

# 2  
Lab. copy

Poor fig 12 from discarded  
plate

Page 57

REVISION OF  
TORNATELLINIDAE  
AND ACHATINELLIDAE  
(GASTROPODA, PULMONATA)

BY  
C. MONTAGUE COOKE, JR.  
AND  
YOSHIO KONDO

BERNICE P. BISHOP MUSEUM  
BULLETIN 221

HONOLULU, HAWAII  
PUBLISHED BY THE MUSEUM  
1960

List of ERRATA  
inside cover

## Errata

page 25, fig. 5

~~57, fig 12~~

235, Vol. 23, not Vol. 3. (Line ~~12~~<sup>11</sup>)

267, Bishop Museum, not British Museum

32, fig. 8, replace Tornatellinoptini  
in fig. with Lamelliderni and  
vice versa.

57, 58, old discarded plates, put in  
the 2nd time following placement  
of figure where no fig before (fig. 12).  
Fig 12 & 13 found to be defective  
(old discarded plate of 1st proofing  
job) so called Editor's attention  
to it. She demurred. director had to  
order a second tipping job (YK 10-VIII-65)

Note on Tetoulina Solem 1972 in Copy #1, p. 18

REVISION OF  
TORNATELLINIDAE  
AND ACHATINELLIDAE  
(GASTROPODA, PULMONATA)

BY  
C. MONTAGUE COOKE, JR.  
AND  
YOSHIO KONDO

BERNICE P. BISHOP MUSEUM  
BULLETIN 221

HONOLULU, HAWAII  
PUBLISHED BY THE MUSEUM  
1960 D.30

Printed by  
Star-Bulletin Printing Co., Inc

*This book was printed with funds from the  
Charles M. and Anna C. Cooke Trust and  
from the G. N. Wilcox Trust.*

ISSUED DECEMBER 30, 1960

*In memory of Henry Augustus Pilsbry,  
who laid the foundation for this work.*



## CONTENTS

	Page
Introduction.....	3
Acknowledgments.....	3
Material and method.....	4
Abbreviations of Terminology.....	6
Review of literature on anatomy.....	8
Pallial organs.....	10
Digestive system (except teeth and jaws).....	10
Free muscles.....	10
Central nervous system.....	11
Genitalia.....	11
Review of literature on teeth and jaws.....	13
Brief review of classification.....	16
Catalog of genera, subgenera, sections.....	17
New groups, species, subspecies, and forms in systematic order.....	18
Types of genera and minor groups.....	20
Distribution.....	22
Anatomy.....	29
Genitalia.....	29
Ovotestis.....	29
Hermaphrodite duct.....	31
Talon.....	31
Carrefour vesicle, or vesicula seminalis.....	31
Albumin gland.....	33
Prostate gland.....	34
Spermatheca and stalk.....	35
Oviduct.....	35
Vas deferens.....	36
Penis.....	36
Appendix.....	37
Reproduction.....	38
Central nervous system.....	38
Jaw, radula, and teeth.....	39
Conclusion.....	40
Summary of anatomical characters.....	44
Systematics.....	50
Bibliography.....	293
Index.....	295
Figures 1 to 123 in text	



# Revision of Tornatellinidae and Achatinellidae (Gastropoda, Pulmonata)

By C. MONTAGUE COOKE, JR. and YOSHIO KONDO

BERNICE P. BISHOP MUSEUM

---

## INTRODUCTION

This revision and consolidation of the orthurethrous families Achatinellidae and Tornatellinidae had its beginning in a simple plan whereby the members of the group Tornatellinidae were to be treated conchologically and anatomically, region by region, beginning with Rapa. The regional results were to be added to the tornatellinid framework represented by volume 23 of the Manual of Conchology. However, because of the complications engendered by the varied types of genitalia, it was at first difficult, later impossible, to stay within the confines of Rapa. We found that, in order to derive a clear understanding of the relationship of the tornatellinid genera, it was essential that the genitalia of all be studied, including those in Achatinellidae. This was wholly in accord with Pilsbry's view (Pilsbry and Cooke, 1914, p. ix),<sup>1</sup> when he wrote that "An entirely satisfactory classification of the genera [of Tornatellinidae] is naturally not to be expected until we are acquainted with their soft anatomy." When Pilsbry made this statement he and Cooke had just completed a monumental monograph on the group which was to be the foundation for this present work.

The study of the Rapan genera, estimated to require six to nine months, took several years. It was started on December 7, 1941, and at the time of Dr. Cooke's death in October 1948 the most important portions had been recorded. There remained only the relatively simple task of integration. His portion of the introduction, the distribution, was only partially complete when he fell ill; but it is given below as he left it, except for routine editing.

The conchological work for this report was done by Dr. Cooke, senior author; the anatomical work by Yoshio Kondo, the junior author.

This work is far from the last word on this group of mollusks and should be considered but a framework for future investigations.

## ACKNOWLEDGMENTS

We are greatly indebted to Dr. Henry A. Pilsbry and to Dr. Horace B. Baker for reviewing the anatomical findings and for their valuable criticisms during the early part of this research. Upon its completion, the manuscript

---

<sup>1</sup> Dates in parentheses refer to the Bibliography, page 293.

received their critical attention; and their advice on numerous points has aided the work materially. We are also obligated to Dr. Nils Hj. Odhner for a rare specimen of the animal of *Fernandezia bulimoides*. And for giving freely of their time toward proofreading the original manuscript we owe a debt of gratitude to Miss Margaret Titcomb, Miss Naida P. Das, and Mrs. Kiyoko S. Kondo.

#### MATERIAL AND METHOD

This paper is concerned principally with (a) the reproductive and (b) the central nervous systems and (c) the radula of the family Achatinellidae. The genitalia are studied in detail. The central nervous system of only a representative number has been studied. The teeth are not treated exhaustively. Only samples have been taken.

At least three animals of each species have been dissected to gain a concept of the genitalia, with the average studied for each species about five to six. Where animals are scarce, only one or two have been dissected. If a record of the number of animals dissected has been kept, it has been given here. For the study of the central nervous system and teeth, at least two specimens of each species have been dissected, often more if animals were plentiful.

Much of the material on which this work is based is the result of more than 40 years of collecting by Dr. Cooke, including a vast store of specimens from the Austral, Mangareva (Gambier), and Society Islands, collected in 1934 when he led the Mangarevan Expedition to these heretofore unexplored areas. Unless otherwise noted, all dates in locality citations are 1934.

Critical Juan Fernandez tornatellinids were contributed by Nils Hj. Odhner of the Riksmuseum, Stockholm.

Animals studied had been collected and preserved by Cooke's own method: drowned for approximately 12 hours, preserved in 50-percent alcohol, extracted in the laboratory, and stored in 75-percent alcohol after a short period of dehydration in 95-percent alcohol.

The dissections of the animals were done by Yoshio Kondo, whose methods follow those of H. B. Baker. Only fully expanded animals were used for genitalia and central nervous system studies.

First, the foot was pinned down at several points. Next, the lung was separated from the body by cutting along the collar line, then pinned down. The dorsal integument of the forebody was slit longitudinally from head to nuchal membrane, which was also cut, as far as the albumin gland. When the body covering was pinned down at appropriate points, the common penial retractor (RM) disconnected from the diaphragm and pinned down to one side, the most important organs of the snail (excepting the ovotestis) were exposed as shown in figure 1. After the animal was mounted for study, the first step was to determine whether the penis was innervated by the cerebral or pedal ganglion (*Partulina dubia*, fig. 1, by cerebral: PN); the next, to determine

whether the ommatophoral retractor was free or passed through the penioviducal angle (in *P. dubia* it passes through this: Rt Omm). Next, the various nerves and other tissues were cleared away from the genitalia, the genitalia separated from the body and remounted separately for closer examination.

The macroscopic ontogeny of a few species of Achatinellidae were studied, most of them in the subadult or paraneanic juvenile substages. In one species, *Lamellovum auriculella*, a fairly good series of the youngest to the oldest juvenile substages was dissected and illustrated.

The study of the central nervous system required the dissection of additional animals. The principal nerves were traced from point of origin to termination. A drop of methyl violet among the organs helped delineate the nerves.

In this work, teeth were processed, stained in methyl violet, and mounted in Canada balsam by a complicated method now regarded unnecessary.

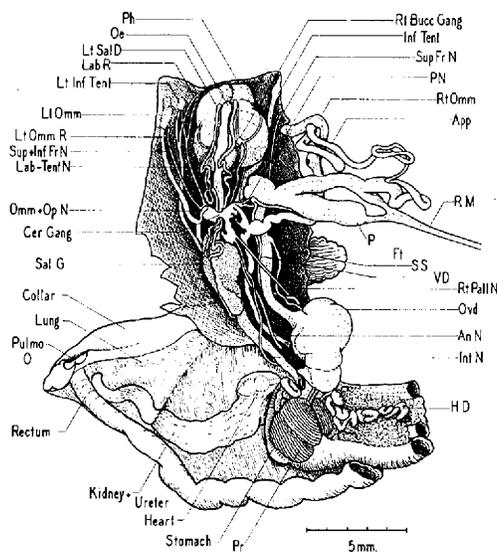


FIGURE 1.—Gross anatomy of most internal organs of *Partulina dubia* discussed under material and method. Left: Ph = pharynx, Oe = oesophagus, Lt Sal D = left salivary duct, Lab R = labial retractor, Lt Inf Tent = left inferior tentacle, Lt Omm = left ommatophore, Lt Omm R = left ommatophoral retractor, Sup + Inf Fr N = superior + inferior frontal nerve, Omm + Op N = ommatophoral + optic nerve, Cer Gang = cerebral ganglion, Sal G = salivary gland, Pulmo O = pulmonary orifice, Pr = prostate. Right: Rt Bucc Gang = right buccal ganglion, Inf Tent = inferior tentacle, Sup Fr N = superior frontal nerve, PN = penial nerve, Rt Omm = right ommatophore, App = appendix, RM = common retractor, P = penis, Ft = foot, SS = spermathecal stalk, VD = vas deferens, Rt Pall N = right pallial nerve, Ovd = oviduct, An N = anal nerve, Int N = intestinal nerve, HD = hermaphrodite duct.

The digestive system is simple. It consists of a prominent pharynx (Ph) or buccal mass which contains the radula. The oesophagus (Oe) leads off from the dorsal surface and goes through a ring formed by the principal ganglia just posterior of which the left and right salivary gland (Sal G) wrap themselves around it. It widens into the crop, or stomach, near the prostate (Pr); thence into the intestine, which is twice reflexed (Pilsbry, 1900, pl. 17, fig. 3, *Achatinella dolei*); and becomes the hindgut and rectum, which empties into the pulmonary orifice (Pulmo O).

The lung is plain, with microscopic veins transverse to the pulmonary vein, which arises out of the anterior end of the heart to run anterior and paralleling the ureter. The kidney is parallel with the heart; its division from the ureter is not obvious (Kidney + Ureter).

The terminology of the genitalia follows that of Pilsbry and Baker in part; the terminology of the nervous system follows Baker.

All drawings and measurements, both shell and anatomical, are based on camera lucida projections.

The first species dissected was *Pitya pagodiformis*, followed by *Lamellovum globosum*. Their affinity was thus early established and the status of *Pitya* finally fixed. However, a comparison with Pilsbry's dissection of *Auriculella* and with Odhner's *Tornatellina*, *Fernandezia*, and *Pacificella* provided no clue to relationship. Nor did the diverse genitalia of the new genera—*Antonella*, *Perakua*, and *Tubuaia*—shed any light in that direction. It was not until animals of all available genera were studied that tenuous evidence was seen, yet much remains obscure.

#### ABBREVIATIONS OF TERMINOLOGY

Abd, abdominal	D, duct
Ac, acoustic	Dor, dorsal
ALP, anterolateral pedal	Ec, ectocone
An, anal	Emb, embryo
Ant, anterior	En, entocone
At, atrium	Epi, epiphallus
App, appendix	Fo, folds
App V, appendical "verge"	Fov, vertical folds
AVP, anteroventral pedal	Fot, transverse folds
b, bulge in appendix = appendical "verge"	Fl, flagellum
Bucc, buccal	Fol, follicle
c, central tooth	Fr, frontal
Ch, chamber	Ft, foot
Ca, carrefour	G, gland
Cau, caudal	Gang, ganglion
Cer, cerebral	GO, genital orifice
Col, columellar	
Conn, connective	
Cop, copulatory	HD, hermaphrodite duct
CVP, caudoventral pedal	HG, hermaphrodite gland; ovotestis

Inf, inferior	Pt, part or in part
Int, intestinal	Pulmo, pulmonary
Lab, labial	R, retractor
Lat, lateral	R App, appendical retractor
L.P, lateral pedal	RM, common retractor
L.t, left	RP, penial retractor
M, muscle or muscle tissue	Rt, right
MC, muscle cord	S, stalk
MVP, medioventral pedal	Sal, salivary
MW, muscular wall	Sec, Secretory
N, nerve	Sec-ejac, secretory-ejaculatory
Nuc, nuchal	sN, small innominate nerve connecting two or more other nerves
O, orifice	Sp, spermatheca
Odont, odontophoral	Sphr, "spermatophore" or sperm mass
Oe, oesophageal	Sup, superior
Omm, ommatophoral	SS, spermathecal stalk
Op, optic	T, teeth
Ov, ovum or ova	Ta, talon
Ovd, oviduct or oviducal	Ut, uterus or uterine
P, penis	V, verge
Pal, palatal	Vag, vagina, vaginal
Pall, pallial	Ve, valve
Pap, papilla	Vel, velum of interior of penis
Par, parietal	Vest, vestigial
Ped, pedal	VD, vas deferens
Pil, pilaster	VDO, vas deferens orifice into penis (see Y)
Pil 1, same as P Pil	Vent, ventral
Pil 2, 3, secondary, tertiary pilasters	Vivip, viviparous
PLP, posterolateral pedal	VS, "vesicula seminalis" or carrefour vesicle
P Pap, penial papilla	X, junction of spermathecal stalk with oviduct
P Pil, principal pilaster	Y, junction of vas deferens with penis (see VDO)
Pleu, pleural	
Post, posterior	
PN, penial nerve	
Pr, prostate	
Preut, preuterine	
PS, penial stalk	

The terminology for the apertural armature is given on figure 2. Pilsbry (1916, vol. 24, p. vii) gives a detailed discussion of the terminology of the apertural teeth, illustrating it in his figure 1.

In this paper the usual terms applied to the supra- and subcolumnellar lamellae are upper and lower.

The palatal plicae run spirally. Ribs are parallel to the growth lines, cutting across the path of the plica at right angles.

The measurements of the shell are shown here in figure 3, and dimensions are taken from the figure. Length or height is measured from apex to the bottom extremity, usually the base of the aperture, along the axis of the shell. The

diameter, or width, is used for the lateral measurement at its widest portion. The height of the last whorl is the distance between the end of the penultimate whorl and the basal line. The axis of the aperture is the distance between the end of the last whorl and the columellar base. The diameter of the aperture is the distance between the outermost columellar edge to the point directly opposite. Owing to the nature of the aperture, these points are not always constant and sometimes may be taken from that portion to slightly above, as indicated by the fine broken lines. The projection of these alternative points show that practically no difference in measurement exists.

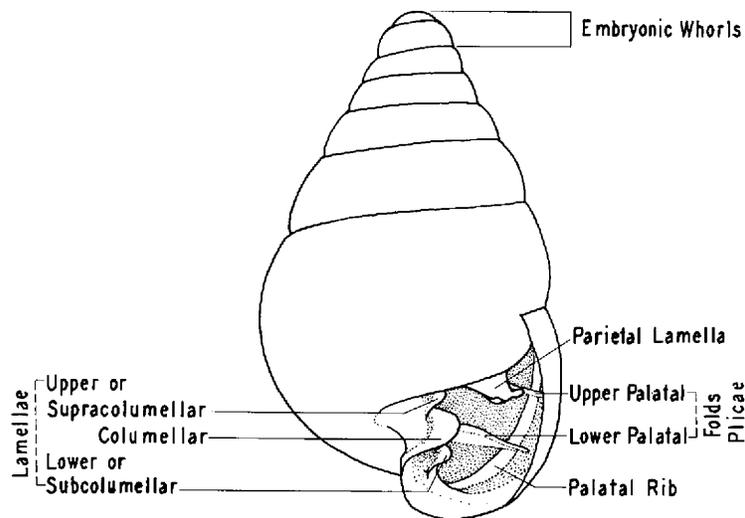


FIGURE 2.—Terminology for apertural armature.

The height of the parietal lamella is shown by dotted lines in figure 3. All scales on figures are for 1 mm. unless otherwise labeled.

Color nomenclature is after Robert Ridgway's "Color standards and color nomenclature" (1912).

#### REVIEW OF LITERATURE ON ANATOMY

The anatomy of the following achatinellids has been treated previously as follows:

Pallial organs: *Achatinella* by Semper (1870); *Partulina dolei* by Pilsbry (1900); *Auriculella* by Pilsbry (1915-1916); *Tornatellaria* by Pilsbry (1915-1916); *Tornatellinops* (= *Pacificella*) *variabilis* by Odhner (1922); *Partulina redfieldii*, *P. horneri*, *P. virgulata*, and *P. mauiensis* by Neal (1928); *Newcombia canaliculata* by Neal (1928); *Achatinella lehuiensis* var. *meinecke* by Neal (1928).

The digestive system, except teeth and jaws, has been treated as follows: *Partulina dolei* by Pilsbry (1900) and *Achatinella vulpina* by Pfeffer (1877).

Free muscles have been treated as follows: *Partulina dolei* by Pilsbry (1900); *Achatinella*, *Partulina*, *Newcombia*, and *Perdicella* (in part) by Neal (1928).

The central nervous system has been treated as follows: *Fernandezia bulimoides* (in part) by Odhner (1922); *Tornatellinops variabilis* (in part) by Odhner (1922); *Partulina redfieldii* (in part) by Neal (1928).

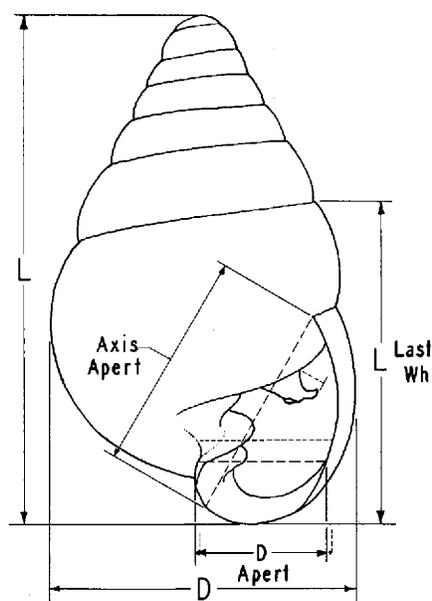


FIGURE 3.—Measurements of shell.

The genitalia have been treated as follows: *Achatinella lorata* by Semper (1870); *Achatinella stewartii producta* by Binney (1884); *Achatinella vulpina* by Pfeffer (1877); *Partulina dolei* by Pilsbry (1900); Achatinellidae by Pilsbry (1912-1916); *Achatinella abbreviata*, *A. stewartii*, *A. viridans*, *A. byronii*, *A. lila*, *A. simulans*, *A. lorata nobilis*, *A. mustelina*, and *A. vulpina* by Pilsbry (1915-1916); *Partulina redfieldii kamaloensis*, and *P. confusa* by Pilsbry (1915-1916); *Newcombia philippiana* by Pilsbry (1915-1916); Tornatellinidae by Pilsbry (1915-1916); *Auriculella pulchra*, *A. cerea*, and *A. westerlundiana* by Pilsbry (1915-1916); *Tornatellina bilamellata* by Odhner (1922); *Fernandezia bulimoides* by Odhner (1922); *Tornatellinops variabilis* by Odhner (1922); *Newcombia canaliculata*, *N. pfeifferi*, and *N. cumingi* by Neal (1928); *Perdicella helena*, *P. mauiensis*, and *P. carinella* by Neal (1928);

*Partulina horneri*, *P. dubia*, *P. virgulata*, *P. tessellata*, *P. rufa*, *P. proxima*, *P. redfieldii*, *P. natti*, *P. mighelsiana*, and *P. mighelsiana* var. *bella* by Neal (1928). *Achatinella viridans*, *A. decipiens*, *A. stewartii* var. *producta* color form *dunkeri*, *A. vulpina*, *A. lehuiensis* var. *meineckei*, *A. lorata* var. *pulchella*, and *A. turgida* by Neal (1928).

#### PALLIAL ORGANS

Semper (1894, p. 70) studied the pallial organs of an unknown species of *Achatinella* and classified it with those mollusks with completely enclosed kidney and secondary ureter (Stylommatophoren mit vollständig geschlossenem Niere- und Darmharnleiter).

Pilsbry (1900, pp. 565-566, pl. 17, fig. 3) fully describes and figures the pallial organs of *Partulina dolei* (Baldwin) and points out the significance of the direct ureter (Orthurethra) as compared with the sigmoid type (Sigmurethra). Later, Pilsbry describes the same mollusk and figures it (Pilsbry and Cooke, 1915, p. 57, pl. 20, fig. 3). He says that the kidney is narrow and long, extending nearly to the collar, where it opens on the intestinal side via a small pore. He adds that the apex is turned back a short distance, in the form of a narrow, fleshy ridge; that the heart lies parallel with the kidney; that a broad pulmonary vein runs posteriad alongside the ureter; and that a mesh of arteries and veins was not seen.

Pilsbry (Pilsbry and Cooke, 1915, p. 66) also describes the pallial organs of *Auriculella* and *Tornatellaria* as achatinelloid.

Odhner (1922, p. 250) describes the pallial organs of *Tornatellinops variabilis* as being orthurethrous and achatinelloid.

Neal (1928, pp. 35-36, figs. 11, 12) describes and figures the pallial organs of four species of *Partulina*, one *Newcombia*, and one *Achatinella*.

#### DIGESTIVE SYSTEM (EXCEPT TEETH AND JAWS)

Pfeffer (1877, p. 330) mentions the buccal mass of *Achatinella vulpina* (Férussac) as proportionately larger than that in helicids.

Pilsbry (1900, p. 566, pl. 17, fig. 3) describes and figures the pharynx, oesophagus, salivary glands, stomach, and intestine of *Partulina dolei*. (See also Pilsbry in Pilsbry and Cooke 1915, pl. 20, fig. 3.) He states that the salivary gland forms a complete ring around the oesophagus; that the oesophagus is long, unusually slender, without a crop; that the stomach is much lengthened, curved at the end; and that the intestine is unusually long.

#### FREE MUSCLES

Pilsbry (1900, pp. 566-567, pl. 17, fig. 5) made a study of the retractor muscles of *Partulina dolei*. According to him (p. 565), the principal difference

between the achatinellid and partulid muscle systems is the fact that in the partulid the right ocular retractor unites with the tail retractor, whereas in the achatinellid neither of the retractors unites with the tail retractor.

Neal (1928, pp. 35-36) found that in all but one species of a total of 23 species and in the varieties studied, the buccal retractor muscle was attached to the tentacular retractor. In *Partulina mighelsiana* (Pfeiffer) the two muscles were not attached.

#### CENTRAL NERVOUS SYSTEM

Little work has been done on the central nervous system, merely a superficial survey of the ganglia. Odhner (1922, pp. 242-243, 251, figs. 16, 21) dissected the nervous system of *Fernandezia bulimoides* (Pfeiffer) and *Tornatellinops variabilis* (Odhner). The ganglia plus their commissures were treated, but their principal nerves were not followed. Neal (1928, footnote, p. 39, fig. 16) dissected the nerve collar of *Partulina redfieldii* (Newcomb) and found a subcerebral commissure such as those reported by Watson (1923) in the genera *Ena*, *Rachis*, and *Chondrina*; but only two of the principal nerves were described.

#### GENITALIA

Semper was probably the first to dissect achatinellid genitalia (*Achatinella lorata* Férussac). He figured it (1870, pl. 16, fig. 23), but he apparently omitted it from the text. Probably for this reason, and because it was not indexed, many subsequent authors have missed it entirely. Pilsbry did not review it (Pilsbry and Cooke, 1914, pp. lii-lvii; 1915, pp. 59-60), although he noted the figure (1914, p. 278). Semper's dissection and figure are excellent, the terminology quite modern. It is notable that he recognized the prostate as such, for this organ can easily be confused with the albumin gland. He probably saw the reduced albumin gland, for he did extricate the spermatheca (*bursâ seminalis femina*, Semper) from the prostate follicles, as the figure indicates. He also recognized the penial retractor (although it is unlabeled), the appendix or flagellum as an adjunct of the penis (gl. p., probably = glandula penis), and the ovotestis (*glandula hermanphrodita*, Semper).

Binney (1873, pp. 337-338, pl. 15, fig. 4), among numerous other species, dissected, described, and figured the genitalia of *Achatinella stewartii producta* Reeve. Binney reports that, owing to poorly preserved material, the dissections were difficult to make. He was somewhat misled by the penial and appendical retractors which he thought might be ducts and by the common retractor, which he thought to be the prostate gland. Also, the appendix appeared to Binney to be either a dart sac or a prostate gland. The terminology is the same as that of Leidy.

Pfeiffer (1877, pp. 330-334, figs. 1-3) dissected, described, and figured the genitalia of *Achatinella vulpina*. He made a careful dissection of the prostate

(*Binney's ovary*) and corrected Binney on this point. He also noted the true functions of the penial, appendical, and common retractors.

Pilsbry (1900, p. 566, pl. 17, figs. 7, 7a) describes and figures the genitalia of *Partulina dolei*. Except for the omission of the ovotestis and for the designation of the prostate as the "albumin gland," Pilsbry's morphological details are excellent. (See discussion on albumin gland in relationship of subfamilies, under Achatinellinae.) He evidently saw the interior of the penis. The lumen of the penis is described as being narrowed above by two large pilasters. This pilaster, now considered to be a single reflected organ, is one of the principal characteristics of the family.

Pilsbry (Pilsbry and Cooke, 1914, p. ix) gives an excellent summary of the genital organs of the family Achatinellidae. He must have found the true albumin gland after his *Partulina* dissection, for in his diagnosis the "albumin gland" reverts to the prostate. Later, Pilsbry (Pilsbry and Cooke, 1915, p. 58) gives a more detailed diagnosis of the achatinellid genital organs, as well as dissections and illustrations of nine *Achatinella*, one *Newcombia*, and two *Partulina* (p. 60, pls. 12, 13, 14). He also gives (p. 66) the diagnosis of the genitalia of what was then considered the separate family Tornatellinidae. The family diagnosis is based upon the genus *Auriculella*, the genitalia of which is of the "Achatinellid type, except that the appendix has no retractor muscle." Three species of *Auriculella* genitalia (pl. 22) are figured by Pilsbry.

Odhner (1922, p. 235) dissected *Tornatellina*, *Fernandezia*, and *Tornatellinops* [= *Pacificella*]. On the basis of the extraordinary genitalia (large seminal vesicles; vestigial penis) he limits the Juan Fernandez mollusks to Tornatellinidae, in which he tentatively includes *Tornatellinops*, which he thinks may belong to a distinct family [? family Pacificellidae, Steenberg, 1925, p. 202]. *Auriculella* and its allies he places in the Auriculellidae. The genitalia of the Juan Fernandez genera are so odd Odhner cannot be criticized for making such an extravagant delimitation. He includes the ovotestis of the three genera studied, although, as he himself admits later (in a letter to Cooke, Mar. 6, 1943), the ovotestis of *Tornatellinops* is "rather schematical."

Neal in her painstaking work (1928, pp. 34-43) with the genitalia of three species of *Newcombia*, 13 *Partulina*, and seven *Achatinella* shows that—though the organs are not fundamentally different among the genera—slight but consistent size differences in the penis of *Perdicella*, together with the primitive webbed condition of the appendical retractor, justify its elevation from sectional to generic rank. The subsequent chapter (pp. 44-49) Neal devotes to the dissections of age groups from the aneanic substage to the paraneanic substage and up to the gravid ephebic stage (total = six growth stages) of *Achatinella viridans* Mighels. This research unearths a most interesting fact, that in the very immature stages (groups D-F) the appendix lacks a retractor or is just beginning to form one and that in the youngest stage (group F) the appendix is absent.

## REVIEW OF LITERATURE ON TEETH AND JAWS

The teeth and, or, jaws of the following achatinellids have been treated previously: *Achatinella bulimoides* (teeth) by Heynemann (1867); *Elasmias manilensis* (teeth) by Semper (1870); *Auriculella*, *Achatinella*, *Partulina* (teeth and jaws) by Bland and Binney (1873); *Achatinella vulpina* by Pfeffer (1877); *Auriculella*, *Achatinella*, *Partulina* (teeth and jaw) by Binney (1884); *Elasmias apertum* (teeth) by Binney (1884); *Lamellidea oblonga* (teeth) by Binney (1884); *Auriculella*, *Achatinella*, *Partulina*, *Newcombia* (teeth and jaws) by Gwatkin, Suter, and Pilsbry (1895); *Tornatellides chathamensis* (teeth) by Dall (1896); Achatinellidae (teeth and jaw) by Pilsbry (Pilsbry and Cooke, 1914, 1915); *Achatinella lorata* (jaw) by Pilsbry (1915); *Achatinella lorata nobilis* (teeth) by Pilsbry (1915); *Achatinella vulpina* (teeth) by Pilsbry (1915); Tornatellinidae (teeth and jaw) by Pilsbry (1915); *Elasmias apertum* (teeth) by Pilsbry (1915); *Elasmias manilensis* (teeth) by Pilsbry (1915); *Tornatellides chathamensis* (teeth) by Pilsbry (1916); *Tornatellina bilamellata* (teeth) by Odhner (1922); *Fernandezia bulimoides* (teeth) by Odhner (1922); *Tornatellinops variabilis* (teeth and jaw) by Odhner (1922); *Fernandezia bulimoides* (teeth) by Peile (1929).

As far as can be determined, Pilsbry is the only investigator who has figured the jaw of an achatinellid (Pilsbry and Cooke, 1915, pl. 14, fig. 3, *Achatinella lorata*). References to the jaw are found in the following pages, which review the literature on teeth.

Heynemann (1867) was the first to study the achatinellid teeth (*A. bulimoides* Swainson). For that early date and the equipment of that period, his observations are surprisingly good. According to him, the teeth are all similar, the medians and laterals undifferentiated; the median teeth the smallest, increasing in size outward. The teeth are shaped like a rake with a small handle, the front ones recurved, broadened, toothed, the six cusps projecting more or less as tuberosities, the two outermost the largest. Small or short teeth appeared to be present when suitable strata were examined. In some specimens, two additional cusps were found behind the outer two cusps. Heynemann's figures (1867, pl. 1, figs. 2, 2a) are excellent in that they clearly illustrate the shouldered, chelate, incurved condition of the cusps which is apparent in *Achatinella* teeth. Heynemann also made a comparison of the achatinellid teeth with the athoracophorid teeth and noted their remarkable similarity. (See also Knight, 1859, pp. 381-382, pl. 66, figs. 9, 10.) As most of the subsequent authors have repeated this information, further discussion here is terminated with Pilsbry's note (Pilsbry and Cooke, 1914, p. xii). "The Athoracophoridae have also evolved teeth wonderfully similar to those of Achatinellidae. This is evidently a case of convergent evolution, as the relationship must be remote." Heynemann saw no jaw in *A. bulimoides*.

Semper (1870) prepared the radula of *Elasmias manilensis* (Dohrn) but not in its entirety, and he was unable to define the rhachidian. The tooth had a long, fine, crooked median cusp with a small cusp on each side. Pilsbry (1915, p. 114) states, "It is obvious that Semper's 'middle cusp' is really the basal plate." An inspection of Semper's figure (1870, pl. 16, fig. 13) leaves no room for doubt as to Pilsbry's diagnosis that the tooth was mounted upside-down, the median cusp being obscured by the basal plate.

Bland and Binney (1873) found that the jaw of Achatinellidae was very delicate, very thin, transparent, and arcuate, with the ends blunt. The teeth are arranged in shallow V-shaped rows. The rhachidian, lateral, and marginal teeth are all alike, the first smaller and symmetrical; long, narrow, bluntly truncate below, curving and widening above, first gradually, then rapidly; the apex twice the width of the base, reflected, slightly produced, seven-cuspid, central cusp smallest. The formula in one specimen is 175-1-175. The teeth of *Achatinella stewartii* (Green) are figured by Binney. Later, Binney (1884) summarizes his work on *A. stewartii*, adding a description and figure of *Elasmias apertum* (Pease) teeth plus a short description of the teeth of *Lamellidea oblonga* (Pease). The teeth of both are of the same type as those of *Achatinella*, *s.s.*

Pfeffer (1877) gives the tooth formula for *Achatinella vulpina* as 180-1-180  $\times$  155 rows.

Pilsbry (1895) describes the jaws and teeth of *Achatinella*, *Partulina*, and *Tornatellina*. The jaw is excessively delicate; the teeth arranged in very oblique transverse rows. For the form of the teeth, the reader is referred to Pilsbry's plate 11, fig. 52. (Gwatkin *et al.*)

Gwatkin (Gwatkin *et al.*, 1895), after studying *Achatinella*, *Partulina*, *Newcombia*, and *Auriculella*—together with *Amastra*, *Laminella*, and *Leptachatina*—divided the achatinellids from the amastrids by the dentition. The achatinellid teeth are described as being of the same type: "Base narrow, head rather broad, with four, five, six, or seven small tentacles (exactly as in *Janella* and *Tornatellina* and the marginals only of *Succinea*)."

Suter (Gwatkin *et al.*, 1895) studied the dentition of *Achatinella turgida cookei* (Baldwin), *A. fuscobasis lyonsiana* (Baldwin), and *Partulina dolei* (Baldwin). He described and figured the radula of *Partulina dolei* and the rhachidian plus two marginals of *A. fuscobasis lyonsiana*, noting that the rhachidian of the latter was bicuspid, whereas no reflection could be seen in the others. The laterals and marginals appeared to resemble the marginals of *Succinea*.

A. H. Cooke (1895, p. 234) gives a short account of the achatinellid teeth and figures those of *A. vulpina* (Férussac) in his figure 140, E. On page 443 he includes *Tornatellina* in the family Achatinellidae, giving no reason; but doubtless his conclusion is based on the similarity of the teeth.

Dall (1896) figures one tooth of *Tornatellides chathamensis* (Dall) from Chatham Island, Galapagos, sketched by Binney. The cusps appear to be eroded or broken.

Pilsbry (Pilsbry and Cooke, 1914, p. ix) notes that in Achatinellidae the "jaw was wanting or extremely thin, indistinctly plaited vertically. Radula broad and short. Teeth excessively numerous, arranged in V-shaped transverse rows; rake-like, composed of narrow basal plate and a broad recurved portion bearing numerous unequal cusps." In discussing the morphology of the achatinellid teeth Pilsbry says (pp. x-xii) that he believes the achatinellid radula had lost both central and lateral teeth, leaving only the marginals, and that the marginals were derived from those of some unspecialized group of ground snails with multicuspid marginals. Pilsbry's view on the Athoracophoridae teeth is given above, under Heynemann. A short review of literature to 1914 is given by Pilsbry (p. lvii).

Suter (1913, p. 768) sketchily describes the jaw and teeth of Achatinellidae. He mentions two types; the first evidently a résumé of his original study on *A. fuscobasis lyonsiana* (see above); the second, interesting in that the central is described as unicuspid, the laterals as bicuspid, and the marginals as multicuspid. He does not identify the second type.

Pilsbry (Pilsbry and Cooke, 1915, p. 59) describes and figures the thin delicate jaw of *Achatinella lorata* Férussac as being "composed of narrow, more or less overlapping, vertical elements, which seem completely united" though not converging toward the middle. In some of the species there are no jaws, only a cuticle. The radula bears 150 teeth in a half row (*A. lorata nobilis* Pfeiffer); all teeth are alike, or rastriform, the basal plate narrow, long, widening and recurving anteriorly, with five to seven acute cusps, the lateral the largest. Some species have narrow "central," bi- to tricuspid teeth; others lack central teeth, or if they are present, they are not distinguishable from marginals. Pilsbry illustrates the characters of the teeth of *A. vulpina* and *A. lorata nobilis* (pl. 20, figs. 1, 2) and gives a good review of the literature up to 1916 (pp. 59-60). On the family Tornatellinidae Pilsbry notes (pp. 66-68) that the teeth are similar to those of Achatinellidae. He also discusses *Elasmias aper-tum* and *E. manilensis*, as found by Binney and Semper, and finds them to be the same type as those of *Achatinella*. Pilsbry reproduces a tooth of *Tornatellides chathamensis* from Dall (pl. 44, fig. 17).

Odhner (1922, pp. 235, 240, fig. 14) finds the radula of *Tornatellina bilamellata* Anton to be achatinelloid. The teeth are multicuspid, having large and small denticles. The teeth of *Fernandezia bulimoides* Pfeiffer (Odhner, p. 242) are rastroid. Neither one has a jaw. The jaw of *Tornatellinops variabilis* (Odhner) is thin, consisting of a few smooth hyaline bandlike segments (p. 250); teeth achatinelloid (Odhner's fig. 19), with rake-like edges, eight-cuspid, ectocone strong, mesocones feebler; median tooth lacking.

Steenberg (1925, pp. 193-195), following Odhner's paper, reviews the teeth as given by Pilsbry and Odhner. The variability of the genitalia led Odhner to suggest the erection of four families: Achatinellidae, Tornatellinidae, Auriculellidae, and Pacificellidae (p. 202) as proposed by Odhner (1922, p. 235).

Peile (1929, p. 268, fig. 1) shows that the *Fernandezia bulimoides* teeth are the same as those of *Tornatellina* and *Achatinella*.

#### BRIEF REVIEW OF CLASSIFICATION

The first attempt at bringing order into the classification of Tornatellinidae was made by Pilsbry in 1910. His system is given below.

Genus Auriculella  
 Elasmias  
 Section Elasmias  
 Lamellovum  
 Tornatellina  
 Tornatellina  
 Lamellina  
 Lamellidea  
 Elasmatina  
 Tornatellides  
 Tornatellides  
 Tornatellaria

Genus *Fernandezia* was then classified under Amastridae.

In 1915 the classification by Pilsbry and Cooke was slightly modified. The genera and subgenera bracketed together were considered closely related. *Fernandezia* was still excluded.

Genus {Lamellovum  
 Elasmias  
 Tornatellina  
 Section Lamellidea (Lamellina)  
 Tornatellinops  
 Elasmatina  
 Tornatellides  
 Subgenus Waimea  
 {Tornatellaria  
 Gulickia  
 Auriculella

In 1922 Odhner included *Fernandezia* in the family, created *Pacificella*, and limited Tornatellinidae to the Fernandezian forms, relegating the extra-Fernandezian to Auriculellidae.

As a result of Odhner's work, Pilsbry and Cooke in 1933 made additional revisions to their order. *Lamellidea* was substituted for *Tornatellina*, *Strobilus*

was reinstated, *Pityts* was included (formerly in Endodontidae), and the new subgenus, *Atea*, was added.

The reconstituted classification of Tornatellinidae would have stood as follows:

Lamellovum  
 Elasmias  
 Tornatellina  
 Fernandezia  
 Lamellidea  
   Lamellidea  
   Tornatellinops  
   Atea  
 Strobilus  
 Pityts  
 Tornatellides  
   Tornatellides  
   Waimca  
 Gulickia  
 Auriculella

#### CATALOG OF GENERA, SUBGENERA, SECTIONS

Subclass Pulmonata  
 Order Stylommatophora  
   Suborder Orthurethra  
   Family Achatinellidae  
   Subfamily Pitytsinae  
   Tribe Pitytsini  
   Genus Strobilus  
   Subgenus Strobilus  
   Tautautua  
   Tanga  
   Genus Pukunia  
   Mangaoa  
   Mitiperua  
   Taitaa  
   Section Taitaa  
   Taireva  
   Taraia  
   Genus Apopityts  
   Pityts  
   Lamellovum  
   Subgenus Lamellovum  
   Maitua  
   Tribe Antonellini  
   Genus Antonella  
   Perahua  
   Tribe Tubuaiini  
   Genus Celticola  
   Subgenus Celticola  
   Meryticola  
   Nesonoica

- Genus *Tubuaia*
  - Subgenus *Tubuaia perplexa* (group)
  - Tubuaia gouldi* (group)
  - Tubuaia voyana* (group)
- Subfamily Lamellideinae
  - Tribe Tornatellinoptini
    - Genus *Tornatellinops*
  - Tribe Lamellideini
    - Genus *Lamellidea*
      - Subgenus *Lamellidea*
      - Elamellidea*
      - Atea*
- Subfamily Tornatellinae
  - Tribe Tornatellimini
    - Genus *Elasmias*
      - Tornatellina*
      - Fernandezia*
- Subfamily Tornatellidinae
  - Tribe Tornatellidini
    - Genus *Tornatellides*
      - Subgenus *Tornatellides*
        - Aedituans*
        - Waimea*
  - Tribe Tornatellariini
    - Genus *Philopoa*
      - Tornatellaria*
- Subfamily Auriculellinae
  - Tribe Auriculellini
    - Genus *Auriculella*
      - Gulickia*
- Subfamily Achatinellinae
  - Tribe Achatinellini
    - Genus *Newcombia*
      - Perdicella*
      - Partulina*
        - Subgenus *Baldwinia*
        - Partulina*
        - Partulinella*
        - Eburnella*
    - Genus *Achatinella*
      - Subgenus *Bulimella*
        - Achatinellastrum*
        - Achatinella*

## NEW GROUPS, SPECIES, SUBSPECIES, AND FORMS IN SYSTEMATIC ORDER

- |                                     |                                    |
|-------------------------------------|------------------------------------|
| Pitysinae, new subfamily            | <i>Tautautua</i> , new subgenus    |
| Pitysini, new tribe                 | <i>Strobilus perfragilis</i>       |
| <i>Strobilus turritus basalis</i>   | <i>Tanga</i> , new subgenus        |
| <i>Strobilus opeas</i>              | <i>Strobilus brevis</i>            |
| <i>Strobilus opeas intermedius</i>  | <i>Strobilus brevis subsimilis</i> |
| <i>Strobilus subtilis</i>           | <i>Strobilus brevis pumilus</i>    |
| <i>Strobilus subtilis similaris</i> | <i>Pukunia</i> , new genus         |
| <i>Strobilus acicularis</i>         | <i>Pukunia acuta</i>               |
| <i>Strobilus acicularis raphis</i>  | <i>Pukunia margaritae</i>          |

Pukunia pellucida	Celticola, new genus
Mangaoa, new genus	Celticola pilsbryi
Mangaoa perissa	Celticola pilsbryi proxima
Mitiperua, new genus	Celticola pilsbryi incerta
Mitiperua simplex	Celticola pilsbryi latior
Mitiperua simplex subcostata	Meryticola, new subgenus
Mitiperua simplex convexior	Celticola arborea
Taitaa, new genus	Celticola arborea sororcula
Taitaa, new section	Nesonoica, new subgenus
Taitaa dacryma	Celticola conoides
Taitaa arauana	Celticola anatonuensis
Taireva, new section	Tubuaia, new genus
Taitaa striatula	Tubuaia gouldi nannodes, new form
Taitaa zimmermani	Tubuaia cremnobates
Taraia, new section	Tubuaia cylindrata
Taitaa neanica	Tubuaia cylindrata philolichen
Taitaa terebriformis	Tubuaia voyana rapaensis
Apopitya, new genus	Tubuaia inconstans
Apopitya andersoni	Lamellideinae, new subfamily
Pitya scalaris	Tornatellinoptini, new tribe
Pitya scalaris form A	Tornatellinops concolorans
Pitya alpestris	Lamellideini, new tribe
Maitua, new subgenus	Lamellidea micropleura
Lamellovum auriculella	Elamellidea, new subgenus
Lamellovum leptospira	Elasmiatini, new tribe
Lamellovum solitaria	Elasmias ovatum exiguum
Lamellovum costata	Elasmias simplicimum
Antonellini, new tribe	Tornatellinini, new tribe
Antonella, new genus	Tornatellidinae, new subfamily
Antonella trochlearis radricula	Tornatellidini, new tribe
Antonella trochlearis fusiforma	Tornatellides oswaldi
Antonella trochlearis nesiotica	Aedituans, new subgenus
Antonella pfeifferi	Tornatellides neckeri
Antonella tenuis	Tornatellariini, new tribe
Perahua, new genus	Philopoa, new genus
Perahua grandis	Philopoa singularis
Perahua bakeri	Auriculellini, new tribe
Tubuaiini, new tribe	Achatinellini, new tribe

An illustrated synopsis of the tribes of Achatinellidae is given in figures 7, 8, and 9. Selected to represent the tribes are:

- Achatinellini: *Achatinella concavospira*  
 Auriculellini: *Auriculella auricula*  
 Tornatellariini: *Tornatellaria newcombi*  
 Tornatellidini: *Tornatellides oblongus*  
 Tornatellinini: *Fernandezia bulimoides* (after Odhner)  
 Elasmiatini: *Elasmias apertum*  
 Lamellideini: *Lamellidea oblonga*  
 Tornatellinoptini: *Tornatellinops variabilis*  
 Tubuaiini: *Tubuaia perplexa*  
 Antonellini: *Antonella trochlearis*  
 Pitysini: *Pitya pagodiformis*

## TYPES OF GENERA AND MINOR GROUPS

## PITYSINAE

- Strobilus: *S. turritus* Anton  
 Strobilus: *S. turritus*  
 Tautautua: *S. perfragilis*  
 Tanga: *S. brevis*  
 Pukunia: *P. acuta*  
 Mangaoa: *M. perissa*  
 Mitiperua: *M. simplex*  
 Taitaa: *T. dacryma*  
     Taitaa: *T. dacryma*  
     Taireva: *T. striatula*  
     Taraia: *T. neanica*  
 Apopitys: *A. andersoni*  
 Pitys: *P. pagodiformis* (E. A. Smith)  
 Lamellovum: *L. globosum* Petit  
     Lamellovum: *L. globosum*  
     Maitua: *L. auriculella*  
 Antonella: *A. trochlearis* Pfeiffer  
 Perahua: *P. grandis*  
 Celticola: *C. pilsbryi*  
     Celticola: *C. pilsbryi*  
     Meryticola: *C. arborea*  
     Nesonoica: *C. conoides*  
 Tubuaia: *T. perplexa* (Garrett)

## LAMELLIDEINAE

- Tornatellinops: *T. novoseelandica* (Pfeiffer)  
 Lamellidea: *L. pepomum* (Gould)  
     Lamellidea: *L. pepomum*  
 Elamellidea: *L. tantalus* (Pilsbry and Cooke)  
 Atea: *L. adamsoni* Pilsbry and Cooke

## TORNATELLININAE

- Elasmias: *E. aperta* (Pease)  
 Tornatellina: *T. bilamellata* (Anton)  
 Fernandezia: *F. wilsoni* (Pilsbry)

## TORNATELLIDINAE

- Tornatellides: *T. oblongus* (Anton)  
     Tornatellides: *T. oblongus*  
     Aedituans: *T. neckeri*  
     Waimea: *T. rudicostatus* (Ancey)  
 Philopoa: *P. singularis*  
 Tornatellaria: *T. newcombi* (Pfeiffer)

## AURICULELLINAE

- Auriculella: *A. auricula* (Férussac)  
 Gulickia: *G. alexandri* Cooke

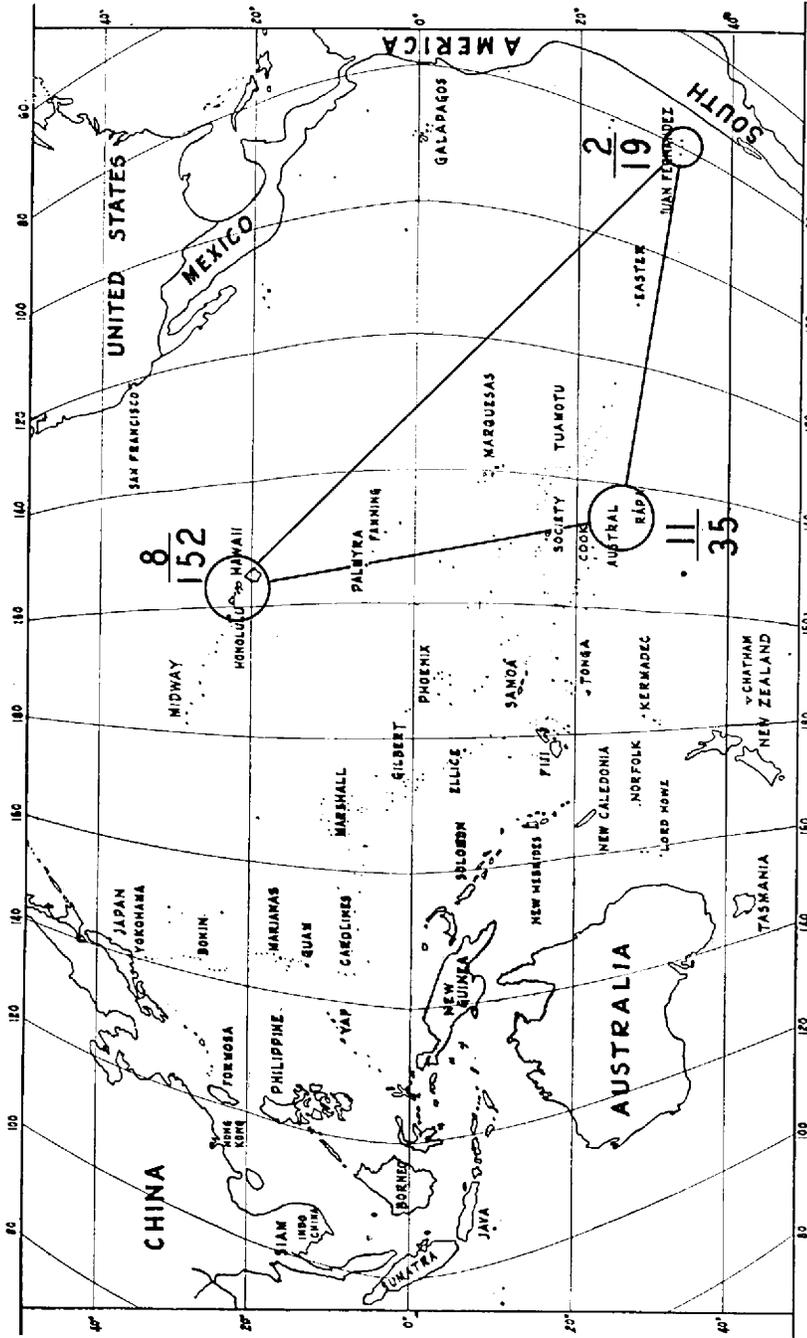


FIGURE 4.—Three generic centers of evolution in Achatinellidae. Austral Islands: 11 genera, 35 species; Juan Fernandez: two genera, 19 species; Hawaiian Islands: eight genera, 152 species. Approximate distances: Australs to Juan Fernandez, 3,900 miles; Juan Fernandez to Hawaiian Islands, 5,000 miles; Hawaiian Islands to Australs, 2,700 miles.

