absent but never entirely absent within a
 - series; when present, low, linear, laminate, or beaded.....cylindrata

T. perplexa Group

Tubuaia with palatal plicae in two discontinuous rows; upper palatal fold either bifid or twin; with palatal rib or without; parietal lamella strongly sinuous; columella bi- or trilamellate.

- A. Upper palatal fold bifid, folds mounted on ribs

BB. Not striate

- CC. Typically 3.78×2.2 mm., outlines slightly convex, whorls fewer and flatter than above; columella of juveniles without broad undulating lamella but with two folds of nearly equal development, the columellar lamella the broader (Mangareva)......gouldi nannodes
- AA. Upper palatal fold twin; rib present or absent
 - B. Palatal ribs present; folds mounted on ribs
 - C. Typically 3.2 × 1.45 mm., elongate-conic, spire elongate and convex, whorls convex, the last narrow; columella of juveniles with three strong lamellae (Rurutu, Rimatara).....perplexa

BB. Palatal ribs absent; folds mounted directly on palatal wall

- C. Typically 2.84 × 1.35 mm., short, bluntly pointed, whorls slightly convex, supracolumellar lamella of juveniles plate-like, as are lower two; palatal plicae very strong, high (Rurutu)......bakerorum
- CC. Typically 3.13×1.45 mm., long, subacutely pointed, whorls convex; supracolumellar lamella of juveniles linear, lower two subtransverse; palatal plicae very weak, upper faintly twinned, many not appearing so (Rurutu).....amoebodonta
- Tubuaia gouldi (Pfeiffer), Cooke and Kondo, B. P. Bishop Mus., Bull. 221: 151, fig. 71, a-d, 1960.
 - Tornatellina gouldi Pfeiffer, Zool. Soc. London, Proc., 335, 1856.—Pilsbry and Cooke, Man. Conch. 23: 141, 1915.

Tubuaia gouldi nannodes Cooke and Kondo, B. P. Bishop Mus., Bull. 221: 153, fig. 71, e-f, 1960.

Tubuaia garrettiana, new species (fig. 2, a-d).

Shell (fig. 2, a) oblong-conic, color whitish to pale straw yellow, thin, subtransparent, with silky sheen, finely striate on upper whorls. Spire short, outlines slightly convex, tapering regularly. Suture well-impressed. Whorls 6.3, embryonic whorls obtuse, postembryonic whorls convex, last whorl long and tapering fairly even to base. Aperture vertical, subauriform, outer margin even. Parietal lamella fairly strong, compressed, oblique, about 0.75 whorl long. Columella vertical, weak. Palatal lamellae none. Peristome thin, erect.

Length 3.5 mm., diameter 1.75 (50 percent); apertural axis 1.16, diameter 0.90 (78 percent); last whorl 2.06 (59 percent); parietal lamella 0.13.

Subadult (fig. 2, b) usually with striae plainly visible on last whorl, with thinner, strongly sinuous parietal lamella; remnant of upper palatal plica only, on low rib near peristome, also another rib farther inward with or without remnant of lower palatal fold and remnant of upper palatal fold; vestiges of columellar and of subcolumellar lamellae, which is a little stronger than columellar. Length 3.5 mm., whorls 6.0.

Paraneanic specimens (fig. 2, c) with distinct striae on all whorls except embryonic. Parietal lamella thinner than in adult, with two strong sinuosities, margin of undulations bent inward. Palatal ribs strong (three in figured specimen), bidentate, lower fold semilunate, upper fold small, bifid, oblongish. Columella trilamellate; supracolumellar lamella thin, subvertical; columellar lamella widest, subtransverse, slanted downward; subcolumellar weak, a little steeper than columellar lamella. Length 3.3 mm., whorls 6.0.

Metaneanic specimen (fig. 2, d) same as paraneanic in external features. Parietal lamella thinner, sinuosities (two in number) and bend in margin even more pronounced. Palatal ribs three, folds as in paraneanic specimen. Columella trilamellate; supracolumellar lamella thicker than in paraneanic; columellar lamella not slanted but flat and more transverse; subcolumellar lamella wider and also more transverse than in paraneanic. Length 3.0 mm., whorls 5.5.

Ananeanic stage. Shell smoother, apertural dentition (except parietal lamella) the same as in metaneanic, lobes of parietal lamella more angularly bent. Length 2.0 mm., whorls 4.5.

"Gambier [Margareva] Islands" ex Fulton collection acquired by C. Montague Cooke, Jr. and presented to Bishop Museum, February 3, 1933. "This [including other genera] is probably the same lot as represented in the British Museum in lots collected by J. C. Lambert [a lieutenant in the British Navy]. British Museum No. 86.6.9. 587-591 etc." (Cooke, original label catalog).

Cooke said that this statement was based on the generic and specific associations, in addition to the similar proportions. Holotype 10154; paratypes 10155-10157, 115409-115414 (398 specimens). Additional paratypes: ex Garrett collection, "Gambier Isles," 3223-3224 (12 specimens); Mangareva, northeast of Vaitutai Bay, alt. 1-3 ft., fossil, Cooke and Anderson,¹ June 9, 1934, 139020 and 139022 (nine specimens).



FIGURE 2.—*Tubuaia garrettiana*, "Gambier [Mangareva] Is.": a, adult (holotype); b, subadult, oblique view of aperture; c, paraneanic, frontal view; d, metaneanic, frontal view, turned slightly to left.

As is usual in this genus, the greatest development in the apertural armature occurs in the metaneanic stage. From this point onward a gradual absorption of these denticles takes place until finally all but the parietal and supracolumellar lamellae disappear. It seems that the columellar lamella is absorbed before the subcolumellar lamella, as the former is much more reduced.

¹ Unless otherwise indicated, Donald Anderson.

In some juvenile specimens the columellar lamella is weakly sinuous or there is, at least, a shallow dip on the periphery reminiscent of the columellar lamella of T. gouldi.

T. garrettiana is similar to T. perplexa, but is much larger, has deeper sutures, hence much more convex whorls, is proportionately much broader, and has a large obtuse embryonic whorl, whereas that of T. perplexa is small and acute. T. garrettiana is light in color, silky, and striatulate, whereas T. perplexa is brown and glossy, and has growth lines only, not striae. In the juveniles the upper palatal fold of T. perplexa is twin, whereas that of T. garrettiana is bifid. Otherwise the apertural armatures of the two are nearly identical.

In length, *T. garrettiana* ranges from 3.0 to 4.0 mm., the mean being about 3.6 mm. (60 specimens measured).

The species is named for Andrew Garrett, who gave it the manuscript name "Tornatellina gambierensis."

- **Tubuaia perplexa** (Garrett) Cooke and Kondo, B. P. Bishop Mus., Bull. 221: 146, figs. 68, *a-d*; 69, *a-h*, 1960.
 - *Tornatellina perplexa* Garrett, Acad. Nat. Sci., Philadelphia, Proc., 24, 1879.—Pilsbry and Cooke, Man. Conch. 23: 145, pl. 34, figs. 12, 13; pl. 36, fig. 2, 1915.
- Tubuaia affinis (Garrett) Cooke and Kondo, B. P. Bishop Mus., Bull. 221: 149, fig. 70, a-d, 1960.
 - Tornatellina affinis Garrett, Acad. Nat. Sci., Philadelphia, Proc., 23, 1879. —Pilsbry and Cooke, Man. Conch. 23: 177, 1915.

Tubuaia bakerorum, new species (fig. 3, *a-b*).

Shell (fig. 3, a) narrowly ovate, color russet, thin, transparent, glossy, growth lines very fine. Spire slightly convex, tapering fairly evenly to apex. Suture weakly impressed, whorls six; embryonic whorls small, subacute; postembryonic whorls nearly flat, weakly convex; last whorl narrow. Aperture vertical, elongate, subauriform. Parietal lamella fairly strong, thin, about 0.5 whorl long. Columella linear, sigmoid. Palatal folds none. Peristome thin, erect.

Length 2.84 mm., diameter 1.34 (47.5 percent); apertural axis 1.13, diameter 0.61 (54 percent); last whorl 1.74 (61.5 percent); parietal lamella 0.16.

Juvenile (fig. 3, b, para-metaneanic). Parietal lamella thin, sinuous, margin bent strongly inward. Lower palatal fold semilunate; upper palatal fold twin, small, tuberculate; palatal rib none. Columella trilamellate; supracolumellar lamella fairly broad, subvertical; columellar lamella broadest, subtransverse; subcolumellar lamella smallest, subtransverse. Length 2.5 mm., whorls 5.5.

Austral Islands: Rurutu, Mount Manureva, southeast slope, in small patch of native forest, on ferns, alt. 1,100 ft., Zimmerman, Anderson, and Kondo, Aug. 30, 1934, holotype 10158; paratypes 148779 (five specimens). Additional paratypes: southwest slope of Mount Manureva, taken by beating *Blechnum*, alt. 1,100 ft., Zimmerman, Aug. 28, 1934, 10159, 148685 (nine specimens); 148779 dissected.

The adults of T. bakerorum and T. perplexa differ considerably. T. bakerorum is shorter and proportionately more convex than T. perplexa; the spire is less pointed, the embryonic whorl more obtuse, and the body whorl is longer in proportion to total length. The suture of T. bakerorum is less impressed, hence the whorls more flattened. The parietal lamella appears to be slightly longer and thinner. Finally, whereas the shell of T. perplexa is a pale honey yellow, that of T. bakerorum is a rich, deep brown.



FIGURE 3.—a, b, *Tubuaia bakerorum*, Rurutu: a, adult (holotype); b, para-metaneanic, oblique view into aperture. c-e, *T. amoebodonta*, Rurutu: c, adult (holotype); d, paraneanic, oblique view of aperture; e, metaneanic, oblique view of aperture (upper palatal fold almost imperceptible, twin).

The principal differences between the juveniles of the two species are in the apertural armature. T. perplexa has a transverse palatal rib, which T.bakerorum lacks. Both the supra- and subcolumellar lamellae are plate-like in T. bakerorum, but in T. perplexa the supracolumellar fold is not plate-like and the subcolumellar fold is much smaller. T. bakerorum is a rare species (total specimens, 14), which was collected on only two occasions. It is named in honor of H. Burrington Baker of the University of Pennsylvania and his family.

Tubuaia amoebodonta, new species (fig. 3, *c-e*).