## ACHATINELLINAE

- Newcombia: *N. plicata* (Pfeiffer)  
 Perdicella: *P. helena* (Newcomb)  
 Partulina: *P. virgulata* (Mighels)  
     Partulina: *P. virgulata*  
 Partulinella: *P. marmorata* (Gould)  
 Baldwinia: *P. physa* (Newcomb)  
 Eburnella: *P. variabilis* (Newcomb)

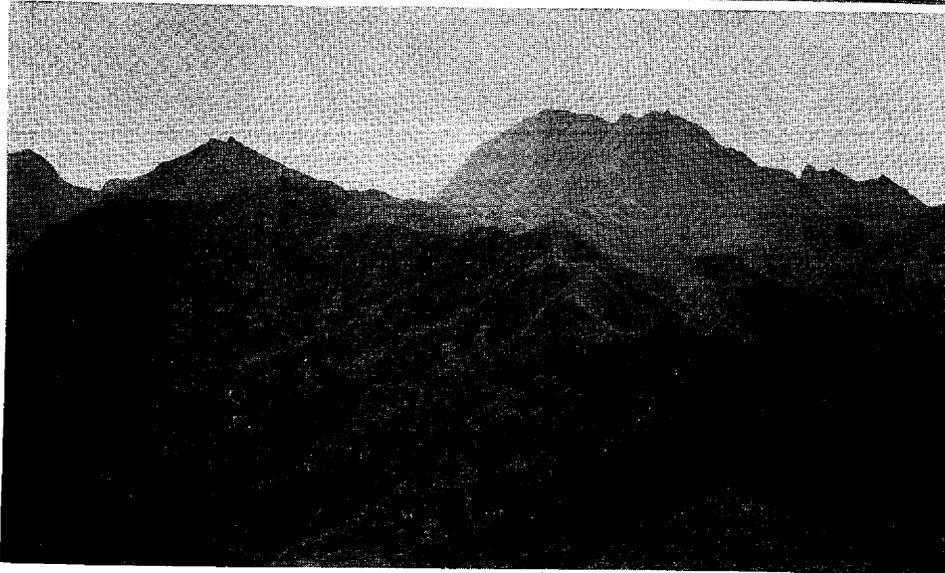
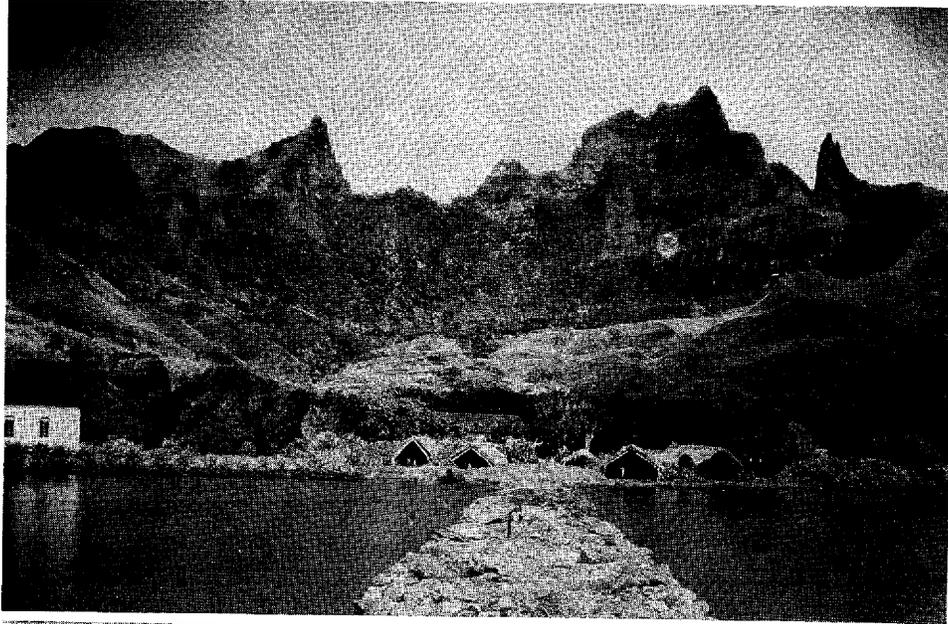
## DISTRIBUTION

The family Achatinellidae is limited to the islands in and bordering the Pacific Ocean. Three species have been reported outside of this area, from Lombok and Java in the East Indies and from Mauritius and Bourbon in the Indian Ocean. These three species belong to the genus *Elasmias*, the most widespread member of the family, and have undoubtedly been distributed through human agency.

Throughout its distribution there are three principal centers of generic evolution, shown on the accompanying map (fig. 4): (1) the Austral Islands, including Rapa, with 11 genera, (2) the Hawaiian Islands, with eight genera, and (3) the Juan Fernandez Islands, with two genera. The number of species referable to these genera are, more or less: Australs, 35; Hawaiian Islands, 152; and Juan Fernandez, 19. The centers are located at approximately the following points: Australs, latitude 22° to 27° S., longitude 144° to 145° W.; Hawaii, latitude, 19° to 22° N., longitude 155° to 160° W.; Juan Fernandez, latitude 33° S., 80° W. Approximate distances between these centers are: Hawaii to Rapa 2,700 miles; Rapa to Juan Fernandez 3,900 miles; Juan Fernandez to Hawaii 5,000 miles.

In the Australs nearly all the genera belong to the group Pitysiinae, a subfamily almost entirely confined to Rapa. Of this group, the subgroup, or tribe Antonellini (two genera, five species), is limited to Rapa alone and the tribe Pitysiini (eight genera, 26 species) extends, in a small way, into the other islands of the Austral group (fig. 11). One of its members (*Taitaa*) is found in the nearest islands of Raivavae, Tubuai, and Rurutu. The third tribe of this subfamily, Tubuaiini (two genera, 12 species), has a genus (*Celticola*) restricted to the Australs but also has a relatively widespread member (*Tubuaia*), species of which may be found in the Kermadec, Cook, and Austral Islands, Mangareva, Pitcairn, and the Society Islands (Garrett).

In the Juan Fernandez Islands (Masafuera, Masatierra) off the coast of Chile are two restricted genera of the subfamily Tornatellinae (tribe Tornatellinini) with 19 species between them forming a second and a most paradoxical center of generic evolution. Much can be learned by a thorough collection of the land-shell fauna of these islands, particularly the tornatellinids, and a systematic study of their anatomy. For many years the Fernandezian genera



**Top:** Rapa, Maitua valley from Ahurei jetty, a rich shell country; peaks are, left to right, Mangaoa (1,434 feet), Tautautu (1,784 feet), and Pokumaru (1,916 feet); photo by J. F. G. Stokes. **Bottom:** Rapa, forest southeast of Morongota fortress, its rocky rounded peak in left middle ground; Mount Perahu (2,077 feet), right background; Mount Putaketake (1,194 feet), left background. Although much native forest has been destroyed, several patches like that in foreground remain.

*Tornatellina* and *Fernandezia* have posed a provocative enigma, but the present study has shed some light on it by our stumbling onto its affinity to *Elasmias*. Further discussion will be found under *Elasmias*.

In the Hawaiian Islands are eight endemic genera, restricted in their distribution to the islands of this group. Four genera (*Achatinella*, *Newcombia*, *Perdicella*, and *Partulina*) comprise the subfamily Achatinellinae and are limited to the islands of Oahu, Molokai, Lanai, Maui, and Hawaii. The genus *Auriculella*, of Auriculellinae, has the same distribution. Neither Achatinellinae nor Auriculellinae is represented on the island of Kauai except by introduced species. *Gulickia*, of the same group as *Auriculella*, is known only from west Maui. The genus *Tornatellaria* of the subfamily Tornatellidinae is represented by endemic species on all the Hawaiian Islands except Kauai, whereas the monotypic genus *Philopoa* is known only from the small island of Nihoa.

Most of the genera of the family, of which 26 are recognized in this paper, are highly restricted in their distribution, as shown in the following table.

TABLE 1

ONE ISLAND	ONE GROUP	GROUPS OF ISLANDS*	WIDELY DISTRIBUTED
<i>Achatinella</i> , Oahu	<i>Auriculella</i> , Hawaiian Is.	<i>Tubuaia</i>	<i>Elasmias</i>
<i>Antonella</i> , Rapa	<i>Celticola</i> , Australs		<i>Lamellidea</i>
<i>Apopitys</i> , Rapa	<i>Fernandezia</i> , Juan Fernandez		<i>Tornatellides</i>
<i>Gulickia</i> , Maui	<i>Newcombia</i> , Hawaiian Is.		<i>Tornatellinops</i>
<i>Lamellovum</i> , Rapa	<i>Partulina</i> , Hawaiian Is.		
<i>Mangaoa</i> , Rapa	<i>Perdicella</i> , Hawaiian Is.		
<i>Mitiperua</i> , Rapa	<i>Taitaa</i> , Australs		
<i>Perahua</i> , Rapa	<i>Tornatellaria</i> , Hawaiian Is.		
<i>Philopoa</i> , Nihoa	<i>Tornatellina</i> , Juan Fernandez		
<i>Pitya</i> , Rapa			
<i>Pukumia</i> , Rapa			
<i>Strobilus</i> , Rapa			

\* Kermadec, Cook, Austral and Society Islands, Mangareva, and Pitcairn.

Apparently, 12 genera are restricted to single islands, nine of them to Rapa. Nine genera are known only from island groups, five of them from the Hawaiian Islands. One genus (*Tubuaia*), as shown on the map (fig. 67), is apparently limited mainly to the southernmost islands of the central Pacific: the Kermadec, Cook, Austral, Mangareva, and Society Islands. Only four of the 26 genera have a widespread distribution: *Elasmias* (Tornatellininae), *Lamellidea* and *Tornatellinops* (Lamellideinae), and *Tornatellides* (Tornatellidinae). There is little doubt that their wide distribution is due, for the most part, to human agency.

The genus *Lamellidea* has been taken from the Palau Islands in the west to the Marquesas in the east and from the Izu and Hawaiian Islands in the north

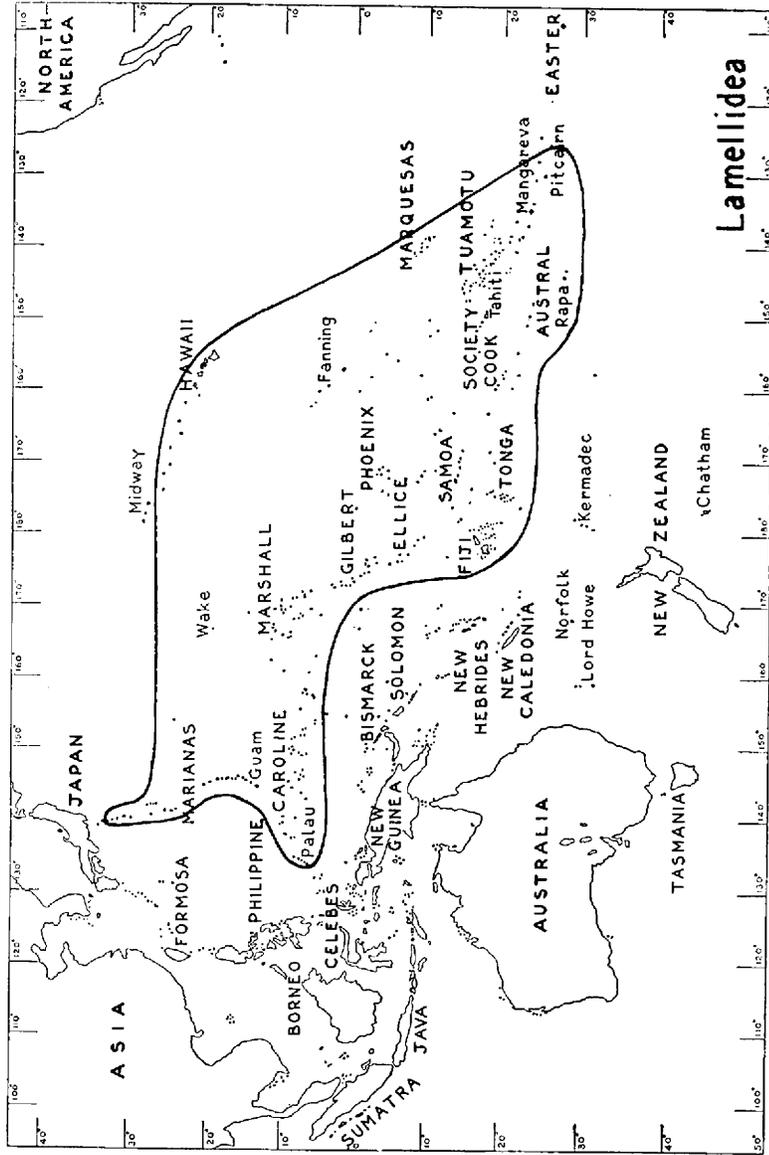


FIGURE 5.—Distribution of genus *Lamellidea*. (Broken lines point to extralimital localities.)

to Rapa in the south. It has not been reported from any of the islands west of Fiji in the south Pacific. (See map, figure 5.)

The genus *Tornatellinops* is known to inhabit a large proportion of the Pacific islands, as shown on the accompanying map (fig. 6). The wide dissemination of *T. variabilis* (Odhner) is undoubtedly due mainly to human agency (map, fig. 77). The westernmost island having *Tornatellinops* is one of the Ryukyus. The northernmost islands from which the genus is reported are the Izu Islands, just south of Japan, and Kure (Ocean), in the northwestern part of the Hawaiian chain. Easter Island is the easternmost record of its occurrence, and in the south a few species have been reported from Pitcairn, Rapa, Lord Howe, and New Zealand. To date, no species have been reported from the Gilbert Islands. Undoubtedly, one or more species will be found there with intensive collecting.

The genus *Tornatellides* has a remarkable distribution (map, fig. 104), having been reported almost entirely from the peripheral islands of the Pacific: To the northwest, Hongkong and Formosa; to the north, the Hawaiian Islands; to the east, the Marquesas; to the southeast, Pitcairn and Mangareva; to the south, the Society Islands, the Australs, the Kermadecs, and New Zealand. Within this perimeter the only islands from which *Tornatellides* has been recorded is Ebon in the Marshalls. This species had been referred to as *Tornatellides simplex* Pease [= *oblongus* Anton] by Pilsbry and Cooke. The genus is apparently absent from all the high islands within the perimeter; that is, from Samoa, Tonga, Fiji, the Carolines, and Marianas, all of which have received considerable attention from collectors. Another anomaly is the presence in the Galapagos Islands of a single species, *T. chathamensis* (Dall), which is apparently more closely related to the Hawaiian form of species than to *T. oblongus*, which is widely distributed throughout the islands of the southeastern Pacific from the Marquesas to the Cook and Society Islands. (After this was written, the late Dr. Pilsbry called our attention to two species of *Tornatellides* from islands off Mexico.) The distribution of this genus is covered more fully in the systematic discussion.

*Elasmias* is the most widespread genus of the family. (See map, figure 96.) It is not confined entirely to the oceanic islands of the Pacific but has been collected in Australia, in Papua, in three of the islands of the East Indies (Natuna, Lombok, and Java), in the Philippines, and in Mauritius, Reunion, and the Maldivé Islands in the Indian Ocean.

In Pilsbry's estimation (Pilsbry and Cooke, 1915, p. 114) *Elasmias* represents a form "probably not far removed from the ancestral Tornatellinid stock." The similarity between the genitalia of *Elasmias* on one hand and *Fernandezia* and *Tornatellina* on the other can hardly be accounted for by convergent evolution. Possibly the Juan Fernandez genera, by virtue of their isolation and lack of competition, have retained their early ancestral anatomical characters:

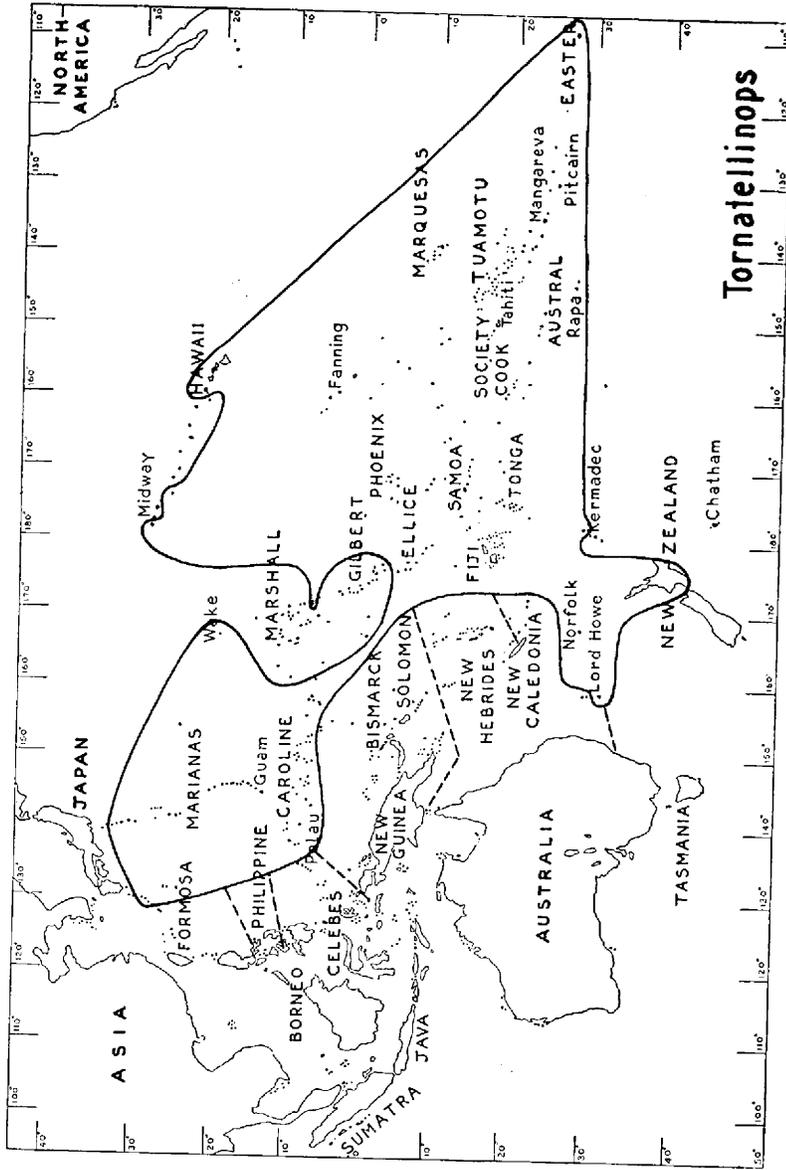


FIGURE 6.—Distribution of genus *Tornatellinops*. (Broken lines, etc.,) [ex Fig. 5.]

conchologically, there seem to be no connecting characters.

The four and only distinct species of *Elasmias* are from the Hawaiian, Society (Tahiti, Moorea), and Austral Islands (Rapa, Rurutu), along the eastern rim of the distributional area.

Except for the four forms of *Elasmias*, the 17 species from the entire area of distribution can be divided into two types which more or less overlap each other. To identify unlocalized material accurately is almost impossible, as some of the species have been described without comparison with a representative collection.

Most of the species of *Elasmias* have been collected near sea level, and many have been taken on garden and other cultivated plants. This fact, together with the rather close resemblance of most of the species recognized, leads us to believe that the wide distribution of the genus undoubtedly took place after the advent of man to the peripheral islands of the eastern Pacific and, further, that much of this distribution has occurred since Europeans entered the area. This may explain the presence of the genus on the islands of the Indian Ocean, in the East Indies, in Australia, and in the Philippines, for no other member of the family is represented in their faunas. Iredale (1944, p. 308) expresses virtually the same opinion.

The very wide distribution of *Elasmias apertum* throughout the islands of the southeast Pacific is almost paralleled by *Tornatellides oblongus*, *Lamellicidea oblonga*, *L. pusilla*, and *Tornatellinops variabilis*.

The high percentage of endemism among the genera of Achatinellidae is, without doubt, due primarily to isolation. If it has taken a comparatively long period of time for a genus to evolve, it seems strange that the majority of the genera are restricted in their distribution, for the agencies which distributed the early primitive types have undoubtedly continued to function and are still potential distributors. The only altered factors are land areas which were once somewhat larger.

Of the many authors who have discussed the distribution of plants and animals in the Pacific oceanic area, some believe that only land connections account for the rather logical distribution of flora and fauna. Advocates of the land-bridge theory have strongly opposed advocates of other natural means of distribution such as winds, ocean currents, and birds.

We know practically nothing of the geography of the ocean floor between most of the groups of islands, nor do we know the contours of the ocean floor between the individual islands of many of the groups. Before we are able to discuss any possible land connections or larger land masses, we must have a clear picture of the appearance of the entire ocean floor of the Pacific Basin. The dissimilar distribution of many of the genera and subfamilies of land mollusks in the Pacific is opposed to any large land mass at any single period in the past, as a few of numerous examples illustrate.

The genus *Thaumatodon* (Endodontidae) extends from Palau to New Zealand and from Hawaii to Rapa. Within this area it is probably represented on all the high islands. The genus *Charopa*, considered in the broad sense of years ago, is known to inhabit the same area with the exception of the Hawaiian Islands, the Marquesas, Mangareva, and the Austral Islands. The genus is most strongly represented in the southwest Pacific.

The subfamily Diplommatinae is well represented in the faunas of the high islands west of and including Fiji, with a subgenus (*Moussonia*) in Samoa. No species of the subgenus has been recorded from any island east of Samoa. The zonitid subfamily Trochomorphinae occupies nearly the same area as the Diplommatinae except that it extends eastward to include the Society Islands. It is entirely absent in the Cooks, the Australs, the Tuamotus, the Marquesas, and the Hawaiian Islands.

The family Helicinidae undoubtedly occurs on all the islands of the Pacific as far east as Mangareva and the Marquesas. One of the genera (*Pleuropoma*) occupies nearly the whole of this area. *Omphalotropis* is reported from most of the high islands and atolls in all island groups, but it does not occur in the Hawaiian Islands and its presence in the Marquesas is doubtful.

The above examples show that each group of terrestrial mollusks has its own peculiar distribution. Each pattern of distribution may be paralleled or overlapped to some degree by that of another, but usually some peculiar divergence at a significant point raises a question. Present knowledge can supply only speculative answers.

#### ANATOMY

An over-all picture of the anatomical findings in the study of the families Tornatellinidae and Achatinellidae will be found in the synopsis of genitalia (figs. 7-9). Eleven principal types of genitalia, one (*Tubuaia*) with an interesting variant during the juvenile paraneanic substage, were found; these represent the tribal subgroups of the six subfamilies in the proposed consolidation.

#### GENITALIA

##### OVOTESTIS

One of the most important diagnostic features of the genitalia is the type of ovotestis or hermaphrodite gland (figs. 7-9). Except for the subfamily Tornatellinae (fig. 8), each subfamily is characterized by a definite type of ovotestis: unilobate or multilobate.

For a quick means of discriminating between *Tornatellinops* (Lamellideini) (fig. 8) and *Tubuaia* (Tubuaiaini), figure 9, a good dissection of the ovotestis is essential. The male and female parts of both genera are so similar that a

quick differentiation depends almost entirely upon the character of the ovotestis. Innervation of the penis may also be resorted to, but this entails considerable labor.

While the ovotestis may be broadly divided into two major categories, unilobate and multilobate, they may be further analyzed and divided into five types: (1) the true unilobate (type, *Elasmias*), (2) the apparently bilobate (type, *Atea*), (3) the bilobate to trilobate (type, *Tornatellides*), (4) the true multilobate (type, *Achatinella*), and (5) the clustered form (type, *Fernandezia*). The first type is apparently a simple sac, which is often slightly indented distally, sometimes quite deeply. In the second form the ovotestis has a deeper distal indentation than usual so that it appears to be bilobate. However, no

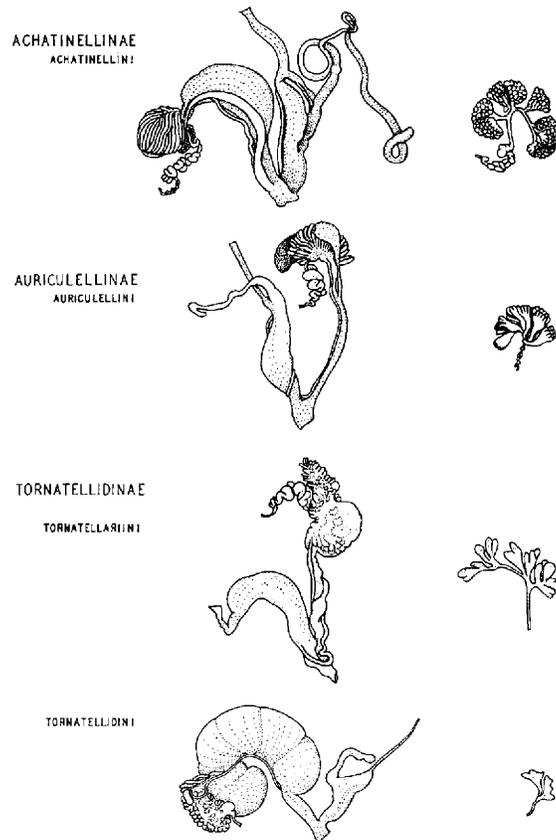


FIGURE 7.—Synopsis of tribes of Achatinellidae: Achatinellini (represented by *Achatinella concavospira*), Auriculellini (*Auriculella auricula*), Tornatellariini (*Tornatellaria newcombi*), Tornatellidini (*Tornatellides oblongus*).

separate efferent ducts to the hermaphrodite duct are apparent, hence it is, in reality, only a modification of the first form. The bilobate to trilobate type (3) is the usual condition in *Tornatellides*, in which case the indentations have not only divided the ovotestis but each lobe is connected with the hermaphrodite duct by a separate efferent duct. The true multilobate type of ovotestis is the commonest and consists of numerous lobes, up to 10 or so, and always appears to be heavily packed. The clustered form of ovotestis is a novelty. As all the efferent ducts appear to meet at the same point, the gland differs somewhat from the true multilobate type in which the efferent ducts enter the hermaphrodite duct separately and at some distance from each other.

#### HERMAPHRODITE DUCT

In the adults the hermaphrodite duct is usually distended and convoluted. In Pityisini it is always heavily swollen and convoluted. The distension is caused by the storage of large amounts of gonadal products, which, at least in *Achatinella*, consist principally of an enormous number of spermatozoa.

#### TALON

The talon is a small U-shaped or sigmoid termination of the hermaphrodite duct near the carrefour. In *Achatinellidae* it is usually hidden and difficult to detect, and the typical shape is missing in many specimens.

#### CARREFOUR

Like the talon, the carrefour is a small inconspicuous organ, a continuation of the hermaphrodite duct, and usually hidden under the follicles of the albumin or prostate glands. It is generally ovate or oblong and assumes the role of a "crossroad" where the product of the hermaphrodite gland, albumin, and prostate glands appear to be received and dispersed to the vas deferens, uterus, and the carrefour vesicle, if the last organ is present.

#### CARREFOUR VESICLE, OR VESICULA SEMINALIS

Odhner (1922) first discovered the peculiar "vesicula seminalis" in *Tornatellina bilamellata* and *Fernandezia bulimoides*. In *Fernandezia bulimoides* it is a large, cylindrical, hollow organ; in *Elasmias* it is minute; and in both it originates at the carrefour and terminates in the columellar muscle, where its tip is attached. That the vesicle is a storage organ is indubitable, for it is a hollow cylinder connected with the carrefour. One of our most surprising discoveries in the *Elasmiatini* is the presence of an organ of an identical nature. This fact came to light after preliminary dissections of *Elasmias* were completed, but before the critical analysis was started. What was for some time regarded as a peculiar retractor of the upper female region connecting it with the columellar muscle was carefully removed in dissection and found to be a small but definite

vesicle. However, were it not for the fact the Odhner had first found the “vesicula seminalis,” the vesicle of *Elasmias* would probably have been overlooked, for it was the Tornatellinini vesicle that served as a clue toward its identification. The occurrence of this vesicle in Elasmiatini and Tornatellinini brings the two closer together, but not as close as Lamellideini is to Tornatellinoptini or as close as the tribes of Pitysinae. This remote relationship is explained by the fact that the ovotestis of Elasmiatini and Tornatellinini differ radically from each other and by the knowledge that, whereas the interior of the Elasmiatini appendix is simple like that of Tornatellinoptini, that of Tornatellinini is complex.

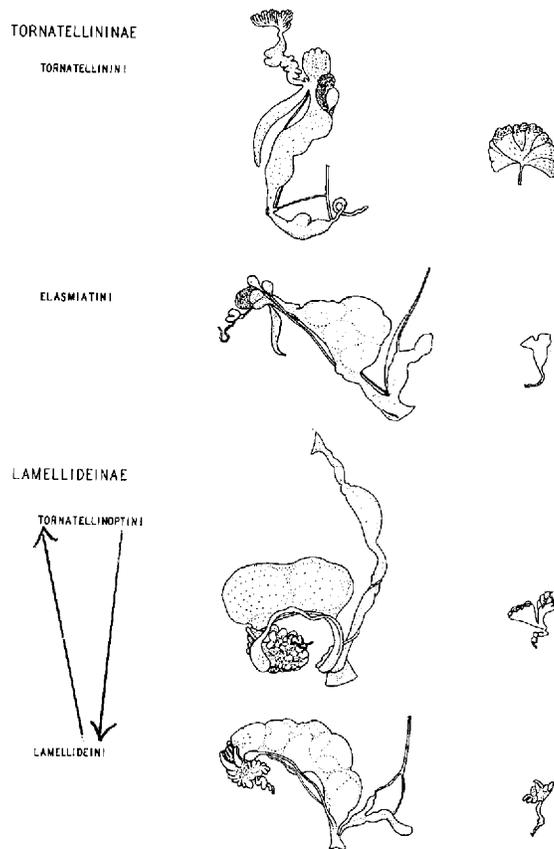


FIGURE 8.—Tornatellinini (*Fernandezia bulimoides*, after Odhner), Elasmiatini (*Elasmias apertum*), Lamellideini (*Lamellidea oblonga*), Tornatellinoptini (*Tornatellinops variabilis*).

The carrefour vesicle discussed herein is not to be confused with that discussed and illustrated by Neal (1928, p. 36, fig. 13). The seminal vesicle referred to by Neal is probably a mislabeling for the preuterine chamber (fertilization chamber of authors), a bulge commonly found in the uterus immediately below the carrefour. Partially formed embryos are found there in many animals. (See preuterine chamber in *Achatinella concavospira*, *Partulina mighelsiana*, *Perdicella helena*, *Newcombia cumingi*.)

## ALBUMIN GLAND

The albumin gland is a variable organ in the Achatinellidae. It ranges from minute to large and, in relation to the prostate, may be classified as dominating or relatively reduced. In general, it is a fair-sized organ with numerous follicles

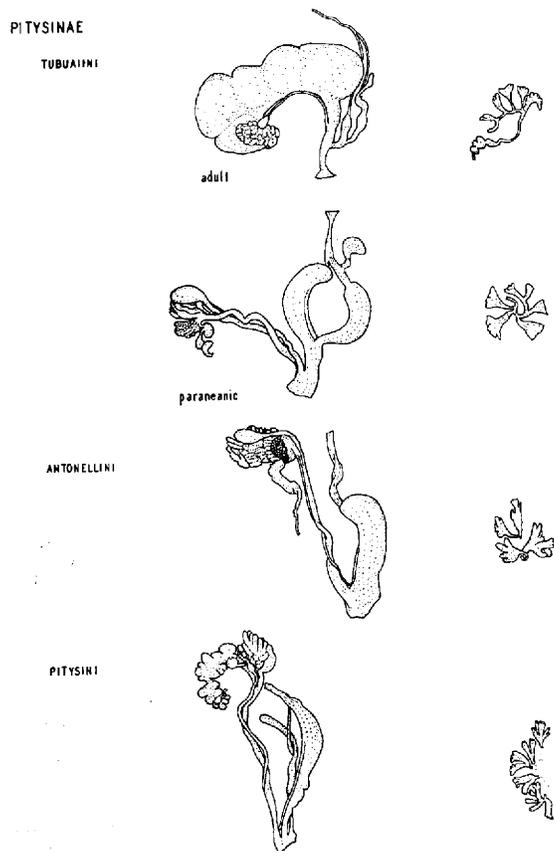


FIGURE 9.—Tubuaiini (*Tubuaia perplexa*), Antonellini (*Antonella trochlearis*), Pitysini (*Pitys pagodiformis*).

which are either erect and rooted to a central core, thus radiating outward, or lie sprawled all over each other in indefinite arrangement. This gland forms a head at the distal termination of the oviduct. In the adult of Pityisini and Antonellini the albumin gland is vestigial or, in many, apparently absent. When present, it is a small mass of numerous minute lobes. In the subadult or the paraneanic substage the gland is large and dominating. (See *Pityis pagodiformis*, *Strobilus subtilis*, *Taitaa dacryma*, *Pukunia acuta*, *Antonella tenuis*.) Why the gland gradually diminishes as maturity approaches, is not known. Its large size in the late juvenile stage and its minuteness in the adult stage suggest that utilization diminishes as age advances. Thus it appears that with age, members of the tribes may change over from functional females to functional males. Further, with the diminution of the albumin gland a corresponding enlargement of the prostate gland takes place until the upper female parts are dominated by a large head of prostate follicles.

In Tubuaiini the above peculiar characteristic, noted for Pityisini and Antonellini, is reversed. Here the subadult or paraneanic members of the tribe repeat the change in the mature pitysinine genitalia, and this is accomplished faithfully even to the diminution of the albumin gland. Apparently, members of the tribe Tubuaiini function as females in the adult stage and as a males in the subadult stage.

In the subfamily Achatinellinae the albumin gland is minute, but apparently never totally absent. However, unlike the Pitysinae, there appears to be no stage in its development where the albumin gland dominates.

The albumin gland in the Auriculellinae is small in comparison to the prostate but cannot be said to be minute. In both the subfamilies Achatinellinae and Auriculellinae the follicles are numerous, rather small, and apparently arranged radially with their roots attached to a common central core, for only the tips are visible.

In the remaining subfamilies (Tornatellidinae, Tornatellinae, Lamellideinae) the albumin glands are relatively inconspicuous but definitely dominating, as compared to the prostate. The follicles are fairly numerous and rather small, and they may either sprawl or radiate from a central core.

#### PROSTATE GLAND

Typically, the prostate is a gland with few to numerous digitate follicles. The exception may be found in Elasmiatini (see *Elasmias peasianum*), where the follicles are merely short and squat and have relatively large protuberances or diverticuli.

Among members of the oviparous tribes the prostate is nearly always large and dominating. The gland is composed of large digitate follicles, roughly arranged like a fan. The few dissections in Tornatellariini show that the prostate is either as large as or larger than the albumin gland. Since the juvenile pros-

tate is quite small, as compared to the albumin gland, the prostate probably dominates in normal adults.

Among the viviparous tribes the prostate is reduced [with the exception of Achatinellini and Tornatellariini (*Philopoa*)]. The prostate is usually a diminutive organ, paucifolliculate, and often surfaced with some black pigment. The follicles are short-clavate to fairly long-digitate. Sometimes the prostate is apparently absent, in which case a careful search near the carrefour will reveal a few inconspicuous follicles on the vas deferens. In *Philopoa* the prostate appears to be equal in size to the albumin gland. The prostate of Achatinellini is peculiar in two ways: (1) it is relatively strongly developed, especially since the albumin gland is minute and (2) it is formed of very long follicles which form a compact bundle enclosing tightly the spermatheca.

#### SPERMATHECA AND STALK

Except in the Achatinellini, where it is enclosed within the prostate follicles, the spermatheca is always free and joined to the albumin or prostate glands, on which it rests by fine membranous threads, or it is only partially overgrown by follicles of the glands. Although its position is usually near the prostate, in many gravid individuals it is pulled down and rests on the upper uterus. It ranges from small to fairly large and is roughly ovate, some having a blunt point distad. Very often, simple, compact, elongate masses of sperm are found within the spermatheca, but in no specimen did any horny covering surround them.

In general, the stalk empties into the oviduct (indicated by X in the figures) below the lowest or oldest embryo or egg. The exception is Tornatellidini, in which the spermathecal stalk enters the oviduct well above the first or earliest embryo at the point where the uterus joins the carrefour (see *Tornatellides oswaldi*, *T. oblongus*). In general, the stalk of the adult in viviparous groups enters the oviduct at a point well below the half-way level. In the oviparous groups the entrance is anywhere from just below the carrefour to almost at the atrium. In juvenile viviparous snails the stalk may be well above the half-way point, depending upon the number of embryos present (see *Lamellidea oblonga*, *Celticola pilsbryi*).

#### OVIDUCT

The oviduct in the viviparous achatinellids is almost always large, sac-shaped, and diaphanous. The portion generally referred to as the uterus usually composes the larger, upper part of the tube; the vagina is narrow and short. Tornatellidini are the exception.

In the oviparous snails, the oviducal distention occurs only when the eggs are present. Ordinarily the oviduct is very narrow and tubular, rarely translucent. The vagina is long in the tribes Pityisini and Antonellini. In Tornatellariini it is about half the oviducal length. The vagina is short in Achatinellini.

## VAS DEFERENS

The vas deferens is a thin tube, ordinarily narrow, and always free. Immediately upon leaving the carrefour, it follows the oviduct to the latter's termination and curves upward, following the penis to the apex or entering it somewhere between the apex and midbody. In many members of the oviparous tribes such as Pityisini, Antonellini, and Auriculellini the width of the vas deferens equals the oviducal width, exceeding it in others. Like the oviduct, it is elastic and, rarely, bulges somewhere along its length with a mass of sperm.

## PENIS

The family exhibits a varied assortment of penial types (figs. 7-9). Every tribe is characterized by a penial type peculiar to itself, although some of them have superficially similar types. All except Auriculellini and Elasmiatini are equipped internally with a recurved pilaster. In some, the pilaster is modified either toward simplicity or toward complexity. All are characterized by the lack of an epiphallus except the Auriculellini, which have a small one. In the majority, the penis is equipped with an appendix. The penis varies from vestigial to longer than the female parts. Some species produce individuals (*Tubu-  
aia voyana*, *Lamellidea oblonga*) without penis. The retractor, when present, is always terminal.

A vestigial or highly reduced penis is a mere pimple on the larger appendix. It is difficult to trace unless the penial retractor is followed. The penial retractor, in turn, requires careful search and handling as it is a very thin, delicate thread. The interior of the vestigial penis may contain vestiges of the achatinellid pilaster (*Fernandezia*) or may be entirely free of it (*Elasmias*). The vas deferens always terminates at or near it. A somewhat larger penis, but comparatively small, is found in Tornatellinoptini. It is  $\pm 0.25$  the oviducal length, narrow, and usually pointed. The interior has a modest recurved pilaster.

The next type, a little larger and longer than the foregoing, is the penis found in Tubuaiini. The Tubuaiini penis is of interest because it is the final result of a penis which, in its ontogeny, has passed through a much larger type (the pitysinid) and, apparently, partially atrophied to a relatively insignificant organ. Within is a recurved pilaster.

The largest, but not the longest, penial type is found both in Achatinellini and in Pityisini. Ordinarily it is large, fairly long ( $\pm 0.5$  oviducal length to as long or longer), and club-shaped. The pilaster within is large and impressive, ascending dorsad from the stalk, recurving at the apex, and descending a short distance, usually to the level of the appendix, as a semi-pendulous tongue.

A unique type of penis is found in Auriculellini. It is without pilaster and is the only one equipped with an epiphallus, which is small. The appendix is terminal or nearly so and without a retractor, in contrast to all the aforementioned, wherein the appendices emerge off the penis at a somewhat low level and are all equipped with retractors.

The penis of Tornatellidini is similar to that of Auriculellini in external morphology. It also is unique and superficially resembles the penis of Auriculellini, the appendix being terminal (or nearly so) and retractorless. It has no epiphallus, but does have a modified pilaster.

The non-appendiculate penises do not arrange themselves into several well-defined types as do those with appendices. They are all similar in one respect: they are cylindrical, vermiform, or sometimes clavate. In length, they range from a small fraction of the oviducal length to longer than the oviducal length. Those dissected have shown typical pilasters.

One of the rare peculiarities of the family is the fact that some individuals in the genera *Lamellidea* (Lamellideini) and *Tubuaia* (Tubuaini) lack a penis. In these the vas deferens either enters the atrial region directly or does not enter at all, in which circumstance, the vas deferens either has become detached and lies free in the coelom or is absent.

#### APPENDIX

The family is characterized by three principal types of appendices, as indicated by the interior arrangement. They are (1) secretory, (2) secretory-ejaculatory, and (3) copulatory. In reality, however, all the appendices are secretory in one way or another and the terminology above is arbitrary to indicate types of appendix in the light of what we have interpreted as their principal (and apparent) functions.

The secretory type of appendix is a simple blind tube, smooth or slightly pebbled within. It is found in Tornatellidini only. Its principal function, aside from being perhaps stimulatory, appears to be that of a mechanism for the production of sperm masses. No sperm masses have been found so far in the few species of *Tornatellides* dissected.

The secretory-ejaculatory appendix has a simple, thin, delicate tube within. In those snails having a well-developed penis in addition to an appendix the purpose of the appendix can be assumed to be chiefly secretory. But in *Elasmiatini*, in which the penis is vestigial and apparently non-functional, the appendix may be a substitute copulatory organ (see *Elasmias peasianum*). We believe that the inner tube, besides secreting a substance to cement the sperm together, ejects the sperm mass.

There are two well-defined types of secretory-ejaculatory appendices. First (a) the pitysinid, which is a large, somewhat fleshy inner tube (see *Lamellovum auriculella*), usually coiled once upon itself (see *Elasmias peasianum*), composed of longitudinal layers of muscular tissue, terminating at, opening into, and attached to the wall near the blind end. Second (b) the auriculellid, a straight inner tube of small diameter, is composed of muscles arranged circularly instead of longitudinally (see *Auriculella auricula*) and thinning out toward the distal end, perhaps in the same manner as that of a. In a are

Pityisini, Tubuaiini, Tornatellinoptini, and Elasmiatini. In *b* are Auriculellini and Achatinellini.

The true copulatory type of appendix is found only in Tornatellinini (seen in *Fernandezia* only). The interior of this appendix is complexly ridged with a good series of stimulator folds, chiefly circular in the upper part, whereas in the region of the vestigial penis the stimulators are composed of longitudinal ridges plus muscular pilasters.

The general rule is that the appendix has a retractor, which is one of the two branches of the main penial retractor (common retractor). In Auriculellini and Tornatellidini this rule does not apply. Both are without appendical retractors. Appendical retractors are never attached apically as in the penial retractors but always well below the apex.

#### REPRODUCTION

Reproduction is either ovoviviparous or oviparous. Where ovoviviparous (viviparous) the embryos are nearly always multiple in adult gravid specimens. The extremes are from one to two in the genera of Achatinellinae (these are the counts of the embryos only in the uterus proper, disregarding the small protoembryos of the preuterine chambers) to 20 to 22 in *Fernandezia bulimoides*. The average for all genera appears to be about five to seven, in various stages of development. These are arranged in the uterus from the very young (upper uterus) to the oldest (near lower part of oviduct). Graduated stages occupy the interval. Very young embryos are never enclosed within a calcareous shell, as in some species of *Partula*, but are enclosed by thick layers of a white or yellow substance which is taken to be the yolk mass. The older embryos are with shell.

Where oviparous, the uterus is rarely seen with egg; but if such are found, the general rule is one egg for each adult gravid specimen. Rarely, two or three eggs are found together at the same time in the uterus. Some eggs are spherical or nearly so; many are oval.

The genera of Achatinellidae are divided on the basis of method of reproduction, as follows:

Oviparous: *Perahua*, *Antonella*, *Pukunia*, *Taitaa*, *Mitiperua*, *Mangaoa*, *Strobilus*, *Lamellovum*, *Apopitys*, *Pitys*, *Tornatellaria*, *Gulickia*, and *Auriculella*.

Viviparous: *Celticola*, *Tubuaia*, *Lamellidea*, *Tornatellinops*, *Elasmias*, *Fernandezia*, *Tornatellina*, *Philopoa*, *Tornatellides*, *Perdicella*, *Newcombia*, *Partulina*, and *Achatinella*.

#### CENTRAL NERVOUS SYSTEM

The central nervous system is of the concentrated type. The principal penial nerve stems from either the pedal or the cerebral ganglion. There is a consoli-

with  
shell

duction of the labial and inferior tentacular nerves to form a large labio-tentacular nerve, a condition also found in the Pupillidae (Steenberg, 1925, pl. 32, fig. 7).

In some members the labial, tentacular, and nuchal nerves are combined to form an even newer combination. In others the nuchal may combine with the frontal nerves. The frontals are usually two in number where the penis is innervated by the pedal ganglion, but where it is innervated by the cerebral ganglion the inferior frontal nerve is modified into the penial nerve or merely gives off a branch to the penis while continuing anteriorly to the lower basal region of the ommatophore. The inferior frontal nerve is almost always connected with the ommatophoral by a small innominate nerve.

#### JAW, RADULA, AND TEETH

No jaw was found in any of the species dissected for the teeth, but Pilsbry's figure and description (Pilsbry and Cooke, 1915, p. 57, pl. 14, fig. 3) is sufficient for the present.

Two classes of cusps are recognizable in Achatinellidae. In class A, the cusps are large, heavy, long, and few in number and usually occupy the middle and two ends of the head of the tooth. For the purposes of this paper, this class shall henceforth be referred to as cusps or cones (ecto-, ento-, and mesocones). In class B, the cusps are usually aculeate and more delicate and shorter than the principal cusps; they are between the principal cusps or behind and below them. They are usually fewer in number than the principal cusps, sometimes greater in number, but often absent. These shall be referred to as cusplets.

Granted that all the achatinellid teeth are marginals, as postulated by Pilsbry, the fact remains that in some species the central, or median, tooth is distinguished from the others either by size or by its shape. In this paper the term central is used.