Adult shell (fig. 3, c) similar in all ways to illustrated specimen of *T. perplexa* (B. P. Bishop Mus., Bull. 221, fig. 68, b) except for whorls, which are slightly more convex and darker in color.

Length 3.13 mm., diameter 1.45 (46.3 percent); apertural axis 1.03, diameter 0.71 (69 percent); last whorl 1.77 (56.5 percent); parietal lamella 0.13.

The metaneanic juvenile (fig. 3, e) differs from that of T. perplexa in three important ways: (1) transverse palatal rib is absent, (2) palatal folds are weak, and (3) upper palatal fold is weak and appears faintly twinned. Columella trilamellate; parietal lamella sinuous and bent inward at periphery. Length 2.5 mm., whorle 5.5.

Ananeanic specimens with apparently non-twinned upper palatal fold, but base of fold somewhat more thickened than palatal wall, indicating incipiency of twinning. Both palatals very strong. Length 1.5 mm., whorls 4.0.

Austral Islands: Rurutu, southeast slope of Mount Manureva, hanging valley west of Moerai village, in patch of *Aleurites* trees, on fern roots, on tree trunks, and on dead leaves on ground, alt. 500-600 ft., Anderson and Kondo, Aug. 30, 1934; holotype 10160; paratypes 10161-10162, 11572-11580 (35 specimens).

T. amoebodonta is an anomalous species, found only once, closely associated with T. voyana manurevae. The two were originally considered variants of a single type of shell, but a mixture was later suspected. A critical study revealed subtle but definite differences on the basis of which T. amoebodonta was separated. A species of Lamellidea, possibly oblonga, was with the two abovementioned species.

The adult of T. amoebodonta differs from that of T. v. manurevae in being shorter, in having a narrower apex, in having a narrower body whorl which does not taper evenly to the base, in its narrower whorls, in the spiral aciculations of many specimens, and in having more whorls (6.3:6.0).

In the paraneanic specimens of T. amoebodonta (length, 3.0 mm.; whorls, 6.0) the columellar lamellae are very strong, even persisting into the subadult stage in a reduced state, whereas in T. v. manurevae these lamellae are lost early. (See figure 3, d.)

In the metaneanic stage (fig. 3, e) the columella is trilamellate, the parietal lamella is strongly sinuous, the two palatals are always present, the upper one twin; but in T. v. manurevae the columella is bilamellate, the parietal folds are weakly sinuous, and the palatal plicae are absent in most of the specimens.

This species may well be intermediate between the groups of T. perplexa and T. cylindrata.

Of the 37 specimens collected, 10 are adults and 27 are juveniles. Of the 27 juveniles, 10 have twin upper palatal plicae, five are indeterminate, nine are paraneanic, or subadult; and three are ananeanic, therefore not to be relied upon for apertural dentition.

Tubuaia sp. ?

A species distinct from T. perplexa, T. affinis, T. bakerorum, and T. amoebodonta was collected on Rurutu on the south slope of Mount Manureva, on fern roots, in a patch of native forest at the base of a cliff, at 1,000 to 1,150 ft., Zimmerman and Anderson, Aug. 25, 1934; 148246-148248 (12 specimens). No adults were collected.

In juveniles (paraneanic and younger) the last whorl is globose and large and the apex is more conical than in T. *perplexa*. The parietal and columellar lamellae are nearly the same; but the palatal plicae differ to some extent from those of T. *perplexa*: there is no rib and the lower palatal fold is higher, longer, and semicontinuous (that is, each foldlet is connected to the following one by a low but distinct ridge). The upper palatal fold is twinned, as in the type species. This species fits into the *bakerorum* subgroup.

Table 3.—Dimensions of T. perplexa Group (ascending order of length)

Species	L,ENGTH	DIAMETER	Percent	Apertural Axis	DIAMETER	PERCENT	Parietal Lamella	Last Whorl	PERCENT	W HORLS
bakerorum	2.84	1.35	47.5	1.13	0.61	54.0	0.16	1.74	61.5	6.0
amoebodonta	3.13	1.45	46.3	1.03	0.71	69.0	0.13	1.77	56.6	6.3
perplexa	3.20	1.45	45.0	1.13	0.68	61.5	0.13	1.87	58.0	7.0
affinis	3.42	1.72	50.0	1.29	0.84	65.0	0.11	2.16	63.0	6.5
garrettiana	3.50	1.75	50.0	1.16	0.90	78.0	0.13	2.06	59.0	6.3
gouldi nannodes	3.78	2.20	53.5	1.33	1.18	88.7	0.30	2.29	60.5	6.5
gouldi	4.88	2.63	54.0	1.79	1.30	72.5	0.34	2.90	59.5	7.0

T. CYLINDRATA GROUP

Usually with two discontinuous palatal plicae, the upper plica single, not split as in the *perplexa* group, usually appearing as rows of flattened beads, the lower rarely continuous (in the exception, *T. voyana*, palatal plicae range from two or one to none within a series, with only a few of the subspecies biplicate). Parietal lamella ranges from strongly sinuous to not sinuous. Columella either bi- or trilamellate (in *T. voyana* subcolumellar fold is vestigial, showing in some specimens as a small fold, not at all in others).

Key

A. Lower palatal fold continuous or distantly and shallowly discontinuous, in the latter case forming elongate ridges; upper palatal fold discontinuous, folds beaded or at least of shorter length than those of lower palatal fold; parietal lamella not sinuous; columella bilamellate; shell small, typically 2.58 × 1.22 mm. (Henderson Island) ________hendersoni

- AA. Lower and upper palatal folds, when present, discontinuous, mostly beaded; parietal lamella from strongly sinuous to weakly so; columella bilamellate or trilamellate or a combination of both within a series.

 - BB. Palatal folds always present, plicae two or one (very rare).
 - C. Columella both bi- and trilamellate within a series; subcolumellar lamella, when present, very weak to faint (vestigial); parietal undulations very strong, strong, or weak.
 - D. Typically 2.58 mm., more or less; parietal undulations strong, never weak or extra strong.
 - E. Typically 2.58 × 1.26 mm., subcylindrical; whorls 6 to 6.25, smooth; subcolumellar lamella from comparatively strong and tuberculate to faint and subvertical, sometimes absent; Rapa......cylindrata
 - EE. Typically 2.03×1.06 mm., adult roughly resembling juvenile of *cylindrata*; more ovate, smoother, and glossier than *cylindrata*, whorls about 5.5; subcolumellar lamella weak as in *cylindrata*, sometimes absent (Rapa)cylindrata philolichen
 - DD. Typically 2.6 mm., more or less up to about 3.23 mm.; parietal undulations very strong, strong, to weak...... voyana subspecies in part (*christiani* to *rapaensis*); table 5
 - CC. Columella either bi- or trilamellate, never mixed (unless very young and subcolumellar lamella undeveloped); subcolumellar lamella, when present, distinct, not weak or faint as above; parietal undulations fairly strong to strong.
 - D. Columella bilamellate
 - E. Typically 3.68 × 1.61 mm., whorls nearly 7, upper whorls eroded by subacid water, slightly convex; growth striae strong and widely spaced (Rapa) cremnobates
 - E.E. Typically 4.6×2.0 mm., not elongate but usually subcylindrical from last whorl to third, thence subconic to apex; whorls 7.5, smooth, sometimes eroded, shouldered; growth striae fine (Pitcairn Island)..fosbergi
 - DD. Columella trilamellate
 - E. Typically 3.3×1.7 mm., whorls 6; supra- and subcolumellar lamellae blunt (Kermadec Islands)..raoulensis

Tubuaia fosbergi, new species (fig. 4, a-d).

Shell cylindric-turretted, color sayal brown, dull, thin, subtranslucent, pitted, scarred, and pinpointed with erosion; growth striae fine. Spire subcylindrical from last to third whorl, subconic from third whorl to apex, tapering slowly and gradually from last whorl to 0.75 of way above, then abruptly tapered beyond. Suture well-impressed. Whorls 7.5; embryonic whorls small, sharp; postembryonic whorls narrow, shouldered above; last whorl flattened on right side, forming upper and lower angles. Aperture slightly oblique, auriform, outer margin very lightly flattened by shallow sulcus. Parietal lamella strong, about one whorl long, outer 0.8 high, remainder of interior low. Columella faintly sigmoid, thickened up to outer obtuse angulation. Palatal folds none. Peristome thin, unreflected. Length 4.6 mm., diameter 2.0 (43.5 percent); apertural axis 1.42, diameter 0.84

(59 percent); last whorl 2.36 (51 percent); parietal lamella 0.23.

Paraneanic stage (fig. 4, b). Shell transparent, lighter in color than adult, shining. Columella bilamellate: supracolumellar lamella linear; columellar lamella broad, semi-



FIGURE 4.—Tubuaia fosbergi, Pitcairn: a, adult (holotype); b, paraneanic, oblique view; c, metaneanic, frontal view; d, meta-ananeanic, frontal view.

lunate, subtransverse, deeply seated; subcolumellar lamella absent. Parietal lamella somewhat thinner than in adult, no undulations visible. Palatal wall biplicate, folds interrupted, denticles widely spaced exteriad, closely spaced interiad, upper with eight denticles, lower with two to three fewer. Length 4.16 mm., whorls 7.0.

Metaneanic stage (fig. 4, c). Shell pale, transparent, shining. Columellar lamella stronger, extending farther out. Parietal lamella quite strongly sinuous with two broad undulations. Palatal denticles more distinct than in paraneanic specimens, quite high, compressed, four above, three below, the remainder absorbed but scars visible. Length 3.16 mm., whorls 6.5.

Meta-ananeanic stage (fig. 4, d). Shell pale, transparent, shining. Columellar lamella extending farther out than in metaneanic specimens, its termination coalescing with supracolumellar lamella. Parietal fold similar to that of metaneanic specimens. Palatal plicae about same as metaneanic but scars of absorbed denticles stronger. Length 2.02 mm., whorls 5.0.

Pitcairn Island: Middle Hill, on dead *Pandanus* leaves, alt. 700 ft., Fosberg, June 14, 1934; holotype 135141; paratypes 135142-135147 (12 specimens), 10138-10139; dissected 135142 and 141871. Additional paratype: north slope, back of village [Adamstown], on dead *Pandanus* leaves on one tree, alt. 600 ft., Cooke and Anderson, June 13, 1934, 141871 (one specimen).

Only 14 specimens of this species, in two colonies, were collected, owing to a gale which forced the party to leave the island. Of the 14, only three can be considered adult. Of these three, one is 4 mm. long (135143), one is 5 mm. long (141871), and the holotype is 4.6 mm. long.

This species differs from T. *myojinae* in size, shape, and apertural armature. It is much longer and the whorls of the spire are more compressed axially and more convex; it lacks the subcolumellar fold; the palatal denticles are more numerous, the folds longer; and the parietal lamella is broad for a greater length, with fewer undulations.

This species is named for Raymond Fosberg, one of the botanists on the Mangarevan Expedition, who collected 13 of the specimens.

- Tubuaia cremnobates Cooke and Kondo, B. P. Bishop Mus., Bull. 221: 153, fig. 72, a-f, 1960.
- Tubuaia cylindrata cylindrata Cooke and Kondo, B. P. Bishop Mus., Bull, 221: 155, fig. 73, a-c, 1960.
- Tubuaia cylindrata philolichen Cooke and Kondo, B. P. Bishop Mus., Bull. 221: 156, fig. 73, d, e, 1960.

Tubuaia myojinae, new species (figs. 5, *a-h*; 6).

Shell (fig. 5, a) convex-conic, color sayal brown, thin, upper part opaque, last two whorls transparent with patches of opacity, glossy, growth striae fine, faint. Spire with slightly convex outlines, tapering gradually to apex. Suture simple, moderately impressed. Whorls 6.3; embryonic whorls fairly large, obtuse; postembryonic whorls convex; last whorl oblong, tapering evenly to base. Aperture vertical, subauriculate, outer margin very slightly flattened by incipient sulcus. Parietal lamella strong, oblique, 0.75-0.85 whorl in length, outer third high, remainder very low, gradually disappearing. Columella faintly sigmoid, inner margin thickened, obtusely angled and projecting at its outer edge; remnant of columellar folds visible as tiny tubercle in oblique aspect. Palatal folds none. Peristome thin, erect.

Paraneanic stage (fig. 5, f). Columella trilamellate; supracolumellar lamella linear, subvertical; columellar wide, subtransverse; subcolumellar small, vertical, flat, compressed, the edge facing laterad. Parietal fold with two shallow sinuosities interiad, not noticeable frontally but seen through shell from back. Palatal folds two, interrupted, each with two widely separated denticles plus signs of third remnant (upper fold not visible in illustration). Length 3.0 mm., whorls 6.3.



FIGURE 5.—*Tubuaia myojinae*, Raivavae: a, adult (holotype); b, elongate form of typical specimen; c, conical form; d, fusiform shell; e, subcylindrical form; f, paraneanic, oblique view; g, metaneanic, oblique view; h, ananeanic, frontal view.

Para-metaneanic stage. Columella trilamellate, all lamellae much weaker than in paraneanic stage. Parietal with three sinuosities, the first clearly visible frontally. Palatal folds with three upper denticles, two lower.

Metaneanic stage (fig. 5, g) substantially the same as para-metaneanic. Some specimens have threadlike connections between palatal denticles or folds are continuous. Length 2.16 mm., whorls 5.0.

Ananeanic stage (fig. 5, h). Supracolumellar lamella vertical; columellar lamella fairly wide, transverse; subcolumellar lamella absent (not formed). Parietal fold not sinuous. Palatal wall with one strong lower denticle and very low, fairly long upper fold. Length 1.2 mm., whorls 3.5.

Infants are miniature of ananeanic but without palatal folds.

Elongate form of typical specimen (fig. 5, b), 0.43 mm. longer, narrower, otherwise the same as typical form.

Conical form (fig. 5, c). Spire with straighter outlines than typical form, embryonic whorls sharper, whorls flatter, last whorl wider, less evenly tapering to base. Parietal lamella perceptibly weaker, lower, thinner. Columellar lamella weaker. Palatal folds weaker. Suture lightly impressed.

Fusiform type of shell (fig. 5,d) longer than typical form, whorls flatter, embryonic whorls sharper, suture very lightly impressed, last whorl narrow and tapering evenly to base. Apertural armature typical.

Subcylindrical form (fig. 5, e) slightly shorter than typical, spire narrower, with flatter whorls, last whorl narrower and tapering much more evenly to base. Color of juveniles tawny olive, in contrast to sayal brown of typical juvenile.

	Figure 5, <i>a-e</i>	Length	DIAMETER	Percent	Apertural Axis	Diameter	Percent	Parietal Lamella	LAST WHORL	Percent	W HORLS
c	conical	2.87 mm.	1.45	50.5	1.06	0.64	60.7	0.13	1.77	62.0	6.0
е	subcylindrical	2.87	1.32	46.0	0.97	0.64	66.5	0.13	1.68	58.6	6.0
а	typical	2.97	1.35	45.7	1.00	0.64	64.5	0.19	1.77	59.7	6.3
b	elongate	3.40	1.42	41.7	1.06	0.64	60.5	0.16	1.84	54.0	6.5
d	fusiform	3.62	1.52	41.7	1.32	0.71	54.0	0.13	2.20	60.5	6.0

Table 4

Austral Islands: Raivavae, second valley west of Pic Rouge, northwest side of ridge, on leaves and trunk of *Glochidion* and *Celastrus* and on lichens growing on their trunks, alt. \pm 425 ft., Anderson, August 5, 1934; holotype 10124; paratypes 146448-146457 (43 specimens), 10125-10127 (elongate form same as typical form, 10125). Conical form, 0.25 mile west of Ahuoivi Point, nearly all found on young coconut trees, alt. 5 ft., Cooke, Anderson, and Kondo, Aug. 9, 1934, 10129, 147056-147059 (62 specimens). Fusiform forms, Mount Araua, in clump of *Scirpus*, alt. 1,247 ft., Zimmerman, Aug. 14, 1934, 10130, 147621-147622 (10 specimens). Subcylindrical form: Marae Unurau, \pm 0.25 mile southeast of Pic Rouge, under stones and on dead leaves, alt. 50 ft., Cooke, Anderson, and Zimmerman, Aug. 3, 1934, 10131, 146089-146091 (seven specimens).

The holotype retains a small remnant of the columellar fold, indicating that complete maturity had not been attained. However, no specimens in the lot lacked that vestige.

The infant is a simple shell without palatal folds or subcolumellar lamella. The ananeanic stage has palatal plicae, the lower plica well developed, the upper scarcely visible but longer in extent. Fullest armatural development takes place in the metaneanic stage or close to it. At this stage all three columellar folds are well developed, the parietal lamella attains the maximum number of sinuosities, and the palatal plicae attain the greatest number of denticles. In maturity the shell reverts to simplicity, since all palatal plicae, the two lower columellar folds, and the sinuosities of the parietal lamella are resorbed. A small basal tubercle persists in the subadult or near-adult stage for some time.

Including the typical one, four forms are discernible within the species. Of these, only two, the fusiform and the subcylindrical, were collected in pure colonies and thus appear to be distinct forms. The conical form, which may be only a variant of the typical form, occurs either separate from or together with the typical form. A thorough collection from Raivavae will undoubtedly reveal other new forms and intermediates.

The typical form of the species ranges through the entire length of the island of Raivavae (fig. 6), from sea level to 1,400 feet. The conical form was collected from the east, west, and south, ranging from sea level to 900 feet. The fusiform shell was collected only on Mount Araua near the center of the island at 1,247 feet and on its southern slope at 1,000 feet. The subcylindrical form was collected twice, at the south and southwest, at 50 feet and near sea level.

T. myojinae resembles T. cremnobates from Rapa, which is approximately 290 miles southeast of Raivavae. T. cremnobates is, however, much longer (3.7 mm. versus 2.97), has more whorls (7 versus 6.3), is darker in color, and has coarser growth striae than T. myojinae, which is nearly smooth with weak growth striae. Juvenile T. myojinae have a definite and unique subcolumellar fold, which is vertical and compressed and faces the peristome. T. cremnobates has no subcolumellar fold. Occasional specimens have a thickening below the columellar lamella, but this appears to be only a vestige.

The species is named for the Mangarevan Expedition ship Myojin Maru. Although the ship was christened the *Islander* on the day of its departure from Honolulu, the name did not become official until sometime after the expedition returned.

- Tubuaia raoulensis (Pilsbry and Cooke), Cooke and Kondo, B. P. Bishop Mus., Bull. 221: 156, 1960.
 - Tornatellina raoulensis Pilsbry and Cooke, Man. Conch. 23: 180, pl. 39, figs. 9-11, 1915.



FIGURE 6.—Distribution of the four forms of *Tubuaia myojinae* on island of Raivavae: enclosed areas indicate mountains, and mountain names are adjacent to these areas; altitudes, in feet, are within the areas or below names; place names are along the coastline.

In a previous paper (B. P. Bishop Mus., Bull. 221, pp. 157-159, 1960), Cooke and Kondo enumerated a series of localities where T. voyana (Pilsbry and Cooke) was collected. At that time the samples showed evidences of subspeciation. A closer study of the series in question and of others in the Bishop Museum collections has substantiated the existence of at least 12 subspecies.

T. voyana voyana is now restricted to the Cook Islands. The form figured by Cooke and Kondo (1960, fig. 74, a, b) is transferred to T. voyana teutuensis.

In the absence of juveniles from the type locality, Mauke in the Cook Islands, comparisons have been made with those from Mangaia, the adults of which are similar to those from Mauke. Adults of the subspecies are compared with a paratype from Mauke (BBM 189794 ex Academy of Natural Sciences, Philadelphia, 83154).

The subcolumellar lamella is vestigial; many specimens have a weak, some a well-defined, tubercle. The two-plicate palatal armature is considered normal; the loss of one or both, a degenerate condition.

The differentiation of the 12 subspecies of T. voyana through their adults is difficult, for every subspecies has nearly identical characteristics of size, shape, coloration and simplified apertural armature. Only T. v. vaiaunanae is sufficiently small to be easily segregated from the others.

Among the juveniles, especially in the metaneanic stage, the subspecific differentiations are more evident. Differentiation is dependent principally upon palatal plication, bolstered by the columellar and parietal plicae.