The radula of the Achatinellidae (see *Achatinella fuscobasis lyonsiana*, fig. 122, *o, p*) is short and broad; the anterior end is recurved and closed by the membrane above; the posterior and nascent end thin; and the caudal end curved ventrad. Stain is taken on heavily at the anterior end, weakly at the caudal end. The teeth are arranged in shallow V-shaped rows, the internal points of each row meeting at the median line and forming an 80 to 90 degree angle, or each half row forming a  $\pm 45$ -degree angle with the median line.

The teeth are all alike, rake-shaped, or rastriform; the basal plate narrow and long, gradually widening apicad and recurving into a broad head bearing large cusps and smaller denticles. Central teeth are smaller than marginals or as large, the largest teeth in about the middle of a half row. Ectocones and entocones, single or paired, are incurved or outcurved. The mesocone is smaller and shorter, the cusplets aculeate, fine, delicate, sharply pointed, shorter than cusps, situated below and (or) behind or between principal cusps.

## CONCLUSION

The anatomical study of the available Achatinellidae-Tornatellinidae animals has led to the construction of the single family Achatinellidae, comprising six subfamilies, 11 tribes, and 26 genera. Although our inclination was to continue the separation of Achatinellidae from Tornatellinidae, no other conclusion but the one arrived at seems possible in the light of our findings. Before the final conclusion was reached two other courses were taken into consideration, namely to create six families or to leave Achatinellidae as a separate family and create five subfamilies in Tornatellinidae. The first course was rejected; the alternative course parallels the view of Pilsbry. Pilsbry's belief that conchological differences are fundamental is well known and requires no elaboration (1927, p. vii). To be sure, the members of the family Achatinellidae of Pilsbry and Cooke are giants as compared with the tornatellinids; and the gaudy coloration of its members is remarkable in view of the drabness of most of the tornatellinids. Nevertheless, the unique quality of "Achatinellidae" is in shell size and coloration alone and can be ascribed to either mutation or to rejuvenation of the race upon its discovery of a new habitat (Pilsbry, 1914, p. xii). Its genitalia, on the other hand, are basically similar to those of Pitysiinae, differing only in two principal respects: (1) its spermatheca is bundled within the prostate follicles, whereas in Pitysiinae it is free; and (2) the interior of its appendix is structurally different from that of Pitysiinae and either closely resembles that of Auriculellinae or is identical with it. Furthermore, anatomically it would seem more logical to set aside Pitysiinae as a separate family because of its theoretically primitive position or to separate Tornatellininae from its fellows because of its unique genitalia or, finally, Auriculellinae because it possesses a distinct epiphallus and completely lacks the achatinellid pilaster.

The lack of cohesion between the subfamilies is remarkable. One is forced to the conclusion that the family is an ancient one, having lost a great many intermediate members in its evolution. Thus, no "family tree" can possibly be constructed to show the relative position of the subfamilies to each other. That some connecting links did exist at some earlier period and were later obliterated is highly probable, as evidenced by at least one known link, that between Tubuaiini and Pitysiini. That the absence of linkage proved confusing to earlier investigators is evidenced by the fact that, at one time or another, two, three, and even four family titles have been either assigned or proposed for the Achatinellidae.

Lacking any material to create a phylogenetic "tree," it becomes necessary to give a few important characteristics to explain the stratification of the subfamilies as presented in this work (fig. 10).

The characteristic common to all the subfamilies is the rastriform teeth. An orthurethrous kidney with a reflected ureter is also shared by all.

SUBFAMILY	TRIBE	GENUS	T ras- roid	PN cer	RO free	HG multi	X below ov or emb	AG mi- vivep	RE PVS	APPENDIX with rm	sec- ejac	ab- sen	PENIS long	with pil	with epi	
ACHATINELLINAE	ACHATINELLINI	Achatinella														
		Partulina														
		Newcombia														
AURICULELLINAE	AURICULELLINI	Perdicella														
		Auricella														
TORNATELLIDINAE	TORNATELLARINI	Gulickia														
	Philopoa															
TORNATELLININAE	TORNATELLIDINI	Tornatellaria														
	Tornatellides															
	Tornatellina															
LAMELLEIDINAE	ELASMIATINI	Fernandezia														
	Elasmas															
PITYSINAE	LAMELLEIDINI	Lamellidea														
	TORNATELLINOPTINI	Tornatellinops														
TUBUATINI	ANTONELLINI	Tubuaria														
		Celticola														
PITYSINI	PITYSINI	Antonella														
		Perahua														
PITYSINI	PITYSINI	Lamellovum														
		Pitys														
		Appilyis														
		Taitaa														
		Mitiperua														
		Mangaea														
Pukunia																
Strobilus																

FIGURE 10.—Graphic summary of anatomy studied, abbreviations as follows: T = teeth rastroid; PN = penial nerve originating at ped = pedal ganglion or at cer = cerebral ganglion; RO = retractor of ommatophore free of peni-oviducal angle; HG = hermaphrodite gland multilobate; X = insertion of spermathecal stalk below ov = ovum (or ova) or emb = embryo(s); AG = albumin gland minute; REP = reproduction; vivip = viviparous; VS = seminal vesicle or carrefour vesicle; with = with appendix, with rm = retractor muscle, cop = copulatory, sec = secretory, sec-ejac = secretory-ejaculatory; penis absent, vest = vestigial, short, long, with pil = pilaster, with epi = epiphallus. (See explanation under conclusion.)

Penial innervation (fig. 10) divides the family into two great groups: that in which the penis is innervated by the pedal ganglion (Pitysiinae) and that in which the penis is innervated by the cerebral ganglion (remaining five subfamilies). Of these Pityisini is considered the lowest. Antonellini is a derivative of Pityisini, having secondarily lost its appendix. Tubuaiini is a derivative of Pityisini in a direction markedly differing from that of Antonellini. Its paraneanic genitalia is like that of Pityisini. In view of this and the fact that the aperture of the juvenile Tubuaiini shell is relatively simply lamellated as compared with that of Pityisini, the tribe must be considered a degenerate member. Its position is above Antonellini.

There is a close similarity between the genitalia of *Tubuaia* and *Tornatellinops*. If the penial complex of *Tubuaia* were slightly reduced and the multilobate ovotestis were reduced to a unilobate one, a transition into *Tornatellinops* would occur. No better proof of the closeness of *Tubuaia* and *Tornatellinops* can be given than the interesting fact that in numerous species of these genera the factor that determines their generic status is the dissection of the ovotestis. The loss of the appendix in Lamellideini is secondary, as it was in Antonellini. In some species of *Lamellidea* a lack of penis (Watson's "aphallic") was noted. This peculiarity is also shared by *Tubuaia*, although it is found in fewer members of this genus.

The connection between Lamellideinae and Tornatellinae appears to be remote; but because both *Tornatellinops* and *Elasmias* have identical interior appendical structures and both have a unilobate ovotestis, a distant relationship is inferred.

Conchologically, Elasmiatini and Tornatellinini do not resemble each other even remotely, but anatomically they are very close to each other. Both have vestigial penises and both have the unique carrefour vesicle. These tribes are believed to be even more degenerate than Lamellideinae.

The stratification of half of the subfamilies being accounted for, it now remains to attempt an explanation of the remaining three members.

Achatinellinae is without doubt the most recently evolved subfamily. Its handsome coloration, great size, and simplified aperture are sufficient evidence for this hypothesis. Its position is unquestionably at the summit of the strata.

The position of Auriculellinae is certainly next to that of Achatinellinae although anatomically it has diverged more than Achatinellinae, hence could be placed above Achatinellinae. The changes are the loss of the achatinellid pilaster and the formation of a small but distinct epiphallus. Because the interiors of the appendices of Auriculellinae and Achatinellinae are similar, perhaps identical, there must be some relationship between these subfamilies.

Tornatellidinae occupies an unknown position as it is not even distantly related to the three lower subfamilies and is related to Auriculellinae only in an externally similar penial complex. The interior of its appendix is a simple

tube (without the usual inner tubular structure) unlike that of Auriculellinae, so that the external similarity may be only coincidental. The placement of Tornatellidinae in this position (fig. 10) may not be inappropriate, for it is at this point that the ommatophoral retractor changes over from its place outside of the peni-oviducal angle to a position within it. Tornatellariini possibly derives from Tornatellidini.

It now remains to give a short account of some of the minor but important genitalial parts which serve to indicate relationships between tribes and subfamilies.

The achatinellid pilaster, the fleshy ridge that ascends the penial interior and generally is semipendulous below the apical recurvature, or a modification of that ridge, serves as a connecting link between all the tribes except Auriculellini and Elasmiatini where it is absent.

Only Auriculellini has an epiphallus. Its presence may or may not be correlated with the absence of the typical pilaster.

Three types of appendices are known: (1) the secretory and tubeless (Tornatellidini), (2) the copulatory (Tornatellinini), and (3) the secretory-ejaculatory (all others). The secretory-ejaculatory type is further divisible into the pitysinid and the auriculellid types. In pitysinids the interior organ of the appendix is a loose and easily protrusible tube; in the auriculellid it is much narrower, apparently not loose, and apparently unprotrusible. The auriculellid is shared only by Achatinellini and Auriculellini. Sharing the pitysinid appendix are: Pityisini, Tubuaiini, Tornatellinoptini, and Elasmiatini. These tribes are thus fairly close to each other.

Reduction of the albumin gland, coupled with a strong development of the prostate is a characteristic common to Pitysinae and Achatinellinae. Undoubtedly, this is an indication of relationship, as this phenomenon has no correlation with the mode of reproduction (Pitysinae, oviparous; Achatinellinae, viviparous). The converse to reduction of the albumin gland is a strong development of it but, curiously enough, this is very rarely accompanied by reduction of the prostate. This character may also be an indication of relationship among its common possessors.

Generally, the type of ovotestis is no indication of relationship except, perhaps, in Tornatellinoptini and Elasmiatini.

The presence of the carrefour vesicle in Elasmiatini and Tornatellinini serves not only to isolate them from others but at the same time affirms the relationship created by penial reduction.

Whether the ommatophoral retractor is free of the peni-oviducal angle or enclosed within it is of some importance in Achatinellidae. Fortunately its behavior has been logical to the extent that the stratification of the subfamilies and tribes has been confirmed by it (fig. 10). It is entirely free in Pitysinae, Lamellideinae, and Tornatellininae; it wavers in Tornatellidini; and it is enclosed in Tornatellariini, Auriculellinae, and Achatinellinae.

In general, the spermatheca is free and the stalk enters the oviduct near the atrium. The spermatheca is enclosed in Achatinellinae only, and this peculiarity sets this subfamily apart from the remaining members. In Tornatellidini, the stalk enters the oviduct near the carrefour, above the embryo. This is a drastic departure from the usual and certainly emphasizes the divergence of Tornatellidini from its contemporaries. In Pityisini and Antonellini an erratic behavior is noticeable, the stalk usually entering the oviduct anywhere above the midpoint. Conversely, in Auriculellinae the stalk usually enters near the midpoint or below it. Normal behavior of spermatheca and stalk is usually found in Lamellideinae, Tornatellinae, Tubuaiini (adult), and Tornatellariini.

The diversity of anatomical types may possibly lead one to conclude that the genital variations were induced by mutation. Such a possibility has been examined but, decidedly, cannot be upheld. Mutations do not occur in such numbers as they appear to have occurred in Achatinellidae. If the theory of mutation is to be applied anywhere at all, it may be called upon to explain the phenomenon expressed by the shell of Achatinellinae. The logical explanation of the anatomical diversity is that the family is of great age and that most of the intermediate forms have been destroyed through numerous factors.

The present work is based largely upon the works of Pilsbry and Cooke who clarified the subject so that effective research could be done upon it. Pilsbry's anatomical incursions into the achatinellids and tornatellinids led him to expect great taxonomic changes at some later date. The work of Odhner and this study have, it is thought, justified Pilsbry's expectations. However, research is by no means final. *Gulickia* and *Waimea* must be found and dissected. They may possibly clarify the positions of their respective subfamilies. And thorough collection and study of the Juan Fernandez Achatinellidae may reveal other anatomical types. Additional collecting in the Australs, the Society Islands, the Marquesas, and elsewhere may uncover anatomical types unknown at present and may furnish some of the connecting links that are now believed extinct.

#### SUMMARY OF ANATOMICAL CHARACTERS

Figure 10 is a graphic summary of the anatomical characters of the family Achatinellidae as they were found to be distributed in the subfamilies, tribes, and genera. These groups are arranged according to the ascending order which appears most logical, as evidenced by the anatomical findings. As stated elsewhere in this paper, the relationship between the various members of the family is tenuous except for Tubuaiini and Pityisini. In order to derive some concept of the order of relationship, however tenuous, it has been necessary to construct a table of anatomical characters which would show the presence or absence of certain anatomical features within the different groups.

The principal separation of the family Achatinellidae into two great groups is performed by innervation of penis, by the pedal ganglion, or by the cerebral

ganglion. The ensuing four subdivisions—ommatophoral retractor free, oovestis multilobate, entrance of spermathecal stalk below egg (ovum) or embryo, albumin gland minute—being more or less continuous, or at least logically discontinuous, tend not only to confirm the correctness of the division by penial innervation but also to show that the taxonomic arrangement may be correct. These possibilities are strongly supported by an additional characteristic (appendix, secretory-ejaculatory type) which is one of the few links binding several groups together.

The over-all picture that one derives from the study of the chart is one of discontinuity, or the absence of enough intermediate links between subfamilies. This is more evident in the four middle subfamilies (Auriculellinae, Tornatellidinae, Tornatellininae, Lamellideinae), whereas the three tribes of Pitysiniae share many characteristics, as the solid bars indicate. The tenuity of relationship between the larger groups indicates either great age and long isolation of the groups or destruction of the direct links leading to the highly variegated forms of today, or both.

In the ensuing paragraphs, the characters depicted in the chart are treated individually and in some detail.

**Teeth.** The one anatomical feature common to all members of the family is rastriform teeth. It is indicated by a solid bar (fig. 10) vertically through the first column. The consolidation of what have hitherto been considered separate families (Tornatellinidae and Achatinellidae) is dependent principally upon the rastriform teeth, though there are other factors.

**Innervation of the penis.** Of importance second only to dentition is the penial innervation of the family. In Pitysiniae the innervation of the penis is by nerve fibers originating at the pedal ganglion, whereas in the remaining five subfamilies (except where questioned) the innervation is by nerve fibers originating at the cerebral ganglion. This differentiation divides the family into two great groups which, when placed in what seems to be their natural order, seem to indicate that they are (a) the more primitive and (b) the less primitive, or relatively evolved, group. In all probability, the penises of tribe Tornatellinini will be found to be innervated by nerve fibers emanating from the cerebral ganglion, if its genital similarity is any indication of its proximity to tribe Elasmiatini.

**Ommatophoral retractor.** Of equal consistency but probably of less fundamental importance than penial innervation is the tendency of the ommatophoral retractor either to pass through the peni-oviducal angle or to remain free (or outside) of this crotch. The bar is solid nearly three-fourths of the way. In Tornatellidinae (tribe Tornatellidini) the solidity becomes diluted (checked bar). It is here that, depending upon the species (within one species at least, *Tornatellides oblongus*), the retractor of the ommatophore either

passes through the peni-oviducal angle or does not do so (for statistics see under *Tornatellides*). This seems to indicate that a transitional point has been reached, leading into the type in which the ommatophoral retractor habitually passes through the crotch (Tornatellariini, Auriculellini, Achatinellini). Note that all those in which the retractor is not free are confined to the Hawaiian Islands.

**Ovotestis.** The distribution of the ovotestis (multilobate or unilobate) shows a break near the middle. The sequence is orderly though discontinuous, and this consistency tends to give support to the primary division based upon penial innervation and also to the taxonomic arrangement depicted to the left of the chart. Note that the unilobate ovotestis is found in one subfamily (Lamellideinae) and in part of another (Tornatellinae, tribe Elasmiatini), indicating some kind of relationship between the two subfamilies.

**Junction of spermathecal stalk and oviduct.** Ordinarily the junction of the spermathecal stalk and the oviduct occurs below the oviducal contents (eggs or embryos), but in tribe Tornatellidini the spermathecal stalk joins the oviduct at the carrefour or near it and well above the embryos. This phenomenon is unique and serves to emphasize the fact that tribe Tornatellidini is an extraordinary group, for its ommatophoral retractor also behaves in an odd manner. A third peculiarity of this group is the absence of the appendical "verge."

**Reduced albumin gland.** The reduced albumin gland occurs in both the lowest and highest groups (Pitysinae, Achatinellinae). In tribe Tubuaiini, the gland is rudimentary only in the paraneanic stage, wherein the genitalia are pitysinoid. For this reason that portion of the bar is checkered. Between the two extremes is a large group in which the gland is ordinarily large or small but not minute. Reduction of the albumin gland argues in favor of some remote relationship between Achatinellinae and Pitysinae.

**Reproduction.** The reproductive habit (oviparous or viviparous) probably has very little bearing on the relationship between subfamilies. It is placed here because it is interesting in itself. Note that in tribe Tornatellariini one genus, *Tornatellaria*, is oviparous and the other (*Philopoa*) is viviparous.

**Carrefour vesicle.** The carrefour vesicle is present in only the subfamily Tornatellinae. The small distribution of this character indicates the uniqueness of the organ and serves to emphasize how far the subfamily has diverged from its nearest contemporary, Lamellideinae.

**Appendix.** The column for the presence of the appendix has three well-distributed breaks indicating that the occurrence of the appendix in various groups is quite regular. Only in Auriculellinae, Achatinellinae, and Tornatellinae are the corresponding non-appendiculate members absent. The absence

of these members, at least in Auriculellinae and Achatinellinae, is probably an indication of the youthfulness of these groups.

**Appendix with retractor.** Ordinarily, one could expect the bar in this column to parallel the one to its left. However, in Auriculellini and Tornatellidini, the retractors are absent. This is one of the characteristics linking the two tribes together, though very remotely.

**Copulatory, secretory, secretory-ejaculatory appendices.** The type of appendix, as indicated by its interior morphology, is of some importance in classification and is an indication of relationship. The principal trend is toward the secretory-ejaculatory type, of which two forms are recognizable, the auriculellid and the pitsinoid. The former links the subfamilies Auriculellinae and Achatinellinae, whereas the latter forms a bond between Pitysinae, Lamellideinae, and Tornatellinae.

**Penis.** The lack of penis in individuals of *Lamellidea* and *Tubuaia* is probably one of the strangest phenomena in the entire family. In time, examples will probably be found in other genera. All genera of Tornatellinae are characterized by the highly reduced, or vestigial, penis. This type of penis, together with the carrefour vesicle, makes the subfamily Tornatellinae unique. The terms short and long, as applied to the penis, are arbitrary. In general, we use the term short for a penis approximately one-fourth the oviducal length. Ordinarily, though there are some exceptions, the short penis is also small and, conversely, the long penis is usually large. In *Antonella* and *Lamellidea* are both types, depending upon the species (checked bars in graph). Tubuaiini also have both types but, in contrast to the others mentioned above, the penis is usually short in the adult. However, in its pitsinid stage (paraneanic substage or subadult) the penis is usually quite long. (These two portions of the vertical bar are checkered.)

**Pilaster.** The vertical bar indicates that the achatinellid pilaster is present in all the members except in Auriculellini and Elasmiatini. Genus *Tornatellina* is questionable but, by analogy with *Fernandezia*, may be expected to have a vestigial pilaster. This category is most important in indication of relationship, as can be seen by its near solidity.

**Epiphallus.** Like reduction of the penis in Tornatellinae, the presence of an epiphallus is unique in the subfamily Auriculellinae. Its absence in the remainder of the family may indicate that Auriculellinae is, anatomically, the most recently evolved member.

In view of the fact that special anatomical studies have necessarily been limited to samplings of available representative species, a tabulation of these species is hereby provided (table 2). The reason for this list is twofold: to facilitate tracing those that were sampled and to provide a basis for future research for anyone inclined to fill in the gaps which are so conspicuous.

TABLE 2 (X = dissected; O = appendix absent)

SUBFAMILY	SPECIES	INTERIOR PENIS	INTERIOR APPENDIX	CARREFOUR COMPLEX	GENITAL ONTOGENY	NERVOUS SYSTEM	TEETH
Achatinellinae	<i>Achatinella concavospira</i>	X	X	X		X	X
	<i>A. fuscobasis lyonsiana</i>						X
	<i>A. turgida</i>	X					
	<i>A. viridans</i>	X					
	<i>A. lehuiensis meineckeii</i>	X					
	<i>Partulina dubia</i>	X	(in part)			(in part)	
	<i>P. redfieldii</i>	X	X				
	<i>P. virgulata</i>	X	X				
	<i>P. mighelsiana</i>	X	(not figured)				
	<i>Newcombia canaliculata</i>	X	X				
Perdicellinae	<i>N. cumingi</i>	X		X			
	<i>Perdicella helena</i>	X	X	X		(in part, not figured)	
	<i>P. mauriensis</i>	(not figured)					
	<i>Auriculella auricula</i>	X	X	X	para- to metaneanic	X	X
	<i>A. castanea</i>	X					
Auriculellinae	<i>A. olivacea</i>	X					
	(not figured)						
Tornatellidinae	<i>Tornatellides oblongus</i>	X	X	X	paraneanic	(in part)	X
	<i>T. oswaldi</i>			X			
	<i>T. neckeri</i>	X	X		metaneanic		
	<i>Philopoa singularis</i>	X	O				
	<i>Tornatellaria newcombi</i>	X	O			(not figured)	X
Tornatellinae	<i>Fernandezia bulimoides</i>	X	X	X	meta- and aneanic	(in part)	X
	<i>Elasnias peasianum</i>	X	X	X	(not figured)		
	<i>E. apertum</i>						X
Lamellideinae	<i>Tornatellinops concolorans</i>	X	X		para- and metaneanic	(in part)	X
	<i>T. variabilis</i>				para- to metaneanic		
	<i>T. baldwini</i>				para- and metaneanic	(not figured)	



## SYSTEMATICS

## FAMILY ACHATINELLIDAE

As revised, the family Achatinellidae consists of the combined families Achatinellidae and Tornatellinidae, now reduced to subfamilies. Included are those groups treated monographically by Pilsbry and Cooke in the Manual of Conchology (1912-1916, vols. 22, 23) with additions from the works of Odhner, Hyatt, Pilsbry, and others. The definitions of the families have been given by Pilsbry and Cooke. However, we have added a few redefinitions of the genitalia to the anatomical descriptions given by Pilsbry and Cooke.

Jaw when present, thin, delicate.

Radula short, broad, recurved outwardly at anterior end.

Teeth all of single uniform type, all believed to be modified marginals, rastriform; base narrow, expanding above, and recurved into broad multicuspid reflection, consisting of numerous aculeate cusps and denticles.

Kidney orthurethrous, kidney plus ureter nearly as long as lung, narrow, opening on intestinal side, with narrow, fleshy ridge recurved posteriad at tip for a short distance.

Lung without macroscopically visible network of veins, with pulmonary vein adjacent to kidney.

Reproductive habits: oviparous or viviparous. Eggs borne singly, very rarely two or three. Embryos borne singly or up to 22.

Ommatophoral retractor either through peni-oviducal angle or not through or, rarely, both (*Tornatellides*).

Genitalia: penis occasionally lacking, reduced, small, or well developed; with appendix or without; without epiphallus (one exception). Internally, penis with ascending recurved pilaster (two exceptions) or with a modification of it. Internally, appendix either plain, with ejaculatory apparatus, or modified for copulation. Penial retractor always present, terminal; retractor of appendix either present or absent, subterminal; if both present, then off common retractor; common retractor off nuchal membrane (diaphragm). Vas deferens free, following oviduct to atrium thence recurving and following penis upward; entrance into penis terminal or subterminal; often adherent to penis from origin or sometimes from some distance above it. Ovotestis (hermaphrodite gland) unilobate to multilobate. Hermaphrodite duct usually distended and convoluted. Talon small. Carrefour small, often hidden in albumin and prostate gland follicles. Carrefour vesicle present or absent. Albumin gland minute to large, multifolliculate. Prostate either small and paucifolliculate or large and multifolliculate. Spermatheca small or large, usually ovate, lying on prostate or between prostrate and albumin glands or tightly enclosed within prostatic follicles (*Achatinellinae*); stalk very short to long, entering immediately into carrefour-uterus junction or at any point on oviduct, or near atrium.

## ANATOMICAL KEY TO SUBFAMILIES AND TRIBES

- A. Penis with appendix.
  - B. Penis reduced; penial and appendical retractors present.
    - C. Ovotestis unilobate; interior of appendix with simple tubular apparatus, without pilasters or corrugations for copulation; vestigial penis internally plain; carrefour vesicle minute.....**Tornatellinae, Elasmiatini.**
    - CC. Ovotestis multilobate; interior of appendix complexly plicate and corrugated for copulation; vestigial penis with small muscular pilaster; seminal vesicle large.....**Tornatellinae, Tornatellinini.**

- BB. Penis not reduced.
  - C. Penis with retractor; appendix without.
    - D. Oviparous; penis with epiphallus; spermathecal stalk joining oviduct at half way or below.....**Auriculellinae, Auriculellini.**
    - DD. Viviparous; penis without epiphallus; spermathecal stalk joining oviduct at base of carrefour.....**Tornatellidinae, Tornatellidini.**
  - CC. Penis and appendix both with retractor.
    - D. Oviparous; ommatophoral retractor free of peni-oviducal angle; penial nerve off pedal ganglion; albumin gland minute or absent in adult; prostate large, follicles large.....**Pitysinæ, Pityisini.**
    - DD. Viviparous.
      - E. Ovotestis unilobate.....**Lamellideinae, Tornatellinoptini.**
      - EE. Ovotestis multilobate.
        - F. Ommatophoral retractor free; penial nerve off pedal ganglion (right); penis small ( $\pm 0.25$  oviducal length); sometimes without penis; spermatheca free.....**Pitysinæ, Tubuaiini.**
        - FF. Ommatophoral retractor not free, between peni-oviducal angle; penial nerve off cerebral ganglion (right or left); penis large, clavate ( $\pm 0.3$  to  $0.5$  oviducal length); spermatheca tightly enclosed in prostate follicles.....**Achatinellinae, Achatinellini.**
- AA. Penis without appendix.
  - B. Ovotestis unilobate, sometimes deeply cleft and appearing bilobate (subgenus *Atea*); occasionally without penis.....**Lamellideinae, Lamellideini.**
  - BB. Ovotestis multilobate.
    - C. Ommatophoral retractor free of peni-oviducal angle; penis innervated by pedal ganglion (right); albumin gland of adult minute, follicles minute; prostate large, follicles large; oviparous.....**Pitysinæ, Antonellini.**
    - CC. Ommatophoral retractor not free, passing through peni-oviducal angle; penis innervated by cerebral ganglion (right); albumin gland of adult not minute, follicles fairly large; prostate equal to or slightly smaller than albumin gland, follicles fairly large; viviparous (*Philopoa*) or oviparous.....**Tornatellidinae, Tornatellariini.**

## SUBFAMILY PITYSINAE

Penis innervated by pedal ganglion. Right ommatophoral retractor free of peni-oviducal angle. Penis with or without appendix, with reflexed achatinellid pilaster or a modified one. Appendix, when present, with retractor; internally equipped with secretory-ejaculatory apparatus ("verge"). Albumin gland either (a) minute, often absent in adult and large in juvenile (subadult, paraneanic stages) or (b) large in adult and minute, often absent, in juvenile. Prostate large if albumin gland is minute or small; prostate small if albumin gland is large. Spermatheca free. Ovotestis multilobate. Oviparous or viviparous.

The subfamily Pitysinæ includes all tornatellinid land shells, exclusive of *Lamellidea*, *Tornatellinops*, and *Elasmias* found in the Austral (Tubuai), Tuamotu, Cook, and Kermadec Islands. A portion of the group (Tubuaiini) consists of shells closely resembling *Lamellidea* and *Tornatellinops*. A greater part

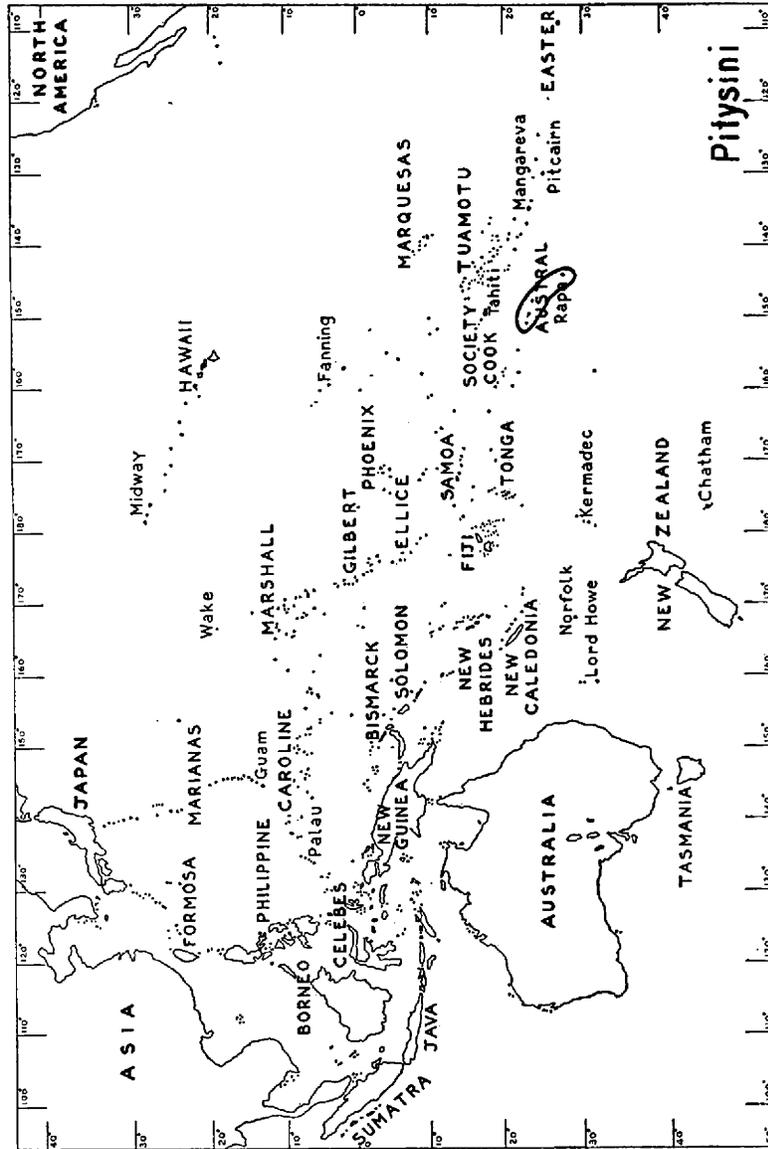


FIGURE 11.—Distribution of tribe Pityisini.

(Pitycini, Antonellini) is composed of 10 genera, which are greatly divergent from each other and which find their greatest development on the tiny island of Rapa. The divergence is culminated in the genus *Pityis*, a group characterized by costate pagodiform shells.

#### TRIBE PITYSINI

With appendix. Albumin gland minute in adult. Interior of penis with recurved achatinellid pilaster ending in semi-pendent papilla. Oviparous.

Pitycini embraces eight genera of a wide variety of forms, most of them with many whorls (8 to 11); all but one (*Taitaa*) confined to Rapa. A large group is comprised of multi-whorled aciculate shells, mostly minute; in it are also shells difficult to differentiate from *Tubuaia*. One group consists of globose shells, related to which are those that resemble species of *Auriculella* and having a complex columella structure based upon three to four lamellae. One genus (*Pityis*) is pagodiform, umbilicate, ornamented with thin ribs, and so distinct that its true tornatellinid position could be determined only by its genitalia. Several genera of the tribe are paucispecific, having turritid, ovate-conic, or broadly elongate shells, with or without costae. Another group extends beyond Rapa into Raivavae, Tubuai, and Rurutu, and consists of minute, subglobose, or subcylindrical shells. (See map, figure 11, for distribution.)

Type genus: *Pityis*.

#### GENERA

*Ovotestis* multilobate ( $\pm 8$  to 10): lobes robust, compact; follicles short-stout, adherent to each other. Hermaphrodite duct heavily distended, convoluted. *Albumin gland* minute or absent; follicles minute, numerous, round or ovate. *Prostate* very large, paucifolliculate; follicles large, digitate, distended. *Spermatheca* large, ovate, usually with blunt, slightly produced apex, lying on prostate or at its edge, stalk short, emptying into oviduct almost immediately below carrefour except when gravid (see *Pukunia acuta*, fig. 24a), never extending below 0.25 of distance; vagina, therefore, composing nearly entire length of female tube. *Talon* small, making hairpin turn. *Carrefour* roughly ovate. *Oviduct* narrow, subcylindrical, long. *Vas deferens* as wide as oviduct or slightly narrower. *Penis* large (ratio, width to length, 1 : 7)<sup>2</sup>, long (0.3 to equal oviducal length; ratio, penial length to oviducal length, 1 : 1.5), clavate; without epiphallus; vas deferens orifice subterminal; internally equipped with large, ascending stimulator pilaster, recurving at apex to descend and forming semi-pendent fleshy lingual process or penial papilla which terminates near upper third of penis, the papilla adherent to penial wall at one edge via thin membrane, with a translucent velum across inner angle of apical curvature. *Appendix* large, as long as penis or longer (ratio, width to length, 1 : 16; penial length to appendical length, 1 : 1.4; appendical length to oviducal length, 1 : 1.05); with median bulge caused by secretory-ejaculatory apparatus; apex blunt (for interior of appendix, see *Lamelloxum auriculella*). *Retractor* robust, usually short, bifid, off diaphragm; penial retractor terminal; appendical retractor near middle. *Atrium* short.

The genitalia of the genera of Pitycini are fundamentally so close to each other that the above generalized description will cover the entire group. In general, all the genera of Pitycini are so much alike that it is impossible to

<sup>2</sup> Ratios are the average of 12 specimens, five genera.

differentiate one genus from another by means of the genitalia. An exception is the species *Pukunia acuta*.

#### KEY TO GENERA OF PITYSINI

- A. Shells costate or subcostate, Rapa.  
 B. Shells umbilicate.....**Pitys, in part (pagodiformis)**.  
 BB. Shells imperforate.  
 C. Costae thin, cuticular.  
 D. Costae widely spaced, whorls 5 to 9, diameter more than 50 percent of length.  
 E. Whorls 5 to 6, convex, increasing rapidly, embryonic whorls transversely striate, parietal lamella absent....**Mangaoa**.  
 EE. Whorls 7 to 9, flat or slightly convex, embryonic whorls spirally striate, parietal lamella strong.....**Pitys, in part (scalaris, alpestris)**.  
 DD. Costae narrowly spaced, whorls 9 to 10, diameter less than 40 percent of length.....**Apopitys**.  
 CC. Costae low, thick, not cuticular.  
 F. Shell ovate, parietal lamella moderate, columella with two rather weak, rapidly ascending lamellae, juveniles without palatal folds.....**Mitiperua**.  
 FF. Shell globose-conic, parietal lamella strong, columella with four lamellae, juveniles with two to six continuous or interrupted palatal folds.....**Lamellovum (in part)**.  
 AA. Shells nearly smooth, finely striate with lines of growth, sometimes with slightly raised striae.  
 G. Distribution, Rapa.  
 H. Columella slightly sigmoid, inner face margined with a rapidly ascending low lamella, juveniles with a strong slowly ascending columellar lamella.....**Pukunia**.  
 HH. Columella nearly straight or slightly concave.  
 I. Shells slender, diameter 25 to 40 percent of length; columella narrow, very slightly calloused. Juvenile columella with none, two, or three low oblique lamellae, when present.....**Strobilus**.  
 II. Shells not slender; diameter 44 to 61 percent of length. Columella heavily calloused, sometimes furnished with lamellae, juveniles with four strong thick sub-horizontal columellar lamellae.....**Lamellovum (in part)**.  
 GG. Distribution Raivavae, Tubuai, and Rurutu. Shells small, globose-conic, subcylindrical, or subulate; columella with two or three lamellae which persist up to adult stage; palatal folds one or two.....**Taitaa**.

Genus *Strobilus* Anton

*Strobilus* Anton, 1839, Verzeichniss der Conchylien, 46 (subgenus of *Clau-silia*).—Pilsbry and Cooke, 1915, Man. Conch. 23 : 134 ; 1933, Nautilus 47 : (2) : 60.

*Strombilus*, Alton [Anton], 1839, Gray, 1847, Zool. Soc. London, Proc. 175. Type *St. turritus* (synonym of *Tornatellina*).

*Elasmatina* Petit, 1843, Zool. Soc. London, Proc., 2.—Gray, 1847, Zool. Soc. London, Proc., 175. Type *E. subulata* (synonym for *Tornatellina*).—Pilsbry and Cooke, 1910, Nautilus 23 (10) : 123 ; 1915, Man. Conch. 23 : 188.

"Shell ovate, or turrated, fragile, transparent; columella one or many toothed, with lamelliform teeth; lip thin, acute." (Petit, *Elasmatina*.)

"The shell is very long, slender, turrated or conic, composed of 9-10 flattened whorls; aperture armed with a strong parietal lamella; columella simple or lamellate. Type, *T. turrita* Anton." (See Pilsbry and Cooke, 1915, Man. Conch. 23 : 188.)

*Shells* small (2.8-7.0 mm. long), imperforate, narrowly turrated to elongate-ovate, outlines straight to slightly convex, thin, subtransparent to translucent, glossy or somewhat dull, the surface usually very finely striatulate with lines of growth. *Whorls* 6 to 11, nearly flat to convex, in most species increasing very slowly and regularly, embryonic whorls smooth and glossy or with microscopically very fine, close spiral lines, in some specimens papillate, sometimes slightly oblique to axis. *Parietal lamella* rather strong, long, entering aperture for about 1.5 whorls. *Columella* unarmed or furnished with one or two minute oblique lamellae. *Palatal wall* unarmed. *Aperture* small to medium, vertical. *Peristome* thin, erect, occasionally slightly thickened within but without a well-defined lip.

Juvenile specimens generally thin and transparent, showing complete apertural armature through shell. Parietal lamella strong, simple (in only one species, *S. brevis*, is free margin sinuous). Columella furnished with three to no lamellae. Palatal wall may or may not have palatal folds.

Type: Location unknown.

Pilsbry and Cooke reestablished the senior generic name *Strobilus* in 1933.

The genus *Strobilus* is confined to Rapa. All the species are terrestrial and probably slightly subterranean in habits. At first, specimens were taken under stones and on the ground covered over by dead, damp leaves. It was later discovered accidentally that they lived about one-fourth inch or more under the soil surface. If the earth is exposed and rubbed vigorously, the minute snails will crawl out. In woods they are difficult to see, but in the open areas they are collected in good series. An excellent series of 60 or more living specimens was found in an open area on the day their habitat was discovered.

The species of *Strobilus* do not form a tight group but differ from each other in somewhat important characters, such as spirally striate or smooth and glossy embryonic whorls, and in the presence or absence of columellar or palatal folds in immature specimens.

## KEY TO SPECIES OF STROBILUS

- A. Adult shell with 6 to 7 whorls, 2.8-3.0 mm. long, diameter 40 percent of length.  
 Juveniles with three columellar folds, two palatal.....**S. brevis.**

- AA. Adult shells with 8 to 11 whorls, diameter 25 to 37 percent of length.
- B. Shells with nearly straight outlines, whorls convex.
- C. Shells more than 5 mm. in length.
- D. Shells with strong parietal lamella; juveniles with two columellar folds and a long, lower palatal fold.....**S. turritus.**
- DD. Shells with weak palatal lamella; juveniles without columellar or palatal folds.....**S. perfragilis.**
- CC. Shells less than 4 mm. long; juveniles with two columellar folds and no palatal fold.
- E. Shells with 10 convex whorls, length 3.7 mm.....**S. acicularis raphis.**
- EE. Shells with eight slightly convex whorls, length 3.1 mm.....**S. acicularis.**
- BB. Shells with slightly convex outlines, whorls flatly convex.
- F. Shells more than 5.8-7.0 mm. in length with 10 to 11 whorls; juveniles with two columellar lamellae; embryonic whorls spirally striate.....**S. opeas.**
- FF. Shells less than 4 mm. in length; juveniles with three columellar lamellae; embryonic whorls spirally striate.....**S. subtilis.**

In addition to the characters given in the above key, the species may be recognized by the presence or absence of the following characters: Embryos marked with fine microscopical spiral striae (*S. subtilis*, *S. acicularis*, *S. a. raphis*, *S. perfragilis*). Embryos smooth and glossy, with no spiral lines visible under high microscopical lens (*S. turritus*, *S. opeas*, *S. brevis*). Strong parietal lamella in all species except *S. perfragilis*. Juveniles with three columellar lamellae (*S. brevis*, *S. subtilis*). Juveniles with two columellar lamellae (*S. turritus*, *S. acicularis*, *S. a. raphis*, *S. opeas*, *S. perfragilis*). Juveniles with no columellar lamellae (*S. perfragilis*). Juveniles with two palatal folds (*S. brevis*). Juveniles with one palatal fold (*S. turritus*, *S. opeas*, *S. subtilis*). Juveniles with no palatal fold (*S. acicularis*, *S. a. raphis*, *S. perfragilis*).

#### Subgenus **Strobilus**

Turrite or aciculate shells with 8 to 11 whorls, ranging from 2.8-7 mm. Juveniles have only one palatal fold or none, usually two columellar lamellae, rarely three (*S. subtilis*), and moderate or strong parietal lamella.

Type species: *Strobilus turritus* Anton.

Species: *S. turritus*, *S. t. basalis*, *S. opeas*, *S. o. intermedius*, *S. subtilis*, *S. s. similaris*, *S. acicularis*, *S. a. raphis*.

**Strobilus (Strobilus) turritus turritus** Anton (figs. 12, *a-i*; 13, *a-c*).

*Strobilus turritus* Anton, 1839, Verzeichniss der Conchylien, 46.

*Balea turrita* Pfeiffer, 1842, Symbolae 2: 55.

*Tornatellina turrita* Pfeiffer, 1848, Mon. Hel. Viv. 2: 391.—Küster, 1852 (-1859), Conch.-Cab., Pupa, 1 (15): 153, pl. 18, figs. 22, 23.

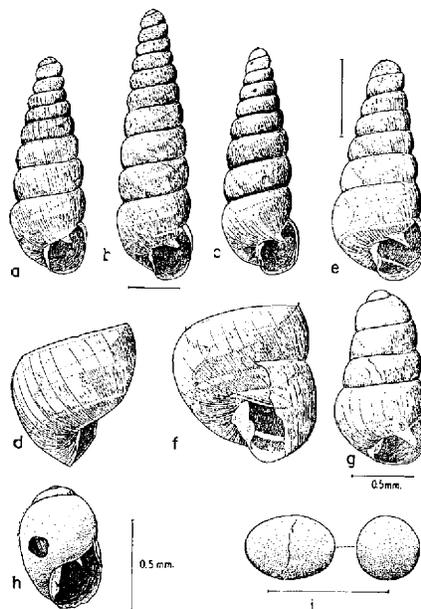
*Achatina* (*Leptinaria*) *turrita* Pfeiffer, 1855, Malak. Blätt., 170.

*Cionella* (*Tornatellina*) *turrita* von Martens, 1860, Albers Die Heliceen, 259.

*Tornatellina* (*Elasmatina*) *turrita* Pilsbry, 1910, Nautilus 23 (10): 123.—  
Pilsbry and Cooke, 1915-1916, Man Conch. 23: 188, pl. 53, fig. 15.

*Tornatellina archimedes* Beck, 1837, Index Molluscorum, 80. *Nomen nudum*, with varieties *major* and *minor*.

*Elasmatina subulata* Petit, 1843, Zool. Soc. London, Proc., 2.



*This was red-*  
*See copy #3*

FIGURE 12.—*Strobilus* (*Strobilus*) *turritus turritus*: a, adult (4.48 × 1.6 mm.) agreeing with Anton's measured specimen (4.5 × 1.5 mm.); b, adult, usual size (5.6 mm.); c, measured specimen (4.73 × 1.6 mm.), suture deeper than usual; d, profile of juvenile (parametaneanic); e, juvenile (same as d), showing single spiral palatal fold; f, juvenile (same as c), latero-oblique view, showing columellar and lower folds; g, juvenile (ananetic); h, embryo from an egg; i, egg, lateral and frontal views.

"Shell turritid, elongate; with nine narrow whorls, the last a little larger than the penultimate, moderately convex; suture deep; aperture acutely oval with a lamella on the columella; fragile, finely striate, glossy, light brown. Diameter three-fifths, length two and one-fourth lines [1.4 × 4.5 mm.]" (Anton; type whereabouts unknown.)

"Shell very small, imperforate, needle shaped, thin, shining, brown or corneous; with ten nearly flat whorls, the last equaling one fourth of the length; columella simple; aperture oblong-obovate; lip simple, acute; parietal fold lamelliform. Length 5, diam. 1½ mm." (Pfeiffer)

"Shell conic-elongate, cylindrical, transparent, pale corneous; with ten convex whorls, suture linear, impressed; apex obtuse; aperture obliquely obovate; columella furnished with

a lamellalike and inwardly decurrent tooth; lip thin, acute. Length 6, diam. 2 mm." (Petit.)

Shell turrated, very slender, color chamois, very thin, transparent, the columellar, parietal, and inner whorl walls being visible through the shell, glossy, microscopically striate with lines of growth. Spire elongate, narrow, with nearly straight outlines, tapering gradually to a rather blunt apex. Suture well impressed, narrowly margined. Whorls 9 to 11; embryonic whorl increasing rapidly in juvenile specimens, smooth, glossy, no spiral lines visible with a microscope, in adults worn; postembryonic whorls increasing slowly and evenly, flatly convex; last whorl oblong, about 0.4 length of shell, tapering to base. Aperture small, vertical. Parietal lamella high, simple, oblique, very long, length about 1.5 whorls. Columella nearly straight to slightly sigmoid, without lamellae. Palatal wall furnished with a deeply seated, long, low interrupted lower fold, often extending beyond and just below juncture of outer lip (not visible in frontal view). Peristome thin, delicate, erect.

## MEASUREMENTS (IN MILLIMETERS)

Figure 12	Length	Diameter	Apertural axis	Diameter	Last whorl	Parietal lamella
8696 Tumu, a	4.48	1.60 (36%)	1.10	0.84 (76%)	1.75 (39%)	0.15
8695 Tumu, b	5.61	1.60 (28%)	1.10	0.87 (79%)	1.91 (34%)	0.19
8698 Maitua, c	4.73	1.60 (33%)	1.10	0.84 (76%)	1.83 (39%)	0.22

In a juvenile specimen (fig. 12, d-f), whorls 8, length 3.1 mm., aperture more rounded; parietal lamella proportionately higher; columella bilamellate, with a very oblique, low but distinctly lower columellar lamella at its base, uniting with peristome; also another indistinct, low, blunt, nearly vertical lamella accompanying inner margin of columella; palatal wall with a long low fold beginning just below peristome; fold slightly more than a whorl long.

In a younger specimen (fig. 12, g), whorls slightly more than 5, length 1.49 mm., aperture narrow, pointed at both ends; parietal lamella proportionately very high; columella furnished with two nearly equal oblique lamellae; palatal fold very weak and merely indicated.

An embryonic specimen (fig. 12, h) taken from an egg is ovate in outline, length 0.71 mm., whorls about 3; parietal lamella low, vertical; columella nearly straight with very indistinct basal lamella; no indication of palatal fold.

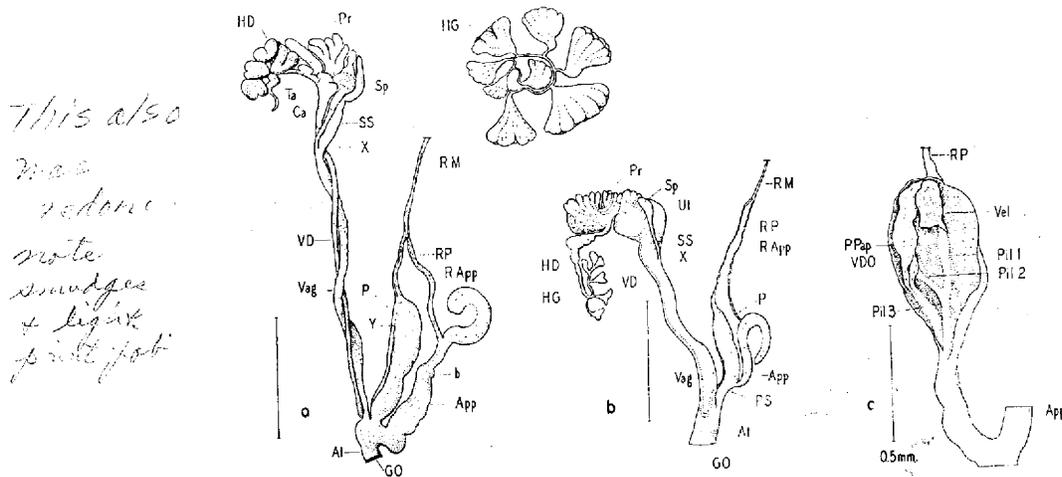


FIGURE 13.—*Strobilus (Strobilus) turritus turritus*: a, genitalia, adult; b, genitalia, subadult or paraneanic stage; c, interior of penis.