By palatal dentition the 12 subspecies may be divided into three groups (table 5): (1) those in which all are biplicate or principally biplicate with a few uniplicate (*christiani* to *rapaensis*); (2) those in which the palatal walls are principally biplicate, some uniplicate, and a few nonplicate (*enokai* to *teutuensis*); and (3) those in which the palatal walls are principally nonplicate, some uniplicate, and a few or none biplicate (*oromanaensis* to *peasei*). When one of the palatal plica is lost, it is usually the upper. In fact, the upper plica is seldom retained (*turivaoensis*).

Except in *christiani*, the columella is principally bilamellate. As compared with T. *perplexa* and other species, the subcolumellar lamella is weak, in fact, considered vestigial. Many subspecies have a vague rise below the columellar lamella giving an indication of the subcolumellar lamella.

The degree of warping or sinuosity in the parietal lamella gives no indication of relationship but does serve to differentiate some forms from others. The sinuosities, or undulations, are fairly uniform for each subspecies except in *rapaensis* and *oromanaensis*, in both of which they are weak and strong. T. v. christiani has the strongest undulations; *peasei*, the weakest. One new subspecies of T. voyana was collected on Rurutu, but lacking a good series and good specimens, I have not described it. It is narrower than any of the other subspecies and about the length of T. v. anceyana. The juveniles have two beaded rows of palatal plicae. It was collected at Murivahi (147690-147691), at Teuo (147764), and on Mount Taitaa (147840-147843).

Distribution: "Society Islands" (Garrett), Mangareva Islands, Pitcairn, Austral Islands (Rapa, Raivavae, Tubuai, Rurutu, Rimatara), and Cook Islands (Mauke, Mangaia). This is an area bounded by 28 degrees of longitude (130°W. to 158°W.) and 12 degrees of latitude (16°S. to 28°S.). The longest distance between islands (Mangaia to Pitcairn) is approximately 1,680 nautical miles. Further collecting will undoubtedly uncover many more new subspecies.

In the following key parietal, palatal, and columellar plications refer to those of juveniles in a series. Parietal undulations are given in four degrees: very strong, strong, weak, and faintly sinuous.

Key to Subspecies

MAUKE, MANGAIA

Typically $\pm 3.2 \times 1.45$ mm.; parietal lamella weakly sinuous, shallowly indented; palatal wall all biplicate; columella principally bilamellate, some trilamellate; subcolumellar lamella, when present, very weak.....voyana

Rimatara

Typically 2.9×1.48 mm.; parietal lamella weakly sinuous, shallowly indented or fairly strongly sinuous; palatal wall principally nonplicate, a few uni- and biplicate; columella all bilamellate.....oromanaensis

Rurutu

- Typically 3.3×1.52 mm.; parietal lamella weakly sinuous, shallowly indented; palatal wall principally nonplicate, a few uniplicate, even fewer biplicate; columella all bilamellate......manurevae
- Typically 3.2×1.52 mm.; parietal lamella weakly sinuous, shallowly indented, slightly stronger than in *manurevae*; palatal wall principally biplicate, some uniplicate, a few nonplicate; columella principally bilamellate but a good number of specimens trilamellate; whorls more convex than in *manurevae* and shells appearing more fragile......matonaaensis

RAIVAVAE

- Shell dark, typically 3.3×1.45 mm.; parietal lamella weakly sinuous, shallowly indented; palatal wall principally nonplicate, some biplicate, a few uniplicate; columella principally bilamellate, a good number of specimens trilamellate, subcolumellar fold faint.....turivaoensis Shell lighter than above, smaller, typically 2.62×1.29 mm.; parietal lamella strongly

Rapa

Shell light, typically 3.06×1.53 mm.; length: diameter = 50 percent; parietal lamella
usually weakly, shallowly indented but some strongly sinuous; palatal wall
principally biplicate, rarely uniplicate; columella principally bilamellate, rarely
trilamellaterapaensis
Shell darker, typically 3.36×1.48 mm.; length: diameter = 44 percent; parietal
lamella weakly sinuous, shallowly indented; palatal wall principally biplicate,
some uniplicate, some nonplicate; columella all bilamellateteutuensis

PITCAIRN

MANGAREVA ISLANDS

Typically 2.94 × 1.39 mm.; parietal lamella strongly sinuous, deeply indented; palatal wall all biplicate; columella principally bilamellate, some trilamellate......anceyana
Typically 3.2 × 1.45 mm.; parietal lamella weakly sinuous, shallowly indented; palatal wall principally biplicate, some uniplicate, a few nonplicate; columella principally bilamellate.....enokai

SOCIETY ISLANDS

Typically 3.3×1.48 mm.; parietal lamella faintly sinuous, very shallowly indented, at first glance appearing straight; palatal wall principally nonplicate, some uniplicate, none biplicate; columella principally bilamellate, occasionally trilamellate ______peasei

Tubuaia voyana voyana (Pilsbry and Cooke). Figure 7, a, b.

- Tornatellina (Tornatellinops) voyana Pilsbry and Cooke, 1915, Man. Conch. 23: 179, pl. 35, figs. 12, 13.
- Tornatellina (s.s.) nitida Pilsbry and Cooke, 1915, Man. Conch. 23:145, pl. 34, fig. 11 [not pl. 36, figs. 3, 7, Huahine].
- Tubuaia voyana voyana Cooke and Kondo, 1960, B. P. Bishop Mus., Bull. 221:157 but not fig. 74 a, b [= now T. v. teutuensis, Rapa]. Cook Islands only.

Adult (fig. 7, a) oblong-conic, semitransparent, glossy, clay color, minutely striate. Spire straight, tapering regularly to apex. Suture moderately impressed. Whorls 6; embryonic whorls small, subacute; postembryonic whorls convex; last whorl tapering regularly to base. Aperture subauriform. Parietal lamella strong, about a whorl in length. Columella subsigmoid. Palatal folds none. Peristome thin, unreflected.

Length 3.2 mm., diameter 1.45 (45.5 percent); apertural axis 1.23, diameter 0.74 (60 percent); last whorl 1.97 (61.6 percent); parietal lamella 0.16.

Metaneanic stage (fig. 7, b). Parietal lamella weakly undulant, with two shallow indentations on periphery, the edge bent inward weakly. Palatal wall with two rows of denticles; upper plica with three denticles and scar of fourth; lower plica with two denticles and scars of third and fourth; denticles small, oblong. Columella bilamellate;

supracolumellar lamella sigmoid, fairly strong; columellar lamella broad, subtransverse. Length 2.0 mm., whorls 4.5-5.0.

Palatal wall biplicate 13 out of 13 or (13:13).

Columella bilamellate (9:13), trilamellate (4:13). Subcolumellar lamella, when present, weak.

Type in Academy of Natural Sciences, Philadelphia (83154).

Cook Islands: Mauiki [Mauke], C. D. Voy; paratype in Bishop Museum (ex Philadelphia 83154) BBM 189704 (one specimen). Additional material,

Table 5.—Summary of Tubuaia voyana subspecies (arranged from subspecies predominantly biplicate on palatal wall to those predominantly nonplicate)

		TOTAL Exam-	Tuvr-	PAL	ATAT PI	TCAE	Columel- LAR FOLDS		PARIE- TAL
SUBSPECIES	LOCALITY	INED	NILES	0	1	2	2	3	ITY
christiani	Pitcairn	305	238			238	63	175	very strong
vaiaunanae	Raivavae	49	30			30	13	17	strong
anceyana	Mangareva	5	4			4	3	1	strong
voyana	Mauke Mangaia	21	13			13	9	4	weak
rapaensis	Rapa	106	81		3	78	73	8	weak to strong
enokai	Mangareva	672	317	41	96	180	269	48	weak
matonaaensis	Rurutu	34	25	2	6	17	18	7	weak
teutuensis	Rapa	51	18	4	4	10	18		weak
oromanaensis	Rimatara	12	11	7	3	1	11		weak to fairly strong
turivaoensis	Raivavae	165	122	83	10	29	77	45	weak
manurevae	Rurutu	520	394	337	38	19	394		weak
peasei	Society	8	8	5	3		7	1	faint

typical or closely so: Mangaia, Oneroa Makatea, under stones or logs, alt. 115 ft., Buck, Feb. 14, 1930, 10128 (figured juvenile), 97640-97641 (three specimens); Oneroa Makatea, under stones or logs, alt. 115 ft., Jan. 10, 1930, 97518-97520 (seven specimens).

The above description is based on the paratype in Bishop Museum. The figured specimen is slightly longer than the type described by Pilsbry and Cooke (Man. Conch. 23:179) and has more whorls. The type measures 3.0×1.5 mm., has 5.5 whorls.



FIGURE 7.—a, b, Tubuaia voyana voyana, Mauke: a, adult; b, metaneanic, oblique apertural view (note weakly sinuous parietal lamella, biplicate palatal wall, and bilamellate columella). c, T. v. oromanaensis, Rimatara, adult (holotype). d-h, T. v. manurevae: d, adult (holotype); e, metaneanic, oblique apertural view illustrating (1) bilamellate columella and (2) nonplicate palatal wall; f, gerontic specimen with angular body whorl; g, broader than typical specimen; h, with flatter whorls than typical specimen.

Tubuaia voyana oromanaensis, new subspecies (fig. 7, c).

Shell nearly identical with paratype of T. v. voyana in size and outline except for slight difference in shape of last whorl, which is less regularly tapering to base.

Length 2.99 mm., diameter 1.48 (50 percent); apertural axis 1.16, diameter 0.74 (64 percent); last whorl 1.80 (60.5 percent); parietal lamella 0.16.

Juvenile parietal lamella weakly undulant, with shallow indentations, edge bent inward weakly.

Palatal wall: biplicate (1:11), uniplicate (3:11), nonplicate (7:11). Columella: bilamellate (11:11).

Austral Islands: Rimatara, Oromana Hills, taken by beating ferns and shrubs, alt. 250 ft., Zimmerman, Sept. 4, 1934; holotype 10137; paratypes 149122-149123 (17 specimens).

T.v. oromanaensis is 0.2 mm. shorter than T.v. voyana and slightly wider. It differs from the typical subspecies in having irregular palatal dentition.

Tubuaia voyana manurevae, new subspecies (fig. 7, d-h).

Adult (fig. 7, d) larger and slightly longer than paratype, otherwise very close to it. Length 3.3 mm., diameter 1.52 (46 percent); apertural axis 1.26, diameter 0.71 (56 percent); last whorl 2.0 (61 percent); parietal lamella 1.3.

Metaneanic stage (fig. 7, e). With broader body whorl; parietal lamella weakly sinuous, shallowly indented. Length 2.75 mm., whorls 5.3.