Egg (fig. 12, *i*) elliptical, circular in cross section, with calcareous shell,  $0.73 \times 0.53$  mm., 8700.

Adult genitalia (fig. 13, *a, c*): *Ovotestis* eight-lobate; lobes heavy; follicles large. *Prostate* small, with about eight digitate follicles, some adhering together at their bases. *Spermatheca* small, elliptical; stalk short, broad. *Talon* small, not recurved (in figured specimen). *Carrefour* small, oval. *Penis* relatively small, short ( $\pm 0.3$  oviducal length). Interior of penis slightly modified from the typical: ascending pilaster narrow, Y-shaped (Pil 1, Pil 2); velum larger than typical, semi-transparent, campanulate; papilla a mere elongate, high, fleshy ridge, apex diminishing in size into low ridge descending into penial stalk; vas deferens emptying under tip of papilla (VDO). *Appendix* fairly large, longer than penis, semi-transparent, "verge" visible (b). *Retractors* thin, long. *Atrium* short.

Paraneanic genitalia (fig. 13, *b*). *Ovotestis* immature, six-lobate; follicles undifferentiated macroscopically. Duct small, just starting convolutions, slightly swollen. *Prostate* relatively large; follicles few, short-clavate. *Spermatheca* small; stalk very narrow, short. Uterus enlarged, several times vaginal diameter. *Vagina* fairly wide (five times width of vas deferens). *Penis* small, short, with long stalk. *Appendix* vermiform, hooked. *Retractors* very thin, long, bifurcation high. *Atrium* long, wide.

Dissected 140228 (adult genitalia, interior of penis), two specimens; 137695 (paraneanic), five specimens; 138253 (juvenile, unfigured), one specimen; 140229 (immature, unfigured), two specimens; 143245 (age unknown, fragmentary, unfigured), one specimen.

Opana (Anton), or Opara (Pfeiffer). "Found by Mr. Cuming in decayed grass" (Petit).

Rapa: Tumu Valley, east of Mount Pukutaketake, in talus slope at foot of cliffs near southern waterfall, alt. 150-200 ft., C. M. Cooke, Jr., July 13, 8695, 8696 (figured specimens), 140228-140230 dissected. Maitua, just inside of native forest, under stones and on dirt, alt. about 600 ft., Anderson and Cooke, July 1, 8698 (figured specimen from 137695-137699), dissected. Maitua, under ferns, alt. 500 ft., Margaret Stokes, Aug. 15, 1921, 53233, embryo (fig. 12, *h*). 8699. Kopenena Valley, south fork, alt. 200-600 ft., Kondo, July 24, 143248 (fig. 12, *g*).

Specimens referable to the typical form are more or less abundant on the western side of the inner half of Ahurei Bay, covering 1.5 miles from Tumu to Maungaeae Valley. They occurred in native forests from about 200 to 800 feet. A few lots were taken on the western slope of the principal mountain range. In addition to the lots mentioned above, Bishop Museum has more than 40 lots collected in this area, five of which were collected in Maitua in 1921 by Margaret Stokes. Of all the lots in the Museum collection, those from Tumu have been selected to represent the species, since Cuming undoubtedly collected in the immediate neighborhood, and since specimens agreeing with Anton's measurements are from this area. One of these is illustrated (fig. 12, *a*). On the whole, the adult specimens are larger, ranging in size up to 5.6 mm. in length (fig. 12, *b*). A representative from Maitua (fig. 12, *c*) has a deeper suture and slightly more convex whorls.

*Elasmatina subulata* Petit is included on the authority of Pfeiffer. None of the shells here referred to *Strobilus turritus* (from localities Cuming could

have visited) agrees in the measurements given by Petit and Pfeiffer,  $6 \times 2$  mm. It is possible that both these authors had a small form of *S. opeas* from a locality which Cuning may have visited. This observation cannot be verified without examining both Petit's and Pfeiffer's original material. Until this can be done, it seems wisest to agree with Pfeiffer's decision. However, he believed the two forms to be included in his material, one somewhat larger than the other.

***Strobilus (Strobilus) turritus basalis*, new subspecies (fig. 14, a-c).**

No tangible differences between adults of species and subspecies, but juveniles in same stage of development have one distinct differentiating character. In juveniles of the subspecies *basalis* columella is slightly sigmoid and lacks a lamella. In place of a lamella, there is a low basal fold just below and outside columella, which it parallels; visible through shell. In most juveniles of the subspecies palatal fold is shorter than in those of species, being little more than 0.75 whorl long. Parietal lamella is very slightly stronger.

Length 5.05 mm., diameter 1.45 (29 percent); apertural axis 1.18, diameter 0.83 (70 percent); last whorl 1.74 (35 percent); parietal lamella 0.22.

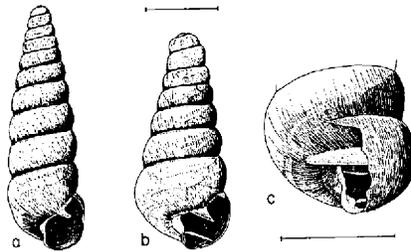


FIGURE 14.—*Strobilus (Strobilus) turritus basalis*: a, adult, holotype; b, juvenile (paraneanic), palatal fold short; c, juvenile (same as b, latero-oblique view), columellar lamella absent and replaced by low basal fold.

Rapa: Mount Mangaoa, northeast ridge (type locality), in small ravine, under stones and dead leaves, alt. about 800 ft., Anderson<sup>3</sup> and E. C. Zimmerman, July 29; holotype 8701; illustrated juvenile 8702; paratypes 138415-138418 (138415 dissected). In addition to the type colony, three colonies were located on the same ridge up to about 1,100 ft. This form was also collected near the cemetery, close to Ahurei Village, alt. 50-100 ft., Cooke, 143703-143704, and in the southeastern valleys of Mount Ororangi, alt. 500-600 ft., Anderson and Cooke, 138506-138510. On eastern ridge of Mount Perahu, alt. 900-1,500 ft., Anderson and Kondo, shells were found which are, at present, included with this subspecies (140300, 142840, 142841).

The subspecies was not associated with the typical form in any of the 11 colonies from which it was taken.

<sup>3</sup> Donald Anderson unless otherwise specified.

**Strobilus (Strobilus) opeas opeas**, new species (figs. 15, *a-d*; 16, *a-f*).

*Shell* (fig. 15, *a*) subcylindrical, clay color, translucent, minutely striatulate with growth lines. *Spire* straight to slightly convex in outline, upper half tapering gradually to apex. *Suture* lightly impressed. *Whorls* 10.5, increasing very slowly, flatly convex, indistinctly shouldered just below sutures; apical whorls worn in adults, in juveniles slightly swollen, smooth, glossy, without spiral lines under a strong lens; last whorl oblong, tapering slowly to base. *Aperture* vertical, longer than broad. *Parietal lamella* strong, long, simple, slightly obliquely seated. *Columella* nearly vertical, hardly sigmoid, inner face slightly thickened, with an indistinct low, oblique lamella near its base. *Palatal folds* none when viewed frontally. *Peristome* erect, indistinctly, minutely thickened.

Length 7.04 mm.; diameter 2.36 (33 percent); apertural axis 2.0, diameter 1.4 (70 percent); last whorl 3.14 (45 percent); parietal lamella 0.27.

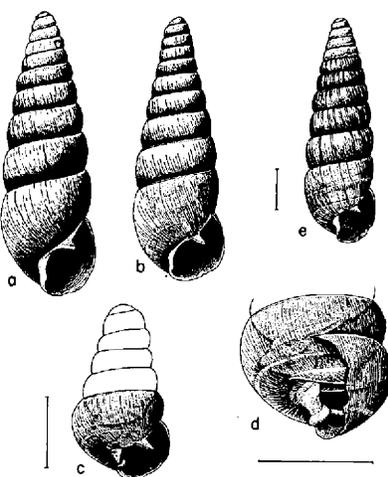


FIGURE 15.—*a-d*, *Strobilus (Strobilus) opeas opeas*: *a*, adult; *b*, subadult; *c*, juvenile (metaneanic); *d*, juvenile, latero-oblique view, columella. *e*, *S. (S.) o. intermedius*, adult.

In nearly mature specimen (fig. 15, *b*), whorls 10, length 6.6 mm., last whorl semi-transparent; parietal lamella visible through shell, about 1.25 whorls long; columellar lamella slightly stronger than in adult; with low palatal fold deeply seated, about 0.5 whorl in length.

In a younger specimen (fig. 15, *c, d*), whorls about 6, length 2.46 mm., parietal lamella very strong; columellar lamella proportionately much stronger than in adult, basally situated, blunt, thick, slightly obliquely seated, extending to outer margin; above it, close to parietal wall, is a deep-seated, oblique, indistinct swelling; palatal fold low, somewhat more than one whorl long.

Adult genitalia (fig. 16, *a, b*). Typical, with following differences: *ovotestis* 10-lobate; prostate relatively large, follicles numerous (about 20), digitate; *spermatheca* large, bluntly pointed; stalk very short, joining oviduct immediately; *penis* 0.6 oviducal length; *appendix* enlarged below (optical section with eversible organ typical of subfamily); *common retractor* long, others short (in figure, penial retractor strongly contracted so that appendical retractor appears to come off penial head). Interior of penis with similar transparent type of papilla, but apex free, not descending down stalk as low narrow ridge; ascending pilaster also Y-shaped; velum large, campanulate; orifices of vas deferens under tip of papilla. *Atrium* short.

Teeth (fig. 16, f) alike, small, delicate, six-dentate. All cusps apparently paired and cusplets absent. Length 6 microns, width  $\pm 3$  microns. This is about the smallest tooth studied to date.

Juvenile genitalia. Paraneanic, metaneanic, and aneanic stages show evolution of genitalia (fig. 16, c-e). Paraneanic stage is between Tubuaiini and Pityisini; metaneanic resembles adult *Tornatellinoptini*. In aneanic stage, penis and appendix are mere blunt protuberances, their retractors meeting immediately, common retractor very thin, long (7.5 times penial length), oviduct a long undifferentiated tube.

Dissected 140513 (adult genitalia, interior of penis, teeth), four specimens; 142969 (para- and metaneanic), three specimens; 13500 (aneanic), two specimens.

Rapa, north of bay: Area, back of village (type locality), under stones, alt. 250-400 ft., Kondo, Anderson, and Cooke, July 15; holotype 8703, subadult

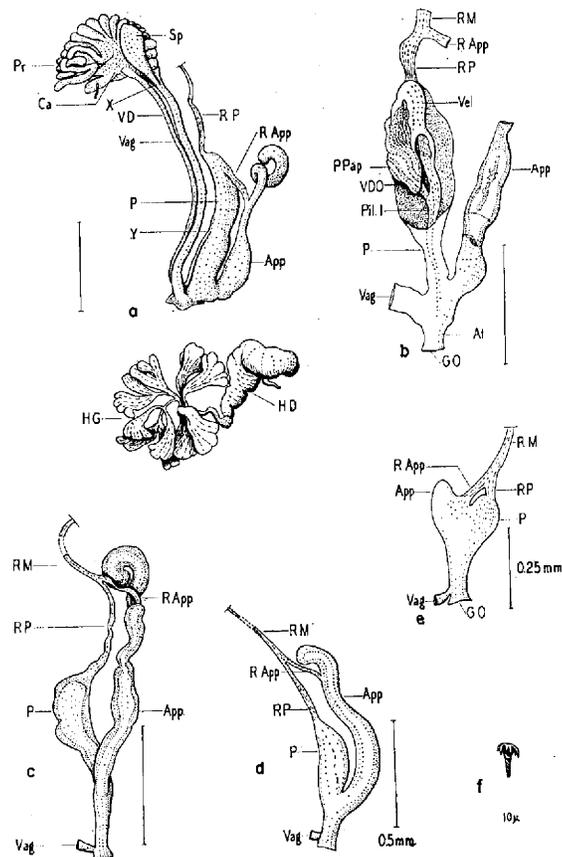


FIGURE 16.—*Strobilus (Strobilus) opeas opeas*: a, genitalia, adult; b, interior of penis and appendix; c, penial complex, subadult or paraneanic; d, penial complex, metaneanic; e, penial complex, aneanic; f, tooth. (10 microns = 8 mm.)

8704, juvenile 8705; paratypes, or syntypes, 140513-140514. Mount Ruatara, northeast slope, alt. about 750 ft., Kondo, July 26, 143499-143500; same locality, alt. about 800 ft., Kondo, July 26, a few specimens with distinct narrow lip, 143528. Mount Perahu, east ridge, alt. 1,200-1,500 ft., Kondo, July 21, 142837. South of bay: Mount Tepiahu, under dead leaves, alt. about 500 ft., Kondo and Cooke, July 23, 142969. Mount Tanga, north slope, under stones, alt. 300-700 ft., Anderson, Toto, Terii Pare, July 31, 143801.

In addition to the six colonies mentioned above, this species was collected in 19 colonies north of the bay between Area and Mount Perahu. From south of the bay come nine additional lots collected from Mount Tepiahu to nearly the eastern tip of the island. The species is especially abundant in the neighborhood of Area village and on the slopes of Mount Tepiahu which are almost opposite each other across the bay.

This species is easily distinguished from *S. turritus* by its larger size; by its slightly flatter whorls, which increase more rapidly with the growth of the shell; and by its more elongate last whorl. The two species did not occur in the same colonies.

***Strobilus (Strobilus) opeas intermedius*, new subspecies (fig. 15, e).**

*Shell* smaller than that of typical form, thinner and lighter in color, cream buff, with silky sheen; slightly, more closely, and evenly coiled. *Spire* more cylindrical, with more convex outlines. *Whorls* 11, increasing more slowly toward base, very lightly convex, surface of median whorls with fine distinct costae which are slightly stronger just below sutures but only indicated on last whorl, which is slightly flattened dorsally. *Aperture* rather narrow, nearly vertical. *Parietal lamella* strong, long. *Columellar lamellae* low, threadlike, very obliquely seated; a low indistinct swelling indicates upper lamella, visible only obliquely. *Palatal fold* low, indicated only when viewed frontally.

Length 5.8 mm., diameter 1.82 (31 percent); apertural axis 1.44, diameter 1.03 (71 percent); last whorl 2.2 (38 percent); parietal lamella 0.23.

Surface in juveniles more strongly costulate than in typical form of same age, and columellar lamellae distinctly stronger.

Rapa: Mount Vairu, southeast slope (type locality), in small valley, under stones, alt. about 900 ft., Anderson, July 26; holotype 8706, paratypes 143455-143457 (dissected). Also collected in two higher localities 140131-140134 and 143483-143485, Zimmerman and Kondo.

Most of the 33 specimens from the three colonies were alive when collected. This subspecies, which was not abundant, is undoubtedly an isolated geographical race, as Mount Vairu is well within the range of the species.

The shells are of about the same length and thickness as those of *S. turritus*. They differ in outline, in the diameter, in the number of whorls, and in the texture of the surface.

***Strobilus (Strobilus) subtilis subtilis*, new species (figs. 17, a-c; 18, a-c).**

*Shell* (fig. 17, a) small, very slender, subcylindrical, isabella color, thin, diaphanous, very finely, delicately, obliquely striatulate with lines of growth. *Spire* elongate, tapering slowly to apex, with very slightly convex outlines. *Suture* simple, lightly impressed. *Whorls*

9; embryonic whorls subpapillate, microscopically spirally striate; postembryonic whorls increasing slowly and regularly, flatly convex, upper whorls slightly shouldered just below sutures; last whorl oblong, slightly flatter than penultimate. *Aperture* small, nearly vertical. *Parietal lamella* strong, oblique, more than 1.25 whorls long. *Columella* nearly vertical, inner face slightly thickened, without perceptible lamellae though they may be indicated by slight irregularities. *Palatal fold* absent, no trace of it is found through the more or less transparent shell. *Peristome* thin, erect along outer margin, lower margin indistinctly thickened.

Length 3.93 mm., diameter 1.16 (31 percent); apertural axis 0.93, diameter 0.63 (68 percent); last whorl 1.32 (34 percent); parietal lamella 0.22.

In juvenile specimens (fig. 17, *b, c*), whorls 6.5, length 2.4 mm., embryonic whorls more distinctly spirally striate; parietal lamella very strong, its free margin flaring outward and weakly sinuous. *Columella* calloused, furnished with three lamellae; supracolumellar lamella obliquely seated, a little weaker than columellar lamella; columellar lamella well developed;

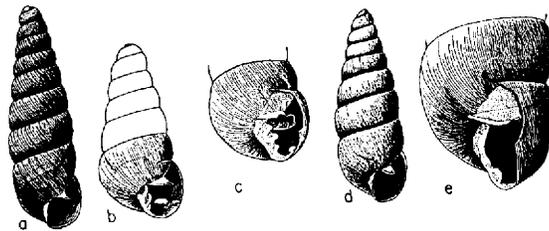


FIGURE 17.—*a-c*, *Strobilus (Strobilus) subtilis subtilis*: *a*, adult, holotype; *b*, juvenile, frontal aspect; *c*, same as *b*, latero-oblique apertural view. *d, e*, *S. (S.) s. similis*: *d*, adult, holotype; *e*, adult, latero-oblique columellar view. (1 mm. = 6.7 mm. for *a, d*.)

subcolumellar lamella weaker than other two, more deeply seated and visible only when viewed obliquely. Lower palatal fold consists of a row of distinctly separated, irregularly spaced, elongate denticles placed on a thin low callus ridge. Row of denticles extends into shell for about 0.66 to 0.75 whorl; beyond denticles callus ridge sometimes continued to just beyond and below juncture of outer lip.

Adult genitalia (fig. 18, *a*). Basically similar to those of *S. turritus* and *S. opeas*. *Ovotestis* eight-lobate; *albumin gland* absent or minute; *prostate* small; *oviduct* very narrow; *penis* large (about 0.75 oviducal length).

Paraneanic genitalia (fig. 18, *b, c*). *Ovotestis* (not figured) undeveloped, thin, follicles short-clavate. *Albumin gland* large, follicles numerous, ovate to round. *Prostate* small, paucifolliculate. *Penis* smaller than in adult, shorter (about 0.6 oviducal length), stalk relatively longer. In specimen with egg, penis subcylindrical.

Dissected 143600 (adult genitalia), two specimens; 138354 (paraneanic), two specimens.

Rapa: Mount Mangaoa, west slope of northeast ridge (type locality), under stones, alt. about 800 ft., Anderson, July 25; holotype 8707 (figured juvenile 8708), paratypes 138354-138357. Teutu, on north slope of Mount Tepiahu, under stones and damp, dead leaves, alt. about 200 ft., Sam Wight and Cooke, July 27, 143600-143601.

Besides the two lots mentioned, Bishop Museum has specimens from 15 other colonies. All but one of these are on the slopes of the ridge paralleling

the southern margin of Ahurei Bay. The exception is the islet of Rapa Iti, just south of the entrance to the bay. These colonies are from Mount Mangaoa, Ahurei, Mount Ororangi, Mount Tepiahu, Teutu, Mount Tanga (south), and Pake Bay.

Adults of *S. subtilis* differ from those of *S. turritus* in size, contour, and type of whorling. Juveniles are more easily separated by the more distinct spiral striations of the embryonic whorls, by the slightly sinuous free margin of the parietal lamella, and by the tridentate columella.

In contour, this species somewhat resembles that of *S. opeas intermedius*. It is most easily recognized by its smaller size, smoother surface texture, and other characters.

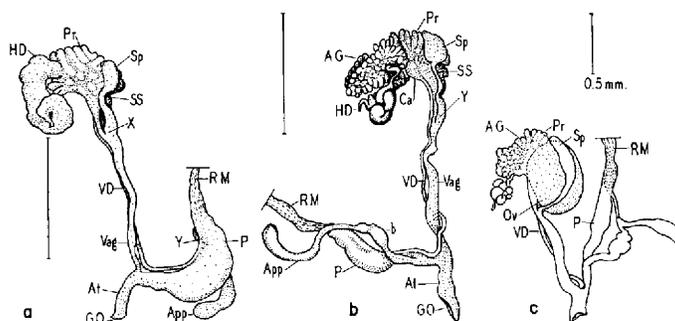


FIGURE 18.—*Strobilus (Strobilus) subtilis subtilis*: a, adult genitalia; b, paraneanic genitalia; c, same as b, but with egg.

Apparently, reproduction starts quite early. Eggbearing in the younger stages and the small penis suggest the possibility that the animal is a functional female at this stage, whereas the large penis and the heavily distended ovotestis of the mature animal suggest it is a functional male. Correlated with the above conditions are the large albumin gland and small prostate in the immature specimens; in the adult, the large prostate and minute albumin gland.

***Strobilus (Strobilus) subtilis similis*, new subspecies (fig. 17, d, e).**

*Shell* shorter and broader than in typical species. Surface texture slightly smoother, the weaker striae less oblique. In a near adult, microscopical fine spiral striae of embryonic whorls just discernible. *Whorls* slightly more convex, spire tapering more rapidly to apex. *Columella* tridentate, subcolumellar lamella almost basal in position, seated slightly lower than in typical form.

Length 3.39 mm., diameter 1.19 (35 percent); apertural axis 0.93, diameter 0.64 (69 percent); last whorl 1.45 (43 percent); parietal lamella 0.16.

*Rapa*: Mount Vairu, small valley on southeast slope, above head of Angairao Bay (type locality), under stones, alt. about 900 ft., Anderson, July 26; holotype 8709, paratypes 143458.

The material available contained three dead adults and two live near-adults.

In the absence of juvenile specimens, this subspecies is tentatively placed with *S. subtilis*, to which it is apparently more closely related. Although it was found outside the range of the species, there is no other known species with which it can be associated. With more abundant material, especially with a series of juveniles, *similaris* might prove to be a distinct species. The position of the subcolumellar lamella may indicate a relationship with *S. turritus basalis*, but it differs from this form in size, in number of whorls, and in type of whorling.

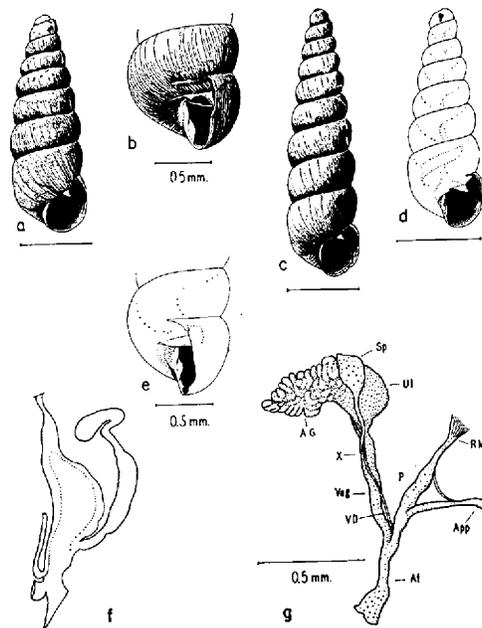


FIGURE 19.—a, b, *Strobilus (Strobilus) acicularis acicularis*: a, adult, holotype; b, juvenile, latero-oblique view. c-g, *S. (S.) a. raphis*: c, adult, holotype; d, juvenile; e, juvenile, latero-oblique columellar view; f, adult penial complex; g, subadult genitalia (minus ovotestis).

***Strobilus (Strobilus) acicularis acicularis*, new species (fig. 19, a, b).**

*Shell* very small, slender, turritid, honey yellow, thin, transparent, somewhat glossy, microscopically striate with lines of growth. *Spire* elongate with nearly straight outlines, tapering gradually to apex. *Suture* simple, well impressed. *Whorls* 8.25; embryonic whorls slightly flattened and shouldered above, glossy, marked with very fine, microscopical, closely spaced spiral lines; postembryonic whorls convex, increasing slowly and regularly; last whorl oblong, slightly flattened. *Aperture* small, vertical, rather wide, its outer margin slightly flattened. *Parietal lamella* not high, slightly oblique, nearly 1.5 whorls long. *Colu-*

*mella* perpendicular, inner face slightly arcuate, thinly calloused, with no indications of lamellae. *Palatal wall* without folds. *Peristome* thin, erect.

Length 3.06 mm., diameter 1.03 (33 percent); aperture axis 0.80, diameter 0.60 (75 percent); last whorl 1.27 (41 percent); parietal lamella 0.10.

Rapa: South of Ahurei Bay, Mount Tepiahu, south slope, under dead leaves, alt. about 500 ft., Cooke and Kondo, July 23; holotype 8714 (figured, 8715), paratypes 142976-142978. North of Ahurei Bay, Area, back of village, under stones, alt. about 400 ft., R. Fosberg, July 1, 143866-143867. Also collected from 19 other colonies: Area, Mount Tanga, Mount Perahu, Tumu Valley, Mount Morongota, Mount Tautautu, Mount Ororangi, Maungaeae Valley, Mount Tepiahu, Maomao Point, and Mount Koara northwest of South Anatauri (Anataari) Bay. The species occurred under similar conditions from a few feet above sea level at Maomao Point to 1,500 ft.

The collection contains few juveniles. In one (fig. 19, *b*), with about six whorls, the parietal lamella is damaged but enough remains to show that it is proportionately stronger than in the adult stage. The columella is perpendicular, nearly straight, the inner face slightly calloused and furnished with two oblique nearly equal lamellae. There are no palatal folds in any of the available specimens.

In Bishop Museum collections, *Strobilus acicularis* is the most widespread species of the genus. The specimens show little colonial variation except in size and in the slightly greater convexity of the whorls, and there are no tangible characters (except in the subspecies *raphis*) by which the species can be separated into geographical races.

*S. acicularis* and its subspecies *raphis* differ from all the species of the genus in their small size, in the lack of palatal folds at all stages of growth, in the equally developed columellar lamellae of immature specimens, and in the distinctly convex whorls.

Although widely distributed, this species is comparatively rare. Few of the lots contain more than a dozen specimens each, probably because of their small size and their habitat. As a rule, specimens from the higher localities are slightly larger (3.4 mm., Perahu, 142886), with 0.50 to 1.0 additional whorl.

In some respects *S. acicularis* seems to be closely related to *S. subtilis*. Both species have microscopically spirally striate embryonic whorls. Adults of *S. acicularis* are slightly smaller; and the juveniles have two oblique, equally developed columellar lamellae and no palatal folds, whereas juveniles of *S. subtilis* have three columellar lamellae, a strongly developed columella, and a prominent disconnected palatal fold.

Both species were taken on Mount Ororangi and Mount Tepiahu, but not in the same colonies. On Ororangi 100 to 200 yards separated the colonies of *S. acicularis* from those of *subtilis*, and on Tepiahu several hundred yards separated the three colonies of *S. acicularis* from the two colonies of *S. subtilis*.

***Strobilus (Strobilus) acicularis raphis***, new subspecies (fig. 19, c-g).

*Shell* very slender, turrated, color cream buff, thin but not transparent, microscopically finely striatulate. *Spire* elongate, tapering very gradually to apex with nearly straight outline. *Suture* well impressed. *Whorls* 10; embryonic whorls slightly flattened, glossy, under high magnification indistinctly spirally striate; postembryonic whorls increasing very slowly and regularly, convex, slightly shouldered above, widest about half-way between suture and periphery; last whorl oblong, slightly flattened dorsally. *Aperture* small, broad, outer margin indistinctly flattened. *Parietal lamella* medium in height. *Columella* nearly perpendicular, faintly concave, inner surface hardly calloused, without appreciable lamellae. *Palatal wall* without folds. *Peristome* thin, erect.

Length 3.77 mm., diameter 1.0 (27 percent); apertural axis 0.74, diameter 0.56 (75 percent); last whorl 1.27 (34 percent); parietal lamella 0.12.

In a juvenile specimen, whorls about 7, length 2.59 mm., parietal lamella simple, proportionately only a little stronger than in adults; columella nearly straight, its inner face only slightly calloused and furnished with two nearly equal, very oblique folds, the lower extending to outer margin of columella. No palatal fold.

Adult genitalia typical, fragmentary. *Ovotestis* five-lobate. *Albumin gland* absent. *Prostate* large, follicles large. *Vagina* long, narrow. *Penis* large, clavate, as long as oviduct, with heavy, relatively long stalk. *Atrium* short.

Paraneanic or subadult genitalia. *Albumin gland* large; follicles numerous, large, short-digitate. *Prostate* not seen. *Uterus* enlarged (without egg). *Penis* small, subcylindrical. *Appendix* small, club-shaped; *retractor* thin. *Atrium* very long, flaring distally.

**Rapa:** Mount Ruatara, northeast slope, near head of Tubuai Valley (type locality), alt. about 750 ft., Kondo, July 26; holotype 8716 (figured juvenile 8717), paratypes 143504-143505. This material consisted of a single colony of 61 specimens.

Adults are easily distinguished from the parent species by their narrow and elongate form. Juveniles of the species and subspecies, whorls about 6, are almost identical. However, the whorls are slightly more convex in the subspecies. *S. a. raphis* is undoubtedly an isolated geographical race, highly localized, as this form occurred with *S. opeas* at only one station. At three other localities on the slopes of Ruatara the only representative of *Strobilus* was the species *opeas*.

Subgenus **Tautautua**

The single species of this subgenus differs from the rest of the species of the subgenus *Strobilus* in its very low parietal lamella and in the absence of a columellar lamella during the juvenile stage.

Type species: *Strobilus perfragilis*.

This subgenus is proposed for a rather unique species which differs from the other species of the subgenus *Strobilus* in its much reduced apertural armature. Most of the specimens were taken on or near the slopes of Mount Tautautu, a peak south of Ahurei Bay, after which the subgenus is named.

***Strobilus (Tautautua) perfragilis***, new species (fig. 20, a, b).

*Shell* turrated to acutely conic, deep colonial buff, exceedingly thin and fragile, translucent with a silky sheen, under a strong lens minutely striatulate; spire elongate, tapering gradually and evenly to apex, outlines nearly straight. *Suture* simple, not deep. *Whorls* 9;

embryonic whorls slightly convex, worn in adults, in juveniles glossy, microscopically minutely sculptured with close spiral lines; postembryonic whorls increasing slowly, regularly, slightly convex; last whorl short, wide, apparently not flattened dorsally. *Aperture* quadrate-oval, outer margin regularly curved. *Parietal lamella* low, about 1.5 whorls long, slightly obliquely seated. *Columella* perpendicular, nearly straight, inner only slightly calloused, unarmed. *Palatal wall* without folds. *Peristome* extremely thin, fragile.

Length 5.08 mm., diameter 1.91 (37 percent); apertural axis 1.35, diameter 1.03 (76 percent); last whorl 2.21 (43 percent); parietal lamella 0.11.

Genitalia (not figured) similar to that of *S. brevis* and *S. acicularis raphis*. *Ovotestis* immature, four-lobate; follicles globular, only two to four per lobe. *Albumin gland* large; follicles very numerous, ovate, round. *Spermatheca* large; stalk short. *Uterus* enlarged. *Vagina* narrow, long. *Penis* clavate, nearly oviducal length; stalk narrow. *Appendix* long, narrow. *Retractors* thin. *Atrium* very short.

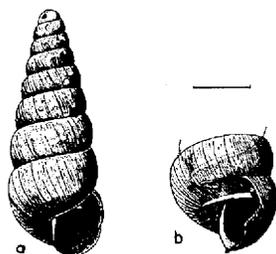


FIGURE 20.—*Strobilus (Tautautua) perfragilis*: a, adult, holotype; b, latero-oblique view of aperture, columellar and palatal folds absent.

Dissected 140030 (adult, juvenile), two specimens; 144767 (paraneanic or subadult), one specimen.

Rapa: Mount Tautautu, northwest slope, at foot of cliff (type locality), under damp stones and dead leaves, alt. about 800 ft., Wight, Kondo, and Cooke, July 25; holotype 8718 (figured juvenile 8719), paratypes 144728, 144767. Maitua, near foot of cliffs, below Mangaoa, under stones in damp woods, alt. about 750 ft., Anderson, July 6, 140030-140031 (dissected). Mount Mangaoa, northeast ridge, alt. 1,000-1,100 ft., Zimmerman and Anderson, July 29, 143756.

Thirty specimens, six of which were alive, were taken from five colonies. Most of the specimens were damaged in transit or during cleaning. No very young specimens were taken; the youngest, with about eight whorls, is without any indication of either columellar or palatal folds. It is probable that this species has none of these folds at any stage of growth, for in all the other species of the genus except *acicularis* both columellar and palatal folds are present until the shell is nearly mature.

This is one of the most distinct species of the genus, as it is the only one in which columellar lamellae are entirely lacking (fig. 20, b); in addition, the parietal lamella is less prominent. Its closest relative is *S. acicularis* from which

it is easily distinguished by its larger size, straighter outlines, and weaker parietal lamella.

Animals of this species were rare and most of those available were torn, indicating that they were difficult to extract. Of two other dissections, one was an adult and one was immature; both were badly mangled so that only the penises were recovered.

#### Subgenus **Tanga**

The shell has 7 whorls, fewer than any species of the typical subgenus, *Strobilus*, in which are 8.25 to 11 whorls. The whorls are slightly flatter and increase more rapidly, and the parietal lamella is higher and slightly shorter. In juveniles, the three columellar folds are much stronger, the columellar fold being well developed. The two rather short palatal folds are about 0.3 whorl long. In the typical subgenus the single palatal fold, when present, extends into the shell for a full whorl to 1.25 whorls. Unlike the other species of the genus, the parietal lamella in juvenile stages has a distinctly sinuous free margin. The subgenus is named for Tanga Peak near the south entrance of Ahurei Bay.

Type species: *Strobilus brevis*, new species.

The juveniles of only one species of *Strobilus* (*s. s.*), *Strobilus subtilis*, have as many as three columellar lamellae which are low and very obliquely placed.

#### **Strobilus (Tanga) brevis brevis**, new species (fig. 21, a-d).

Shell small, elongate, color deep colonial buff, thin, very fragile, subtransparent, glossy, microscopically finely striatulate. *Spire* with slightly convex outlines, tapering slowly to subacuminate apex. *Suture* slightly impressed, indistinctly narrowly margined. *Whorls* 7; embryonic whorls smooth, shining, without microscopical spiral striations; postembryonic whorls flatly convex; last whorl oblong, about 0.5 shell length, tapering slowly to base, faintly flattened dorsally. *Aperture* vertical, longer than broad. *Parietal lamella* strong, oblique, apparently not quite a whorl in length. *Columella* indistinctly sigmoid, not heavily calloused, furnished with a very distinct oblique fold. *Palatal wall* without any indications of folds. *Peristome* thin, erect.

Length 3.01 mm., diameter 1.18 (39 percent); apertural axis 0.91, diameter 0.54 (60 percent); last whorl 1.52 (50 percent); parietal lamella 0.18.

In a juvenile specimen, whorls 6, length 2.15 mm., parietal lamella is proportionately stronger, very obliquely seated, very long, length nearly 1.5 whorls, inner 0.50, low, its free margin flaring outward, and somewhat undulate, its upper face faintly striate, striae nearly parallel to free margin. *Columella* very heavily calloused within, as seen through the shell, with three lamellae, the supracolumellar lamella weakest and more oblique than other two, subcolumellar lamella a little more deeply seated. *Palatal wall* furnished with two continuous folds about 0.3 whorl in length which terminate just inside margin of peristome. Lower fold considerably stronger than upper.

Genitalia immature, typical. *Ovotestis* (recovered in part only) immature; follicles globular. *Albumin gland* large, multifolliculate; follicles short-digitate, mostly V-shaped or split. *Prostate* not seen. *Uterus* enlarged, folded. *Spermatheca* small, round, with spermatophore; stalk narrow, short. *Vagina* long, broad. *Penis* quite large, clavate, about 0.5 oviducal length. *Appendix* small. *Atrium* long, narrow.

Dissected 140302 (paraneanic or subadult), one specimen only.

Rapa: Mount Perahu, east ridge (type locality), under stones, alt. 900-1,000 ft., Anderson, July 13; holotype 8710 (figured specimens 8711, 8712), paratypes 140302-140303. Number 135495, an uncoiled juvenile (fig. 21, c), was collected on same ridge and under same conditions, alt. 1,500-1,850 ft., Anderson, July 28.

This species is rare; only 14 specimens, most of which were alive, were taken from five colonies.

*Strobilus brevis* differs from the other species of the genus on several significant points. The adult has fewer whorls, a shorter parietal lamella, and is

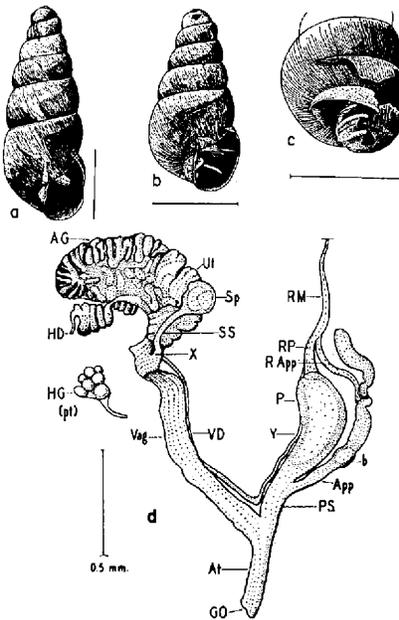


FIGURE 21.—*Strobilus (Tanga) brevis brevis*: a, adult, holotype; b, metaparanecanic; c, metaneanic, uncoiled, latero-oblique columellar view; d, subadult genitalia.

proportionately broader than any species of the genus. Except for its genitalia, it might properly be placed in *Tubuaia*. In the juvenile stages *S. brevis* has a sinuous parietal lamella, a character absent among its fellows and, again, is reminiscent of *Tubuaia*. It has two short palatal folds 0.3 whorl long, whereas the others have one (*Strobilus*) or none (*Tubuaia*). The lower fold is quite short, whereas in the other species of *Strobilus* having this fold it is nearly a whorl long or longer. The columellar folds stand out strongly in *S. brevis*, but they are generally weak in the other species.

**Strobilus (Tanga) brevis subsimilis**, new subspecies (fig. 22, a).

Compared with typical form, shell is slightly broader in proportion to its length, tapering more rapidly to apex, upper outline very slightly more acuminate. Aperture proportionately longer. Parietal lamella not as high and less obliquely seated, columella less caloused within.

Length 2.87 mm., diameter 1.21 (42 percent); apertural axis 0.97, diameter 0.64 (65 percent); last whorl 1.52 (53 percent); parietal lamella 0.13.

Genitalia (not figured) of functional female type, somewhat younger than that of *S. brevis*. Penis and appendix undeveloped; vagina broad, long; uterus bloated. Spermatheca large; stalk short. Albumin gland huge, multifolliculate. Prostate small, just below spermatheca, follicles few, ovate. Hermaphrodite duct thin, narrow, long. Ovary five-lobed, undeveloped, follicles few, clavate to ovate. Atrium short, broad.

Dissected 143828; one specimen only.

Rapa: "Putaketake" (type locality), W. Anderson, July 31; holotype 8713, paratype 143828. Taken by a crew member, giving no additional data. Putaketake is probably a local name for a restricted area a short distance south of Ahurei village (not Mount Puketaketake, north of bay).

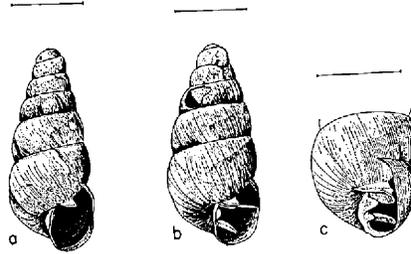


FIGURE 22.—a, *Strobilus (Tanga) brevis subsimilis*, adult, holotype. b, c, *S. (T.) b. pumilus*: b, subadult, holotype; c, subadult, latero-oblique view of apertural armature.

The material consists of two specimens which appear to be adult, and which probably represent a form living at a lower altitude and quite widely separated from the typical form. Unfortunately, there are no juveniles to establish definitely how closely the subspecies is related to the species.

**Strobilus (Tanga) brevis pumilus**, new subspecies (fig. 22, b, c).

The type is not mature. Compared with younger specimens of typical form (*S. brevis brevis*), with same number of whorls but younger, shell is a little darker in color, with wider and more convex outlines. Surface marked with distant, minutely stronger striae. Whorls slightly flatter, increasing more rapidly. Aperture proportionately broader. Free margin of parietal lamella less sinuous, its upper face furnished with a distinct fold parallel to free margin (in typical form this fold is only indicated). Columella less heavily caloused. Other apertural characters follow same pattern as that of typical form.

Length 2.83 mm., diameter 1.28 (45 percent); apertural axis 0.93, diameter 0.65 (69 percent); last whorl 1.53 mm. (54 percent); parietal lamella 0.13.

Rapa: Mount Perahu, east ridge, near apex of peak (type locality); alt. about 1,900 ft., Kondo, July 21; holotype 142912.

The material consists of a single specimen which is not quite mature. Unfortunately, the adult stage is not known. From a comparison between this lone specimen and those of similar age of the typical form, the adult should have at least 0.5 less whorl, be slightly larger in size, have more convex outlines, and have a proportionately broader shell.

#### Genus *Pukunia*, new genus

*Shells* small, 3.5-4.75 mm. in length, imperforate, sublanceolate, subtransparent, glossy, surface microscopically finely striatulate with lines of growth. *Whorls* 8 to 10, flatly convex, increasing slowly and regularly; embryonic whorls smooth, glossy. *Parietal lamella* well developed, long, entering aperture about 1.3 whorls. *Columella* furnished with a low thickened lamella along its inner face. *Palatal wall* unarmed. *Peristome* thin, erect.

In juvenile specimens columella furnished with a strong, spirally ascending, columellar lamella and a minute, nearly perpendicular, deeply seated supracolumellar lamella. Palatal wall armed with low, continuous lower palatal fold about 1.25 whorls long.

Type species: *Pukunia acuta*.

Distribution: Rapa.

This arboreal genus is named after a prominent peak just north of Ahurei Bay. *Pukunia* closely resembles both *Strobilus* and *Antonella* in shell characters. The principal character on which *Pukunia* can be differentiated is in the columella, which always has a low, nearly perpendicular lamella. Juvenile specimens are easily distinguished by the strong spiral columellar lamella.

Anatomically, *Pukunia* (at least *P. acuta*) is the most distinct genus of the Pityisini. Its long oviduct, penis, and appendix are its most important characters. The partly twisted, or convoluted, penis was not seen in any of the other genera of Pityisini.

As far as we know, the genus is arboreal, whereas *Strobilus* and *Antonella* are entirely terrestrial in habit.

#### *Pukunia acuta*, new species (figs. 23, *a-e*; 24, *a-c*).

*Shell* (fig. 23, *a, b*) sublanceolate, narrow, color cinnamon, somewhat thin, translucent to subtransparent, very glossy, under a strong lens faintly striate with lines of growth. *Spire* elongate, tapering gradually to apex, upper portion subacuminate. *Suture* narrow, well impressed, indistinctly narrowly margined. *Whorls* nearly 10; embryonic whorls rather narrow, smooth, glossy; postembryonic whorls increasing gradually, the upper nearly flat, last three slightly more convex; last whorl slightly oblong. *Aperture* small, nearly perpendicular, its outer margin regularly curved. *Parietal lamella* moderately strong, simple, obliquely seated, about 1.3 whorls in length, uniform in height for more than 0.75 of its length. *Columella* nearly straight, its inner face furnished with a thickened nearly straight fold, which terminates rather abruptly at base of columella and forms a low, broad, angular projection when viewed from outside. *Palatal folds* absent. *Peristome* thin, erect.

Length 4.68 mm., diameter 1.78 (38 percent); apertural axis 1.33, diameter 0.96 (74 percent); last whorl 1.96 (42 percent); parietal lamella 0.19.

In a juvenile specimen (fig. 23, *c, d*), whorls nearly 7, length 2.84 mm., last whorl transparent and internal armature clearly visible through shell. Parietal lamella strong, oblique, its free margin flaring outward. Columella furnished with a strong spiral lamella,

terminating on outer margin near base of columella; a second, deeply seated, nearly perpendicular lamella just above columellar lamella. Palatal wall with a low, long, continuous fold about 1.25 whorls in length; fold clearly visible through shell.

In an older specimen (142726A), whorls 8.5, shell thicker, last whorl semitransparent, columellar lamella proportionately weaker. Palatal fold not proportionately weaker.

Egg (fig. 23, *e*) elliptical, circular in cross section,  $0.63 \times 0.48$  mm.

Genitalia basically similar to those of other genera of Pityisini (fig. 24, *a-c*), differing principally in having an extremely elongate penis in the adult stage, as long or longer than oviduct, usually convoluted in part.

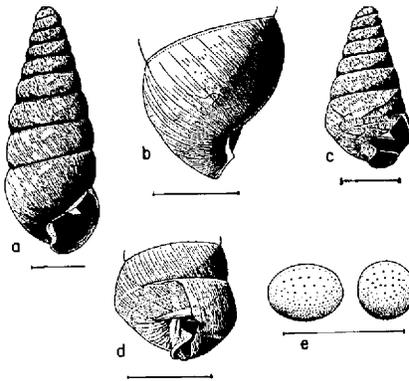


FIGURE 23.—*Pukunio acuta*: a, adult, holotype; b, adult, profile view; c, juvenile; d, juvenile, latero-oblique view of aperture; e, egg, lateral and frontal views.

Adult genitalia (fig. 24, *b*). *Ovotestis* 10-lobate; lobes robust, full; follicles truncate at apex, strongly adnate to each other. *Duct* (not figured) convoluted, distended. *Talon and carrefour* not dissected but presumably typical. *Albumin gland* small. *Prostate* large; digitate follicles fanning. *Spermatheca* large, elliptical; stalk short, stout. *Vagina* fairly broad, long ( $\pm 0.85$  oviducal length). *Vas deferens* narrow (0.2-0.3 vaginal width); insertion (Y) apical. *Penis* elongate, clavate above, narrower below. *Appendix* small, shorter than penis. Common and penial retractors heavy; appendical retractor slender. Interior of penis (fig. 24, *c*) simple, with low pilaster ascending from half-way point, forming small velum at apex, and descending as banana-shaped, semi-pendent papilla with inner margin somewhat raised; orifice of vas deferens just below velum.

Paraneanic genitalia (fig. 24, *a*) similar to that of adult, with following differences: *ovotestis* eight-lobate, undeveloped, translucent, tips of free end of follicles rounded; *albumin gland* larger, follicles also much larger, numerous; *prostate* small, follicles few; *spermatheca* long, elliptical (distended with sperm mass); *uterus* enlarged with three eggs (Ov. 1, 2, 3). *Penis* proportionately shorter; *appendix* longer than penis.

Dissected 142723 (adult, paraneanic, interior of penis), at least three specimens.

Rapa: Mount Perahu, northeast ridge (type locality), arboreal, on leaves of *Veronica* and *Lautea*, alt. about 1,200-1,500 ft., Zimmerman and Anderson, July 21; holotype 8720 (figured juvenile 8721), paratypes 142723-142730.

This species was abundant at all altitudes from above 1,200 feet to the top of the peak, which is slightly more than 2,000 feet, on the leaves of a number of

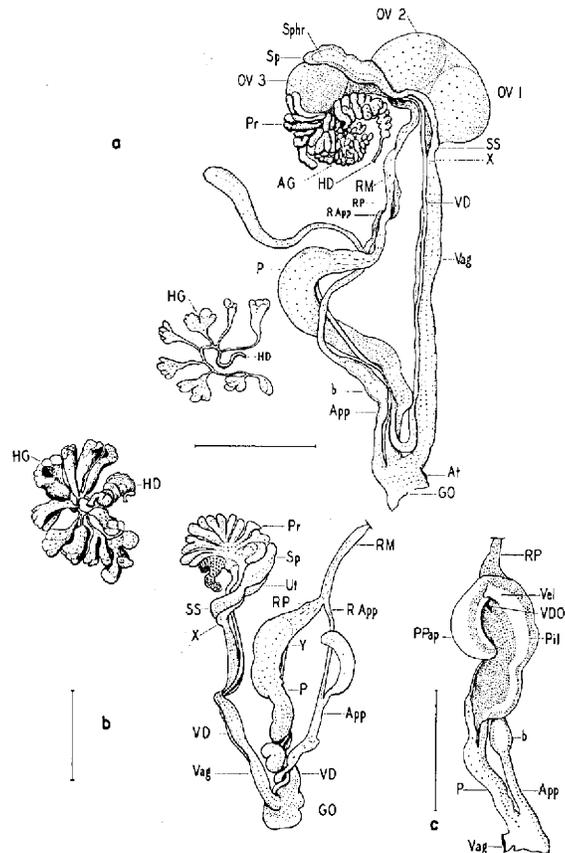


FIGURE 24.—*Pukimia acuta*: a, paraneanic genitalia (note three eggs in uterus); b, adult genitalia; c, interior of penis.

bushes and small trees and on the fronds of birdsnest ferns. It was taken on all three trips up this ridge. The type lot consists of more than 300 specimens.

Three specimens, presumably *P. acuta*, were taken on different trips up the western ridge of Mount Mangaoa. This material consists of two juveniles (137906, 137958) and a badly damaged dead adult (143340). The two juveniles have slightly different characters which may be individual. As a whole, there seems to be no consistent differences between these specimens and those from Mount Perahu. In contrast to the abundance of the species on Mount Perahu, the Mount Mangaoa species appeared to be extremely rare.

As in *Lamellovum globosum*, a cul-de-sac is formed in the nuchal membrane by some parasite. The penial papilla resembles that of *Mangaoa perissa*.

***Pukunia margaritae***, new species (fig. 25, a, b).

*Shell* resembles that of *P. acuta* but is shorter, with 8.5 whorls, proportionately stouter and with slightly flatter whorls; aperture narrower; parietal lamella lower; columella shorter, slightly sigmoid, and with a stronger, slightly spiral lamella; no palatal fold.

Length 3.60 mm., diameter 1.64 (47 percent); apertural axis 1.04, diameter 0.90 (86 percent); last whorl 1.74 (48 percent); parietal lamella 0.14.

Rapa: Mount Morongota, under tree ferns, alt. about 800 ft., Margaret Stokes, 1921; holotype 53241.

The type is the only specimen in the Bishop Museum collection. It is a near-adult, and was dead when collected. There seem to be enough differences between this and *P. acuta* readily to distinguish the two.

Named for Margaret Stokes, who spent several months during 1921 and 1922 on Rapa and who, as far as can be ascertained, was the first person to collect on the island after Cuming visited there in 1828.

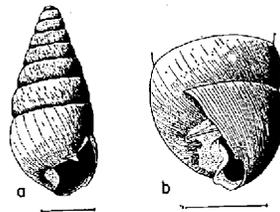


FIGURE 25.—*Pukunia margaritae*: a, subadult, holotype; b, subadult, latero-oblique apertural view.

***Pukunia pellucida***, new species (fig. 26, a-e).

*Shell* small, ovately conic, color pinkish cinnamon, semi-transparent, glossy, under a strong lens less distinctly marked by fine slightly oblique lines of growth. *Spire* with slightly convex outlines. *Suture* simple, lightly impressed. *Whorls* 7.5; embryonic whorls smooth, glossy; postembryonic whorls increasing slowly and regularly; last whorl short, only slightly longer than broad, tapering evenly to base. *Aperture* small, narrow, tapering at both ends. *Parietal lamella* moderately strong, about one whorl long, obliquely seated, free margin slightly flaring outward. *Columella* slightly sigmoid, interior face thickened by a rapidly ascending lamella, which terminates somewhat abruptly at base and outer margin of columella; when viewed obliquely, a rather sharp lamella is seen superimposed on columellar lamella. *Palatal fold* absent. *Peristome* thin, fragile, erect.

Length 3.43 mm., diameter 1.77 (51 percent); apertural axis 1.23, diameter 0.90 (74 percent); last whorl 1.80 (52 percent); parietal lamella 0.14.

In a juvenile specimen, whorls 5.75, length 2.42 mm., parietal lamella proportionately stronger, its free margin flaring more abruptly outward. Columella with a proportionately stronger, spirally ascending lamella; when viewed obliquely, has an indistinct nearly perpendicular, supracolumellar lamella. Palatal fold one (lower) fairly strong, lamella-like, about one whorl long, terminating just inside peristome.

Penis with appendix, but not strongly elongate as in *P. acuta* (not figured).

Dissected 135632 (probably juveniles), two specimens, both torn.

Rapa: Ahurei, on low ridge back of village (type locality), on leaves, dead twigs of guava shrubs growing along trail leading to Maitua, alt. about 75 ft., Zimmerman and Cooke, July 29; holotype 8722 (figured juvenile 8723). Paratypes 135632-135635: back of Maraia Point, near crest of ridge, alt. about 500 ft., W. Anderson, Cooke, and Kondo, July 16, 140389; back of Area village at foot of cliff, under stones and dead leaves, alt. about 250 ft., Anderson and Cooke, July 8, 135850.

Of the 18 specimens referable to this species, 13 are from Ahurei, the type locality. Three of the remaining five were taken back of Ahurei; the fourth, a dead shell, back of Maraia Point; and the fifth was found behind Area village. The fifth specimen undoubtedly fell off its host plant. Although not adult, it is

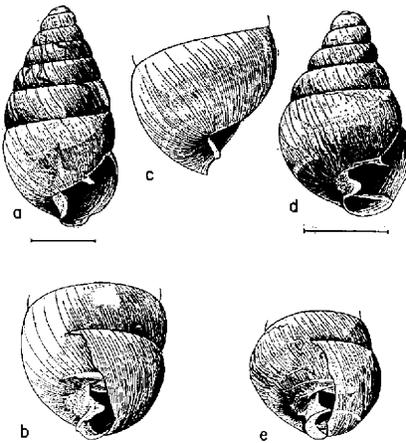


FIGURE 26.—*Pukunia pellucida*: a, adult, holotype; b, adult, latero-oblique apertural view; c, adult, profile; d, juvenile; e, juvenile, latero-oblique apertural view.

so similar to juveniles of about the same age from the type colony that there is little doubt it is this species.

From the quite widely separated localities in which this species was found, it is safe to assume that, under suitable conditions, *P. pellucida* is probably distributed on the slopes facing the bay over a considerable portion of the island. The type lot came from two small guava shrubs.

*P. pellucida* is the smallest of the three species referred to the genus. It is easily recognized by its small size, by its broader form, by its proportionately larger parietal lamella, and by its slightly more calloused columella.

Except for its anatomy and the columellar characters, this species might belong to the genus *Antonella*.

Genus **Mangaoa**, new genus

*Shell* imperforate, elongate, loosely coiled; initial embryonic whorl glossy, under high magnification very faintly wrinkled, wrinkles arranged spirally; second whorl faintly but distinctly, transversely, closely striate; postembryonic whorls ornamented with prominent, thin, widely spaced, slightly flexuous lamellae, continuing to base of shell. *Whorls* convex, separated by a deep suture. *Aperture* longer than broad; parietal and palatal lamellae absent; columella sigmoid, inner face slightly calloused, without distinct lamellae.

In juvenile specimens up to 4.5 whorls, margins of costae delicate, cuticular; parietal lamella sometimes lacking, sometimes an indistinct threadlike line; columella has two low, almost perpendicular, sigmoid, equally developed lamellae, both extending to outer margin.

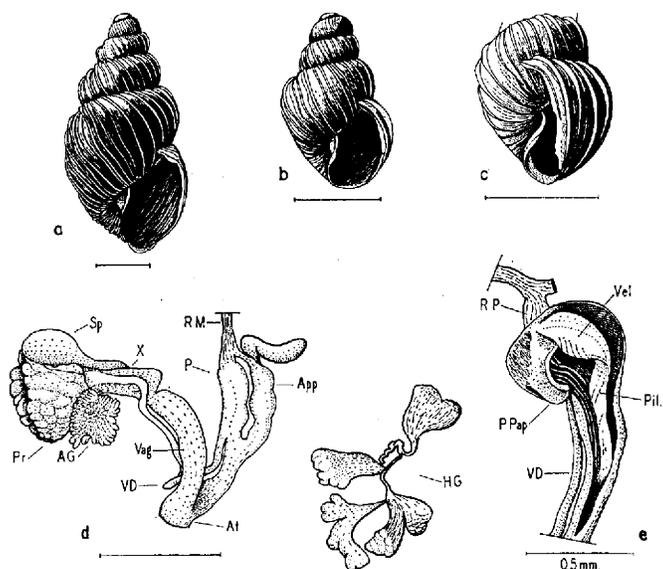


FIGURE 27.—*Mangaoa perissa*: a, adult, holotype; b, juvenile; c, juvenile, latero-oblique view; d, genitalia; e, interior of penis.

Type species: *Mangaoa perissa*.

Distribution: Rapa.

Arboreal, on the higher mountain peaks, this genus is named after one of the highest peaks of Rapa. It is one of the few genera of the family in which the embryonic whorls are transversely striate and in which there is an almost complete absence of apertural lamellae.

***Mangaoa perissa***, new species (fig. 27, a-e).

*Shell* elongate, subfusiform, sayal brown, very thin, translucent, dull, costate, ribs high, slightly flexuous, subcuticular, widely and more or less evenly spaced, extending to base, intercostal spaces marked with fine microscopical close lines. *Suture* deep. *Spire* elongate, with slightly convex outlines, tapering slowly to a somewhat blunt apex. *Whorls* 5.75, loosely coiled, increasing rather rapidly; postembryonic whorls convex, slightly shouldered

above, sloping inward below; last whorl elongate, tapering gradually to base. *Aperture* large, vertical, subovate. *Parietal lamella* absent. *Columella* nearly straight, slightly sigmoid, with indistinct lamellae bordering inner margin and uniting with peristome. *Palatal folds* absent. *Peristome* very delicate, almost cuticular.

Length 4.55 mm., diameter 2.34 (51 percent); apertural axis 1.85, diameter 1.15 (63 percent); last whorl 3.15 (69 percent).

Juvenile specimens up to 4.5 whorls, a few with a very indistinct, rather short parietal lamella, apparently lacking in most specimens. *Columella* furnished with two almost equally developed low lamellae, both extending to outer margin. *Palatal folds* absent.

Adult genitalia typical. *Ovotestis* heavily distended, four-lobate. *Duct* not recovered. *Albumin gland* in well-developed stage; follicles small, numerous, short-clavate. *Prostate* large; follicles numerous, distended, mostly ovate (intestinal groove well marked between upper and lower follicular layers). *Spermatheca* large, ovate; stalk short. *Vas deferens* large, adherent to penis from half way and above, emptying subapically below penial papilla (VDO). *Vagina* long, broader than usual. *Penis* not very large, long ( $\pm 0.8$  oviducal length); interior with slender but well-defined ascending pilaster, velum semi-transparent, penial papilla tongue-shaped with thickened inner marginal ridge, and free near tip, with few narrow secondary pilasters parallel to ascending one. *Appendix* not very large.

Dissected 140282 (adult, interior of penis), one specimen only, animal strongly contracted.

Rapa: Mount Perahu, east ridge (type locality), on *Lautea* and *Celtis*, alt. 900-1,000 ft., Anderson, July 13, holotype 140282; same ridge, on *Lautea* and *Veronica*, alt. 1,200-1,500 ft., Zimmerman and Anderson, July 21, paratypes (juveniles) 142731-142732 (figured juvenile 8724). Mount Mangaoa, one specimen, dead, under dead leaves, Zimmerman, July 25, 143344.

This species may be extremely rare, as the first specimen taken was the only live adult found. Two subsequent trips to the same ridge for additional material yielded only the eight juvenile specimens, which were found at a somewhat higher altitude. The single dead, nearly adult specimen from Mount Mangaoa agrees closely with that from the type locality.

#### Genus *Mitiperua*, new genus

*Shell* imperforate, nearly conic to ovately conic, surface distinctly striate or subcostulate, striae evenly spaced, apical whorls microscopically spirally striate. *Parietal lamella* simple at all stages of growth, rather short, not exceeding 0.5 whorl in length. *Columella* sigmoid, with two obliquely seated, nearly equal lamellae. *Palatal wall* without folds at any stage of growth.

Type species: *Mitiperua simplex*.

Distribution: Rapa, at high altitudes.

*Mitiperua*, named after one of the highest peaks of Rapa, is considered distinct from *Lamellovum* because of its rather low, simple, and shorter parietal lamella, because of its simple columella with only two lamellae, and because of the absence of palatal folds at all stages of growth.

In *Mitiperua* the parietal lamella is proportionately much weaker in immature specimens than in adults, a characteristic shared by *Celticola* (*Nesonoica*) *anatomuensis*.

**Mitiperna simplex simplex**, new species (figs. 28, *a-e*; 29, *a-c*).

*Shell* (fig. 28, *a-c*) narrowly ovately conic, lower whorls ecru olive, shading to isabella color on upper whorls, rather thin, subtranslucent, striate; striae somewhat closely and evenly spaced, not sharp or cuticular, slightly stronger just below sutures, continued to base of shell. *Suture* lightly impressed. *Spire* narrowly conic, with slightly convex outlines. *Whorls* 7.25; flatly convex, initial whorl slightly flattened with distinct suture, second whorl indistinctly shouldered above; embryonic whorls faintly, microscopically striate in juvenile specimens; last whorl broad, truncately ovate. *Aperture* nearly vertical, longer than broad, its outer margin indistinctly flattened. *Parietal lamella* low, entering for about 0.5 whorl, simple, very slightly oblique. *Columella* slightly sigmoid from frontal view, strongly sigmoid when viewed obliquely, terminating in an angular projection when viewed from exterior and separated from parietal wall by broad, deep sinus, hardly calloused except for lamellae. *Columellar lamellae* two, very obliquely seated; supracolumellar lamella delicate, extending to outer margin and uniting with peristome. *Palatal folds* absent. *Peristome* erect, inner margin rather broadly and thinly calloused.

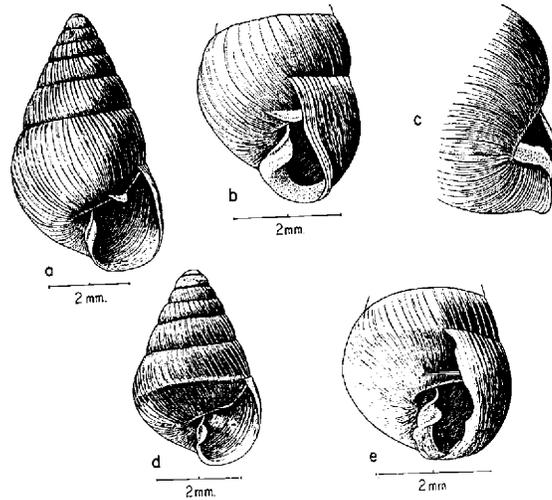


FIGURE 28.—*Mitiperna simplex simplex*: a, adult, holotype; b, adult, latero-oblique view, aperture; c, adult, profile; d, juvenile; e, juvenile, latero-oblique view.

Length 6.57 mm., diameter 3.84 (57 percent); apertural axis 2.72, diameter 1.92 (71 percent); last whorl 4.17 (64 percent); parietal lamella 0.19.

In a juvenile (fig. 28, *d, e*), whorls 6.5, parietal lamella very low, threadlike, proportionately much weaker than in adult specimens; columellar lamellae proportionately slightly stronger. *Palatal folds* absent.

Adult genitalia typical (fig. 29, *a, c*). *Ovotestis* of juvenile recovered in part (all adult ovotestes lost during extraction), follicles short clavate. *Duct and albumin gland* typical. *Prostate* large, multifolliculate; follicles slightly modified from typical: mostly ovate or round, a few short-digitate. *Spermatheca* large, apex pointed; stalk very short. *Vagina* very long, taking up nearly entire length of oviduct. *Penis* large, longer than vagina by about 0.20, curved; retractor short, heavy. Interior of penis with heavy ascending pilaster (Pil 1), with strong velum at apical curvature, ending as short papilla similar to that of *L. globosum*. *Vas deferens*, orifice not determinable, because of transparent penial wall. *Appendix* quite small, retractor short and stout.

Teeth all alike, quite large, stout, more than 100 per half row, seven- to eight-dentate. Cusps short, stout. Ecto- and entocones one to two; when two, outer of pair is behind and below, appearing shorter (tooth c, tooth 2, and tooth 50); one mesocone; one to two shorter cusps between principal cusps. Cusplets not seen and apparently absent. Central tooth: length 7 microns, width 6 microns. Tooth 50: length 11.6 microns. Teeth of this species quite large for size of shell.

Dissected 135498 (adult genitalia, teeth), five specimens; 135499 (ovotestis), one specimen.

Rapa: Mount Perahu, east ridge (type locality), under moss or on dead leaves, in crowns of birdsnest fern (*Asplenium nidus*), alt. 1,500-1,850 ft., Anderson and natives, July 28; holotype 8725 (figured juvenile 8726), paratypes 135498-135500.

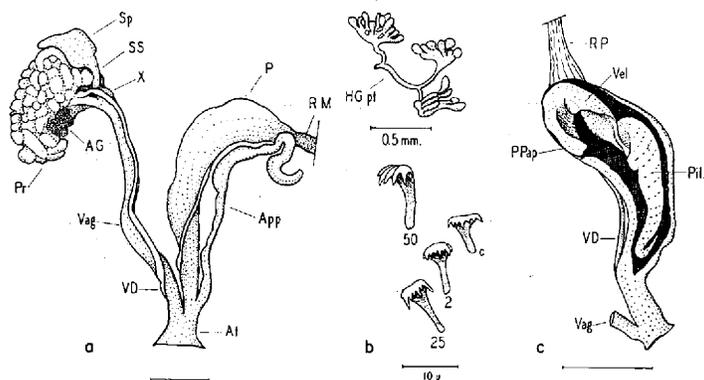


FIGURE 29.—*Mitiperua simplex simplex*: a, adult genitalia; b, teeth, c: central; c, interior of penis.

This species was taken in eight localities other than that of the type lot, but on the same ridge at altitudes from 900 to 1,800 feet. The material collected includes 35 specimens, most of which were alive when taken, representing different stages of growth. The species are not abundant in any single colony, as in only two were there more than two specimens found. Six of the colonies are represented by single specimens. All of the specimens agree closely in size, form, and texture. About one-third of them are ornamented with a broad, light band, of which the upper margin is the insertion of the aperture.

***Mitiperua simplex subcostata*, new subspecies (fig. 30, a, b).**

*Shell* slightly smaller, thinner, and lighter colored (chamois) than that of species, with a faint, broad, darker band at periphery, bordered below by a lighter band. Surface sculptured with more widely spaced and slightly stronger costulae. *Spire* with more convex outlines. *Whorls* 7.5; slightly convex. *Apertural armature* similar to that of typical form.

Length 6.20 mm., diameter 3.66 (60 percent) apertural axis 2.63, diameter 1.83 (69 percent); last whorl 3.75 (61 percent); parietal lamella 0.19.

Rapa: Mount Mangaoa (type locality), on dead leaves under tree fern, alt. 1,000-1,200 ft., Zimmerman, July 25; holotype 143341, paratypes 143342-143343 (not dissected). Mount Mitiperu, half-way to peak, under stones, W. Anderson, July 21, 142930, one dead specimen.

One live specimen (the type) and eight dead ones were collected. Of the nine specimens, seven are marked more or less with the dark peripheral band. Not all of the material is as distinctly sculptured as the type.

**Mitiperua simplex convexior**, new subspecies (fig. 30, c).

Type not quite adult, smaller than typical specimens of about same age; color chamois; outlines of spire more convex; whorls more convex; suture more impressed; columellar folds not as strongly developed.

Length 5.16 mm., diameter 2.86 (56 percent); apertural axis 2.25, diameter 1.31 (56 percent), last whorl 3.24 (62 percent), parietal lamella 0.05.

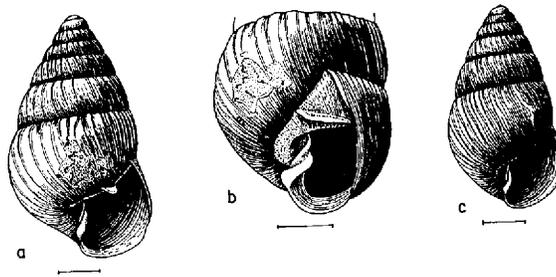


FIGURE 30.—a, b, *Mitiperua simplex subcostata*: a, adult, holotype; b, adult, latero-oblique view. c, *M. s. convexior*, subadult, holotype.

Rapa: Mount Perahu summit (type locality), on dead leaves in crown of birdsnest fern, alt. 2,050 ft., Fosberg, July 28; holotype 144790 (not dissected).

One specimen, which was taken alive, seems to offer enough differences from the typical form to be considered a subspecies. No intermediates were found. Adult specimens probably measure about 6 mm. in length.

Genus **Taitaa**, new genus

Shell imperforate, small, about 2-4 mm. long, dextral, subulate to globosely conic, thin to somewhat thickened, surface glossy, indistinctly marked with fine growth lines to striatulate. *Parietal lamella* strong, obliquely seated, entering from 0.5 to 1 whorl, columella slightly twisted, furnished with one to two oblique lamellae; palatal wall unarmed. *Aperture* ovate, margin thin or slightly thickened, outer wall slightly flattened to faintly sinuous.

Juvenile specimens have apertural armature much stronger and with more elements than adults; these are retained until almost adult stage. *Parietal lamella* proportionately much stronger, nearly straight or flaring outward in cross section, its free margin simple or somewhat sinuous. *Columella* usually furnished with three rapidly ascending lamellae. *Palatal folds* either one or two.

Distribution: Austral Islands (Raivavae, Tubuai, and Rurutu).

The generic title *Taitaa*, after the highest peak on Tubuai (Taita on maps), is proposed for a rather loose assemblage of species found on the three Austral islands west of Rapa. The nearest island, Raivavae, is about 300 miles north-west of Rapa; Tubuai is 95 miles west and slightly north of Raivavae; and Rurutu is 115 miles west of Tubuai.

Six species collected are the only representatives of the Pityisini that have been found outside of the island of Rapa. Furthermore, none of the genera that have been taken on Rapa appear to be closely related to *Taitaa*. No live specimens of two of the species, *T. neanica* and *T. terebriformis*, were taken. Undoubtedly, these two Raivavae species are still living on the island, and there should be a few additional species. Three species of *Taitaa* were taken on Tubuai. Two of them, *T. dacryma* and *T. arauana*, are terrestrial, and were taken on dead leaves and twigs and in hollow dead tree-fern stems. The third, *T. zimmermani*, was found on ferns and low shrubs, also the habitat of *T. striatula* from Rurutu. The two arboreal species, *T. zimmermani* and *T. striatula*, show some relationship and are quite distinct conchologically from the remaining four.

*Taitaa* is used in a generic sense to include the species found outside Rapa. On the basis of their conchological characters and habits the six species are separated into three sections of *Taitaa*: (1) *Taitaa* (*Taitaa*) *dacryma* and *T. (T.) arauana*; (2) *T. (Taireva) striatula* and *T. (Taireva) zimmermani*; (3) *T. (Taraia) neanica* and *T. (Taraia) terebriformis*.

## KEY TO SECTIONS AND SPECIES OF TAITAA

## Sections in Parenthesis

- A. Shells ovate-conic to subulate, juveniles with two palatal folds; Raivavae....(**Taraia**).
  - B. Shell more than 3.5 mm. long, ovately conic, lip slightly thickened in juveniles, lower palatal fold long, upper palatal short, neither beaded.....**T. neanica**.
  - BB. Shell less than 2.5 mm. in length, subulate, lip thin, juveniles with both palatal folds beaded.....**T. terebriformis**.
- AA. Shells subglobose to subcylindrical, juveniles with a single, high, compressed lower palatal fold.
  - C. Shells subglobose, columellar lamella persisting in adult specimens; juveniles with parietal lamella straight in cross section, columella with two lamellae, terrestrial; Tubuai.....**Taitaa (s.s.)**.
    - D. Shell more than 3.5 mm. long. Columellar lamella prominent, thin, high.....**T. dacryma**.
    - DD. Shell less than 2.5 mm. long. Both columellar lamellae low, thickened.....**T. arauana**.
  - CC. Shells very thin and fragile, lower columellar lamella persisting in adults. Juveniles with parietal lamella arcuate in cross section, columella with three almost equally developed lamellae, arboreal; Tubuai and Rurutu.....(**Taireva**).
    - E. Shells less than 2 mm. long, ovate, conic, nearly smooth; Tubuai.....**T. zimmermani**.
    - EE. Shells 2.3 mm. long, subcylindrical, distinctly striatulate; Rurutu.....**T. striatula**.

Section **Taitaa**

Shells small, subglobose. Columellar lamella persisting in adults. Juveniles with two columellar lamellae; palatal wall with single, high (lower) fold.

Type species: *Taitaa dacryma*.

Distribution: Tubuai.

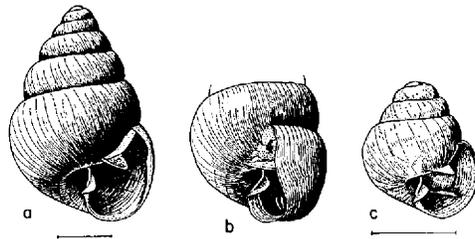


FIGURE 31.—*Taitaa (Taitaa) dacryma*: a, adult, holotype; b, adult, latero-oblique apertural view; c, juvenile.

***Taitaa (Taitaa) dacryma*, new species (figs. 31, a-c; 32, a-h).**

Shell (fig. 31, a, b), globose-conic, clay color, not thin, subtranslucent, dull, minutely distantly striate. Spire ovately conic, with slightly convex outlines, tapering to rather blunt apex. Suture deep, very narrowly margined. Whorls 6.25; embryonic whorls smooth, polished, without distinct demarcation between them and postembryonic whorls; postembryonic whorls convex, slightly shouldered above; last whorl large. Aperture nearly as wide as long. Parietal lamella strong, high, oblique, about 0.75 whorl in length, tapering gradually to its inner termination. Columella slightly sigmoid, with strong subhorizontal lamella extending to margin, with a much weaker perpendicular supracolumellar lamella forming upper and outer margin of columella; columella separated from parietal wall by rather broad V-shaped sinus. Palatal lamellae absent. Peristome thin, delicate.

Length 3.77 mm., diameter 2.55 (68 percent); apertural axis 1.71, diameter 1.03 (60 percent); last whorl 2.45 (65 percent); parietal lamella 0.29.

Juvenile shell (fig. 31, c) glossy and lighter colored. Free margin of parietal lamella not undulate. Columellar folds similar to those of adult, but proportionately somewhat stronger. Palatal wall with low, long, lower fold extending nearly to margin of aperture. This lower palatal fold almost or entirely absent in nearly mature specimens, whorls 5.5.

Egg slightly ovate.

Adult genitalia (fig. 32, b-e) similar to others of Pitysiini. Ovotestis more or less six-lobate, heavy, roughly triangular, appearing stringy; follicles small, numerous, tightly packed. Duct typical. Talon small. Carrefour small, with three protuberances above. Albumin gland minute, on or near talon; follicles minute, scarce. Prostate large, paucifolliculate. Spermatheca quite small; stalk short. Vagina fairly broad. Penis large, clavate, long ( $\pm 0.75$  oviducal length). Interior of penis with modified achatinellid pilaster: remains of ascending pilaster inverted Y-shaped; papilla large, cup-shaped, semi-pendent, fleshy, covering a small flap or valve (Ve); valve small, semi-ovate, pendulous or curled upward against orifice of vas deferens. Appendix large, translucent [figure 32, b, shows it with sperm masses (Sphr) in lower end of blind tube and also in ejaculatory apparatus]. Interior of appendical "verge" (App V) not simple and smooth but with weak, translucent, high, thin vertical folds (Fo<sub>v</sub>) extending a short distance dorsad; also with weak transverse folds (Fo<sub>t</sub>), barely indicated between vertical folds and muscular wall (MW). Retractors short, heavy. Atrium short, fairly broad.

Teeth (fig. 32, h) all alike, delicate, six- to seven-dentate. Apparently with two ecto- and two entocones, one mesocone, plus one or two fine cusplets below principal cusps. Length 6.6 microns, width 3 microns.

Paraneanic or subadult genitalia (fig. 32, *f, g*). Ovotestis thin, transparent, meager or undeveloped, with numerous globules visible within (these may be ova). Albumin gland large, multi-folliculate; follicles round or ovate. Prostate small paucifolliculate. Spermatheca large, multi-folliculate; follicles round or ovate. Prostate small paucifolliculate. Spermatheca large, two to three times that of adult. Uterus almost always distended with one egg (Ov). Vagina narrow. Penis and appendix smaller than in adult. Interior of penis with smaller penial papilla, ascending pilaster very weak, short, double.

Dissected 147812 (adult genitalia, teeth), five specimens; 142375 (interior of penis and appendix), one specimen; 147625 (paraneanic or subadult), one specimen.

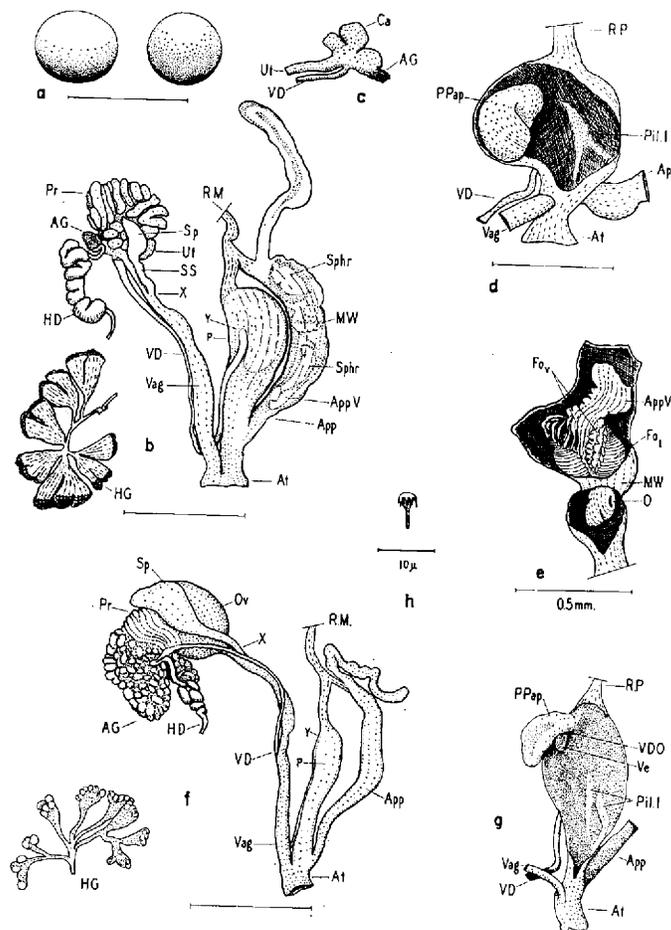


FIGURE 32.—*Taitaa (Taitaa) dacryma*: a, egg; b, adult genitalia (Sphr = spermatophore); c, carrefour complex; d, interior of penis, adult; e, interior of appendix, in part (Fo<sub>v</sub> = vertical folds, Fo<sub>t</sub> = transverse folds); f, paraneanic genitalia; g, interior of penis, paraneanic; h, tooth.

Tubuai (central): Mount Taitaa (Taita, Hydrographic map 1999) north-east slope (type locality) lower part of forest, on dead leaves, alt. 1,000 ft., Anderson and Kondo, Aug. 20; holotype 8727 (figured juvenile 8728), paratypes 147811-147817. Tubuai (west): 0.5 miles south of Araua Village, on dead leaves in jungle of *Hibiscus tiliaceus*, *Pandanus*, and *Barringtonia*, 50 ft. inland from beach, alt. 5-10 ft., Cooke, Aug. 22, 147927-147928; Tavaetu (Teraetu, Hydrographic map 1999), in forest patch in pass north of peak, on dead leaves, alt. 800 ft., Cooke, Aug. 22, 147901-147903.

*T. dacryma* was collected in a number of localities, most of which were above 700 feet, and living specimens were also found in one locality near sea level. It has never been an abundant species in any one locality, but it is probably distributed over the island wherever conditions are suitable.

*T. dacryma* does not seem to fit in with any of the genera or subgenera from Rapa. From the character of the columellar folds, it appears to be closest to the genus *Pukunia*, from which it differs in having a straighter columella, the columellar lamella persisting into the adult stage. The parietal lamella is much stronger in *T. dacryma* but shorter. The juvenile specimens are easily separated by their long, low palatal fold.

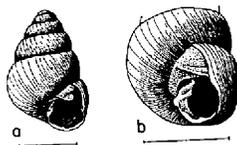


FIGURE 33.—*Taitaa (Taitaa) arauana*: a, adult, holotype; b, adult, latero-oblique apertural view.

***Taitaa (Taitaa) arauana*, new species (fig. 33, a, b).**

*Shell* very small, globose-conic, cinnamon, somewhat thickened, hardly translucent, dull, faintly striate with lines of growth. *Spire* ovate, with slightly convex outlines, apex obtuse. *Whorls* 5.25, slightly convex, upper whorls indistinctly shouldered above, increasing regularly, separated by a distinct suture; last whorl large, flattened behind aperture, with a broad, very shallow depression. *Aperture* rather large. *Parietal lamella* strong, thickened, obliquely inserted, about 0.75 whorl in length; columella only slightly twisted, furnished with two low, thickened, nearly equal and rapidly ascending lamellae, of which the lower extends to the outer margin. *Palatal folds* absent. *Peristome*: lower and outer lip slightly thickened.

Length 2.13 mm., diameter 1.42 (66 percent); apertural axis 0.64, diameter 0.64 (100 percent); last whorl 1.42 (66 percent); parietal lamella 0.13.

Tubuai (western end), back of Araua village (type locality), 200 yds. inland, under dead *Pandanus* leaves, alt. 5-10 ft., Cooke, Aug. 22, holotype 147929.

Only a single dead specimen was found. It differs from *T. dacryma* in size, in the number of whorls, and in the very different columellar lamellae. No juvenile specimen was collected.

Section *Taireva*

Shells small, subcylindrical, striatulate; sub-columellar lamella persisting in adults. Juveniles with three columellar lamellae; palatal wall with single high (lower) fold.

Type species: *Taitaa striatula*.

Distribution: Tubuai and Rurutu.

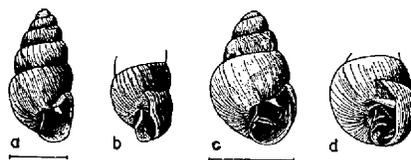


FIGURE 34.—*Taitaa (Taireva) striatula*: a, adult, holotype; b, adult, latero-oblique apertural view; c, juvenile; d, latero-oblique apertural view of c.

***Taitaa (Taireva) striatula***, new species (figs. 34, a-d; 35, a-e).

*Shell* (fig. 34, a, b) subcylindrical, sayal brown, lighter toward apex, thin, subtransparent, dull, under lens striate. *Spire* narrowly conic, with slightly convex outlines, tapering gradually to rather sharp apex. *Suture* well impressed, indistinctly, narrowly margined. *Whorls* 6, increasing slowly and regularly; embryonic whorls smooth, polished, forming a rather acute cone; postembryonic whorls convex; last whorl oblong, slightly flattened. *Aperture* perpendicular, narrow, subauriform, outer margin slightly flattened. *Parietal lamella* high, strong, thin, obliquely seated, about 0.75 whorl in length, its inner 0.5 much lower than outer. *Columella* strongly twisted, outer margin thickened, with a low, deeply seated, lamella-like fold near its base; viewed from outside, columella forms a wide V-shaped sinus. *Palatal folds* absent. Outer margin of aperture thin.

Length 2.31 mm., diameter 1.13 (49 percent); apertural axis 0.87, diameter 0.48 (55 percent); last whorl 1.39 (60 percent); parietal lamella 0.16.

Juvenile specimens, not quite 5 whorls, slightly lighter in color. Columella furnished with three prominent, equally spaced lamellae, the lowest somewhat weaker and more deeply seated. Parietal lamella proportionately high, long, its free margin flaring outward. Palatal (lower) fold strong, high, lamella-like, about 0.3 whorl in length.

Egg (fig. 35, a) ovate.

Near-adult genitalia (fig. 35, b, c) quite similar to that of *T. dacryma*, except for very small size. *Ovotestis* five-lobate, silky, stringy, nearly full. *Duct* swollen, convoluted. *Talon* large, curvature long. *Carrefour* not dissected. *Albumin gland* not seen. *Prostate* large, multi-folliculate. *Spermatheca* large, ovate with blunt point; stalk short. *Uterus* enlarged, recently evacuated (note diaphanous collapsed portion at region of X). *Vagina* long, quite broad. *Penis* small, short for this tribe (probably not fully mature), 0.3 oviducal length, clavate. Interior of penis with only papilla, without valve or remnants of ascending pilaster as in *T. dacryma*; base pierced by orifice of vas deferens (VDO). *Appendix* small.

Paraneanic genitalia (fig. 35, d, e) differ slightly from near-adult: almost always with one egg in uterus. *Spermatheca* smaller. *Penis* and *appendix* reduced; interior of penis with small conical papilla. *Ovotestis* also immature; lobes clavate, translucent.

Dissected 148776 (near-adult, subadult, interior of penis), five specimens. Most of the animals were badly torn. Since those preserved entire within their

shells were few, only two were broken out. Unfortunately, a good adult genitalia could not be found.

Rurutu: Mount Manureva, southeast slope (type locality), in small patch of native forest, on ferns, alt. 1,100 ft., Zimmerman, Anderson, and Kondo, Aug. 30; holotype 8729 (figured juvenile 8730); paratypes 148776-148778, 70 specimens. Mount Teape, on ferns and shrubs, alt. 1,000 ft., Zimmerman, Sept. 2, 144867, two specimens.

*T. striatula* and the following species, *T. zimmermani*, are among the very few of those associated under the subfamily Pitysiinae, which are almost strictly arboreal in habit.

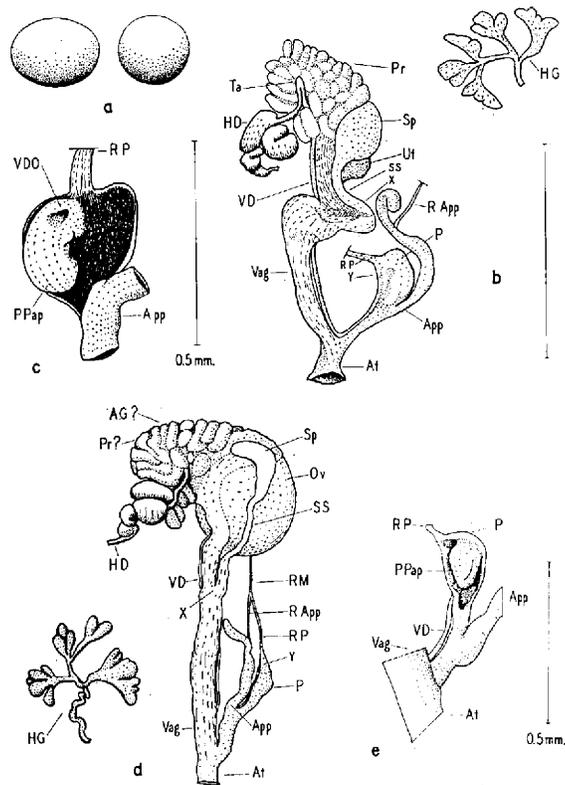


FIGURE 35.—*Taitaa (Taireva) striatula*: a, egg, lateral and frontal views; b, genitalia, subadult; c, interior of penis, subadult; d, genitalia, paraneanic; e, interior of penis, paraneanic.

**Taitaa (Taireva) zimmermani**, new species (fig. 36, *a-d*).

Closely related to *T. striatula*, but smaller, lighter in color (chamois), more conical in outline, spire tapering more evenly to a sharper apex. *Whorls* 5.5, more distinctly striate; last whorl not as flattened dorsally. *Apertural armature* similar in both species but proportionately a little more accentuated in *T. zimmermani*. *Ovotestis* well filled, silky, white. *Albumin gland* (?) or prostate (?) well developed, follicles large, distended, quite numerous. *Penis* clavate. *Appendix* like that of *T. dacryma*.

Length 1.93 mm., diameter 1.03 (53 percent); apertural axis 0.81, diameter 0.48 (59 percent); last whorl 1.52 (78 percent); parietal lamella 0.18.

In juvenile specimens edge of the parietal lamella flares outward more strongly and palatal fold (lower) is somewhat stronger.

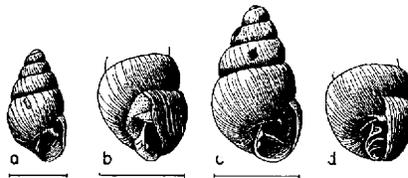


FIGURE 36.—*Taitaa (Taireva) zimmermani*: a, adult, holotype; b, adult, view of columella; c, juvenile; d, juvenile, view of columella.

Dissected 147845, two specimens.

Tubuai: Mount Taitaa, southwest ridge, on ferns, alt. 1,200 ft., Zimmerman, Aug. 20; holotype 8731 (figured juvenile 8732); paratypes 147844-147845, eight specimens. Mount Pane, east ridge, north side of crest, alt. 1,200 ft., Zimmerman, Aug. 23, 148013, two specimens.

This is apparently a rare species, as it was taken only when ferns were beaten for insects. Only one adult was collected, the remainder being immature.

Although only fragments of the genitalia (not figured) were recovered, there was more than sufficient material to indicate that this species belongs to the genus *Taitaa* and to the subfamily Pitysiinae.

### Section **Taraia**

Shells small, smooth or faintly striatulate, upper two columellar lamellae persisting as low, thick ridges in adult specimens. Juveniles with three columellar lamellae, of which middle one is somewhat more pronounced; palatal wall furnished with lower and upper palatal folds.

Type species: *Taitaa neanica*.

The name is based on neanic, or juvenile, in the sense that the vestiges of some of the juvenile characters are retained in the adult.

Distribution: Raivavae.

No live specimens of the two species included in this section were ever found. This section differs from the other two in having an upper palatal fold.

**Taitaa (Taraia) neanica**, new species (fig. 37, a-e).

*Shell*, fossil, elongately conic, color white, fairly thick, opaque, with a dull sheen, growth striae fine, interspersed with faint striatulae. *Spire* quite long, straightly conic, tapering slowly and evenly apicad. *Suture* moderately impressed. *Whorls* 6.5; embryonic whorls obtuse, fairly large; postembryonic whorls slightly convex; last whorl broad, tapering regularly to base. *Aperture* vertical, semiovate, outer margin evenly rounded. *Parietal wall* thickened by callus. *Parietal lamella* strong, compressed, oblique, one whorl long, gradually diminishing in size interiad. *Columella* subvertical, thickened, with two weak lamellae (seen better obliquely), supracolumellar lamella stronger, the columellar lamella weaker, subcolumellar lamella absent. *Palatal wall* thick, lamellae absent. *Peristome* erect.

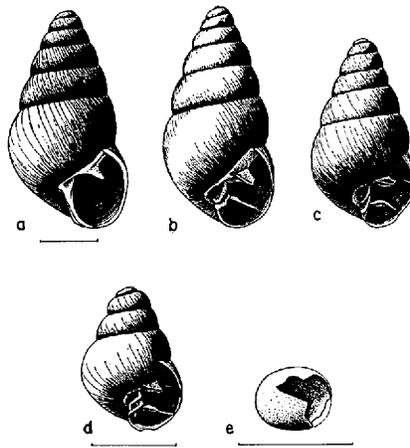


FIGURE 37.—*Taitaa (Taraia) neanica*: a, adult; b, paraneanic; c, parametaneanic; d, ananeanic; e, egg.

Length 3.8 mm., diameter 2.0 (55 percent); apertural axis 1.4, diameter 1.1 (77 percent); last whorl 2.2 (61 percent); parietal lamella 0.23.

Paraneanic juvenile. Columella triplicate, supracolumellar lamella linear, oblique, cutting across front edge of columella; columellar lamella subtransverse, with a slight expansion; subcolumellar lamella weak, small. Parietal wall thinly calloused; parietal lamella thinner than in adult, with one shallow sinuosity visible interiad. Palatal fold one (lower), continuous, inner part high, outer part low, linear. (Length 4 mm., whorls 6.5, 10186.)

Paraneanic to metaneanic stage. Columellar folds thinner, higher than in paraneanic. Parietal lamella with two sinuosities visible, the outer forming a small ridge on free margin of lamella. Palatals two; the lower with a median rise; the upper discontinuous, short, low. (Length 3 mm., whorls 6.0, 10187.)

Ananeanic stage. Last whorl subglobose. Two upper columellar lamellae more transverse, relatively weaker than in para- to metaneanic stages. Parietal lamella thin, with two shallow depressions on margin. Lower palatal fold shaped as in above stage but very much weaker; upper very weak, hardly visible. (Length 1.75 mm., whorls 4.3, 10188.)

Egg elliptical. Diameter 0.58 mm.; length 0.7. (Recovered by squirting shells with water to clean aperture, 10189.)

Raivavae: 0.5 mile southwest of Ahuovi Point, in hau and lime thicket, Cooke, Anderson, and Kondo, Aug. 9 [according to plotted map, near Mato-

tea, just back of beach; this locality is identical with that of *Taitaa terebriformis*]; holotype 10185; paratypes 10186-10189, 147106, 142179.

About 92 specimens of *T. neanica*, including fragments, were collected with *T. terebriformis*. Some unweathered specimens show that the shell is brown in color interspersed with uncolored zones, giving the shell a banded look (142179).

*T. neanica* is nearly the size of *T. dacryma*, but it differs in shape. In armatural formula it is similar to *T. terebriformis*, although the lower fold resembles that of *T. dacryma*, *T. striatula*, and *T. zimmermani*. Of the extra-Raivavae shells, *T. neanica* is closest to *T. striatula* from Rurutu as regards apertural armature.

The differences between *T. neanica* and *T. dacryma* are as follows: *T. neanica* is conical in shape; has three columellar lamellae, two of which persist into the gerontic stage; and has two continuous palatal folds. *T. dacryma* is shaped like a teardrop and has two columellar lamellae and one palatal fold.

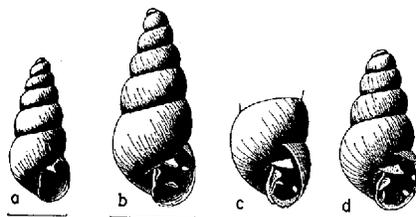


FIGURE 38.—*Taitaa (Taraia) terebriformis*: a, adult, holotype; b, paraneanic; c, paraneanic, latero-oblique apertural aspect; d, metaparaneanic.

***Taitaa (Taraia) terebriformis*, new species (fig. 38, a-d).**

*Shell*, fossil, subulate, color whitish gray, fairly thick, opaque, dull, growth striae fine, faint. *Spire* elongate, outlines straight, tapering evenly apicad. *Suture* well impressed. *Whorls* 6.3; embryonic whorls obtuse, large; postembryonic whorls convex; last quite broad, tapering fairly evenly and gradually to base. *Aperture* vertical, subovate, outer margin rounded. *Parietal lamella* strong, compressed, oblique, approximately 0.5 whorl long, gradually diminishing. *Columella* subvertical, inner margin thickened, lamellae absent. *Palatal wall* slightly thickened, lamellae absent. *Peristome* thin, erect.

Length 2.5 mm., diameter 1.1 (44 percent); apertural axis 0.77, diameter 0.52 (67 percent); last whorl 1.3 (53 percent); parietal lamella 0.13.

Paraneanic juvenile with embryonic whorl tipped to right side of shell. *Columella* triplicate, supracolumellar lamella linear, subvertical; columellar lamella broad, thick, subtransverse; subcolumellar lamella small, deeply seated, subtubercular. *Parietal lamella* with shallow dip visible on margin. *Palatal folds* two, the lower interrupted; denticles short, low, thickened (two visible); the upper also interrupted, weaker than lower (one visible). (Length 2.25 mm., whorls 6.3, 10191.)

Metaneanic-paraneanic stage, columellar lamellae thinner, weaker. *Parietal lamella* the same as in paraneanic. *Palatal folds* smaller but perceptibly higher, both apparently seated on very low callus. (Length 2 mm; whorl 5.5, 10192.)