Palatal wall: nonplicate 85.5 percent (337:394), uniplicate 9.65 percent (38:394), biplicate 4.8 percent (19:394). Columella 100 percent bilamellate.

Austral Islands: Rurutu, southeast slope of Mount Manureva, hanging valley west of Moerai village in patch of *Aleurites* trees, on fern roots, tree trunks, and dead leaves on ground, alt. 500-600 ft., Anderson and Kondo, Aug. 30, 1934; holotype 10146; paratypes 10147-10150, 148793-148808 (926 specimens).

T. v. manurevae differs from its closest neighbor, T. v. matonaaensis, one mile to the east, in having less convex whorls and being slightly larger. In juveniles of matonaaensis the palatal plicae are principally biplicate (17:25), in contrast to those of manurevae, wherein the greatest number are nonplicate. The columella of matonaaensis has either two or three lamellae, whereas the columella of manurevae is bilamellate.

The large number of specimens offers a good idea of the subspecies. Besides the typical form there are the usual longer gerontics with angular body whorl, with or without calloused palatal wall (fig. 7, f); the broader than typical, often shorter, form (fig. 7, g); and forms with flatter and apparently wider whorls than the typical form has (fig. 7, h). Lengths: 3.58, 3.24, 3.30 mm.

With rare exceptions, the plicae in the biplicate specimens are very weak and difficult to discern.

Tubuaia voyana matonaaensis, new subspecies (fig. 8, a).

Adult with slightly more convex spire than paratype, whorls also slightly more convex, parietal lamella slightly stronger, color lighter.

Length 3.23 mm., diameter 1.52 (47 percent); apertural axis 1.16, diameter 0.71 (61 percent); last whorl 1.97 (61 percent); parietal lamella 0.21.

Metaneanic stage with only slightly different parietal lamella than typical, weakly sinuous, with indentations of lamellar margin deeper and edge of margin bent inward slightly. Length 2.2 mm., whorls 4.8-5.0.

Palatal wall: biplicate (17:25), uniplicate (6:25), nonplicate (2:25). Columella: bilamellate (18:25), trilamellate (7:25), weak.

Austral Islands: Rurutu, Mato Naa, upraised coral reef, north side of *makatea* cliff, on dead banana leaves, alt. 20-30 ft., Anderson, Aug. 29, 1934; holotype 10143; paratypes 148715 (dissected)-148719 (47 specimens).

Tubuaia voyana turivaoensis, new subspecies (fig. 8, b).

Longer than paratype, with straighter apex, closer to T. v. peasei in outline.

Length 3.3 mm., diameter 1.45 (44 percent); apertural axis 1.13, diameter 0.71 (63 percent); last whorl 1.94 (58.6 percent); parietal lamella 0.13.



FIGURE 8.—a, Tubuaia voyana matonaaensis, Rurutu, adult (holotype). b, T. v. turivaoensis, Raivavae, adult (holotype). c, d, T. v. vaiaunanae, Raivavae: c, adult (holotype); d, metaneanic, oblique apertural view illustrating strongly sinuous parietal lamella and biplicate palatal wall (faint subcolumellar fold is shown).

Metaneanic stage with weakly sinuous parietal lamella with shallow indentations, palatal wall principally nonplicate. Length 2.25 mm., whorls 5.0.

Palatal wall: nonplicate (83:122), uniplicate (10:122), biplicate (29:122). Columella: bilamellate (77:122), trilamellate (45:122).

Austral Islands: Raivavae, south cliff of Mount Turivao, under Selaginella and Hymenolepis and under their leaves and lichens, alt. 650+ ft., Anderson, Aug. 13, 1934; holotype 10140; paratypes 147511-147514 (58 specimens).

The type locality of T.v. turivaoensis is on the south cliff of Mount Turivao, the easternmost peak of Raivavae. The palatal denticular formula is heterogeneous here but principally nonplicate and the parietal lamella uniformly weak. The shell color is a deep, rich brown. Elsewhere on the island are other colonies which differ in small degree from the typical form. The colony from the other extreme of the island, at the foot of Pic Rouge, is lighter in color, has a more strongly sinuous type of parietal lamella mixed with the weakly sinuous, and the palatal wall is all biplicate (12:12). The Vaiaunana Peninsula colony is like that of Pic Rouge. The Mount Muatapu colony is slightly darker than those of Pic Rouge and Vaiaunana but slightly lighter than that of Mount Turivao. Its parietal lamella is weak, but in palatal plication it is generally absent (7:7).

Other specimens were collected in small numbers from Mount Taraia, Anatonu, and Mount Araua.

Tubuaia voyana vaiaunanae, new subspecies (fig. 8, c, d).

Adult (fig. 8, c) smaller than typical, whorls slightly more convex, last whorl not tapering as regularly.

Length 2.62 mm., diameter 1.29 (49 percent); apertural axis 0.97, diameter 0.58 (60 percent); last whorl 1.55 (59 percent); parietal lamella 0.16.

Metaneanic stage (fig. 8, d) with strongly sinuous parietal lamella, deep indentations, and edge bent inward strongly. Length 2.0 mm., whorls 5.0.

Palatal wall: all biplicate (30:30). Columella: principally trilamellate (17:30), nearly the same number bilamellate (13:30). Subcolumellar fold, when present, weak, tuberculate.

Austral Islands: Raivavae, Vaiaunana Point, south side of peninsula, on dry *Pandanus* leaves on ground, alt. 150 ft., Fosberg, Aug. 6, 1934; holotype 10141; paratypes 10142, 146716-146720 (56 specimens).

T. v. vaiaunanae is the smallest subspecies. Although it inhabits the same island as *turivaoensis*, it differs a great deal from it. T. v. vaiaunanae is 0.68 mm. shorter, has strongly sinuous parietal lamella, and the palatal wall is consistently biplicate, whereas *turivaoensis* nearly always has a weakly sinuous parietal lamella, with the palatal wall principally nonplicate.

Tubuaia voyana rapaensis Cooke and Kondo, B. P. Bishop Mus., Bull. 221: 159, fig. 74, c, e, 1960.

The adult of this subspecies varies only slightly from the typical form, being shorter by 0.14 mm., having a less elongate body whorl, and a slightly more convex outline.

In juveniles apertural armature appears to be somewhat the same. In both, palatal wall is primarily biplicate and bilamellation in columella is predominant. They differ only in parietal sinuosity, which is uniformly weakly sinuous in *voyana*, and both weak and strongly sinuous in *rapaensis*.

Palatal wall: biplicate (78:81), uniplicate (3:81). Columella: bilamellate (73:81), trilamellate (8:81).

Although the undulations of the lamellae of the type lot (Tapui Islet) are uniformly weak, a wide range is shown by the various colonies on Rapa: strong in Tapui and Area; fairly strong in Rapa Iti, Karapo Hari, and Mount Tanga; weak in Tapui, Ahurei, point near Karapo Hari, Mount Koara, and Karapo Hari. In this peculiarity, it is somewhat like T. v. turivaoensis. The conclusion seems to be that no single subspecies, if widespread over an island, can be circumscribed by certain definite characteristics. Each colony appears to take a path of its own, paralleling or diverging in some small way from its fellow colonies.

Tubuaia voyana teutuensis, new subspecies (fig. 9, a).

Tubuaia voyana voyana Cooke and Kondo, B. P. Bishop Mus., Bull. 221: 157, fig. 74, a, b, 1960.

Adult longer and darker than typical form but similar in outline.

Length 3.36 mm., diameter 1.48 (44 percent); apertural axis 1.16 diameter 0.68 (58.6 percent); last whorl 1.97 (58.7 percent); parietal lamella 0.16.

Metaneanic stage close to type, parietal weakly sinuous, indented and bent inward. Length 2.5 mm., whorls 5.0-5.3.

Palatal wall: biplicate (10:18), uniplicate (4:18), nonplicate (4:18). Columella: bilamellate (18:18).

Austral Islands: Rapa, Teutu, on cliff, alt. 250 ft., Wight and Cooke, July 27, 1934; holotype 10151; paratypes 143623 (dissected)-143626 (64 specimens). Additional paratypes 143615 (11 specimens), data as above.

The holotype differs slightly from that illustrated by Cooke and Kondo. It is the same length, but narrower; has a longer apertural axis but smaller diameter; and has a slightly shorter parietal lamella.

T. v. teutuensis is closer to the type from the Cook Islands than to the subspecies known as T. v. rapaensis, which is shorter; is more convex in outline; has smoother whorls and a less tapering body whorl (which is sometimes subtruncate); and has much smaller embryonic whorls. The distance between the two Rapa subspecies is 1.25 nautical miles; the distance between teutuensis and voyana, about 800 nautical miles.

This subspecies is found on the same damp cliff with *Tubuaia cremnobates*; but they are easily separated from each other as the T. v. teutuensis animals are uniformly slate color and those of T. cremnobates are almost solid black.

Besides the typical specimens in the type lot, there are three variants: (1) one extra large specimen 3.75 mm. long, (2) squat specimens with broad body whorl and short spire, and (3) a few small ones, nearly typical in shape.



FIGURE 9.—a, Tubuaia voyana teutuensis, Rapa, adult (holotype). b, c, T. v. christiani, Pitcairn: b, adult (holotype); c, paraneanic, oblique aspect of aperture showing trilamellate columella, very strongly undulating parietal lamella, and biplicate palatal wall. d, T. v. anceyana, Mangareva Islands, adult (holotype). e, T. v. enokai, Mangareva, adult (holotype). f, T. v. peasei, Society Islands, adult (holotype).

Tubuaia voyana christiani, new subspecies (fig. 9, b, c).

Adult (fig. 9, b) nearly identical with paratype except slightly longer and having much stronger parietal lamella.

Length 3.23 mm., diameter 1.52 (47 percent); apertural axis 1.19, diameter 0.71 (59.6 percent); last whorl 1.94 (60 percent); parietal lamella 0.19.

Large adult with slender spire and narrow body whorl (3.5 mm.). Small adult with proportionately wider spire but otherwise typical except shorter (2.75 mm).

Paraneanic stage (fig. 9, c) with very strongly undulating parietal lamella (stronger than in *vaiaunanae* and *anceyana*), edge of which is turned strongly inward; palatal wall always biplicate, plicae very strong, each denticle high. In meta-ananeanic stage upper palatal weakens perceptibly; in infant, upper palatal plica is unformed, showing that lower palatal plica develops first; in embryo both plicae unformed.

Palatal wall all biplicate (238:238). Columella: 73 percent trilamellate (175:238), 27 percent bilamellate (63:238); subcolumellar lamella a perceptible tubercle.

Pitcairn Island: northern slope, above Adamstown, on dead *Pandanus* leaves, alt. 700 ft., Anderson and Cooke, June 13, 1934; holotype 10152; para-types 10153, 141902-141912 (187 specimens). Additional material was collected.

T. v. christiani closely approaches T. v. voyana from Mauke, in that its palatal wall is purely biplicate and the subcolumellar fold is present in many specimens, although more strongly formed in christiani. The principal difference is in the warping of the parietal lamella, that of christiani being very strongly sinuous and bent inward, whereas in voyana it is only mildly so. The parietal lamella is also much stronger in the adult christiani.

The subspecies is named for Fletcher Christian of H. M. S. Bounty.

Tubuaia voyana anceyana, new subspecies (fig. 9, d).

Near-adult much smaller and more slender than either T. v. voyana or T. v. enokai, but parietal lamella much stronger than either. Color similar to that of typical form (clay or near it). Otherwise nearer to type than its neighbor (enokai).

Length 2.94 mm., diameter 1.39 (47 percent); apertural axis 1.06, diameter 0.64 (61 percent); last whorl 1.8 (61 percent); parietal lamella 0.20.

Juvenile parietal lamella strongly sinuous, edge bent inward. Palatal wall biplicate (4:4). Columella: bilamellate (3:4), trilamellate (1:4), subcolumellar weak.

"Gambier [Mangareva] Islands," ex Fulton collection; holotype 10145; paratypes 115377 (four specimens), gift of C. M. Cooke, Jr. For further information see under *T. garrettiana*. Additional paratype 164569 (one specimen), ex Acad. Nat. Sci., Philadelphia 115018, "Purch. Sowerby and Fulton 1916."

Because of the presence of a microscopic vestige of the columellar fold, the type specimen of this subspecies may not be an adult. This specimen is probably smaller than the average, as shown by the presence of a longer paraneanic specimen within the same lot (3.25 mm.), 115377. Another paraneanic specimen (164569) is also quite large (3.25 mm.). The peristome of the type specimen appears to be slightly chipped away.

The subspecies is named for Cesar Felix Ancey who applied the manuscript name "Tornatellina monoliata" to it.

Tubuaia voyana enokai, new subspecies (fig. 9, e).

Adult slightly longer and larger than paratype and much darker, otherwise close to it. Length 3.20 mm., diameter 1.45 (45.5 percent); apertural axis 1.13, diameter 0.71 (63 percent); last whorl 1.94 (60.5 percent); parietal lamella 0.19.

Metaneanic parietal lamella as in typical, weakly sinuous with shallow indentations at periphery. Length 2.3 mm., whorls 5.0.

Palatal wall: biplicate 57 percent (180:317), uniplicate 30 percent (96:317), nonplicate about 13 percent (41:317). Columella: bilamellate (269:317), trilamellate (48:317), subcolumellar fold a faint tubercle.

Mangareva Islands: Mangareva, Mount Mokoto, south cliff, on small fern (*Cyclophorus augustatus*), alt. 1,000 ft., Anderson, June 6, 1934; holotype 10144; paratypes 141558-141564 (161 specimens). Additional paratypes 141590-141594 (31 specimens), Mount Mokoto, south cliff, on cliff and talus,

on ferns, especially *Asplenium nidus*, alt. 1,000 ft., Anderson, June 7, 1934, 141611 (seven specimens); Mount Duff, beyond convent, on cliffs, alt. 800 ft., Zimmerman, June 4, 1934. Other lots were collected on Mount Mokoto. Dissected 141561, 141592.

The subspecies is named for Enos (Enoka) Lyons, assistant engineer of the Myojin Maru.

Tubuaia voyana peasei, new subspecies (fig. 9, f).

Adult more slender than paratype, with sharper apex, flatter and slightly wider whorls, and a more evenly tapering body whorl.

Length 3.30 mm., diameter 1.48 (45 percent); apertural axis 1.19, diameter 0.71 (59.6 percent); last whorl 1.94 (58.6 percent); parietal lamella 0.16.

Juvenile parietal lamella weaker than in typical, faintly sinuous, shallowly indented, appearing straight or nonsinuous at first glance.

Palatal wall nonlamellate (5:8), unilamellate (3:8). Columella: bilamellate (7:8), trilamellate (1:8).

Society Islands: collected by A. Garrett and labeled by him "Tornatellina nitida Pease." Holotype 10136; paratypes 3355 (seven specimens).

The subspecies is named for W. Harper Pease, whose species Garrett believed he had. However, Pease' paratypes, received from the Museum of Comparative Zoölogy, are *Lamellidea pusilla* (Gould).

Race	Length	DIAMETER	PERCENT	Apertural Axis	DIAMETER	PERCENT	Parietal Lamella	Last Whorl	PERCENT	Whores
vaiaunanae	2.62	1.29	49.0	0.97	0.58	60.0	0.16	1.55	59.0	6.0
anceyana	2.94	1.39	47.0	1.06	0.64	61.0	0.20	1.80	61.0	6.0
oromanaensis	2.99	1.48	50.0	1.16	0.74	64.0	0.16	1.80	60.5	6.0
rapaensis	3.06	1.53	50.0	0.97	0.64	66.0	0.13	1.81	58.8	6.0
voyana (typical)	3.20	1.45	45.5	1.23	0.74	60.0	0.16	1.97	61.6	6.0
enokai	3.20	1.45	45.5	1.13	0.71	63.0	0.19	1.94	60.5	6.25
christiani	3.23	1.52	47.0	1.19	0.71	59.6	0.19	1.94	60.0	6.0
matonaaensis	3.23	1.52	47.0	1.16	0.71	61.0	0.21	1.97	61.0	6.0
manurevae	3.30	1.52	46.0	1.26	0.71	56.0	0.13	2.00	61.0	6.0
peasei	3.30	1.48	45.0	1.19	0.71	59.6	0.16	1.94	58.6	6.25
turivaoensis	3.30	1.45	44.0	1.13	0.71	63.0	0.13	1.94	58.6	6.0
teutuensis	3.36	1.48	44.0	1.16	0.68	58.6	0.16	1.97	58.7	6.25

Table 6.—Dimensions of subspecies of T. voyana

Tubuaia hendersoni, new species (fig. 10, a-d).

Shell (fig. 10, a) convex-conic, color cinnamon buff, thin, subtransparent, glossy, growth striae fine. Spire slightly convex, tapering gradually apicad. Suture moderately impressed. Whorls six; embryonic whorls quite sharp, small; postembryonic whorls convex; the last oblong, tapering gradually to base. Aperture vertical, subauriform, outer margin slightly flattened. Parietal lamella strong, compressed, nearly a whorl in

length, gradually lowering interiad. Columella faintly sigmoid, inner margin thickened, projecting at an obtuse angle as usual. Palatal wall with faint trances of two spiral folds. Peristome thin, erect.

Length 2.58 mm., diameter 1.22 (47 percent); apertural axis 0.90, diameter 0.55 (61 percent); last whorl 1.48 (57.5 percent); parietal lamella 0.16.

Elongate form about 0.2 mm. longer, subcylindrical, otherwise as in typical. Length 2.8 mm., whorls 6.5.

Paraneanic to adult same as adult except with deeply seated columellar lamella. Length 2.5 mm., whorls 6.0.

Paraneanic (fig. 10, b). Columella bilamellate; supracolumellar lamella linear, sigmoid; columellar lamella wide, subtransverse, quartermoon-shaped. Parietal lamella



FIGURE 10.—*Tubuaia hendersoni*, Henderson: **a**, adult or near-adult (holotype); **b**, paraneanic; **c**, metaneanic; **d**, ananeanic.

weaker than in adult, lower, not sinuous. Palatal folds two: lower continuous, compressed, quite high, 0.3 length of whorl; upper discontinuous, beaded, beads about six in all, 0.5 whorl long. Length 2.5 mm., whorls 5.5.

Metaneanic stage (fig. 10, c). Last whorl more rotundate than in adult or paraneanic. Parietal lamella as in paraneanic, not sinuous. Lower palatal faint, low; upper semicontinuous, beads more elongate, about six. Length 1.75 mm., whorls 4.75.

Ananeanic stage (fig. 10, d). Supracolumellar lamella weak; columellar strong, transverse. Parietal lamella fairly strong, not sinuous. Lower palatal fold with slight median dip; upper beaded, semicontinuous, about four beads (very rarely lower palatal beaded; 149797, 149838, one specimen each). Length 1.2 mm., whorls 3.5.

Henderson (Elizabeth) Island: northwest end, inland 0.5 mile, alt. 100 ft., sweepings, Fosberg, June 20, 1934; holotype 10132; paratypes 10133-10135, 149849 (\pm 1,200 specimens). Additional paratypes 149645 (dissected) (12 specimens), north end, on dead *Pandanus* leaves, W. Anderson, June 18, 1934.

T. hendersoni differs from T. myojinae in being much smaller and shorter, in having only two columellar lamellae, in having one palatal fold continuous, and in the absence of any undulations on the parietal lamella. In T. myojinae the columella is trilamellate, the parietal lamella sinuous, and the palatal lamellae discontinuous.

The holotype is not a fully mature shell. Faint traces of the positions of the palatal folds are still visible. The numerous gerontic specimens are characterized by a calloused parietal wall, a heavy columella, and opacity of the shell. A few have advanced to the stage where a pseudo-umbilicus is formed by the conjunction of the columella with the parietal callus. Most of the gerontics have a last whorl that appears squarish in outline.

In some juveniles the lower palatal fold is distantly and shallowly disconnected. Juveniles of *T. hendersoni* are easily confounded with those of *Tornatellinops* species from the same locality, which have two continuous spiral palatal folds. The differentiating characteristics between the young of the two species are as follows. *Tornatellinops* species: whorls wider (measured from suture to suture), last whorl large, elongate, and tapering quite slowly to base; parietal lamella uneven, fragile, high and flaring outward; upper palatal continuous, sometimes interrupted once or twice, never beaded, sometimes faint, low. *Tubuaia hendersoni:* whorls narrow, giving shell a tightly coiled appearance, last whorl short, not large, almost globose; parietal lamella even, strong. gradually diminishing interiad; upper palatal fold beaded, some beads connected by low bridges, never continuous.