Raivavae, 0.5 miles southwest of Ahuoi Point [according to plotted map near Matotea, just back of beach], in hau and lime thicket, Cooke, Anderson, and Kondo, Aug. 9; holotype 10190; paratypes 10191-10192, 147107.

Fourteen specimens were collected, but the absence of living shells and the paucity of juveniles make it difficult to determine the exact generic position of this species. It is, however, safer to assign it to the genus *Taitaa* than to *Tubuaia*. The shell is somewhat like that of the *Strobilus turritus* group; and the palatal denticles are, in form and spacing from one another, similar to that of *Pityis pagodiformis*. The tribe Tubuaiini is a very uniform group, the shells being of nearly uniform shape. On the other hand, the tribe Pityisini is rich in variety of forms, sizes, and shapes. All the adults are gerontic, the parietal wall being overlaid by a thick callus.

The differences between *T. terebriformis* and the type species, *T. dacryma*, are as follows: *T. terebriformis* is turritid; the columella is triplicate; the palatal folds are biplicate, separated into denticles. *T. dacryma* is tear-drop shaped; the columella is biplicate; and it has only one palatal fold, which is continuous rather than broken into denticles.

#### Genus *Apopityis*, new genus

*Shell* imperforate, subulate, embryonic whorls finely but distinctly spirally striate, postembryonic whorls distinctly, closely, evenly costate. *Parietal lamella* moderate, slightly more than one whorl in length (in juvenile specimens strong, its free margin sinuous and without tubercles on its lower face). *Columella* with three distinct obliquely seated lamellae. *Palatal wall* with a rather long basal fold.

Type species: *Apopityis andersoni*.

Distribution: Rapa.

This genus is intermediate between *Pityis* and *Strobilus*; but it is apparently closer to *Pityis*, approaching *Strobilus* in form only. It differs in having more distinctly spirally striate embryonic whorls, a costate surface, and three columellar lamellae. In juvenile specimens the parietal lamella is stronger, flaring outward, the free margin distinctly sinuous.

*Apopityis* differs from *Pityis* in lacking an umbilicus, or foveola; in having more convex whorls; in costae which are more closely spaced but not extended near the periphery; and, finally, in the position and in the type of the columellar lamellae. In juvenile specimens the parietal lamella does not have the extreme sinuosity of the free margin. The tubercles of the lower face, a distinct character of the juvenile *Pityis*, are lacking.

#### *Apopityis andersoni*, new species (fig. 39, a-d).

*Shell* subulate, thin, translucent, clay color; distinctly, finely, and closely costate; costae continues, with scarcely any lessening in strength, to axis of shell. *Spire* elongate, narrow, tapering slowly to a rather sharp apex, outline nearly straight. *Suture* well impressed. *Whorls* 9.25; embryonic whorls minutely, closely spirally striatulate, convex, shouldered above, sutures distinct; postembryonic whorls convex, the last oblong, tapering gradually

to base. *Aperture* longer than broad, subauriform. *Parietal lamella* medium in height, erect, a little more than one whorl in length. *Columella* nearly straight, slightly sigmoid, inner face somewhat thickened, furnished with three obliquely seated, thickened low folds. *Palatal wall* with a spirally entering row of three to four rather distinct oblong lower folds united by a low callus; this callus, with its folds, clearly visible through shell when viewed from exterior and about 0.3 whorl long. *Peristome* thin, erect. Viewed obliquely, columella extends to basal palatal wall in a slightly thickened callus, bordered above by subcolumellar lamella.

Length 6.49 mm., diameter 2.45 (37 percent); apertural axis 1.27, diameter 1.12 (70 percent); last whorl 3.01 (45 percent); parietal lamella 0.23.

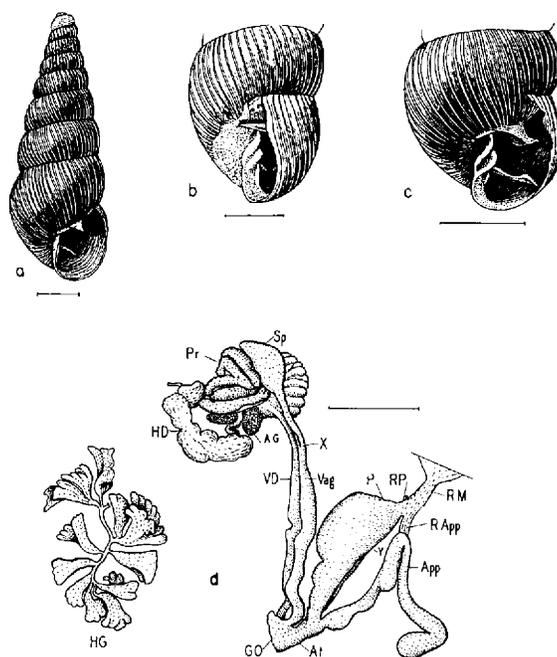


FIGURE 39.—*Apopitys andersoni*: a, adult, holotype; b, adult, latero-oblique view of aperture; c, juvenile, latero-oblique view of aperture; d, genitalia.

In a juvenile specimen with 7 whorls, the parietal lamella is strong, its free margin sinuous and flaring outward, without tubercles on its lower face. Columella furnished with three obliquely seated lamellae, of which columellar lamella is strongest, subcolumellar lamella weakest and somewhat more deeply seated. Palatal fold strong, nearly 0.5 whorl in length, and consisting of four oblong denticles connected by a distinct callus.

Genitalia similar to *Pityis* except for following characters: *ovotestis* 10-lobate; *albumin gland* visible, minute, around carrefour, follicles minute, numerous; *prostate* larger, follicles longer and larger; *spermatheca* larger, stalk longer; *vas deferens* broader but shorter; *penis* with greatly enlarged head, with narrow stalk (length 0.75 of oviducal length); *appendix* more robust, twice penial length; *retractors* short, heavy.

Dissected 138623 (adult), two specimens.

Rapa: Mount Mangaoa, northeast ridge (type locality), in small wooded ravine near crest of ridge, under stones, alt. about 800 ft., Anderson, July 25; holotype 8733 (figured juvenile 8734), paratypes 138362-138366. Additional localities are Mount Vairu, alt. about 1,100 ft., 140135-140136, 143486-143487; Mount Ruatara, alt. about 900 ft., 143555-143556; Mount Perahu, 1,300-1,800 ft., 135448, 135455, 142846, 142889; Maitua Valley, alt. about 500 ft., 135533, 140032-140035, 144205; and Mount Koara, alt. about 800 ft., 142527.

Just over 200 specimens of this species were taken from eight colonies. Nearly three-fourths came from a single colony that was visited three times, whereas the species appeared to be extremely rare in the other seven colonies. Specimens were found in rather scattered colonies from Mount Vairu, north of Ahurei Bay, to Mount Koara, near the southeastern point of the island. All specimens except those found in Maitua Valley came from damp, wooded slopes of peaks or rather high ridges. All live specimens were taken under stones. In two or three colonies, specimens were taken with *Pitys*.

This species, named for Donald Anderson, is much more consistent in all characters than are the species of *Pitys*, varying only in size from colony to colony. Apparently, isolation has not helped to produce recognizable forms although, to judge from the colonies located, *Apopitys* has a wider distribution.

The illustrated animal was strongly contracted, which may account for the enlarged penis head and the short, heavy retractor.

#### Genus *Pitys* Mörch

?*Pitys* Beck, 1837, Index Molluscorum, 9 (*nomen nudum*).—Mörch, 1852,

Cat. Conchyl. Yoldi 1: 6, for *Helix bilamellata* Pfeiffer (not Sowerby) = *pagodiformis* E. A. Smith.

*Pitys* Pilsbry and Cooke, 1933, Nautilus 47 (2): 61 (Tornatellinidae).

*Diaglyptus* Pilsbry, 1892, Man. Conch. 8: 86.

*Diglyptus* Pilsbry, 1893, Man. Conch. 9: 22.

*Shell* umbilicate or imperforate with a shallow foveola, turbinate to elongate, embryonic whorls spirally finely striate, postembryonic whorls strongly ribbed, ribs thin, extended near and at periphery. *Whorls* 7 to 9. *Parietal lamella* strong, long (about 1 whorl in length), obliquely seated. *Columellar lamellae* three, upper two close, parallel, seated on a raised callus, coalescing near their outer terminations and forming a slightly raised prominent nodule or narrow plate. *Subcolumellar lamella* weak, deeply seated, visible only when aperture is viewed obliquely. *Palatal wall* unarmed, sometimes with a low, rather short plica. *Peristome* with outer margin thin, erect; lower margin indistinctly thickened.

Juveniles with apertural armature proportionately more strongly developed than in adults. *Parietal lamella* strong, arcuate in section, flaring outward, its free margin sinuous, its lower surface ornamented with a row of three to four elongate tubercles nearly parallel to its base. *Columella* with three distinct folds; *supracolumellar lamella* thin, high; *columellar lamella* calloused, slightly higher, *subcolumellar lamella* more deeply seated, much more prominent nodule or narrow plate. *Subcolumellar lamella* weak, deeply seated, visible only (*P. scalaris*) with a basal row of three to four elongate tubercles seated on a delicate callus, entering spirally for about 0.3 whorl. In the third species (*P. alpestris*) the palatal fold is simple, not divided into tubercles.

Type species: *Pitys pagodiformis*.

Distribution: Rapa.

The genus, which is confined to the island of Rapa, is the only genus of the family with distinct, high costae. The closest ally of *Pitys* is *Lamellovum*, from which it is easily differentiated by the costae and by the less complex apertural armature.

*Pitys* is terrestrial in habit, but one species (*P. alpestris*) was taken one or two feet above ground, on dead leaves within the crown of a birdsnest fern. This genus was taken only in native forests, from about 200 feet to nearly 2,000 feet. Except for the Area lot, specimens were very rare in all localities in which we collected.

Excluding the species of *Tornatellides* and *Tornatellaria*, *Pitys pagodiformis* is the only species of the family with a distinct umbilicus. This umbilicus is shallow, at most only three whorls deep. Juveniles are imperforate. In *Auriculella* many of the species have been described as being perforate, the perforation more than one whorl in depth. In *Tornatellides* and *Tornatellaria* the perforation is deep, sometimes indicated in embryonic specimens by a minute cleft.

#### KEY TO SPECIES OF PITYS

- A. Shell umbilicate for about two whorls, turbiniform.....*P. pagodiformis*.  
 AA. Shell with shallow foveola, elongate.  
     B. Whorls flattened, base slightly convex.....*P. scalaris*.  
     BB. Whorls convex, base tapering.....*P. alpestris*.

The following forms of *P. pagodiformis* will be treated: *A* from Morongota; *B* from Mount Perahu; *C* from Mount Ruatara; *D* from Area; and *E* from Mount Mangaoa.

***Pitys pagodiformis*** (E. A. Smith). Figure 40, *a, b*.

*Helix bilamellata* Pfeiffer, 1845, Zeitschr. f. Malak., 84; 1848, Mon. Hel. Viv. 1: 188; 1846?, Conch.-Cab., Helix 2: 203, pl. 101, figs. 16-18.—Reeve, 1852, Conch. Icon., Helix, 646, pl. 113; 1859, Mon. Hel. Viv. 4: 157 (*Pitys oparana* Beck).

*Endodonta bilamellata* Albers, 1850, Die Heliceen, 89.

*Pitys bilamellata* Mörch, 1852, Cat. Conchyl. Yoldi 1: 6.—Pease, 1871, Zool. Soc. London, Proc., 474 [= *Endodonta* (*Thaumatodon*) plus *Charopa*].

*Helix* (section *Endodonta* subsection *Laoma*) *bilamellata* Tryon, 1887, Man. Conch. 3: 68, pl. 13, fig. 57.

*Patula pagodiformis* E. A. Smith, 1892, Zool. Soc. London, Proc., 262.

*Patula* (subgenus *Endodonta*, section *Diaglyptus*) *bilamellata* Pilsbry, 1892, Man. Conch. 8: 86.

*Endodonta (Diglyptus) pagodiformis* Pilsbry, 1894, Man. Conch. 9: 22, pl. 5, fig. 54.

*Pitys pagodiformis* Pilsbry and Cooke, 1933, Nautilus 47 (2): 61.

"Shell umbilicate, thin, corneous, longitudinally strongly and regularly plicate; spire elongate, above strongly attenuate, acute; whorls 9, carinate (carina exerted, acute, sub-aculeate), the last with a slightly convex base; umbilicus narrow, open; aperture sub-vertical, subquadrangular, diminished in size by two lamellae; the one entering on the parietal wall, the other, thicker, on the columella; lip simple, erect. Length 4.5, diam. maj. 4.0, min. 3.66 mm." (Pfeiffer.)

Shell umbilicate, umbilicus funnel-shaped, narrow toward apex, enlarging rather rapidly for last three whorls, perspective turbinate, slightly thickened, translucent; color chamois except embryonic whorls, strongly ribbed, ribs widely spaced, uniform, somewhat stronger above and at the bluntly angulate periphery, weak or vanishing on base. Spire broadly conic with slightly concave outlines; apex nipple-like. Whorls 8.75; embryonic whorls distinctly spirally striate; postembryonic whorls flattened above, bluntly angulate at

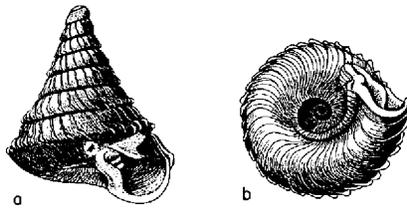


FIGURE 40.—*Pitys pagodiformis*: a, adult, typical form, collected by Cuming (?); b, adult, ventral aspect.

periphery and extending over the rather deep suture; last whorl somewhat flattened below, more convex toward umbilicus. Umbilicus indistinctly margined. Parietal lamella long, strong, flaring outward. Columella heavily calloused, with two parallel, nearly transverse thickened folds; the lower stronger than upper and continued beyond columellar margin, forming a calloused nodule; a third, minute, deeply seated fold is present just above base of columella. Aperture subquadrate, outer lip thin, lower two-thirds thickened. Palatal plicae absent.

Length 4.12 mm., diameter 3.28 (80 percent); apertural axis 1.45, diameter 1.33 (92 percent); last whorl 2.02 (49 percent); parietal lamella 0.30.

Opara [Rapa, May 13-17, 1828], 117332, from Acad. Nat. Sci., Philadelphia, one specimen, illustrated; 167593, from Fulton, one specimen. These two specimens are probably part of the original material collected by Cuming. Nearly typical dead shells were collected in Tumu Valley just north of Morongota, in talus slope at foot of cliff, alt. 150-200 ft., Cooke, July 13, 140224.

We found *P. pagodiformis* in only six localities, five of which yielded 12 or fewer specimens, mostly dead. Area was the exception. As nothing was known of the ecology of *P. pagodiformis*, all suitable conditions were searched. Three weeks of daily searching finally yielded a colony containing a suitable series. The six localities, loosely distributed over more than three-fourths of the slopes facing Ahurei Bay, were separated by bare ridges and valleys; and no colony

occupied more than a few square yards. Each colony had probably been isolated for a long time, and consisted of a fairly distinct geographical race quite consistent in most of its characters.

The species is sedentary in habit and undoubtedly lives under very restricted ecological conditions. Practically all our live specimens were taken under small damp stones in shallow talus, overgrown with large shrubs. Few were taken on dead leaves or twigs. With the scanty material at hand, it seems inadvisable to designate these by subspecific or varietal names.

A comparison with our localized material of the two specimens which were supposedly collected by Cuming indicates that his material came from the slopes leading to Morongota Peak. Cuming's specimens are intermediate in character between our Tumu shells and those taken near the top of Morongota. His are slightly larger than the Tumu ones but have fewer costae (Cuming 31, Tumu 38). In both forms the costae are weak and non-alate and the umbilicus is wide. The Morongota specimens are larger, have straighter outlines, fewer but much stronger costae (22-25, on last whorl), and a narrower umbilicus.

***Pitys pagodiformis* form A (fig. 41, a).**

Shell slightly longer than type form (whorls 9.5), proportionately narrower and somewhat thicker; outlines of spire less concave; costae (22-25) much stronger, decidedly alate just above and at periphery; umbilicus narrower, about two whorls visible when viewed ventrally, without indication of a margin. Columellar folds (in the six mature shells) offer some differences from the typical: supracolumellar fold higher and less calloused, extending to outer margin of columella; columellar fold, on reaching margin, indistinctly bifid, lower fork turning abruptly downward; subcolumellar fold slightly stronger, deeply seated just above base of columella. Low palatal fold in a few mature specimens. Columellar fold in nearly mature specimens well developed, simple, extending to margin of columella.

Figured specimen (8735): Length 4.50 mm., diameter 3.28 (71 percent); apertural axis 1.30, diameter 1.33 (102 percent); last whorl 1.87 (41 percent); parietal lamella 0.30.

Rapa: Mount Morongota, southwest side, near tip of peak, alt. about 800 ft., W. Anderson, Cooke, and Kondo, July 13, 140407.

The material consists of 12 whole or nearly whole specimens.

***Pitys pagodiformis* form B (fig. 41, b).**

Shell nearly same length as typical form, whorls almost 9, of about same proportionate width; umbilicus funnel-shaped, with almost three whorls visible in ventral view, not as distinctly margined. Spire with nearly the same concave outlines. Last whorl with 31 costae (figured specimen); costae somewhat alate above, at, and just below bluntly angular periphery and continued more strongly across base. The two columellar folds coalesce just inside outer margin of columella, and expand above and below, forming a heavily calloused, irregular, almost platelike process.

Figured specimen (135212): Length 3.93 mm., diameter 3.17 (81 percent); apertural axis 1.22, diameter 1.14 (93 percent); last whorl 1.73 (44 percent); parietal lamella 0.34.

Rapa: Mount Perahu, southeast ridge, on dead damp leaves, alt. about 1,000 ft., Anderson, July 13, 135213-135214.

The material contains seven specimens, of which one is fully adult.

***Pityis pagodiformis* form C (fig. 41, c).**

Length 3.1, diameter 2.3 (74 percent); apertural axis 0.95, diameter 1.06 (111 percent); last whorl 1.48 (48 percent); parietal lamella 0.35.

Rapa: Mount Ruatara, northeast slope, alt. about 750 ft., Kondo, July 26, 143498.

A single dead juvenile, taken from Mount Ruatara, probably belongs to a race we found nowhere on Rapa. It does not agree closely with the juvenile of other forms of the same age (just over seven whorls). The outlines of the spire are straighter, the umbilicus narrower, and the diameter is proportionately less. The costae are continued for a greater distance on the base.

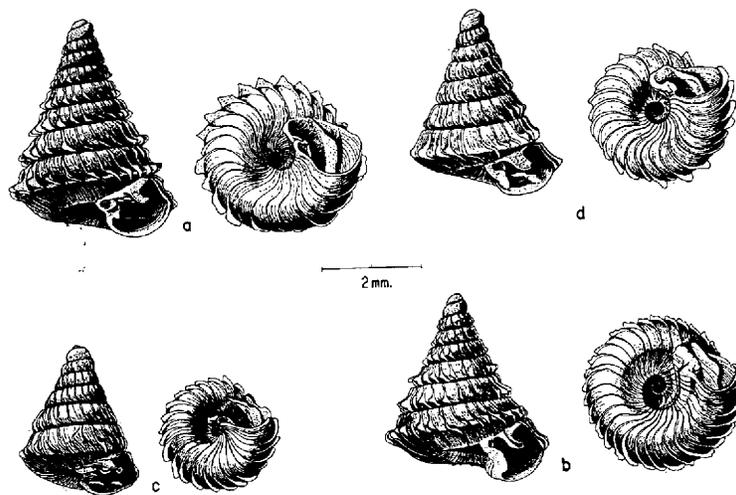


FIGURE 41.—*Pityis pagodiformis*, Rapa: a, form A, Morongota; b, form B, Mount Perahu; c, form C, Mount Ruatara; d, form E, Mount Mangaao.

***Pityis pagodiformis* form D (figs. 42, a-g; 43, a-e).**

Shell (fig. 42, a-c) smaller than typical form, whorls nearly 7.5, thinner, subtransparent, color cinnamon buff; costae (28) plainly visible through shell, finer and more extended near periphery, more distinct on base; umbilicus narrower, with nearly two whorls visible from below. Parietal lamella high, thickened, free margin flaring slightly outward. Columella typical; supracolumellar and columellar folds coalescing more or less on nearing their outer terminations and expanding upward, downward, and inward, forming an irregular narrow platelike protuberance; subcolumellar fold deeply seated and visible only when aperture is viewed obliquely. In adult specimens, with lower peristome slightly thickened, palatal wall is unarmed; in some is an indication of a lower tubercle.

Only one animal containing an egg was found. Egg (fig. 42, g) oval, slightly broken, with thin calcareous shell,  $0.73 \times 0.55$  mm.

Figured specimen: Length 3.52 mm., diameter 2.82 (80 percent); apertural axis 1.22, diameter 1.18 (97 percent); last whorl 1.72 (49 percent); parietal lamella 0.28.

In a nearly mature juvenile specimen (fig. 42, *d, e*), whorls 7, the parietal lamella is proportionately stronger than in adults, a little more than one whorl in length, its outer 0.3 diminishing gradually toward interior, its free margin flaring outward, sinuous, bent into several lobes. Lower face furnished with a riblike process consisting of three to four elongate, more or less connected tubercles, only one of which is shown in the figure. Columella with three folds; supracolumellar fold long, low, not extending to outer margin of columella; columellar fold strong, high, almost transversely seated and reaching columellar margin; subcolumellar fold deeply situated, not visible except in oblique view of aperture, much shorter than other two, very strong and blunt. Lower palatal wall with strong lamella; lamella consisting of two to four (usually three) oblong tubercles arranged in a spiral row; viewed from the exterior, through the shell, these tubercles appear to be united by an indistinct callus extending inward for about 0.5 whorl.

In very young specimens, whorls about 4, apertural armature is proportionately more strongly developed, the supra- and subcolumellar folds not as deeply seated as in older and adult specimens. Juvenile shells up to about 6 whorls are apparently imperforate.

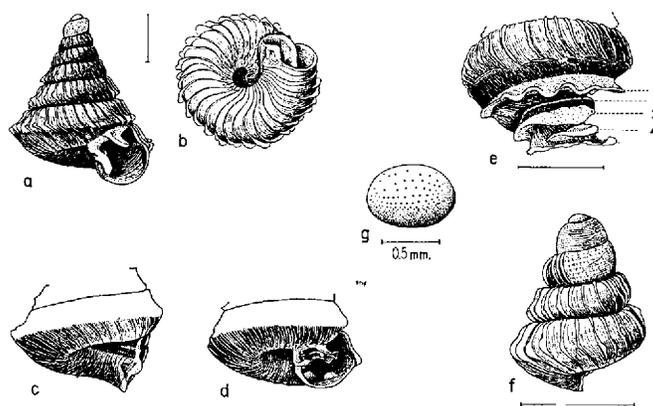


FIGURE 42.—*Pitya pagodiformis* form *D*: a, adult; b, adult, ventral view; c, adult, profile; d, paraneanic, apertural teeth; e, paraneanic, internal architecture of apertural armature, (1) parietal, (2) supra-columellar, (3) columellar, and (4) subcolumellar lamellae; f, ananeanic, boundary between embryonic and postembryonic whorls; g, egg.

Adult genitalia (fig. 43, *a*). *Ovotestis* with about six lobes. *Duct* enormously distended, robust, convoluted. *Talon* small, recurved. *Carrefour* small. *Vas deferens* large, about 0.5 oviducal diameter, entering penis 0.3 way below apex. *Albumin gland* minute or absent. *Prostate* large; follicles few (18 to 20), digitate to ovate. *Spermatheca* large, bluntly pointed; stalk very short, large, ending just below exit of vas deferens from carrefour. *Vagina* long, rather narrow. *Penis* large, nearly as long as vagina, tapering from middle toward both extremities; retractor very short, robust. Interior of penis simple, with ascending reflexed pilaster (Pil 1) terminating in semi-pendent, spoon-shaped tongue or penial papilla (P Pap), furrowed in the inner surface; few short pilasters along midbody. *Appendix* slightly shorter than penis or equal to it in length, narrow, bluntly pointed, with small twin bulges in middle; retractor long, rather thin. *Atrium* short, wide.

Teeth (fig. 43, *e*) all alike, very small, five- to six-dentate. Generally three-cuspid with two to three fine cusplets but occasionally all equally alike. Length 7 microns, width 3 microns.

Paraneanic or subadult genitalia (fig. 43, *c*). *Ovotestis* immature, lobes distally blunt; duct slightly bulging at middle, convoluted. *Albumin gland* large, multifolliculate; follicles small, ovate to round. *Prostate* about 0.3 size of albumin gland, multifolliculate; follicles minute, smaller than those of albumin gland, numerous, ovate to round. *Spermatheca* large,

bulging basally, bluntly pointed, resting on prostate. Stalk very short. Vas deferens and vagina proportionately the same as in adult. Penis differing from that of adult in having large head, narrow stalk; retractor long, thin. Appendix narrow, long, median bulge just developing, distal end curved, rather sharply pointed; retractor thin, long.

In paraneanic specimens, albumin gland well developed and prostate weak, with small follicles. Penial complex weak, not robust. These characteristics are peculiar to all genera of Pitycini.

Younger juvenile (fig. 43, *d*, metaneanic) with small pointed penis, short bluntly pointed appendix, reminiscent of *Tornatellinops* and *Tubuuaia*. Albumin gland, prostate, spermatheca undifferentiated.

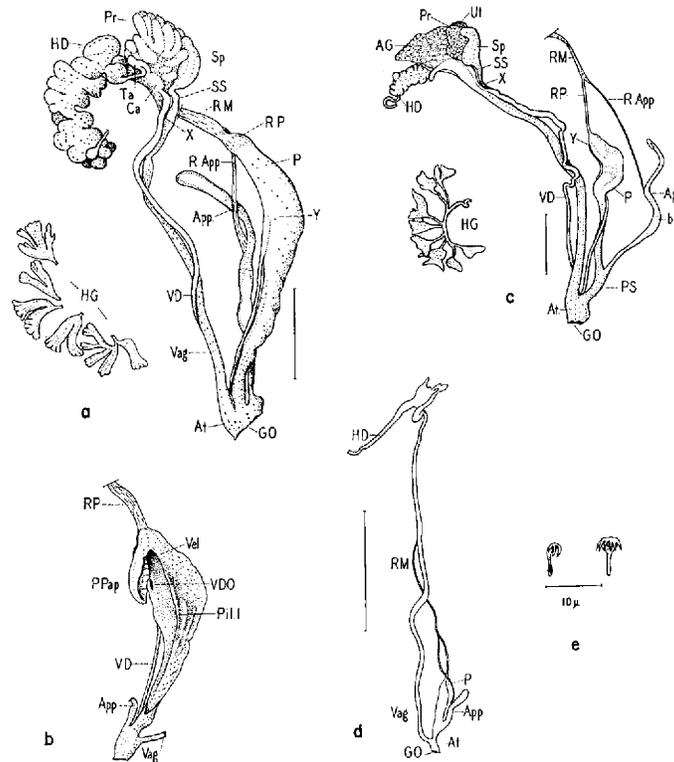


FIGURE 43.—*Pitys pagodiformis* form *D*: *a*, adult genitalia; *b*, interior of penis, adult; *c*, paraneanic genitalia; *d*, metaneanic genitalia; *e*, teeth.

Dissected 135323 (adult, subadult, or paraneanic genitalia; interior of penis), four specimens; 135328 (metaneanic genitalia), two specimens; 135328 (para- to metaneanic, not figured), one specimen.

Rapa: back of Area, under stones, alt. 400 ft., Anderson, July 24, 135323-135330 (figured specimens 8736-8739; 135323A, egg).

The species is abundant in only one locality, a lateral ridge directly back of Area village on the northern side of the bay. This is the second lateral ridge west of the village church, the altitude about 400 feet. The species was taken

on the eastern slope near the trail leading up the ridge, under a thin pile of loose, small, angular, rough stones about three layers thick. Most of the live shells were found below the upper layer and, because of their small size and dark color, were difficult to see under the dense vegetation. Three trips were made to this colony which was about 20 or 30 yards by 2 or 3 yards. More than 500 specimens were taken, of which more than 300 of all ages were alive. As this colony yielded the only satisfactory material, it has served as a basis for our anatomical and growth study of the species.

***Pitys pagodiformis* form E** (fig. 41, *d*).

Shell small, close to form *D* but slightly longer, whorls 8.5, with less concave outlines, umbilicus somewhat narrower, costae fewer (23 on last whorl), more widely spaced and slightly stronger but whorl proportionately shorter.

Length 3.85 mm., diameter 3.12 (82 percent); apertural axis 1.14, diameter 1.33 (113 percent); last whorl 1.41 (37 percent); parietal lamella 0.57.

Rapa: Mount Mangaoa, northeast ridge, small wooded ravine near crest of ridge, under stones, alt. about 800 ft., Zimmerman and Anderson, July 29, 138409-138410; figured specimen 8740.

Form *E* was rare. In fact, it took three collecting trips to the colony for the specific purpose of collecting *P. pagodiformis*. Of the 33 collected, 21 were living (none mature), 11 were dead (two mature; one figured).

***Pitys scalaris*, new species** (fig. 44, *a*).

Shell subimperforate, with small subcircular foveola, elongate-conic, cinnamon buff, distantly and strongly costate. *Costae* obliquely seated, laminate, in peripheral area prominent, alate, diminishing in height on base toward umbilicus (18 on last whorl). *Spire* elongate, with nearly straight outlines, apex acute. *Suture* deep. *Whorls* 9; first 2.5 whorls papilliform, minutely spirally striate (striae more distinct in juveniles), convex, indistinctly shouldered above sutures; postembryonic whorls flattened, bluntly angulate at their peripheries, somewhat extended over sutures; last whorl slightly contracted, trapezoidal, with slightly flattened base. *Aperture* small, subquadrate. *Parietal lamella* thickened, high, free margin flaring outward. *Columella* with three lamellae; supracolumellar lamella prominent, long, separated from columellar lamella by a deep, narrow cleft; columellar lamella strong, thickened, terminating on outer margin of columella in a thick blunt knob; subcolumellar lamella shorter, low, deeply seated. *Lower palatal wall* with low, rather long fold. *Outer peristome* thin erect; lower slightly thickened.

Length 4.12 mm., diameter 2.48 (60 percent); apertural axis 1.14, diameter 1.07 (94 percent); last whorl 1.68 (41 percent); parietal lamella 0.34.

Rapa: Mount Tautautu, northeast face, just below cliffs, alt. 700-800 ft., Kondo, July 25; holotype 8741, paratypes 143303.

The material consisted of 11 dead and one live juvenile.

This species is easily distinguished from *P. pagodiformis* by its narrower form, by the stronger and fewer costae, and by the absence of a distinct umbilicus. The heavy columellar callus of *P. scalaris* is weaker and not as extensive as in *P. pagodiformis*; the supracolumellar fold is more distinct and extends closer to the margin of the columella. As in *P. pagodiformis*, the specimens from separate colonies differ slightly from each other. This is probably

due to their sedentary habit which may have kept the colonies isolated from each other for a considerable time.

***Pityis scalaris* form A (fig. 44, b).**

*Shell* proportionately narrower than typical form, slightly longer, with nearly one less whorl; costae (21 in number) not as widely spaced or as strongly developed.

Length 4.23 mm., diameter 2.44 (58 percent); apertural axis 1.14, diameter 0.95 (83 percent); last whorl 1.75 (41 percent); parietal lamella 0.34.

Rapa: Maitua, below cliffs on north face of Mount Mangaoa, under damp stones, alt. 700-800 ft., Anderson, July 4, 137844-137846 (figured specimen 8742). East Maitua, below cliffs on northeast face of Mount Tautautu, alt. 600-800 ft., Anderson, July 20, 142628-142629.

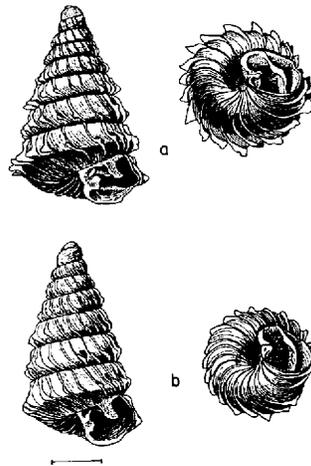


FIGURE 44.—*Pityis scalaris*: a, holotype; b, form A.

This form is extremely rare. The type locality and its immediate vicinity were visited five times, netting eight live and 17 dead specimens. Adults consist of one live and two partly broken dead specimens.

Four specimens of *Pityis scalaris* collected in East Maitua differ in some respects from the Tautautu and other Maitua specimens. The shells are smaller, and the outlines are slightly concave but to a lesser extent than those of *P. pagodiformis*. A nearly adult specimen has 21 costae on the last whorl. All of the specimens are too young or too incomplete to illustrate.

A single dead juvenile, 10117, from Mount Ruatara is tentatively placed under *P. scalaris*. In its narrow form and slightly concave spire, it is very similar to a specimen of about the same age from East Maitua.

**Pityis alpestris**, new species (fig. 45, a, b).

*Shell* imperforate, with a small shallow subcircular foveola, elongate-conic, with rounded tapering base, rather thick, barely translucent, dull, cinnamon buff, costate. *Costae* widely spaced, high, delicate, brittle, well-developed and subulate at periphery (14 on last whorl). *Spire* narrowly conic with straight outlines, apex subacute. *Suture* deep, wide. *Whorls* 7; embryonic whorls convex, indistinctly shouldered above, separated by a rather deep suture; postembryonic whorls uniformly convex, rounded at periphery, hardly exerted above suture, the last whorl slightly contracted. *Aperture* subauriform. *Parietal lamella* long, strong, obliquely seated, free margin slightly bent outward. *Columella* with three folds; supracolumellar fold low, calloused deeply seated; columellar fold high, calloused, extending to margin and ending in a small knoblike callus; subcolumellar fold indicated by a deep-seated swelling on inner columellar wall. *Palatal folds* absent. *Peristome* thin, erect, lower margin hardly thickened.

In a subadult specimen, supracolumellar fold is high and strong, nearly reaching margin of columella. Palatal fold long and continuous, not interrupted as in *P. pagodiformis* and *P. scalaris* (144528).

Length 3.62 mm., diameter 2.02 (56 percent); apertural axis 1.22, diameter 0.99 (81 percent); last whorl 1.89 (52 percent); parietal lamella 0.30.

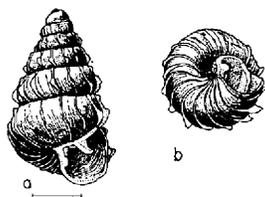


FIGURE 45.—*Pityis alpestris*: a, adult, holotype; b, adult, ventral aspect.

Rapa: Mount Perahu, east ridge, on dead leaves in crown of birdsnest fern, alt. about 1,700 ft., Anderson and Kondo, July 28; holotype 135608. Same locality and habitat, alt. 1,500-2,000 ft., Fosberg, July 21, juvenile paratype 142809. The material collected consisted of one adult and one juvenile.

This species is easily distinguished from *P. scalaris* by its fewer and less angulate whorls, by the more distant costae, and by the tapering base. Neither specimen was taken on the ground, although a form of *P. pagodiformis* is terrestrial in habit on the ridge where *P. scalaris* was collected.

#### Genus **Lamellovum** Pilsbry

*Lamellovum* Pilsbry, 1910, *Nautilus* 23 (10): 123. Type *Tornatellina globosa* (Petit); 1915, *Man. Conch.* 23: 131.

Adult. *Shell* imperforate or with a shallow foveola (*L. auricula*); broadly ovate, subconic or elongate; surface nearly smooth (*L. solitaria*) to costate (*L. costata*). *Whorls* 6.50 to 8. *Parietal lamella* strong and long, its free margin bent more or less outward. *Columella* heavily calloused, furnished with four lamellae, of which columellar lamella is strongest and extends to outer margin. *Palatal wall* unarmed or sometimes with one or two lower tubercles. *Peristome* erect, thin, or very slightly thickened and indistinctly expanded.

Juveniles. Parietal lamella with the free margin strongly sinuous, its lower face plain or with longitudinal ribs. Columella with four lamellae, of which the columellar lamella is much the strongest. Palatal folds two to six, long, continuous or interrupted.

Type species (by original designation) *Tornatellina globosa* = *Elasmatina globosa* Petit. In British Museum?

Distribution: Rapa.

This genus, as recognized, is composed of species in which the columella has four lamellae. The parietal lamella is strong, its free margin slightly bent outward; with or without palatal nodules. In juveniles the free margin of the parietal lamella is sinuous, being bent into two or three lobes. The palatal wall has two to six folds, which may be interrupted or continuous.

#### KEY TO SUBGENERA AND SPECIES OF LAMELLOVUM

- A. Shell broadly ovate, parietal lamella furnished (in adults) with tubercles or ridges, the three lower columellar folds on a very strong thick platelike process extending into aperture and beyond aperture (fig. 46, *b, c*) in a knob-like process. In juvenile shells palatal wall with five or six rather long, parallel, interrupted folds.....**Lamellovum (s.s.) globosum.**
- AA. Shells subtruncate to elongate; parietal lamella without tubercles or ridges; columella with four lamellae, of which columellar lamella is much the strongest and extends to margin of columella, the lower three not coalescing. In juveniles lower palatal fold continuous.....**subgenus Maitua.**
  - B. Surface costate, juvenile specimens with a strong continuous lower palatal fold and several (usually four) interrupted upper folds.....**L. costata.**
  - BB. Surface striate, juvenile shells (paraneanic substage) with one to four continuous lower palatal folds and a single continuous upper palatal fold.
    - C. Adult stage with shallow foveola, about 7 mm. in length, thickened, with prominent ridge connecting columella with parietal wall. Juvenile stage with single lower palatal fold.....**L. auriculella.**
  - CC. With foveola; less than 4 mm. in length, thin.
    - D. Diameter of shell about 60 percent of length, juvenile stage (paraneanic substage) with deep sinus between columellar complex and parietal wall, with a single basal fold.....**L. solitaria.**
    - DD. Diameter of shell about 45 percent of length, juvenile stage (paraneanic substage) without sinus between columellar folds and parietal wall, one lower palatal fold; metaneanic substage with several (about four) lower palatal folds....**L. leptospira.**

**Lamellovum (Lamellovum) globosum** (Petit). Figures 46, *a-g*; 47, *a-f*.

*Elasmatina globosa* Petit, 1843, Zool. Soc. London, Proc., 2.

*Tornatellina globosa* Pfeiffer, 1846, Symbolae 3: 60; 1848, Monogr. 2: 393.

—Küster, 1852 (-1859), Conch.-Cab., Pupa, 1 (15): 154, pl. 18, fig. 27.

*Achatina (Tornatellina) globosa* Pfeiffer, 1855, Malak. Blätt., 170.

*Lamellovum globosum* Pilsbry, 1910, Nautilus 23 (10): 123.—Pilsbry and

Cooke, 1915, Man. Conch. 23: 131, pl. 28, figs. 9-12.

"Elasm. testa ventricoso-conica, pellucida, luteo-virescente; anfractibus 6-7 planiusculis, ultimo maximo, ventricoso, pallidiore; spira conico-acuta; apertura semilunari; ringente;

columella supra medium dente lamelliformi instructa, dente subtus marginato, interdum duplicato, ad basim plicato, plica antice emarginata robuste bilobato lobo superiori ascendente, inferiori subhorizontali; labro acuto long. 4 mill.; larg. 3 mill." (Petit.)

Genitalia smaller than that of *Pitya* (fig. 47, e, f). *Ovotestis* eight- to nine-lobate. *Albumin gland* very small, follicles numerous, barely discernible. *Prostate* as in *Pitya*. *Vas deferens* and oviduct about same size, quite narrow. *Penis* 0.63 oviducal length, internally more complex than in *Pitya*: ascending pilaster long and stronger with heavy terminally truncate papilla (P Pap); velum (Vel) broad, wrinkled; subsidiary or extra velum (Vel 2) between orifice of vas deferens (VDO) and ascending pilaster.

Dissected 138489 (adult genitalia, interior of penis), four specimens.

*Clausilia fissidens* of Mühlfeld (Anton, 1839, p. 46) is a new name, and the species can never be recognized. Its meaning, "cleft tooth," indicates that the author had a specimen of *Lamellovum globosum* before him. Of the species

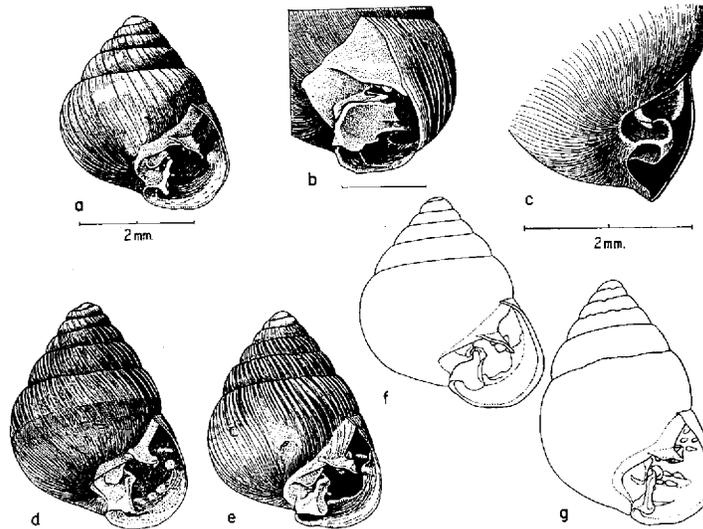


FIGURE 46.—*Lamellovum (Lamellovum) globosum*, Rapa: a, adult, Mount Ororangi; b, adult, columellar view; c, adult, profile showing columellar knob; d, adult, Maitua, banded; e, adult, Mount Perahu; f, adult, Area; g, adult, Morongota.

collected by Cuming, this is the only one to which the name *fissidens* is applicable; both the parietal and columellar lamellae, especially of the subadult, have characteristics appropriate to the adjective.

Pfeiffer (1848, p. 392) made *C. fissidens* Mühlfeld a synonym of *Tornatellina trochiformis* Beck of Juan Fernandez, which is undoubtedly an error in designation as well as in habitat.

According to Petit, the species he described was collected at Opara [Rapa], by Mr. [Hugh] Cuming under stones [May 13-17, 1828].

Collections made by the Mangarevan Expedition indicate that this species is distributed in native forests throughout the island. From nearly a hundred lots, the following six specimens have been selected for figures, measurements, and discussion:

Rapa: Area, ridge north of village, under stones, alt. about 500 ft., Fosberg, July 2, 137768 (fig. 46, *f*)-137769. Mount Perahu, east ridge, on ground, alt. 1,500-1,850 ft., Anderson, July 28, 135492 (fig. 46, *e*). Mount Morongota, near crest of main ridge, southwest of peak, alt. about 800 ft., W. Anderson, Kondo, and D. Anderson, July 16, 144343 (fig. 46, *g*, 8748). Maitua Valley, below Mangaoa, under damp stones, alt. 400-500 ft., Anderson, July 10, 140026 (fig. 46, *d*, 8749). Mount Ororangi, southeast valley, under stones, alt. 500-600 ft., Cooke and Anderson, July 3, 138489-138490; dissected 138489 [fig. 46, *a-c*, 8743; fig. 47, *a*, 8744; fig. 47, *b*, 8745; fig. 47, *d* (egg), 138489]. Mount Tepiahu, south slope, under stones, alt. about 550 ft., Cooke, July 23, 143008-143018; measured specimen 8746 (fig. 47, *c*, 8747).

Cuming's specimens may have been collected on the slopes leading to Mount Morongota, along with *Pitys pagodiformis* (Smith) and *Electrina succinea* (Sowerby), both of which were taken in this locality by the Mangarevan Expedition.

Most of the adult shells from other localities are considerably smaller. Of *L. globosum*, the most widely distributed of the terrestrial tornatellinids of Rapa, there appears to be no localized form. Most specimens from the northern and eastern sides of the bay are slightly larger and more strongly sculptured than those from the southern side, but this is not invariable. In some colonies there is considerable individual variation in the texture of the shells and, especially, in the degree of strength in the striae, whereas in other colonies variation is hardly noticeable.

Extreme specimens from different colonies might appear to form a basis for dividing the species into a few subspecies or geographical races, but in none are the characters sufficiently constant. For example, the form from Ororangi (fig. 46, *a*) is translucent and nearly smooth with weak striae. Maitua shells are slightly larger (fig. 46, *d*) and have somewhat stronger striae (band depicted). Mount Perahu shells (fig. 46, *e*) show distinct striae, as do Area samples (fig. 46, *f*, outline), which, incidentally, are closest to the typical. Morongota samples are larger (fig. 46, *g*, outline) and proportionately narrower. Scattered through a number of colonies are a few specimens ornamented with a dark peripheral band, which may be quite wide or much narrower.

The species is rather rare in most colonies, in only a few of which were more than a dozen live shells taken. Most specimens were found under damp stones; a few, under dead leaves or twigs and logs.

The following description by Pilsbry (Pilsbry and Cooke, 1915, p. 132) is more detailed than that of either Petit or Pfeiffer:

"In this peculiar shell the whorls are moderately convex, though the general outlines of the spire are straight. The surface is distinctly striate, the apex decidedly smaller than in typical *Elasmias*. The parietal lamella is about two-thirds of a whorl long. The inner half is quite low, but the outer is strongly developed, and has pairs of short lamellae upon its lower face, also some projections above the edge on its outer face. The columellar lamella is long, thickened at the edge. Above and below it are small lamellae (supracolumellar and infracolumellar), and the subcolumellar lamella is as strong but not as long as the columellar. Below it there is a very stout lamella, which does not reach far inward, but forms the lower margin of the columellar plate. Above and below the group of columellar lamellae there are deep, narrow sinuses. There are six short, deeply placed, interrupted palatal plicae. The basal lip is thick within. Length 3.7, diameter 3.2; 5¾ whorls." [This description is based on a specimen which had not quite reached maturity.]

In mature specimens the apertural armature is much simpler than in juveniles; the parietal lamella is simpler, its free margin much less sinuous; and the denticles and ridges on the upper and lower faces are less pronounced. The columella is heavily calloused and on it is a complex arrangement of lamellae.

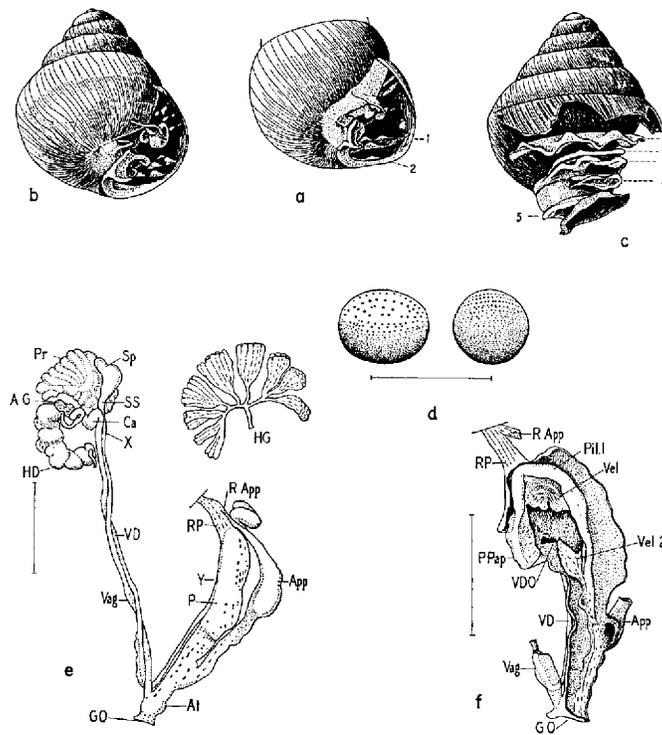


FIGURE 47.—*Lamellovum (Lamellovum) globosum*: a, subadult, palatal teeth (numbers indicate two lower palatals); b, metaneanic palatal teeth; c, interior view of apertural teeth, (1) parietal, (2) supracolumellar, (3) columellar, (4) intracolumellar, and (5) subcolumellar lamellae; d, egg, lateral and frontal views; e, adult genitalia; f, interior of penis.

The supracolumellar lamella is high and thin, separated from the parietal wall by a wide sinus and from the columellar lamella by a narrow, deep sinus. The remaining columellar lamellae (columellar, intracolumellar, and subcolumellar) are on a high, much thickened callus roughly T-shaped in cross section. These lamellae are proportionately much weaker than those of the juvenile and subadult specimens. The columellar complex extends beyond the outer margin of the columella in a high knoblike process (fig. 46, *a-c*). The unique and complicated columella development of *L. globosum* has apparently evolved from a lamellar arrangement somewhat similar to that of *Pityis* but has become much more exaggerated.