Race	L,ENGTH	Diameter	Percent	Apertu ral Axis	DIAMETER	PERCENT	Parietal Lamella	Last Whorl	PERCENT	Whorls
cylindrata philolichen.	2.03	1.06	52.2	0.71	0.48	67.6	0.10	1.32	65.0	5.5
cylindrata	2.58	1.25	48.7	0.94	0.61	65.4	0.19	1.74	67.4	6.25
hendersoni	2.58	1.22	47.0	0.90	0.55	61.0	0.16	1.48	57.5	6.0
myojinae (typical)	2.97	1.35	45.7	1.00	0.64	64.5	0.19	1.77	59. 7	6.3
raoulensis	3.08	1.74	56.4	1.23	0.74	60.6	0.22	1.98	64.2	6.0
voyana (typical)	3.20	1.45	45.5	1.23	0.74	60.0	0.16	1.97	61.6	6.0
cremnobates	3.68	1.61	43.7	1.29	0.84	64.6	0.19	2.09	57.0	7.0
fosbergi	4.60	2.00	43.5	1.42	0.84	59.0	0.23	2.36	51.0	7.5

Table 7.—Dimensions of T. cylindrata group

T. HYGROBIA GROUP

Usually inhabits damp cliffs, the acidulous waters of which tend to erode the shells. Members of this group are, in general, of larger proportions than those of the T. cylindrata group (except T. fosbergi). Usually without palatal plicae, with very weak inconspicuous parietal lamella and columellar lamellae, columella bilamellate. The exception, T. saproderma, has a very strong parietal lamella, which is sinuous in the young, a tubercle on the palatal wall of some specimens, and a strong, transverse columellar lamella in the juveniles.

Key

- A. Parietal fold strong both in adult and juvenile, in the latter weakly sinuous; columella bilamellate, columellar fold strong, wide subtransverse; typically 3.52×1.71 mm. (Mangarevan islands).....saproderma
- AA. Parietal fold weak, low, both in adult and juvenile, not sinuous in the latter; columella bilamellate, columellar fold not broad and subtransverse but weak and subvertical.
 - B. Nearly always smeared with fecal matter; elongate-turrite; parietal lamella relatively strong; columellar lamella relatively strong (Raivavae).
 - C. Typically 4.84 × 2.06 mm.; length: diameter = 42 percent; whorls 6.5coprophora
 - CC. Typically 3.58 × 1.67 mm.; length: diameter = 42 percent; whorls 6.0coprophora diminuta
 - BB. Not smeared with fecal matter; elongate-conic, ovate-conic, or oblong-ovate.
 - C. Growth striae coarse, substriatulate, typically more than 5 mm. long (Raivavae)
 - CC. Growth striae minute, fine; typically 3.68×1.94 mm., oblongovate; whorls six, apical whorls decreasing fairly rapidly but not as pronounced as in *T. saintjohni*; apex rather blunt; last whorl fairly capacious but not as much as in *T. saintjohni*, length: diameter = 53 percent (Rapa).....inconstans

Tubuaia saproderma, new species (fig. 11, *a*-*d*).

Shell (fig. 11, a) elongate-conic, subtruncate at base, color near sayal brown, eroded and pitted above, slightly glossy, subtranslucent, with vague microscopic striae. Spire slightly convex, tapering quite regularly and slowly to apex, penultimate whorl bulging more than others. Suture moderately impressed. Whorls 6.3; embryonic whorls small, subacute; post-embryonic whorls slightly convex, but penultimate more convex; last whorl narrow, not bulging. Aperture vertical, subauriform. Parietal lamella fairly strong, 0.5 whorl long. Columella bilamellate; supracolumellar lamella vertical, weakly sigmoid; columellar lamella a vague, elongate tubercle seated obliquely. Palatal folds none. Peristome thin, erect.

Length 3.52 mm., diameter 1.71 (48.5 percent); apertural axis 1.16, diameter 0.68 (58.5 percent); last whorl 2.0 (57 percent); parietal lamella 0.16.



FIGURE 11.—*Tubuaia saproderma*, "Gambier [Mangareva] Is.": **a**, adult (holotype); **b**, paraneanic, oblique view of aperture; **c**, metaneanic, oblique view of aperture illustrating bilamellate columella, weakly sinuous parietal fold, and nonplicate palatal wall with weak tubercle; **d**, metaneanic with eccentrically placed lower palatal tubercle.

Paraneanic stage (fig. 11, b) less eroded than adult, with thinner parietal fold, much stronger columellar lamella, running nearly parallel with supracolumellar lamella. Length 3.0 mm., whorls 5.5.

Metaneanic stage (fig. 11, c) less pitted than paraneanic, with straighter parietal lamella, which is indented shallowly at margin (some specimens weakly sinuous). Columellar lamella wide, subtransverse; subcolumellar fold none. Palatal wall nonplicate (11:13), rarely with single lower tubercle (fig. 11, d) (1:13) placed eccentrically, or faint remnant of one (fig. 11, c) (1:13). Length 2.75 mm., whorls 5.5.

The youngest specimen of the lot (meta-ananeanic) shows no substantial differences in apertural armature from the metaneanic. Parietal lamella neither indented nor sinuous. Length ± 2.0 mm., whorls 4.5.

Mangareva Islands: ex Fulton collection (see *T. garrettiana* for further details); holotype 10181; paratypes 10182-10184, 115418, 115418a, b, c (55 specimens).

T. saproderma is reminiscent of T. hygrobia from Raivavae, in having a subtruncate last whorl and a fairly long, pointed spire. This similarity is enhanced by the eroded surface, which probably indicates similar hydrophilous habits. However, in T. hygrobia the parietal and columellar lamellae are greatly reduced; in T. saproderma these are very strong. Furthermore, T. hygrobia is a large species (5.2 mm.), whereas T. saproderma is about 1.5 mm. shorter.

Of 31 specimens measured, the longest is 4.0 mm. long; the shortest, 3.0 mm. long. The mean is 3.4 mm., but the type specimen is slightly longer. However, this specimen may not be fully mature, as the minute remains of the columellar lamella is present. Only one specimen approaches maturity (115418b), but even this specimen has a microscopic vestige of the columellar fold. This specimen has not been selected as the type because its body whorl is not wide enough and it is uneroded and is, therefore, not truly representative of the species.

The species is variable. Some specimens are more slender than the typical one, some broader, and some shorter and more squat.

The palatal tubercles of the metaneanic stage are supposedly adventitious, since only one has any remote resemblance to the single bead of a fold (fig. 11, c); the other is placed eccentrically and doubtless is an abnormality (fig. 11, d).

This species was evidently collected on a damp cliff, since the erosion of the shell surface indicates a habit similar to that of T. hygrobia and its fellow species. The dried black animals which are visible through many of the shells indicate that they were alive when collected.

One specimen (115418c) was partially opened by chipping away part of two whorls and in it were found two embryos, the presence of which proves that the species belongs to the viviparous Tubuaiini and not to the oviparous Pitysini.

Tubuaia coprophora, new species (fig. 12, a-f).

Shell (fig. 12, a) elongate-turrite, nearly always smeared with what is apparently its feces, color mars brown with patches, spots, and streaks of cinnamon buff, opaque, dull, growth striae strong, substriatulate, fairly regular, strongly oblique. Spire straight, tapering regularly and slowly to apex, upper part slightly corroded and whitish. Suture moderately impressed, on last whorl vaguely margined by slight dip in striae. Whorls 6.5; embryonic whorls small, subacute; postembryonic whorls weakly convex; last whorl narrow. Aperture vertical or nearly so, ovate or subauriform. Parietal lamella rather weak, low, highest point just behind external termination, almost a whorl in length. Columella bilamellate (fig. 12, b); supracolumellar lamella weak, subvertical; columellar lamella faintly sigmoid, deeply seated but edge visible in frontal aspect. Palatal folds none. Peristome thin, unreflected.

Length 4.84 mm., diameter 2.06 (42.5 percent); apertural axis 1.45, diameter 1.18 (81 percent); last whorl 2.6 (58 percent); parietal lamella 0.09.

Paraneanic (fig. 12, c) broader in outline than adult; thinner, partly transparent, less eroded above, apertural armature as in adult, though some show fairly strong columellar lamella, as in metaneanic stage. Length 3.6 mm., whorls 6.25.



FIGURE 12.--a-f, Tubuaia coprophora, Raivavae: a, adult (holotype); b, oblique apertural view of adult to show columellar and supracolumellar folds; c, paraneanic; d, metaneanic, turned slightly to left; e, ananeanic; f, embryo. g, h, T. c. diminuta, Raivavae: g, adult (holotype); h, oblique view of columella of adult, showing deeply seated columellar lamella.

Metaneanic stage (fig. 12, d) similar to paraneanic in outline but apex more obtuse, semi-transparent, columellar lamella with distinct curvature and more transverse than in adult, palatal plicae none. Length 2.98 mm., whorls 5.5.

Ananeanic stage (fig. 12, e). Apertural armature slightly reduced in strength but still well-defined, palatal plicae none. Length 1.27 mm., whorls 3.5.

Embryo (fig. 12, f). Tip large, body whorl narrow, columellar lamella merely indicated by slight outcurvature on subvertical columella.

Length 0.97 mm., diameter 0.7 (74 percent); apertural axis 0.52, diameter 0.34 (66 percent); parietal lamella 0.02—.

Genitalia. Ovotestis trilobate, penis very small, uterus with about five embryos.

Austral Islands: Raivavae, northeast cliff on Mount Muatapu, Muatapu side of pass, near place wet by stream in wet weather, alt. 550 ft., Anderson and Zimmerman, Aug. 13, 1934; holotype 10168; paratypes 10169-10171, 147501-147507 (416 specimens). Additional material collected on ledge on north cliff, taken where water runs down in wet weather, alt. more than 500 ft., Anderson and Kondo, Aug. 14, 1934, 10172, 147611.

T. coprophora differs from T. saproderma in being much longer and more slender, in having striatulate growth lines, and in having very weak columellar and parietal lamellae. The nearest related species to T. coprophora is T. hygrobia, from which it differs principally in that it carries dried fecal matter on its shell, has stronger columellar and parietal lamellae, and is narrower.

Adults range from about 3.75 to 5.0 mm., with one specimen about 6.0 mm. long (mean, 4.5 mm.). Conspicuous dimorphism not noted.

The dullness of the adult shell surface is due to its habit of covering itself with feces. This habit is interpreted as a measure of protection from enemies or, more likely, from erosion by the slightly acid water on the damp cliffs inhabited by the species.

Juvenile shells gradually lose transparency as they age. The parietal lamella is of the same relative strength and curvature throughout although thinner in the younger stages. In the columellar lamella a slight curvature exists which is strongest in the metaneanic stage. This curvature lessens in the paraneanic stage and becomes nearly straight in the adult.

Tubuaia coprophora diminuta, new variety (fig. 12, g, h).

Shell shorter than typical by 1.26 mm., 0.25 whorls less, spire comparatively broader, in outline closer to paraneanic stage of typical, apertural armature similar, columellar history from juvenile to adult similar. Also smears itself with feces.

Length 3.58 mm., diameter 1.67 (46.6 percent); apertural axis 1.26, diameter 0.88 (69.7 percent); last whorl 2.06 (57.5 percent); parietal lamella 0.07.

Austral Islands: Raivavae, south cliff of Mount Turivao, under *Selaginella* hymenolepis plants and leaves and under lichens, alt. 650 ft., Anderson, Aug. 13, 1934; holotype 10173; paratypes 147508-147510 (32 specimens).

Tubuaia hygrobia, new species (fig. 13, *a-e*).

Shell (fig. 13, a) elongate-conic, color cinnamon brown, semitranslucent, shiny, growth striae strong, substriatulate, regular, not strongly oblique. Spire straight, tapering quite regularly and slowly to apex, upper part strongly scarred, pitted, and eroded.

Suture moderately impressed, the last whorl vaguely margined by slight dip in striae. Whorls seven; embryonic whorls small, subacute; postembryonic whorls weakly convex; last whorl fairly broad. Aperture vertical or nearly so, ovate or subauriform. Parietal lamella weak, low, about a whorl in length. Columella bilamellate; columellar lamella hardly perceptible, very weak, visible only as a small area refracting light differently from columella; supracolumellar lamella vertical, thin. Palatal folds none. Peristome thin, unreflected.



FIGURE 13.—Tubuaia hygrobia, Raivavae: a, adult (holotype); b, paraneanic; c, metaneanic; d, ananeanic; e, embryo.

Length 5.20 mm., diameter 2.40 (46.5 percent); apertural axis 1.64, diameter 1.27 (77.5 percent); last whorl 2.85 (55 percent); parietal lamella 0.04.

Paraneanic stage (fig. 13, b). Sides straighter than in adult, spire more pointed, last whorl semitransparent, with stronger parietal lamella, columellar lamella just showing in frontal aspect, palatal folds none. Length 4.47 mm., whorls 6.5.

Metaneanic stage (fig. 13, c). Penultimate whorl and last whorl semi-transparent. Last whorl broader in relation to height than either paraneanic or adult, parietal lamella

as high as in paraneanic but thinner, columella more curved, columellar lamella as in paraneanic stage, palatal plicae none. Length 2.88 mm., whorls 5.3.

Ananeanic stage (fig. 13, d). Transparent, parietal lamella proportionately as strong as in above juveniles, columellar lamella visible only as a minute tip of columellar curvature, palatal plicae none. Length 1.4 mm., whorls 3.5.

Embryo (fig. 13, e). Globose, parietal lamella proportionately as strong as in ananeanic stage but thinner, columellar lamella absent, palatal folds none.

Length 0.88 mm., diameter 0.68 (77 percent); apertural axis 0.57, diameter 0.40 (72 percent); parietal lamella 0.02.

Genitalia. Only penis and appendix studied; the same as in T. saintjohni.

Austral Islands: Raivavae, north slope of Mount Hiro, on moist base of basalt cliff, alt. 400 ft., St. John, Aug. 10, 1934; holotype 10163; paratypes 10164-10167, 147215 (one specimen dissected)-147223 (149 specimens). (St. John recalls that this species and *T. saintjohni* were collected on a cliff frontage of 200 ft., Feb. 23, 1945.)

Adults range from about 4.3 mm. to 5.5 mm. Conspicuous dimorphism is absent.

Tubuaia hygrobia differs from T. coprophora in being glossy, having broader whorls and a much broader and larger body whorl, in having a very weak parietal lamella and a scarcely perceptible columellar lamella which is weaker than in T. coprophora, and finally in having growth striae which are not strongly oblique.

This species is evidently a lover of very damp situations. Nearly every specimen inspected was more or less strongly eroded (fig. 13, a) by the slightly acid water believed to be characteristic of most of these islands.

Tubuaia saintjohni, new species (fig. 14, *a-g*).

Shell (fig. 14, a) large, ovate-conic, color cinnamon brown, subtransparent, shining, growth striae strong, substriatulate, not strongly oblique. Spire broadly conic, sides straight, tapering regularly and rapidly apicad. Suture moderately impressed, the last whorl margined by slight dip in striae below suture. Whorls 6; embryonic whorls small, subacute; postembryonic whorls weakly convex; last whorl broad, large, subovate. Aperture vertical, ovate or subauriform. Parietal lamella weak, low, 0.5 whorl long. Columella bilamellate; columellar lamella vestigial, visible only as a very slight angle and as a hairline, refracting light differently from columella; supracolumellar lamella vertical, thin. Palatal folds none. Peristome thin, unreflected.

Length 5.25 mm., diameter 2.94 (56 percent); apertural axis 2.02, diameter 1.54 (76 percent); last whorl 3.42 (65 percent); parietal lamella 0.04.

Large adult (fig. 14, b) 0.75 mm. longer than typical, more conical, upper spire heavily eroded, semitranslucent. Length 6.0 mm., whorls 6.0+.

Paraneanic stage (fig. 14, c) similar in shape to adult, growth striae about as strong but parietal lamella very weak, columella still apparently unilamellate, palatal plicae none. Length 4.80 mm., whorls 5.5+.

Metaneanic stage (fig. 14, d). Spire more reduced, growth striae much weaker, parietal lamella comparatively as weak as in paraneanic, columella similar, palatal plicae none. Length 3.7 mm., whorls 5.0.

Ananeanic stage (fig. 14, e). Parietal lamella comparatively stronger than above stages but very thin with small flare near middle. Columella with definite but very weak columellar lamella indicated by median outcurvature, palatal plicae none. Length 1.65 mm., whorls 3.0.

Embryo (fig. 14, f). Globose with a definite but scarcely perceptible peripheral angle. Parietal lamella comparatively stronger than in ananeanic, with greater flare. Columella similar to that of ananeanic.

Length 0.97 mm., diameter 0.83 (86 percent); apertural axis 0.65, diameter 0.46 (70 percent); parietal lamella 0.02.

Genitalia. Ovotestis trilobate; duct long with slight median convolutions, without marked swelling. Penis sometimes recurved at apex, short. Uterus of adult usually with many embryos (10 counted in one specimen). Paraneanic or subadult genitalia pitysinoid.



FIGURE 14.—*Tubuaia saintjohni*, Raivavae: **a**, adult (holotype); **b**, large adult; **c**, paraneanic; **d**, metaneanic; **f**, embryo; **g**, adult, oblique view, with vestigial columellar lamella.

Austral Islands: Raivavae, north slope of Mount Hiro, on shaded moist base of basalt cliff, alt. 400 ft., St. John, Aug. 10, 1934; holotype 10174; paratypes 10175-10180, 147207-147214 (352 specimens). Dissected 147207, 147208 (five specimens).

T. saintjohni is closely related to both T. coprophora and T. hygrobia but differs from them in being much broader and in having a vestigial columellar lamella. It is more closely related to T. hygrobia in having a weak parietal lamella and a very weak columellar fold. A comparison of the embryos of T. saintjohni and T. hygrobia serves to link these two species much more closely. Both embryos are rotund, having fairly wide apertures, and both have the same small initial whorl, whereas the embryo of T. coprophora is not rotund, has a narrower aperture, and has a large initial whorl.

That the columellar lamella is vestigial and the columella only apparently unilamellate is shown by the presence of a definite lamella, vertical and deepseated in one specimen (fig. 14, g) out of a total of 24.

Shells range from about 4.5 mm. to 5.8 mm., with a mean of 5+ mm.

The parietal lamella is comparatively strongest in the embryo and diminishes progressively to the adult.

Named for the botanist Harold St. John, who collected this species and T. hygrobia.

Species	L,ength	DIAMETER	Percent	Apertural Axis	DIAMETER	Percent	Parietal Lamella	Last Whorl	Percent	W horls
saproderma	3.52	1.71	48.5	1.16	0.68	58.5	0.16	2.00	57.0	6.3
coprophora diminuta.	3.58	1.67	46.6	1.26	0.88	69.7	0.07	2.06	57.5	6.25
inconstans	3.68	1.94	52.9	1.45	0.87	60.0	0.08	2.26	61.4	6.0
coprophora	4.84	2.06	42.5	1.45	1.18	81.0	0.09	2.60	58.0	6.5
hygrobia	5.20	2,40	46.4	1.64	1.27	77.5	0.04	2.85	55.0	7.0
saintjohni	5.25	2.94	56.0	2.02	1.54	76.0	0.04	3.42	65.0	6.0

Table 8.—Dimensions of T. hygrobia group

Tubuaia inconstans Cooke and Kondo, B. P. Bishop Mus., Bull. 221:160, fig. 75, a-f, 1960.

All of the species of the *hygrobia* group described above except T. saproderma are closely related. All have weak columellar and parietal lamellae, all lack palatal plicae, and all three live under identical conditions. T. saproderma, which is assumed to be a damp cliff dweller, differs from the other three in having strong columellar and parietal lamellae. It lacks palatal plicae, but some have tubercles which are supposedly adventitious.

On the island of Rapa is a species (T. inconstans) closely related to the three above-mentioned species. T. inconstans has a weak parietal lamella, a bilamellate columella, an extremely weak columellar fold, and no palatal plicae. Both T. inconstans and T. saintjohni have a weak columellar fold. A study of the adults (135747, paratypes) shows that a few of them have a weak vestige of the columellar fold. This species lives on moist cliffs, as do the Raivavae species.

As the animals of *T. coprophora, hygrobia*, and *saintjohni* were poorly preserved complete dissections could not be made for illustrative purposes.

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