Below the columellar lamella the columella is calloused. This callus extends to the base of the palatal wall as a rather thick plate merging into the lip of the peristome (fig. 46, *a*). Within the aperture the palatal wall is slightly thickened with a broad callus. The inner margin bears vestiges of the palatal folds characteristic of juveniles. The peristome is slightly thickened; below the columellar complex it is deeply notched and, flaring abruptly outward, forms a wide, almost spoutlike sinus (fig. 46, *a-c*). There is also a deep sinus between the palatal wall and columellar complex. The embryonic whorls of very young specimens are microscopically, closely, and finely spirally striate.

In juveniles the apertural lamellae are proportionately much more strongly developed than in adults. The free margin of the parietal lamella is more sinuous and the tubercles on both the upper and lower faces are more pronounced (fig. 47, *a-c*). The columellar lamella is long, its free margin sinuous and bent upward; the intracolumellar lamella is shorter, deeply seated, its margin flatly expanded; the subcolumellar lamella is short and strong, with its free margin bent downward. The sinus between the columellar complex and the lower lip is narrow and deep. Five or six interrupted, deeply seated palatal folds are arranged in groups of three. One group, below the margin of the parietal lamella, consists in most specimens of two closely spaced, elongate, deeply seated lamellae mounted on a rather broad callus. On the inner margin of the basal plate is an elongate, deeply seated basal fold.

Measurements of specimens from different localities are shown in table 3.

A peculiarity of this species, and of some others of this subfamily, is the fact that in the nuchal membrane a cul-de-sac is formed at the anchorage of the common retractor, probably by some parasite. The object housed therein is usually tightly compressed into a ball and brown in color. Uncoiled, it is linear.

#### Subgenus **Maitua**

*Shell* from subtrubinate to elongate; surface striate to costulate; three lower columellar lamellae not united into prominent protruding callus plate; palatal fold(s) continuous, not interrupted.

Type species: *Lamellovum auriculella*.

TABLE 3.—LAMELLOVUM GLOBOSUM

SHELL			APERTURE			LAST WHORL			
Length	Diameter	Percent	Axis	Diameter	Percent	Length	Percent Length	Height Fav. Lam.	No. Whorls
3.71	3.55	96	1.77	1.84	104	2.64	74	0.48	6.5 Area
3.81	3.00	79	2.00	1.71	85	2.68	70	0.39	6.5 Perahu
4.26	3.03	71	1.97	1.71	87	3.06	72	0.29	6.6 Morongota
4.00	3.09	77	1.93	1.71	88	2.84	71	0.32	6.3 Maitua
3.39	2.90	85	1.87	1.51	81	2.45	72	0.45	6.25 Ororangi*
3.55	2.79	78	1.71	1.55	90	2.48	69	0.38	6.5 Tepiahu

\* A uterus of one animal from Mount Ororangi contained two eggs (fig. 47, d), which are ovate in form with white calcareous shells and measure  $0.80 \times 0.65$  mm.

Species: *L. auriculella*, *L. costata*, *L. leptospira*, and *L. solitaria*.

*L. solitaria* is represented by a single subadult specimen, and the characters of the adult are, unfortunately, unknown. However, the specimen is so unlike the subadults of the other species that we feel safe in giving it a specific designation.

*L. leptospira* is represented by four examples. The single, damaged adult specimen shows a simple columella that differs from those of *L. costata* and *L. auriculella*, both of which retain vestiges of the juvenile armature. In the palatal armature it differs from *L. costata*, *L. auriculella*, and *L. solitaria* in that it has four lower palatal folds in the metaneanic substage, whereas the others have but one lower palatal fold.

**Lamellovum (Maitua) auriculella**, new species (figs. 48, a-g; 49, a-m).

*Shell* (fig. 48, a-c) imperforate but with shallow foveola, ovately conic, clay color, somewhat thickened, hardly translucent, closely and finely striatulate. *Spire* elongate-conic, with slightly convex outlines below, flatter above, ending in rounded apex. *Suture* very slightly impressed, narrowly and indistinctly margined. *Whorls* 8, nearly flat; first two whorls slightly worn (in very young specimens glossy, the second whorl with very fine, indistinct spiral lines), last whorl tapering to base. *Aperture* subauriform, vertical. *Parietal lamella* high, strong, thickened, its free margin slightly sinuous, not flaring outward. *Columella* heavily calloused within, forming a platelike vertical process on which are three lamellae. *Supracolumellar lamella* deeply seated, rather strong; columellar lamella strong, long, nearly transversely seated, extending slightly beyond outer margin of columella, forming a low projection, connected with parietal wall by a high thickened callus; sub-columellar lamella deeply seated. *Palatal wall* furnished with a short, calloused, deeply seated lower palatal fold. *Peristome* slightly thickened, whitish, its margin weakly expanded; a broad shallow notch below columellar lamella.

Length 7.04 mm., diameter 3.85 (55 percent); apertural axis 2.95, diameter 2.53 (83 percent); last whorl 4.32 (61 percent); parietal lamella 0.61.

In juvenile specimens (figs. 48, d-f), from early age until near maturity, parietal lamella is proportionately stronger, about 0.80 whorl in length, high in front for about half its length, diminishing slowly in height toward interior. Free margin of parietal lamella

sinuous, slightly bent outward, lower margin with two long, slanting ridges. Columella heavily calloused. Four nearly transverse columellar lamellae; supracolumellar lamella high, thick, and deeply seated; columellar lamella high, strong, and extending to outer margin of columella; intracolumellar lamella deeply seated and slightly more prominent than supracolumellar lamella; subcolumellar lamella (absent in adults) a short low tubercle. Two palatal folds; lower palatal fold strong, high, about 0.25 whorl long; upper palatal fold about the same length but not half as high.

Eggs (fig. 48, *g*). The animals of several specimens were gravid, containing a single egg. The eggs are oval with calcareous shells which, under a microscope, look pitted. One measured  $1.16 \times 0.95$  mm.

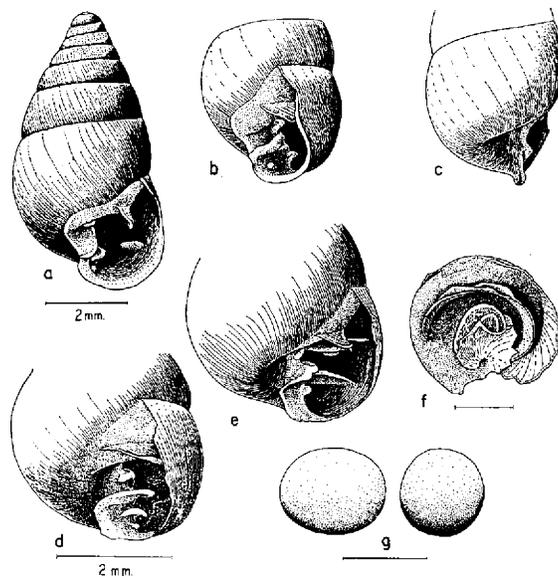


FIGURE 48.—*Lamellovum (Maitua) auriculella*: a, adult, holotype; b, adult, columellar view; c, adult, profile; d, juvenile, columellar view; e, juvenile, frontal apertural view; f, juvenile, internal aspect of parietal lamella; g, egg.

Adult genitalia (fig. 49, *a-g*). *Ovotestis* 10-lobate; duct enormously distended. *Talon* and *carrefour* small: *carrefour* shaped like bird's head, greater curvature above, duct and uterus entering and discharging at opposite ends, vas deferens off middle lateral surface. *Albumin gland* on *carrefour*, minute, paucifolliculate; follicles minute, short-clavate, quite numerous. *Prostate* large; follicles digitate, some forming V's, few. *Spermatheca* small, oval; stalk very short. *Vagina* with small bulge (below X). *Vas deferens* wide above, slightly narrowing below, still more along penis, entering penis terminally or nearly so (Y). *Penis* 0.5 oviducal length; interior with ascending reflexed pilaster terminating in semi-pendent papilla (Pil 1, P Pap); papilla somewhat saddle-shaped, velum campanulate. *Appendix* twice penial length; interior with secretory-ejaculatory apparatus. Secretory portion distal, a plain blind tube; ejaculatory portion composed of muscular wall through which extrudes eversible verge-like organ or appendical "verge" (App V); organ hollow, composed of few folds of semi-transparent muscular tissues, narrowing distad into blind tube. *Common retractor* heavy; penial retractor short, stout; appendical retractor longer, narrower. *Atrium* short, narrow.

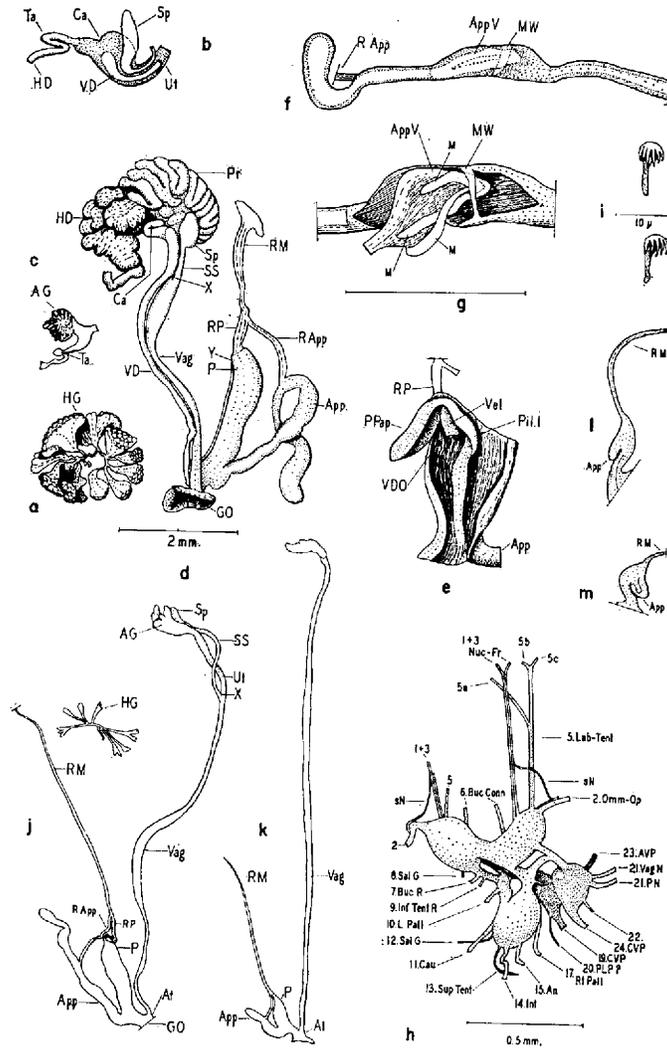


FIGURE 49.—*Lamellovum (Maitua) auriculella*: a, ovotestis of adult genitalia; b, carrefour complex; c, albumin gland; d, adult genitalia; e, interior of penis; f, appendix; g, appendix, interior (in part); h, central nervous system (excluding buccal ganglia); i, teeth; j, paraneanic genitalia; k, metaneanic genitalia; l, m, aneanic genitalia.

Central nervous system (fig. 49, *h*, 1-24) as follows:

*Cerebral ganglion*, right: (1 and 3) Nucho-frontal (Nuc-Fr) nerves, off antero-ventral surface as separate nerves, thenceforth adhering together strongly to near tip, then separating to nuchal and frontal, the nuchal nerve to side of mouth, the frontal nerve to base of ommatophore. [Nuchal nerve in another specimen off labio-tentacular nerves.] (2) Ommatophoral and optic (Omm-Op) nerves off usual place; connected to nucho-frontal nerves by small innominate nerve (sN). (4) No penial nerve off cerebral ganglion (see 21). (5) Labio-tentacular (Lab-Tent) nerves from below ommatophoral nerve, giving off one branch (5a) above midpoint to innervate mouth parts, continuing anteriorly to bifurcate: left branch (5b) to inferior tentacle, the right (5c) to region round base of inferior tentacle. [Some specimens with another branch to nuchal nerve, between 5a and b.] (6) Buccal connective (Buc-Conn) off inner anterior face to buccal ganglion. (7) Right buccal retractor nerve (not figured) and left (Buc R) off caudal surface (in contracted animals this nerve drawn into cerebro-pleural connective).

*Cerebral ganglion*, left: (8) Caudal surface with extra nerve to left lobe of salivary gland (Sal G).

*Pleural ganglia*, left and right: (9) Inferior tentacular nerves (Inf Tent R).

*Parietal ganglion*, left: (10) Large left pallial (L Pall) to body wall.

*Right parietal plus abdominal ganglion*: (11) Caudal (Cau) nerve to columellar muscle and dorsum of tail. (12) Small salivary gland nervelet (Sal G) to salivary gland. (13) Small nerve from left of intestinal nerve to right superior tentacular retractor (Sup Tent). (14) Large intestinal (Int) nerve off apex, along artery. (15) Sizable anal (An) nerve off right edge, going under uterus to integument on right side. (16) Two minute nervelets (not figured) from ventral surface between right pallial and anal nerves, to superior tentacular retractor, right side. (17) Large right pallial (Rt Pall) nerve from right side, crossing over tentacular retractors, over uterus, and under genital retractors, to body wall.

*Pedal ganglion*, left: (18) Three lateral nerves (not figured; sometimes four, as in *Perahua grandis*) apparently from one stem, to anterior, lateral, and posterior positions innervating head and foot. (19) Two ventral nerves, the posterior the larger (CVP). (20) One small nerve from left of caudoventral to sole (PLP?). This may be connected to otocyst (compare with *Perahua grandis*).

*Pedal ganglion*, right: Apparently no anterolateral pedal. (21) Two lateral pedal nerves, one to vagina (Vag N), the other to penis (P N). (22) A small nerve corresponding to number 20 above. (23 and 24) Two ventral nerves as above (AVP, CVP).

*Teeth* all similar in appearance (fig. 49, *i*), small, six- to seven-dentate. Cusps the same size, long. Cusplets not visible. Length  $\pm 10$  microns, width  $\pm 4$  microns.

*Paraneanic genitalia* (fig. 49, *j*). Ovotestis undeveloped, seven-lobate. Albumin gland and prostate undeveloped. Spermatheca small; stalk quite long. Uterus short. Vagina very long, with slight median bulge, narrow at both ends. Penis and appendix slightly developed, resembling tubuaiinid penis. Common retractor very long, thin.

*Metaneanic genitalia* (fig. 49, *k*). Female tube relatively much longer than in paraneanic, upper organs undifferentiated macroscopically. Penis and appendix very short, small, strongly resembling those of *Tornatellinops*; penis nearly conical, apex sharp; appendix bluntly pointed.

*Ananeanic genitalia* (male complex only; fig. 49, *l, m*). Appendix a mere bulge or diverticulum of penis (App), without appendical retractor, only penial retractor.

Dissected 135537 (adult genitalia, carrefour complex, interior of appendix, interior of penis, nervous system), six specimens; 135539 (juvenile genitalia), five specimens.

The ontogeny of the *L. auriculella* penial complex suggests that the order of evolution may be from the appendixless stock of the tornatellinoptinids, thence to the tubuaiinids, and finally to the pitysinids.

Rapa: Maitua Valley, below Mount Mangaao (type locality), about 100 yards below base of cliffs, under damp stones of talus slope, alt. 700-800 ft., Cooke, Kondo, July 20; holotype 8750; figured juveniles 8751, 8752; paratypes 135537-135542; egg 135538.

The type locality, which was visited four times, did not exceed 50 to 75 square yards. Collected live shells, which were fairly abundant, totaled about 100 of all ages. Only eight specimens were found on a similar slope, about 150 yards south of the type locality. Similar talus slopes were investigated in different parts of the island, but no related species were found.

This species is named for the genus *Auriculella*, found in the Hawaiian Islands, which it closely resembles in size and general form.

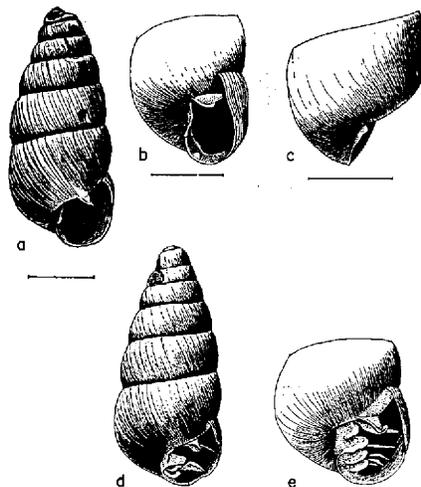


FIGURE 50.—*Lamellovum (Maitua) leptospira*: a, adult; b, adult, latero-oblique apertural view; c, adult, profile; d, subadult, cotype; e, parametaneanic, apertural armature.

***Lamellovum (Maitua) leptospira*, new species (fig. 50, a-e).**

*Shell* elongate, with slightly convex outlines, isabella color, rather thin, subtransparent (axis visible through shell), somewhat glossy, with silky sheen; sculpture consisting of rather fine, blunt, closely spaced striae and microscopically fine spiral lines. *Suture* simple, lightly impressed. *Spire* elongate, tapering slowly to rather sharp apex. *Whorls* about 7.5, slightly convex, increasing slowly and regularly; embryonic whorls marked with microscopically closely spaced spiral lines; last whorl oblong, tapering to base. *Aperture* small, semioval. *Parietal lamella* high, its free margin bent slightly outward. *Columella* nearly straight, furnished with a very oblique columellar fold extending to margin of columella and forming a low long ridge, below which is a minute deeply seated fold. Between columellar fold and palatal wall is a rather thick callus. *Palatal wall* unarmed. *Peristome* thin, erect.

Length 3.71 mm., diameter 1.62 (43 percent); apertural axis 1.11, diameter 0.86 (77 percent); last whorl 1.9 (54 percent), parietal lamella 0.21.

In a juvenile (or subadult) shell, whorls 7.25, not quite mature, parietal lamella is high, its free margin quite strongly sinuous. Columella strongly calloused, with four lamellae, nearly transversely seated. Supracolumellar lamella deeply seated, rather weak; columellar lamella strong, lamella-like, extending to margin; intra- and subcolumellar lamellae well developed but weaker than columellar lamella, and rather deeply seated. Palatal wall with a strong, rather short lower fold and a weaker and longer upper fold.

Length 3.71 mm., diameter 1.65 (44 percent); apertural axis 1.11, diameter 0.86 (77 percent); last whorl 1.77 (48 percent); parietal lamella 0.20.

In an even younger specimen, chamois-colored, whorls 5.5, supra-, intra-, and sub-columellar lamellae nearly equal in size. Palatal wall furnished with four rather weak parallel lower folds and a single equally developed upper fold.

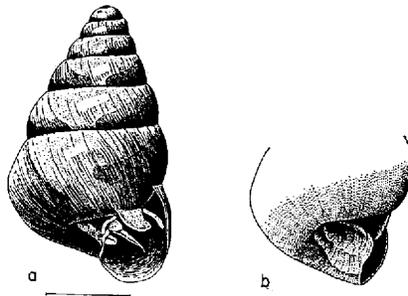


FIGURE 51.—*Lamellovum (Maitua) solitaria*: a, subadult, holotype; b, subadult, profile.

Rapa: Mount Perahu, east ridge (type locality), under moss or on dead leaves in crown of birdsnest fern, alt. 1,500-1,850 ft., Anderson and natives, July 28; cotypes 8753-8754; paratypes 135496-135497, not dissected (figured juvenile 135497).

One damaged adult, two subadult dead shells, and one juvenile live specimen were collected.

The closest relative of *L. leptospira* is *L. solitaria* from the same region. It is here considered as distinct for two reasons: its form and size and its lack of the deep sinus between the columellar folds and the parietal wall.

***Lamellovum (Maitua) solitaria*, new species (fig. 51, a, b).**

*Shell* subadult broadly conic, with slightly convex outlines and somewhat flattened base, cinnamon buff, rather thin, translucent, very glossy, under a strong lens minutely striatulate with lines of growth. *Spire* conic, with rather sharp apex. *Suture* weakly impressed. *Whorls* 7, increasing slowly and regularly, slightly convex; embryonic whorl smooth, glossy, no spiral lines visible under high magnification; last whorl subquadrate. *Aperture* nearly vertical, subauriform, longer than broad. *Parietal lamella* strong, free margin flaring outward and very slightly sinuous. *Columella* heavily calloused, strongly sigmoid, with three almost equally developed strong subhorizontal lamellae. *Supracolumellar and columellar lamellae* extending to margin; subcolumellar lamella more deeply seated. Columellar complex separated from parietal wall by deep, narrow sinus, its outer face white, striate.

Length 3.30 mm., diameter 1.97 (60 percent); apertural axis 1.09, diameter 0.77 (71 percent); last whorl 1.89 (57 percent); parietal lamella 0.26.

Rapa: Mount Perahu, east ridge (type locality), alt. 1,800-1,900 ft., Kondo, July 21; holotype 142918.

The single specimen collected was not quite mature. It is so distinct from any other species found on Rapa that we do not hesitate to describe it.

Its nearest relative is probably *L. auriculella*, from which it differs in size and form; in the characters of the apertural armature, especially its sigmoid columella; and in having a deep sinus separating the columellar complex from the parietal wall. In specimens of *L. auriculella* of the same relative age, the columella is nearly straight.

*L. solitaria* has a much deeper and narrower sinus between the columellar complex and the parietal wall than does *L. globosum*.

**Lamellovum (Maitua) costata**, new species (fig. 52, *a-e*).

*Shell* cylindrical-conic, upper third tapering to apex, honey yellow, thin subtransparent, regularly costate; costae evenly spaced, strong, nearly vertical, extending to or just below periphery; interstices microscopically engraved with very fine, closely spaced spiral lines. *Spire* slightly convex in outline below, nearly straight above. *Suture* impressed, narrowly margined below on last two whorls. *Whorls* 7.5, slightly convex, the first 2.5 glossy, under strong lens, very finely and closely spirally striatulate; demarcation between embryonic and costate postembryonic whorls abrupt; last whorl tapering to base, oblong, indistinctly shouldered just below suture, costae gradually becoming weaker at or just below periphery. *Aperture* nearly vertical, longer than broad. *Parietal lamella* strong, high, nearly one whorl long, free margin simple, scarcely flaring outward. *Columellar lamella* nearly straight, weakly sigmoid, its inner face heavily calloused, with four lamellae. *Supracolumellar lamella* deeply obliquely seated; columellar lamella oblique, long, blunt, extending to margin, uniting with peristome and forming a triangular projection which is separated from parietal wall by a deep wide sinus; intra- and subcolumellar lamellae deeply seated, more or less coalesced, forming a platelike process, extending into and continuing to base of aperture. *Palatal wall* without folds. *Peristome* thin.

Length 5.14 mm., diameter 2.41 (47 percent); apertural axis 1.98, diameter 1.18 (60 percent); last whorl 2.95 (57 percent); parietal lamella 0.31.

*Genitalia*. *Ovotestis* eight-lobate; lobes simple, undeveloped, clavate or flaring distally; follicles not differentiated (this specimen probably nearly adult). *Duct* greatly distended, convoluted. *Talon* small. *Carrefour* small. *Albumin gland* on upper surface of carrefour very small. *Prostate* with few medium-sized digitate follicles. *Spermatheca* large, pyriform; stalk  $\pm 0.3$  oviducal length. *Penis* 0.5 oviducal length, clavate; retractor short, stout. *Appendix* enlarged in middle with twin bulges.

In juvenile specimens, from a very young stage until nearly adult, free margin of parietal fold strongly sinuous and flaring outward. Columella heavily calloused, especially below the strong columellar lamella which is more transversely seated than that in adult stage. Supra-, intra-, and subcolumellar lamellae much weaker, developed in about the same degree and deeply seated. Palatal wall furnished with a strong high continuous lower fold about 0.25 whorl in length and two pairs of much weaker, interrupted upper palatal folds.

Rapa: Mount Perahu, east ridge (type locality), under logs and dead leaves, alt. 1,600-1,800 ft., Kondo, July 28; holotype 8755 (figured juvenile 8766); paratypes 135585A (uncoiled), 135585-135588, 142896.

Nearly 100 specimens were taken in this and other localities on the same ridge, at altitudes from about 1,500 feet to the top of the peak, a little more than 2,000 feet. Of these, about 40 specimens of different ages were alive, but live specimens were not abundant in any one locality. Most of the shells were found under damp stones and leaves, a few in trash between fronds of birdsnest fern 1 or 2 feet above ground.

Undoubtedly the closest relative of *L. costata* is *L. leptospira*, found on the same ridge. *L. costata* is easily distinguished by its larger size and broader proportions, by the surface texture, and by the interrupted upper palatal folds in juvenile specimens. These folds closely resemble those of *L. globosum*, though the lower palatal folds in *L. globosum* are interrupted instead of solid and the columellar complex is entirely different.

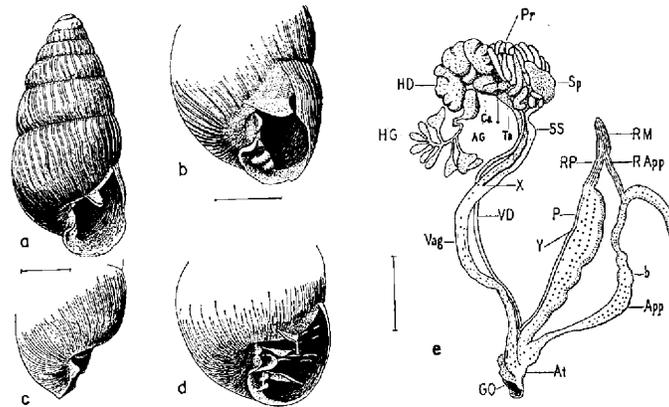


FIGURE 52.—*Lamellovum (Maitua) costata*: a, adult, holotype; b, adult, columellar view; c, adult, profile; d, paraneanic, apertural armature; e, genitalia, near-adult.

#### TRIBE ANTONELLINI

Without appendix. Oviparous. Albumin gland minute. Interior of penis with recurved achatinellid pilaster.

Owing to the limited number of animals, most of them either torn or imperfectly preserved, a good concept of the tribe is not possible. As in Pityisini, the genitalia of some of the species are represented only by the subadult, paraneanic, or other juvenile stages.

Shells of this small tribe are fusiform or subfusiform, smooth, and without parietal tooth, and the two columellar lamellae are simple, ranging from 4 to 9 mm. Whorls 6.5 to 7.5.

Type genus: *Antonella*.

## KEY TO GENERA OF TRIBE ANTONELLINI

- A. Shells with parietal lamella; columella slightly sigmoid, with two rapidly ascending lamellae ..... **Antonella.**  
 B. Shells without parietal lamella; columella strongly sigmoid, with a single lamella ..... **Perahua.**

Genus **Antonella**, new genus

Adult. *Shells* small, 4 to nearly 7 mm. long, ventricose-fusiform to elongate in form, very thin and fragile. *Whorls* 6 to 7.5, flatly convex to slightly convex; last whorl capacious to moderate. *Parietal lamella* moderately to well developed, about one whorl long. *Columella* perpendicular, nearly straight, with two rapidly ascending lamellae which terminate at an acute angle at the outer margin near its base. *Palatal wall* with or without a long uninterrupted basal fold.

Juvenile. Apertural armature proportionately stronger than that in adult. Shells transparent, very thin, fragile.

*Ovotestis* multilobate; lobes bluntly terminate, well defined. *Prostate* large. *Albumin gland* minute in adult. *Spermatheca* large, oval, bluntly pointed, free, lying on prostate or nearby; stalk short, entering oviduct at head or halfway below. *Oviduct* comparatively broader than that of Pityisini. *Vas deferens* narrow. *Penis* without appendix; without epiphallus; short or long (0.3 to 0.6 oviducal length); clavate, broad (ratio of width to length 1:3.5, average of six specimens); internally equipped with achatinellid pilaster. Pilaster narrow below, ascending and broadening above, reflexed at apex into semipendent stimulator. Penial retractor terminal, robust. Vas deferens orifice subterminal. *Atrium* short.

Type species: *Antonella trochlearis* Pfeiffer.

Distribution: Rapa; terrestrial, usually under stones.

The species of this genus differ from those of all other genera from Rapa in the structure of their columellar folds, which consist of two abruptly ascending, nearly equally developed folds which terminate near the base of the columella in an acute angle. Two of the species are easily recognized by their peculiar fusiform outlines. This species is named for Hermann Eduard Anton, who described the first shells from Rapa.

The limited material available indicates that *Antonella* differs from *Perahua* in having a shorter, broader penis. However, it would be most unwise to state that this rule holds, inasmuch as the genus *Perahua* is based on the not quite complete anatomy of only one species. It is expected that penial lengths will range from very long to very short in both genera and that the generic distinction cannot be made except conchologically.

## KEY TO SPECIES OF ANTONELLA

- A. Shells ventricose-fusiform to ovate-fusiform; last whorl capacious, about 0.66 or more length of shell.  
 B. Palatal wall with a long continuous fold at all stages of growth..... **A. pfeifferi.**  
 BB. Palatal wall without fold at all stages of growth.....  
 ..... **A. trochlearis and subspecies.**  
 AA. Shells elongate-turritid, last whorl moderate, about 0.5 length of shell.... **A. tenuis.**

**Antonella trochlearis trochlearis** Pfeiffer (fig. 53, a-i).

*Tornatellina trochlearis* Beck, 1837, Index Molluscorum, 80 (*nomen nudum*), teste Anton.—Pfeiffer, 1842, Symbolae 2: 55; 1848, Mon. Hel. Viv. 2: 393.—Küster, 1852(-1859), Conch.-Cab., Pupa, 1 (15): 151, pl. 18, figs. 18, 19.

*Tornatellina (Tornatellinops) trochlearis* Pilsbry and Cooke, 1915, Man. Conch. 23: 178, pl. 35, fig. 9.

*Achatina (Tornatellina) trochlearis* Pfeiffer, 1855, Malak. Blätt., 170.

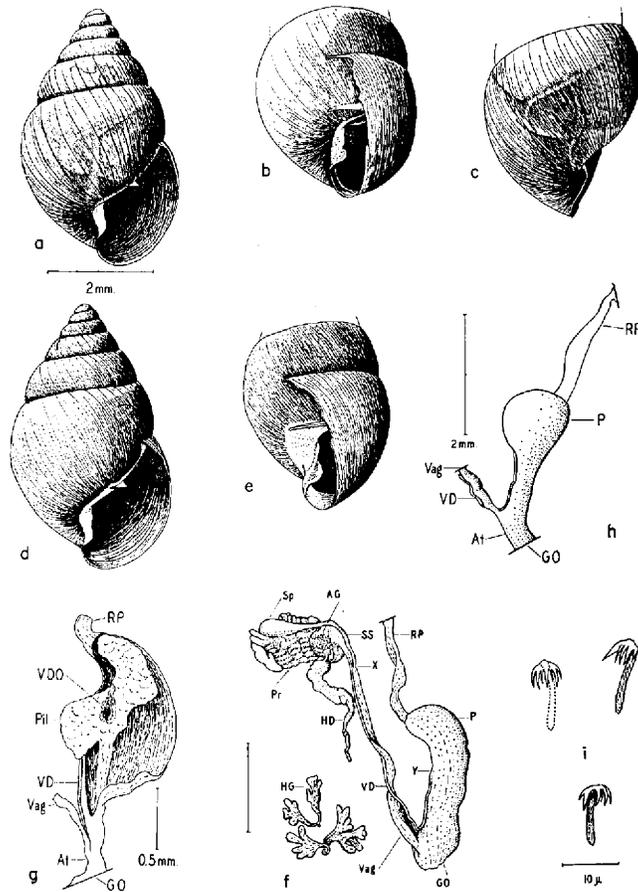


FIGURE 53.—*Antonella trochlearis trochlearis*: a, adult, typical specimen; b, adult, columellar view; c, same, profile; d, large form; e, large form, columellar view; f, genitalia, adult; g, interior of penis; h, penis, strongly contracted; i, teeth.

*Cionella (Tornatellina) trochlearis* von Martens, 1860, Albers Die Heli-  
ceen, 259.

*Strobilus pellucidus* Mühlfeld, Anton, 1839, Verzeichniss der Conchylien,  
46 (*nomen nudum*).

Shell thin, very fragile, transparent, color honey yellow. Whorls 6.5; embryonic whorls without spiral lines, somewhat glossy; postembryonic whorls faintly striate, with lines of growth increasing slowly and regularly, the last whorl enlarging very rapidly and occupying more than half the bulk of the shell. Aperture large, longer than broad. Parietal lamella simple, rather weak, slightly oblique, long, entering about 1.25 whorls into aperture. Columella perpendicular, subtruncated below by a rather weak, rapidly ascending slightly sinuous columellar lamella which terminates at outer margin; in addition, a very weak, nearly vertical upper lamella extends close to outer margin of columella, forming an acute angle with columellar lamella. Palatal wall without folds at all stages of growth. Peristome erect, very thin, fragile. Viewed horizontally from outside, there is only a low elevation fairly close to parietal wall on outer margin of columella.

Length 4.86 mm., diameter 2.97 (61 percent); apertural axis 2.38, diameter 1.59 (66 percent); last whorl 3.43 (70 percent); parietal lamella 0.14.

A juvenile specimen (144802), whorls 5.5-6, is just over 4 mm. long. Parietal lamella proportionately hardly stronger than at adult stage; columellar lamellae only slightly more so.

In even younger specimens (from Maitua, 143953), whorls 4.5, 2.5 mm. long, parietal lamella proportionately about same height, but columellar lamellae much stronger.

Larger specimens (from Maitua, collected at 400-700 ft.) have same number of whorls. Shells lighter in color (chamois), thicker, not as transparent, columellar lamellae a little more distinct.

Length 6.54 mm., diameter 3.95 (60 percent); apertural axis 3.18, diameter 2.27 (71 percent); last whorl 4.64 (71 percent); parietal lamella 0.18 (illustrated specimen).

Adult genitalia. *Ovotestis* multilobate (all but four lobes lost); follicles short-clavate, some bluntly pointed. *Duct* slightly enlarged in middle, not strongly convoluted. *Talon and carrefour* not dissected. *Albumin gland* small, on carrefour; follicles minute, ovate. *Prostate* large; follicles numerous, digitate. *Spermatheca* large, ovate or oblong. Stalk short, inserting into oviduct almost immediately. *Vagina* long, nearly oviducal length, narrow. *Vas deferens* narrow, Y at middle of penis. *Penis* long ( $\pm 0.66$  oviducal length), broad (ratio, width to length, 1:3.5), robust (in contracted animal, penis fist-shaped). Interior of penis simple, with narrow ascending pilaster branching into shapeless masses, lower pendent; orifice of vas deferens between masses of pilaster tissues. *Atrium* short.

Teeth alike, seven-dentate. Two ecto-, two ento-, and one mesocone but sometimes all paired, with two cusplets between mesocone(s) and outer cusps. Length 11-13 microns, width 4.6 microns.

Dissected 144801 (adult genitalia, teeth), about six specimens; 144802 (interior of penis, contracted penis), two specimens.

"Dohrn [1863, Malak. Blätt., p. 158] has suggested that the species belongs to the Auriculaceae," according to Pilsbry, who also gives the following translation of Pfeiffer (1842): "Shell ventricose-fusiform, glossy, pellucid, pale corneous. Whorls 6, flattened, the last shorter than the spire, tapering basally. Aperture oblong; peristome simple, lamella of parietal wall of the aperture transverse, large, acute. Length 4, diameter 2 mm."

Pfeiffer (1842, p. 55) gives the measurements as length 4 mm., diameter 2.5. Küster (1852, p. 151), who studied specimens from Pfeiffer, gives a somewhat fuller description:

Shell small, swollen fusiform, shining, transparent, light corneous, finely striate on the latter whorls; the spire conic, quite high. The six whorls flat, the last broad, shorter than the spire, strongly attenuate below, the suture hardly impressed, somewhat irregular, the last whorl somewhat deeper striate at the margin, so that the intervals appear as weak papillate, somewhat distinct elevations. The aperture is oblong, small; the peristome sharp, erect; the palate of the mouth wall large, oblique, sharp, whitish; columellar fold weakly developed, columella margin short, descending in a rather steep curve. Height  $1\frac{1}{2}$  lines, diameter  $\frac{3}{4}$  lines [3 mm.  $\times$  1.5]. Sometimes there appears a flat insignificant fold on the palatal wall; it appears to be a more developed individual. (Translation from German.)

Type in Germany.

Rapa (Opana of Anton, for *pellucidus*; Opara of Pfeiffer): Mount Tanga (south of Ahurei Bay), south side, under stones, alt. 700-800 ft., Anderson, Toto, and Terii Pare, July 31 (figured specimen 8757); paratypes 144801-144802. Maitua, at foot of cliffs, on very damp leaves, alt. about 800 ft., Anderson and Cooke, July 4, paratypes 143950-143953 (dissected); on upper slope leading to cliffs below Mangaoa, large specimens, under stones, alt. about 700 ft., Anderson, July 4 (figured specimen 8758), paratypes 137872-137873; on ground, alt. 400 ft., Margaret Stokes, June 6, 1921, 53212.

In the Museum collection are 17 lots totaling 48 specimens, 10 lots of which came from Maitua Valley. None of the lots has more than a few specimens. The largest includes eight live specimens, whereas most lots have only one or two. This species appears to be very rare in any locality, perhaps because we failed to discover the optimum condition under which it lives.

All the specimens we interpret as the typical form were found south of Ahurei Bay, at Maitua, Mount Mangaoa, Ahurei, Teutu, and Mount Tanga (south). These occurred in both dense and open forests from an altitude of about 100 feet, usually under stones.

Pfeiffer's material was probably received from Anton, and may have been Mühlfeld's original specimens of *pellucidus*, since both Anton's variety description (1839, p. 46) and Pfeiffer's variety description (1848, p. 394, *Beta*) were undoubtedly based on identical specimens. Küster did not consider this a variety but a more fully developed individual.

The form we have selected to represent the species agrees fairly closely with Pfeiffer's description. The only difference is that Pfeiffer describes the parietal lamella as "magna," a term that could not be applied to our specimens. Furthermore, Pfeiffer's specimen is only 4 mm. with 6 whorls, whereas our figured specimen is 4.86 mm. with 6.50 whorls. The difference in size may be due to age, or our specimens may represent a geographical race.

Owing to imperfect preservation, the more delicate parts such as the ovotestis, the albumin gland, the prostate, and the internal structures of the penis were too soft for ordinary handling. These organs should be reexamined when better animals are available.

**Antonella trochlearis radicula**, new subspecies (fig. 54, *a, b*).

Shell longer than any specimens of the typical form, more convex in outline, indistinctly acuminate toward apex, in shape intermediate between typical form and *fusiforma*. Shell not transparent, quite thin, ecru olive in color.

Length 6.86 mm., diameter 3.70 (54 percent); apertural axis 3.18, diameter 2.23 (70 percent); last whorl 5.11 (70 percent); parietal lamella 0.23.

Rapa: Kopenena Valley (type locality), dead on ground, alt. 200-600 ft., Wight and Kondo, July 24; holotype 8759, paratypes 143208. Mount Ruatara, northeast slope, alt. about 800 ft., Kondo, July 26.

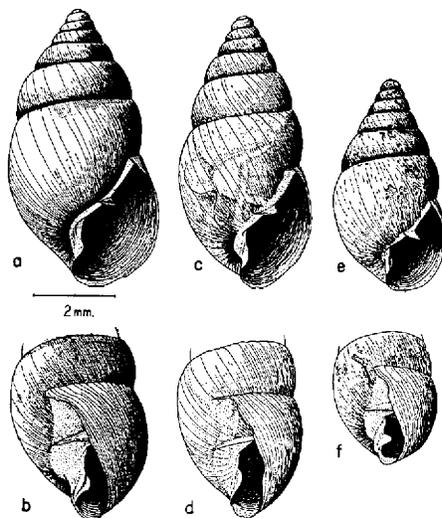


FIGURE 54.—*a, b*, *Antonella trochlearis radicula*: *a*, adult, holotype; *b*, adult, columellar view. *c, d*, *Antonella trochlearis fusiforma*: *c*, adult, holotype; *d*, adult, columellar view. *e, f*, *Antonella trochlearis nesiotica*: *e*, adult, holotype; *f*, adult, columellar view.

The six lots total 43 specimens, of which 19 are in the type lot. Four lots were collected on Mount Ruatara at various altitudes above 700 feet, the fifth lot, found near the apex of Mount Vairu, at more than 1,100 feet.

Only one specimen was alive, a juvenile from Mount Ruatara (143532). This specimen has just over six whorls; is about 5 mm. long; and is thin, sub-transparent, and chamois in color.

This subspecies, with a wider distribution than the species, was taken in localities on the northwestern to northeastern sides of the bay, a distance of more than three miles along the ridge. Specimens from the various localities show no appreciable differences.

**Antonella trochlearis fusiforma**, new subspecies (fig. 54, c, d).

Shell longer and proportionately narrower than that of *A. trochlearis*, thin, fragile, transparent, glossy, color ecru olive. *Spire* elongate. *Whorls* 7, last whorl oblong, tapering very slowly to base. *Aperture* long, narrow. *Parietal lamella* low or moderate. *Columella* perpendicular, not as distinctly truncate at its base and with a slightly stronger fold than in *trochlearis*.

Length 6.73 mm., diameter 3.49 (52 percent); apertural axis 4.82, diameter 1.82 (38 percent); last whorl 4.43 (66 percent); parietal lamella 0.23.

Rapa: Mount Tevaitahu (type locality), in ravine on west slope, under stones, alt. about 750 ft., Anderson, July 9; holotype 8760, paratype 142480.

A single lot of two live specimens was collected. Because of the limited material, *fusiforma* is considered a subspecies of *trochlearis*. With more specimens, especially juveniles, its status might be raised. It is easily recognized by its size and form.

**Antonella trochlearis nesiotica**, new subspecies (fig. 54, e, f).

Shell proportionately narrower than that of typical form, thicker, almost opaque. *Spire* narrowly conic, with straight outlines. *Whorls* 7, increasing more slowly and regularly, last whorl not as capacious, slightly shorter in proportion to total length. *Parietal and columellar lamellae* somewhat stronger.

Length 5.56 mm., diameter 2.82 (51 percent); apertural axis 2.37, diameter 1.50 (63 percent); last whorl 3.36 (60 percent); parietal lamella 0.27.

Rapa: Karapo Rahi Islet (Karapo Hari on chart 2011, U. S. Hydrographic Office map), near southernmost tip of Rapa (type locality), under stones, alt. 50-300 ft., Anderson, July 18; holotype 140649.

The type was the only specimen taken. *Nesiotica*, which means "belonging to an island," is the most distinct of the subspecies of *trochlearis*. In the stronger development of the parietal and the columellar lamellae, it appears to approach *A. pfeifferi* but entirely lacks the palatal fold. It is also a much larger shell. With a full series of adults and juveniles, this subspecies might be given species rank.

**Antonella pfeifferi**, new species (fig. 55, a-g).

*Strobilus pellucidus* Mühlfeld (Anton's var., no. 1693-2), 1839, Verzeichniss der Conchylien, 46.

*Tornatellina trochlearis* Beta Pfeiffer, 1848, Mon. Hel. Viv. 2: 394.

"V. [ariety] slenderer, with a delicate ridge at the base of the aperture." (Anton)

Shell narrowly ovate-fusiform, somewhat thickened, translucent, color chamois in dead state, slightly glossy, nearly smooth, under a lens minutely striate with lines of growth. *Spire* conic, with slightly convex outlines below, indistinctly attenuate above. *Suture* simple, lightly impressed. *Whorls* 6.75; apical whorl slightly swollen; postembryonic whorls flatly convex; last whorl oblong, tapering gradually to base. *Aperture* long, its outer margin regularly curved. *Parietal lamella* strong, slightly more than one whorl long, obliquely seated. *Columella* perpendicular, its inner face thickened with a distinct rapidly ascending, slightly sigmoid lamella, and with a nearly straight upper columellar lamella. These lamellae unite at an acute angle at the outer basal margin; above them and close

to parietal wall is a low, indistinct, deeply seated callus. *Palatal wall* armed with a distinct continuous basal fold, slightly more than 0.5 whorl long. *Lip* erect, margined within by an indistinct callus.

Length 4.0 mm., diameter 2.2 (55 percent); apertural axis 1.81, diameter 1.19 (65 percent); last whorl 2.59 (65 percent); parietal lamella 0.28.

A nearly mature specimen (fig. 55, *c, d*), with just over six whorls is 3.61 mm. long, cream buff in color. Shell thin, semitransparent. Parietal lamella just over a whorl long, its upper surface microscopically and obliquely striate. Columellar lamellae proportionately somewhat stronger. Palatal fold, which is clearly visible through shell from exterior, considerably more than one whorl long.

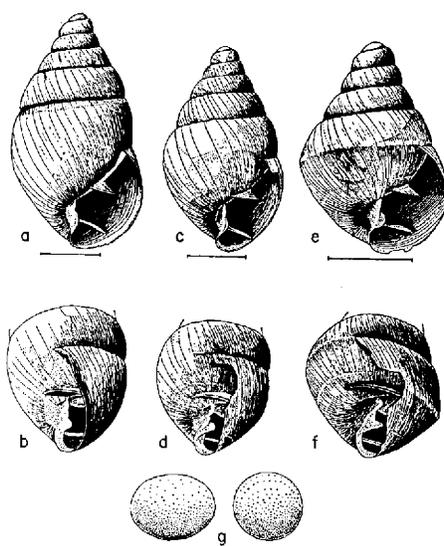


FIGURE 55.—*Antonella pfeifferi*: a, adult, holotype; b, adult, latero-oblique apertural view; c, paraneanic; d, paraneanic, latero-oblique view; e, metaneanic; f, metaneanic, latero-oblique view; g, egg.

A younger specimen (fig. 55, *e, f*), whorls 5.5, length 2.50 mm., is bluntly angulate at periphery. Parietal lamella proportionately stronger, obliquely striate, as in older specimens. Columella with proportionately stronger lamellae than in older and adult specimens; uppermost swelling lacking. In other characters it agrees with older juvenile specimens.

Egg elliptical (fig. 55, *g*), only one found.

Genitalia. Five specimens, not quite mature, were dissected (not figured), all in very poor condition and so badly torn in extraction that parts of the genitalia were difficult to identify, but penises sufficiently entire so that the generic position of species was determinable. Penis long and broad (ratio, width to length, 1:5.6).

Vas deferens enters penis subapically. Atrium short.

Dissected 137701, two specimens; 137650, 137651, 144535, one specimen each.

Rapa: Maitua (type locality), in native forest, under stones, alt. about 600 ft., Anderson, Cooke, July 2; holotype 8761 (figured juveniles 8762, 137702),

paratypes 137701-137705 (dissected). Additional paratypes: Maitua, in coffee plantation, on ground, alt. about 400 ft., Margaret Stokes, June 8, 1921, 53213; Mount Tautautu, north slope, under stones, alt. about 800 ft., Cooke, July 25, 143327.

The holotype was a recently dead adult, one of the very few in our series. The Museum collection has five other lots, two collected by Mrs. Stokes near Ahurei village (53192, 53259), and three lots from Maitua collected by the Mangarevan Expedition (137650-137653, 137623-137624, 144535-144536). Of the 38 specimens, the total of eight lots, only 12 were alive and none of these was adult. All specimens came from a very small portion of the island and agree closely with each other.

The small size, the narrow outlines, the strong parietal lamella, and the presence of a palatal fold easily separate this species from *A. trochlearis*.

***Antonella tenuis*, new species (fig. 56, a-e).**

*Shell* elongate, narrowly conic-turritid, color cinnamon buff, thin, fragile, subtransparent, rather glossy, microscopically striate with lines of growth. *Spire* elongate, conic-turritid, with nearly straight outlines. *Suture* simple, slightly impressed. *Whorls* 7.5; embryonic whorls smooth, glossy; postembryonic whorls increasing slowly and regularly, slightly convex; last whorl oblong, tapering gradually to base. *Aperture* medium, subovate, its outer margin regularly curved. *Parietal lamella* slightly obliquely seated, just over one whorl long. *Columella* perpendicular, nearly straight, inner surface slightly thickened, with two rather weak, rapidly ascending lamellae. *Palatal wall* armed with a low, continuous, threadlike fold, about one whorl long. *Peristome* thin, erect.

Length 4.47 mm., diameter 1.84 (45 percent); apertural axis 1.41, diameter 0.91 (64 percent); last whorl 2.16 (53 percent); parietal lamella 0.14.

In a juvenile specimen (fig. 56, d) whorls nearly 6, length 2.64 mm., parietal lamella strong, its free margin flaring outward. Columellar lamellae rather strong, of nearly equal development. Palatal fold well developed, compressed, about 1.25 whorls long.

Genitalia (fig. 56, e) juvenile. *Ovotestis* not recovered, presumably similar to that of *A. trochlearis* (apical half of animal missing). *Duct* recovered in part, showing sigmoid talon. *Albumin gland* large; follicles numerous, relatively large, short-clavate, round or ovate. *Prostate* fairly large, paucifolliculate; follicles digitate, fanning. *Uterus* distended, long (0.5 oviducal length). *Spermatheca* large, ovate, filled with sperm mass; stalk long ( $\pm 0.5$  oviducal length). *Vagina* narrow, quite short. *Vas deferens* narrow (0.2 vaginal width), entering penis 0.3 way below apex (Y). *Penis* small (ratio, width to length, 1:4), short (0.3 oviducal length), subcylindrical. *Retractor* large, long. *Atrium* short.

Dissected 140231 (paraneanic or subadult), one specimen only; 140519, 135331, 135852, 135215 (all poorly preserved or badly torn).

Rapa: Area, back of village (type locality), under stones, alt. about 400 ft., Anderson, July 24; holotype 8763 (figured juvenile 8764), paratypes 144663-144664. Area, under stones, alt. 250-450 ft., Cooke, Kondo, Anderson, July 15, 140519-140520. Tumu Valley, under stones, alt. 150-200 ft., Cooke, July 13, 140231.

Specimens were also taken at Mount Atanui, Mount Ruatara, Mount Pe-  
rahu, Kopenena Valley, Mount Tevaitahu, Mount Tautautu, Maitua Valley,  
Ahurei village, and Mount Ororangi.

Bishop Museum has 24 lots containing 44 specimens, of which 21 were taken alive. The species is evidently distributed over a large part of Rapa. However, it seems to be extremely scarce in any locality, as our largest lot (the type lot) has only six specimens. Only four lots have as many as three specimens each; most contain only one or two. Only three or four specimens can be considered fully adult. The figured type is gerontic, as the callus nodule between the parietal lamella and the columella indicates. This character is also found in one of the dead shells.

Except for characters of the columella, this species might belong to the genus *Pukunia*, but the anatomy shows no relationship whatsoever to that genus. A fair comparison between *A. tenuis* and *A. trochlearis* cannot be made because of the discrepancy in age. However, two major differences are evident in *A. tenuis*: the penis is comparatively shorter and the spermathecal stalk is much longer.

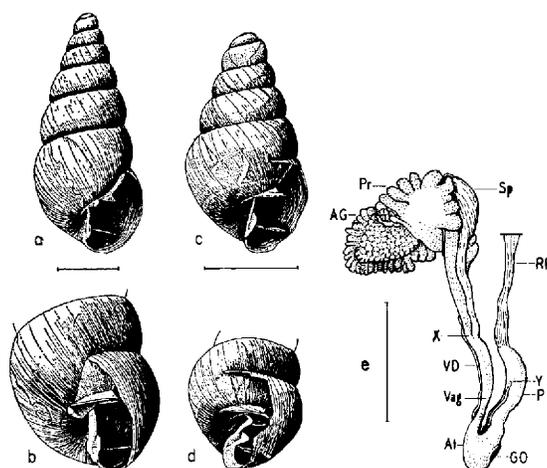


FIGURE 56.—*Antonella tenuis*: a, adult, holotype; b, adult, latero-oblique apertural aspect; c, metaneanic; d, metaneanic, latero-oblique view; e, genitalia, immature, minus hermaphrodite gland.

#### Genus *Perahua*, new genus

*Shells* medium or small, thin, subtransparent. *Embryonic whorls* glossy, under a strong lens microscopically spirally striate. *Parietal lamella* absent at all stages of growth. *Columella* sigmoid, internal face margined with a strong, long lamella entering for about two whorls, terminating near base and projecting outward over columella. No indication of a palatal fold at any stage of growth.

Type species: *Perahua grandis*.

Distribution: Rapa.

Species of this genus were taken only on the upper slopes of Mount Perahu

at altitudes above 1,200 feet. One of the species, *P. grandis*, is strictly arboreal; and it is assumed that this is true of the second, *P. bakeri*.

The genus is characterized by the peculiar form of the columella and by the total lack of a parietal lamella. Anatomically it is related to *Antonella*, from which it is easily separated by conchological characters.

***Perahua grandis***, new species (figs. 57, a-f; 58, a-h).

*Shell* (fig. 57, a-c) acuminate ovate to subfusiform, color of last whorl ecru olive, shading to snuff brown near apex, thin, fragile, last whorl subtransparent, columella visible through shell, upper whorls translucent, surface with oily gloss, finely striate with lines of growth. Under a strong lens, surface, especially in front of aperture, marked with minute, closely spaced, spiral lines, which are less distinct on upper whorls. Embryonic whorls minutely, closely, spirally striate. *Spire* acuminate conic with slightly convex outlines. *Suture* simple, lightly impressed. *Whorls* 7.5; embryonic whorls slightly flattened, with distinct sutures; postembryonic whorls flatly convex, increasing slowly and regularly

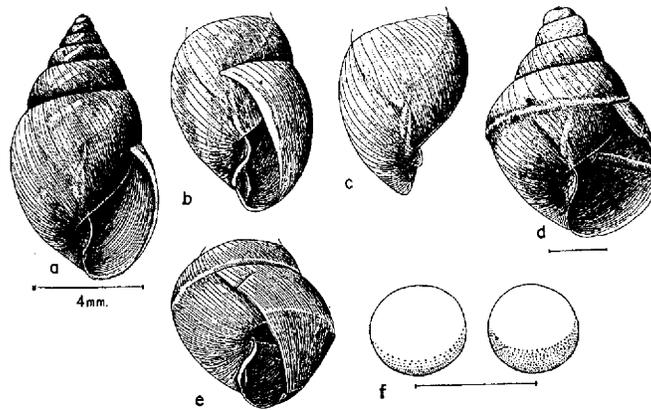


FIGURE 57.—*Perahua grandis*: a, adult, holotype; b, adult, columellar view; c, adult, profile; d, meta-ananeanic stage; e, meta-ananeanic stage, columellar aspect; f, egg.

at first, more rapidly below; last whorl large, oblong, occupying more than three-fourths bulk of shell, tapering gradually to base. *Aperture* rather narrow, more or less pointed at both ends, outer margin regularly curved. *Parietal lamella* entirely lacking at all stages of growth. *Columella* vertical, slightly calloused, sigmoid, margined with a rapidly ascending, strongly sigmoid lamella, ascending within shell for nearly two whorls; lamella terminating below in a rather prominent knob, which is slightly arched over outside of columella; below this lamella a smaller, deeply seated subbasal fold, entering more perpendicularly, scarcely visible in frontal view. *Palatal wall* unarmed. *Peristome* erect, extremely thin, fragile.

Length 9.05 mm., diameter 5.40 (60 percent); apertural axis 4.73, diameter 2.30 (48 percent); last whorl 7.63 (84 percent).

A juvenile specimen (fig. 57, d, e), whorls nearly 5, length 4.03 mm., ivory yellow in color, thin, fragile, transparent, with a broad blunt keel on periphery. Viewed from within, keel is represented by a shallow groove. With growth of shell, keel gradually becomes weaker and disappears by time shell attains maturity. Columellar lamellae proportionately weaker and less sinuous than in adult stage.

An egg (fig. 57, f) taken from uterus has a white calcareous shell. It is nearly spherical, only slightly longer than broad and measures  $0.80 \times 0.70$  mm.

Adult genitalia (fig. 58, a-d). *Ovotestis* large, eight- to 10-lobate; follicles numerous, small, short-clavate, distinct, tightly packed. *Duct* not found (animal incomplete). *Albumin gland* small; follicles very numerous, minute, ovate or round. *Prostate* large; follicles numerous, not large, digitate or short-clavate. *Spermatheca* large, ovate; stalk very short, entering oviduct almost immediately. *Vagina* long, constituting nearly entire length of oviduct, very narrow, tapering below. *Penis* vermiform, longer than oviduct (ratio, oviductal length to penial, 1:1.34), convoluted, twisted around vas deferens two to three times, of nearly equal diameter throughout except for slightly larger head and narrower root (ratio, length to diameter, 14:1). Interior of penis simple with ascending pilaster enlarging at apex (Pil 1), recurved, without velum, papilla (P Pap) similar to ascending pilaster, both ending soon as very narrow ridges.

Central nervous system (fig. 58, e) as follows:

*Cerebral ganglion*, left: (1) Nuchal nerve off anteroventral part of ganglion (next to and left of labio-tentacular nerve, 5), joining frontal nerve and appressed to it until frontal nerve innervates base of ommatophore, thence bifurcating. Shorter nerve innervates wall of head near base of ommatophore, longer nerve continues to upper lip (1a). (2) Ommatophoral-optic nerve off usual angle of ganglion, to superior tentacle (right ommatophoral-optic nerve not passing through peni-oviductal angle). (3) Frontal nerve off fronto-latero-ventral part to left of nuchal nerve, to base of ommatophore. (4) No penial nerve off right cerebral ganglion. See 27a, PN. (5) Large labio-tentacular nerve off fronto-ventral part to left of buccal connective, thence directly anteriad along large muscle that is attached to inferior tentacle and head wall. Nerve bifurcates before reaching anchorage of muscle, the principal nerve (5a) inserting into inferior tentacular retractor near terminal. Of the other branch, one (5b) crosses over inferior tentacle and innervates wall of head; the other branch continues a short way and again bifurcates into two sets of nervelets. Posterior nervelet (5c) goes directly to right and innervates side of buccal mass; anterior branch trifurcates. Of these three nervelets, one (5d) innervates buccal mass just anterior to 5c; of the other two, the anterior nervelet (5e) innervates head parts anterior to inferior tentacular retractor and posterior nervelet (5f) ventrad of this muscle. (6) Buccal connective off medio-ventral part of ganglion to left buccal ganglion. (7) Small buccal retractor nerves off posterior surface. (8) Acoustic nerve (right) from latero-ventral part between cerebro-pedal and cerebro-pleural connectives, directly ventrad alongside pleuro-pedal connective (not figured) to otocyst, which is located at origin of nerves 21 and 28. (9) Subcerebral nerve not seen, but undoubtedly exists.

*Pleural ganglion*, left, and pleuro-pedal connectives: (10) Small nervelet to left superior tentacular retractor at junction of two tentacular retractors. (11) Another small nervelet to left of inferior tentacular retractor.

*Parietal ganglion*, left: (12) Fairly large left pallial nerve to body wall. (13) Small subsidiary nervelet to salivary gland.

*Right parietal plus abdominal ganglion*: (14) Caudal nerve to columellar muscle and dorsum of tail. (15) Long intestinal nerve along aorta. (16) Anal nerve under uterus to integument (not followed further). (17) Right pallial nerve to integument to right.

*Pleural ganglion*, right: Fair-sized nerve bifurcating into nervelet (18a) leading into large foot muscle on floor of body; (18b) nervelet leading to right inferior tentacular retractor.

*Pedal ganglion*, left (around edge): (19) Two large anterolateral pedals. (20) One broad but thin and transparent lateral pedal, anterior part reaching over large foot muscle to insert in integument; posterior part in muscle. (21) One small nerve (PLP?) off posterior end of otocyst to large foot muscle and also to foot. (22) Bifurcating postero-lateral pedal to foot and tail.

*Pedal ganglion*, left (ventral): (23) One anteroventral pedal, bifurcating and innervating sole. (24) One medioventral pedal. (25) One large caudoventral (CVP) with three branches.

*Pedal ganglion, right*: All nerves similar to left except that lateral pedals are two in number. Anterior nerve innervates penis and posterior nerve innervates vagina. The nerves are: (26) anterolateral pedal (ALP); (27a) penial (PN); (27b) vaginal (Vag N); (28) posterolateral pedal? (corresponding to 21); (29) posterolateral pedal (PLP); (30) anteroventral pedal (AVP); (31) medioventral pedal (MVP); (32) caudoventral pedal (CVP).

*Teeth* (fig. 58, h) all alike, quite large. Central tooth (c) smallest, slightly modified, six-dentate. Others usually with broad head, eight- to 10-dentate, all sharp. One ecto-, one ento-, and one mesocone plus two to four cusplets between and below, between mesocone

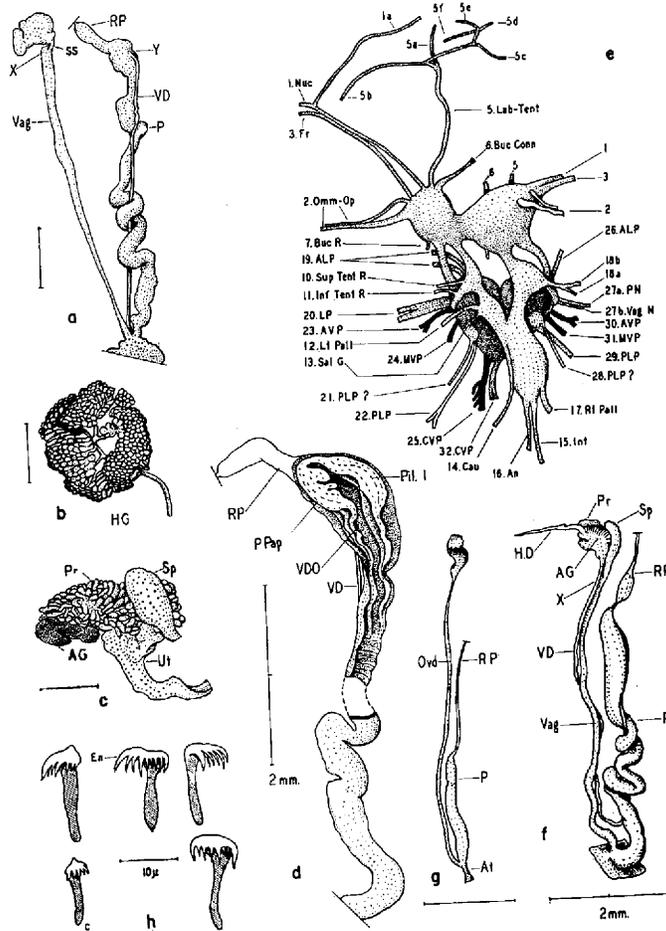


FIGURE 58.—*Perahua grandis*: a, adult genitalia; b, hermaphrodite gland or oovestis; c, upper organs; d, penis, interior; e, central nervous system, except buccal ganglia; f, parametaneanic genitalia, minus hermaphrodite gland; g, meta-ananeanic genitalia; h, teeth, central plus laterals.

and one of outer cusps. Entocone (En) always larger than ectocone. Central tooth: length  $\pm 11.6$  microns, width 4 microns. Marginal tooth: length  $\pm 17.3$  microns, width  $\pm 8.3$  microns.

Para-metaneanic genitalia (fig. 58, *f*). Penis proportionately same length and size. Spermatheca more slender; other organs less developed.

Meta-ananeanic genitalia (fig. 58, *g*) undeveloped. Penis very short, slender.

Dissected 135602 (adult genitalia, in part; teeth), two specimens; 142774 (adult genitalia, teeth), two specimens; 135603, 135457 (nervous system), three specimens; 135604, 135606 (juveniles), one specimen each.

Rapa: Mount Perahu, east ridge (type locality), on leaves of *Freycinetia*, *Veronica*, *Lautea*, and other shrubs, alt. 1,600-1,800 ft., Kondo, Anderson, and natives, July 28; holotype 8765 (meta-ananeanic specimen 8766 figured), paratypes 135602-135607. Same locality, on leaves of shrubs, alt. 1,400-1,500 ft., Anderson, July 21, 142774.

The Bishop Museum collection has an additional nine lots of the species, containing 84 specimens, of which only one dead and two live specimens are adults. The species is rare and scattered, and it is distributed on Mount Perahu's eastern ridge between 1,200 and 1,800 feet.

This is the largest species of the family found on Rapa. Its size approaches that of the largest species of *Auriculella* from the Hawaiian Islands, being only 1 to 2 mm. shorter. It is considerably shorter than some species of *Fernandezia* from Juan Fernandez, of which three or four species are 11 to 12 mm. long. However, it is much larger than any of the known species from the central Pacific islands.

The species is easily recognized by its large size, by the extremely fragile shell, by the lack of a parietal lamella, and by its characteristic columella.

The picture of the genus is necessarily incomplete, owing to the lack of complete animals. In all probability the same condition exists in *Perahua* as in *Antonella tenuis*, which is characterized by a large albumin gland and small prostate in the paraneanic stage.

***Perahua bakeri*, new species (fig. 59, *a-d*).**

*Shell* elongate-conical, isabella color, rather thin, semi-transparent, minutely striate with lines of growth, slightly accentuated just below sutures, under a strong lens faint spiral lines indistinctly visible, surface with a rather dull oily sheen. *Spire* elongate, tapering gradually, with slightly convex outline. *Suture* simple, lightly impressed. *Whorls* 7; embryonic whorls slightly flattened, glossy, microscopically indistinctly spirally striate, slightly shouldered above; post-embryonic whorls increasing slowly and regularly, flatly convex; last whorl oblong, with a broad indistinct depression near aperture. *Aperture* elongate, its outer margin slightly flattened. *Parietal wall* without lamella. *Columella* vertical, its inner face margined with a strongly sigmoid lamella extending inward for more than one whorl, terminating on outer wall and forming a distinct arch over columella. Viewed laterally from outside, margin of columella regularly curved. An indistinct additional fold is indicated about half-way between lamella and base of columella which may take the place of basal fold in *P. grandis*. *Parietal lamella* absent. *Palatal wall* unarmed. *Peristome* thin, erect.

Length 5.95 mm., diameter 2.95 (50 percent); apertural axis 2.54, diameter 1.36 (53 percent); last whorl 3.68 (62 percent).

Genitalia recovered in part (fig. 59, *d*). Penis long, relatively narrow, upper half the broader, thin, transparent (ratio of width to length, 1:9).

One egg, semispherical.

Juvenile specimens none.

Dissected 142848.

Rapa: Mount Perahu, east ridge, alt. 1,200-1,500 ft., Kondo, July 21; holotype 8767, paratype 142848.

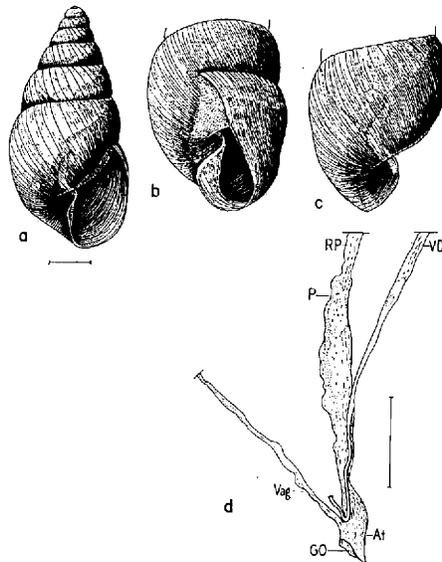


FIGURE 59.—*Perahua bakeri*: a, adult, holotype; b, adult, columellar view; c, adult, profile; d, penis.

Bishop Museum has three lots consisting of four specimens, two collected alive, two dead. Each of the extra two lots (135501, 142892) consists of a single dead specimen taken from 1,500 to 1,800 feet on Mount Perahu. No information is available as to whether or not the species is arboreal.

*P. bakeri*, named for Professor H. B. Baker of the University of Pennsylvania, differs from *P. grandis* in its smaller size, narrower outlines, and simpler columella. The lower columellar lamella, merely indicated in two examples, is absent in the others. The small yield resulting from three collecting trips indicates that *P. bakeri* is an extremely rare species.

Only two, badly preserved and torn specimens were available for dissection. The result, though unsatisfactory, is sufficient for identification purposes.

## TRIBE TUBUAIINI

With appendix. Viviparous. Adolescent genitalia recapitulate adult Pityisini genitalia. Albumin gland well developed and dominant in adult. Interior of penis with simple recurved achatinellid pilaster ending in semipendent papilla.

Adult shells are not clearly distinguishable from those of some of the other tribes. Some externally resemble species of *Lamellidea* and *Tornatellinops*. Others superficially resemble the small species of *Taitaa*. Juveniles of a few have apertural teeth like those of *Lamellovum* (*Maitua*). Length: 2.03-5.84. Whorls: 5.25 to 7.75. Parietal lamella weak, moderate, or strong.

In juveniles, parietal lamella weak, moderate, or strongly sinuous. Palatal wall without folds; or lower fold present, upper fold vestigial; or two folds. Columella two- or three-lamellate, some predominantly two-lamellate with vestigial third, others predominantly three-lamellate with a few two-lamellate among them.

Type genus: *Tubuaia*.

## KEY TO GENERA AND SUBGENERA OF TUBUAIINI

- A. Shells nearly smooth, marked with fine lines of growth.....**Tubuaia**.  
 AA. Shells marked with fine, raised cuticular transverse striae.  
   B. Shells elongate to cylindrical, embryonic whorls without fine spiral striae.  
     C. Shells about 6 mm. in length, whorls 7 to 7.5. Juveniles with a strong sinuous parietal lamella; columella furnished with three strong sub-horizontal lamellae; palatal wall furnished with a long distinct lower palatal fold.....**Celticola** s.s.  
     CC. Shells less than 3.5 mm. in length. Juveniles with rather weak rapidly ascending columellar lamellae; palatal wall unarmed.....**subgenus Meryticola**.  
 BB. Shells conical, embryonic whorls with fine spiral sculpture.....**subgenus Nesonoica**.

Genus *Celticola*, new genus

Shells 2.25-6+ mm., whorls 5.25 to 7.75, elongate to conic, rather thin, translucent, distinctly striate. Embryonic whorls smooth or minutely spirally striate. Parietal lamella usually moderate, occasionally strong, sometimes weak. Columella usually with three lamellae, rarely two, the upper two stronger than the lowest, which is deeply seated. Palatal folds two, or one plus vestigial upper, or none.

Type species: *Celticola pilsbryi*.

Distribution: Rapa, Raivavae.

The four species and their subspecies of *Celticola* are easily differentiated from the other genera of these islands by their peculiar striae. The genus is related to *Tubuaia*, from which it principally differs in its surface sculpture and habitat. *Celticola* lives on tree trunks. *Tubuaia* is terrestrial.

KEY TO SUBGENERA AND SPECIES OF *CELTICOLA*

- A. Shells with 6 to 7.5 whorls, 5-6.5 mm. in length.
- B. Spire with convex outlines, whorls flatly convex, sutures shallow, striae rather closely spaced, interstices marked with fine, close, spiral lines, lower whorls slightly shouldered at upper third of whorl, embryonic whorls smooth and glossy; juveniles with a long lower palatal fold, sometimes with a short, very weak upper palatal fold; Rapa.....**C. (*Celticola*) pilsbryi.**
- BB. Spire with nearly straight outlines, elongate-conic to conic, whorls convex separated by a well-impressed suture. Striae rather widely spaced, interstices minutely, longitudinally striatulate. Embryonic whorls finely, spirally striatulate. Juveniles without palatal folds.....**subgenus *Nesonoica*.**
- C. Spire elongate-conic, striae very weak, length over 6 mm., Raivavae.....**C. (N.) anatonuensis.**
- CC. Spire conic, striae distinct, length less than 5.5 mm., Rapa.....**C. (N.) conoides.**
- AA. Shells with 5 to 5.5 whorls, less than 3.5 mm. in length, subcylindrical; embryonic whorls smooth, glossy; juveniles without palatal folds; Rapa.....**C. (*Meryticola*) arborea.**

Subgenus *Celticola*

*Shells* 5-5.84 mm., whorls 6.5 to 7.75, ovate-turrite, thin, glossy, surface irregularly striate. Parietal lamella moderate to strong; in juveniles weakly to strongly sinuous. Palatals in juveniles two, or lower one strong and upper vestigial. Columellar lamellae three, conspicuously developed in juveniles, upper two strong, lowest deeply seated.

Type species: *Celticola* (*Celticola*) *pilsbryi*

Distribution: Rapa, chiefly on bark of *Celtis* trees.

***Celticola* (*Celticola*) *pilsbryi* *pilsbryi*, new species (figs. 60, *a-c*; 61, *a-f*).**

*Shell* (fig. 60, *a, b*) ovately turritid, isabella color, thin, translucent, glossy, with a silky sheen, the surface closely and somewhat irregularly striate, striae disjointed; last 3 whorls indistinctly angled at upper 0.33 of each whorl; above angle striae are oblique, on angle slightly accentuated and stronger, below angle striae are nearly perpendicular; just above center they are decidedly stronger, forming a narrow raised band. Surface marked with microscopically close spiral lines. *Spire* elongate, with slightly convex outlines. *Suture* shallow, narrowly margined below. *Whorls* 7.25, embryonic whorls smooth, glossy; postembryonic whorls increasing slowly and regularly; last whorl oblong. *Aperture* nearly twice the diameter. *Parietal lamella* moderate, perpendicular, about 0.33 whorl long. *Columella* perpendicular, slightly sigmoid, its inner face calloused, furnished with three lamellae; supra- and columellar lamellae long, ascending rapidly, of about equal development, columellar lamellae extending to and uniting with peristome; subcolumellar lamella short, situated on a heavy callus, deeply seated and visible only when aperture is viewed obliquely. *Palatal wall* unarmed. *Peristome* thin, erect.

Length 5.84 mm., diameter 2.70 (46 percent); apertural axis 2.23, diameter 1.20 (51 percent); last whorl 3.43 (59 percent); parietal lamella 0.17.

A juvenile specimen with 6 whorls (fig. 60, *c*), 3.5 mm. long, has a distinct, beaded, low peripheral keel. Parietal lamella proportionately stronger than in adults, simple, its free margin slightly arched outward. In an opened specimen, same age, parietal lamella nearly one whorl long, outer half well developed, inner half indicated by a mere thread. Columella conspicuously tridentate; columellar lamella strong, nearly transversely seated; supracolumellar lamella weaker, more obliquely ascending; subcolumellar lamella deeply

seated on a heavy callus, short, transverse. In an opened specimen, the two upper lamellae are long, accompanying columellar lamella for almost a complete whorl; subcolumellar lamella short. Palatal wall with a lower fold, which is partially but not completely disconnected and is one whorl or slightly more long. A few specimens have a much shorter indistinct upper palatal fold, which can be seen only through the shell, its position indicated by a faint whitish line.

At a younger stage, about 5.5 whorls, periphery furnished with a slightly sharper keel; parietal lamella proportionately stronger, its free margin flaring outward and slightly sinuous; columella more heavily calloused; lower palatal fold stronger and upper palatal fold sometimes visible when viewed from the front.

Adult genitalia (fig. 61, *a, b, d*) similar to that of *Tubuaia*, multiembryonate (15 in oviduct). *Ovotestis* from another specimen (subadult?), eight-lobate; follicles few, short-clavate. *Duct* small, slightly swollen, convoluted. *Albumin gland* well developed; follicles few, short-digitate to ovate. *Prostate* not seen, possibly hidden. *Upper uterus* heavily distended, wrinkled. *Oviduct* distended, diaphanous. *Vagina* short. *Spermatheca* small; stalk fairly broad, long, emptying into oviduct below lowest embryo (X). *Vas deferens*

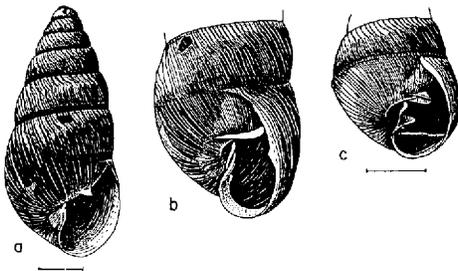


FIGURE 60.—*Celticola (Celticola) pilsbryi pilsbryi*: a, adult, holotype; b, adult, columellar aspect; c, juvenile, apertural aspect.

narrow, thin; Y subapical. *Penis* same as in *Tubuaia*, apex bent in this individual. Interior of penis presumably similar to that of *Tubuaia*. *Appendix* long, narrow. Interior of appendix like that of *Lamellovum auriculella*: with eversible "verge" (App V) or secretory-ejaculatory apparatus anchored to appendical wall (MW) by muscular connection; verge-like organ composed of tissue with double walls (A-A; a; b = efferent channel; c = mouth); with a simple hollow tube ending blindly distad (D-D); in cross-section heavily muscular on two opposing sides, thin and membranous on the other sides (B-B; C-C). *Retractor* long, thin, bifid, penial and appendical branches short. *Atrium* short. A second adult genitalia had a full ovotestis, small albumin gland (AG), very small prostate, and a transparent oviduct with 16 embryos. Penis quite long, narrow, with slightly enlarged ovate apex; appendix nearly subcylindrical, narrow.

Paraneanic genitalia (fig. 61, *c*) in transitional pitysinid stage (note ovotestis, embryos). Ovotestis as in adult, seven-lobate. Duct small. Albumin gland small, follicles few, ovate. Prostate fairly large but diminishing; follicles numerous, ovate. Oviduct distended with five embryos; all embryos heavily coated with yolk masses, the lowest with shell partially visible. Spermatheca large, curved, with coiled sperm mass (Sphr). Stalk broad, 0.5 oviducal length. Vagina 0.5 oviducal length, large, long. Vas deferens narrow; Y apical. Penis pitysinid, long (0.75 oviducal length), clavate; stalk long, narrowing below. Appendix as long as oviduct. Penial retractors heavy, appendical retractors less so. Atrium very short, broad, flaring.

Ana-metaneanic stage (fig. 61, *e*) without distal free appendage to appendix. Retractors both terminal. Penis short, broad. Appendix longer, tapering distad.

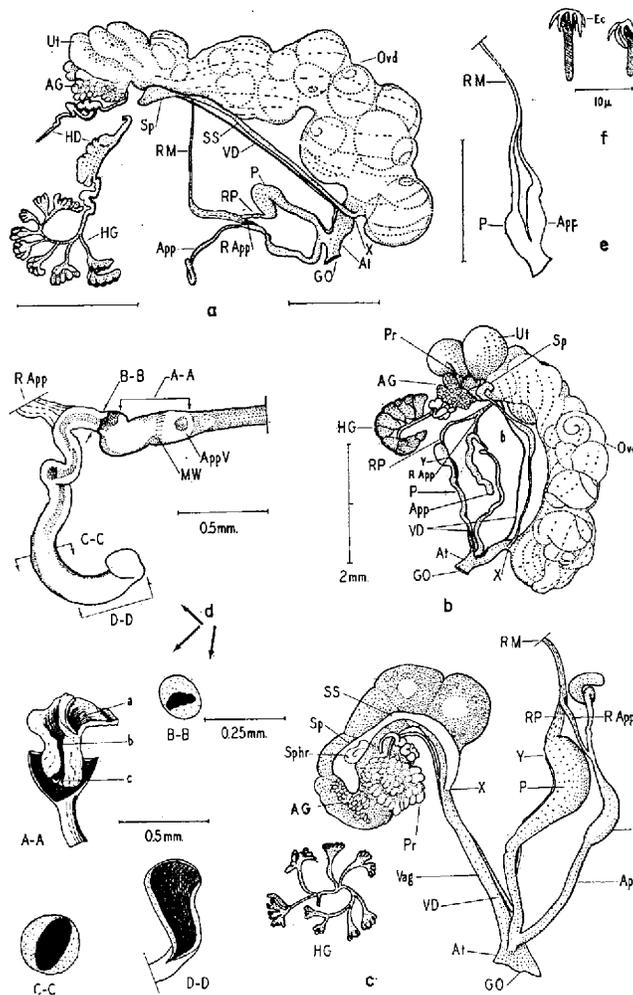


FIGURE 61.—*Celticola (Celticola) pilsbryi pilsbryi*: a, adult genitalia (ovotestis from another, perhaps younger, individual); b, genitalia, less mature than a; c, paraneanic (pitysinid) genitalia; d, appendix, optical section (App V = verge of appendix, MW = muscular wall, sections A-A, B-B, C-C, and D-D shown below, A-A = everisible "verge," a = hollow wall, b = efferent channel, c = mouth of organ opening into lower appendix); e, anametaneanic genitalia, distal tip of appendix absent; f, teeth.

Teeth (fig. 61, f) all alike, seven to eight-dentate, two ecto-, two ento-, one mesocone plus two fine cusplets between mesocone and each side cusp. Other cusplets may be present, but not evident in this preparation. First ecto- and entocone usually behind second. Length 13 microns, width 6 microns.

Dissected 140334 (adult genitalia, interior of appendix, teeth), four to five specimens; 135348 (paraneanic), two specimens; 135349 (ana-metaneanic), two specimens.

Rapa: back of Area (type locality) in crevices of bark of trunks and branches of *Celtis paniculata*, alt. 300-400 ft., Kondo and Anderson, July 15; holotype 8768, paratypes 140332-140340. Additional material was collected back of Area and also back of Atanui Bay, Mount Pukunia, Mount Vairu, Mount Ruatara, eastern ridge of Mount Perahu, Mount Morongota, in Kopenena Valley and on the crest of the ridge back of Point Maraia.

This species occurs at altitudes of about 150 feet to above 1,500 feet and seems to be distributed over a little more than the northern half of the island. The Mangarevan Expedition collected 23 lots of the typical form numbering more than 400 specimens, more than half of which were taken on the ridge back of Area Village.

The species, named for the late Dr. H. A. Pilsbry, Academy of Natural Sciences, Philadelphia, is most commonly found in crevices of the bark of *Celtis* trees. In fact, wherever this tree grew near or in the native forests, *C. pilsbryi* or one of its subspecies was almost certain to be found. A few were taken under the loose bark of one or two other species of trees.

The species shows considerable variation in size, outline, and apertural characters, even in individual lots. Those from Mount Perahu have adults similar to the typical specimen; with juveniles, the free margin of the parietal lamella is somewhat sinuous, but not as strongly so as in the two subspecies.

***Celticola (Celticola) pilsbryi proxima*, new subspecies (fig. 62, a, b).**

*Shell* smaller than that of typical species, with an additional 0.5 whorl, more cylindrical in outline, with weaker striae, not perceptibly accentuated at periphery, slightly lighter shade of clay color. *Whorls* 7.75, more closely coiled, narrower and with a proportionately shorter last whorl. *Parietal lamella* flares outward. *Columellar lamellae* stronger.

Length 5.54 mm., diameter 2.45 (45 percent); apertural axis 2.14, diameter 1.07 (50 percent); last whorl 3.0 (54 percent); parietal lamella 1.71.

In a juvenile specimen with about 6 whorls and 3.5 mm. long, peripheral keel is less distinctly defined and less crenulate than in typical form of same age; parietal lamella much stronger, its free margin strongly sinuous; columellar lamellae stronger and upper palatal fold almost invariably present.

Rapa: East Maitua (type locality), northeast side of Mount Tautautu, on trunks of *Celtis paniculata* and *Meryta choristhanta*, alt. 700-800 ft., Anderson, July 20; holotype 8770 (figured, metaneanic stage, 8771), paratypes 144612-144619.

This subspecies occupies the east-central portion of the island, including the slopes of the ridge connecting Mount Tevaitahu on the north to Mount Mangaoa on the south and Mount Tautautu, on the slopes of which most of our specimens were found.

**Celticola (Celticola) pilsbryi incerta**, new subspecies (fig. 62, *c, d*).

*Shell* elongate, rather slender, honey yellow, quite thin, subtransparent, with a satiny gloss, weakly and irregularly striate with lines of growth. *Spire* with nearly straight outlines, ending in a rather blunt apex. *Suture* shallow, simple, narrowly margined. *Whorls* 6.5 (holotype immature), embryonic whorls eroded and pitted, postembryonic whorls increasing very slowly and regularly, nearly flat. *Parietal lamella* high, its free margin strongly sinuous. *Columella* sigmoid, calloused, with three strong lamellae, the columellar lamella extending to and forming outer margin of columella, subcolumellar lamella somewhat deeply seated, its lower face irregularly calloused. *Palatal wall* with upper and lower folds, the lower high, thin, lamella-like, nearly a whorl long and the upper fold low, indistinct.

Length 4.33 mm., diameter 2.06 (47 percent); apertural axis 1.59, diameter 0.9 (57 percent); last whorl 2.45 (57 percent); parietal lamella 0.32.

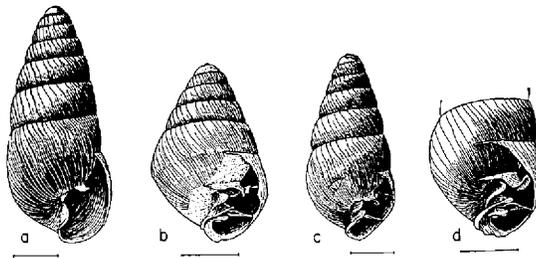


FIGURE 62.—*a, b*, *Celticola (Celticola) pilsbryi proxima*: *a*, adult, holotype; *b*, juvenile (metaneanic). *c, d*, *C. (C.) p. incerta*: *c*, subadult, holotype; *d*, subadult, latero-oblique apertural view.

Rapa: Mount Perahu, on *Bidens* or *Coprosma*, taken while beating for insects, alt. 1,400-1,500 ft., Zimmerman, July 21, holotype 135560; same locality beating *Bidens*, alt. 1,500-1,700 ft., Zimmerman, July 28, 135627, one specimen.

No adult sample of this subspecies was taken; the second specimen, though somewhat older than the holotype, is badly broken. *C. p. incerta* is probably a localized derivative of *C. pilsbryi* from the same ridge, and its nearest relative, apparently, is *C. pilsbryi proxima*. Compared with specimens of the same age, *C. p. incerta* is narrower and smoother and lacks the peripheral angle. The parietal lamella is stronger, with a sinuous free margin, and the lower palatal fold is more prominent and more strongly developed.

**Celticola (Celticola) pilsbryi latior**, new subspecies (fig. 63, *a-d*).

*Shell* slightly shorter than that of typical subspecies with the same number of whorls (7.25), proportionately wider, with slightly straighter outlines, of nearly the same color or slightly darker, glossier, striae not as strong, more weakly accentuated at periphery;

aperture proportionately broader; parietal lamella stronger, simple; columellar lamellae more prominent.

Length 5.19 mm., diameter 2.75 (53 percent); apertural axis 1.84, diameter 1.29 (70 percent); last whorl 3.12 (60 percent); parietal lamella 0.21.

Juvenile specimens of subspecies differ from those of typical subspecies much more than do adults. In one specimen (fig. 63, *b*), 6 whorls, 3.37 mm. in length, striae much weaker and peripheral angle merely indicated. Parietal lamella much stronger, its free margin calloused, arched outward, lobed, and sinuous, sometimes with a rib on its outer face. Columellar lamellae much more strongly developed, their free margins calloused; columellar lamella with a rib on its upper face; subcolumellar lamella heavily calloused and trabeculated. Lower palatal fold stronger, its free margin slightly undulate, upper fold vestigial. In younger specimen, 5 whorls, from a different colony (Pake Bay) parietal, columellar, and palatal lamellae all much more strongly developed. Columellar lamella extends above and outside of margin of columella. (See figure 63, *c, d*.)

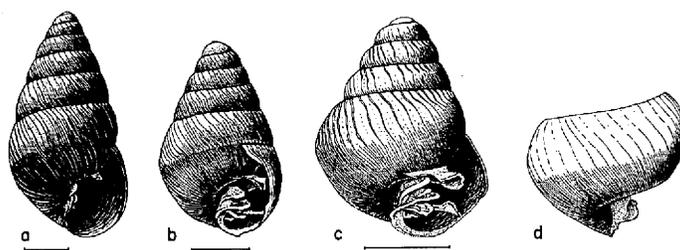


FIGURE 63.—*Celticola (Celticola) pilsbryi latior*: a, adult, holotype; b, metapara-neanic; c, metaneanic; d, metaneanic, profile.

Rapa: Mount Tepiahu (type locality), small valley on southern slope, on trunks, branches, and twigs of *puru* trees (*Meryta choristhanta*), alt. about 550 ft., Kondo, July 23; holotype 8772 (figured juveniles 8773, 137982), paratypes 143092-143098. Pake Bay, southern slope of Mount Tanga, Kondo, July 6, 137982.

Additional material collected on the slopes of Mount Tepiahu, Mount Orangi, Mount Tanga, and Mount Koara, and on Karapo Rahi Islet consists of 12 lots containing slightly more than 100 specimens, of which more than 50 are in the type lot.

This subspecies is apparently distributed over a large part of the southeast quadrant of the island of Rapa, as specimens were taken in widely separated localities in this area. Adults are somewhat difficult to differentiate from the typical subspecies, but the juveniles are easily recognized. In their apertural characters, the juveniles are somewhat similar to those of species included in *Lamellovum* subgenus *Maitua*.

#### Subgenus *Meryticola*

*Shell* very small, 2.5-3.5 mm. long with only 5 to 5.5 whorls, increasing rather rapidly. Embryonic whorls smooth, glossy; postembryonic whorls minutely but distinctly striate; striae stronger just below sutures. Parietal lamella simple, rather weak, nearly

one whorl long. Columella slightly sigmoid, without lamellae. In juveniles parietal lamella proportionately slightly, if at all, stronger than at adult stage. Columella with two weak threadlike rapidly ascending lamellae. Palatal folds absent.

Type species: *Celticola arborea*.

Distribution: Rapa.

Adults of *Meryticola* are easily distinguished from those of *Celticola* by their smaller size and fewer and more rapidly increasing whorls. Juveniles are much more distinct, as the columella lacks the strong, more transverse columellar lamellae and the distinct palatal folds. In size and form the shells superficially resemble those of *Lamellidea*, subgenus *Elamellidea*. The two genera are found under the same conditions.

***Celticola (Meryticola) arborea arborea*, new species (fig. 64, a-d).**

*Shell* oblong, subcylindrical, slender, sayal brown, thin, translucent, slightly glossy, striate, striae rather widely spaced, fine, distinct, slightly oblique, somewhat accentuated just below sutures. *Spire* slender, subcylindrical, with indistinct convex outlines. *Sutures* slightly oblique, crenulate, lightly impressed, margined below with a broad, shallow sulcus on the last two whorls. *Whorls* 5.5; embryonic whorls smooth, glossy; postembryonic whorls striate, increasing rather rapidly, flatly convex, slightly shouldered above; last whorl oblong, more than half total length. *Aperture* longer than broad, its upper outer margin indented. *Parietal lamella* weak, simple, almost perpendicular, nearly a whorl long, its inner half threadlike. *Columella* slightly sigmoid, its inner face calloused, unarmed. *Palatal wall* without folds. *Peristome* thin, erect.

Length 3.22 mm., diameter 1.45 (45 percent); apertural axis 1.10, diameter 0.81 (74 percent); last whorl 2.03 (63 percent); parietal lamella 0.10.

A juvenile, 4.33 whorls, 1.9 mm. long, has a rather weak parietal lamella, scarcely proportionately stronger than at adult stage. Columella with two weak, rapidly ascending lamellae. No trace of palatal folds.

Genitalia small, similar to that of subgenus *Celticola*. *Ovotestis* five-lobate; lobes short-clavate or with broadly flattened apex; follicles very few. *Duct* swollen, convoluted. *Albumin* gland large; follicles large, ovate to short-digitate. *Prostate* very small; paucifolliculate (three visible in figure). *Talon and carrefour* not dissected. *Oviduct* diaphanous, distended (three embryos). *Spermatheca* small, ovate, with sperm mass; stalk thin, narrow, entering oviduct below lowest embryo (X). *Vas deferens* partially recovered, thin; Y median. *Vagina* short. *Penis* fairly large, oblanceolate, quite long (0.3 oviducal length) for this group. Appendix large, long (equal to oviducal length); bulge fairly large. *Retractor* bifid, long, fairly heavy; both penial and appendicular retractors of same size as common retractor. *Atrium* short.

Dissected 143099 (adult genitalia), five specimens.

Rapa: Mount Tepiahu, south slope, near head of small valley, on trunks, branches, and twigs of *puru* trees, alt. about 550 ft., Kondo, July 23; holotype, 8774 (figured, metaneanic 8775), paratypes 143099-143106. Also taken at Morongota, near crest of ridge, alt. about 800 ft., and on ridge back of Area village, under lichens on tree trunks, alt. 300-450 ft.

Dissection revealed a peculiar penis with penial and appendicular branches apparently in the process of either extrusion or retraction. The basal bulge at the penial stalk appeared to be the ejaculatory mechanism of the appendix. Figure 64, d gives an idea of how eversion occurs.

This species is represented in the Museum collection by four lots totaling 183 specimens, of which 167 are included in the type lot. They were taken at widely separated localities, indicating that the species is more or less distributed over the major portion of the forested areas. Its small size, color, and habit of living on bark and under lichens make its detection extremely difficult.

*C. arborea* is easily distinguished from the other arboreal species from Rapa. Its most important characters are its small size, the few and rather rapidly increasing whorls, and the broad, shallow sinus just below the sutures.

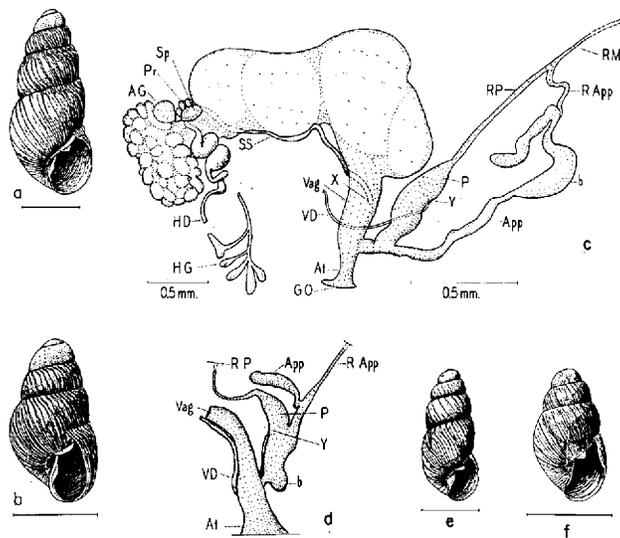


FIGURE 64.—a-d, *Celticola (Meryticola) arborea arborea*: a, adult, holotype; b, meta-neanic; c, genitalia; d, penial complex, appendix arrested in retraction or protrusion. e, f, *C. (M.) a. sororcula*: e, adult, holotype; f, meta-neanic.

***Celticola (Meryticola) arborea sororcula*, new subspecies (fig. 64, e, f).**

*Shell* smaller than that of *C. arborea*, with nearly the same number of whorls (5.25), thinner, glossier, with weaker striae which are stronger just below sutures, becoming much weaker below. Parietal lamella thicker and higher at all stages of growth. Characters of columella and palatal wall similar to those of species. (Juvenile shown in figure 64, f.)

Length 2.25 mm., diameter 1.0 (44 percent); apertural axis 0.77, diameter 0.51 (66 percent); last whorl 1.48 (65 percent); parietal lamella 0.06.

Genitalia as in other species.

Dissected 143444 and 143445, two specimens.

Rapa: Mount Vairu, east slope, on bark of *Meryta* and *Celtis* trees, alt. 850-900 ft., Zimmerman and Anderson, July 26; holotype 8776 (figured, meta-neanic 8777), paratypes 143444-143447.

The Museum has two lots made up of 21 specimens from Mount Vairu, only two specimens of which are adult.

This is the smallest species of the family to be taken on Rapa. In size, general appearance, and habits it is somewhat similar to *Lamellidea* (*Elamellidea*) *tantalus* from Oahu, Hawaiian Islands. The adults of the two, if found on the same island, might be difficult to segregate.

***Celticola* (*Meryticola*) *arborea*, subspecies?**

A single juvenile specimen with 4.25 whorls (144620) was taken from tree bark on Mount Tautautu at an altitude of 600 to 700 feet. It differs slightly from *sororcula* in that the surface is smoother and the whorls are slightly more convex.

Subgenus **Nesonoica**

*Shells* 5-6+ mm., conic to elongate-conic, thin. Whorls increasing slowly and regularly, convex, separated by a rather deep suture. Embryonic whorls closely, spirally striate, convex, separated by a deep suture, viewed from above, initial 0.5 whorl is slightly immersed. Surface marked with distinct, thin, widely spaced vertical striae. Parietal lamella strong, oblique, simple. Columella with three low, blunt, rapidly ascending lamellae. Palatal wall unarmed at all stages of growth.

In juveniles, columellar lamellae more strongly developed than in adult, but lamellae not prominent.

Type species: *Celticola conoides*.

Distribution: Rapa, Raivavae.

The only representative of the type species taken alive, a juvenile, was not dissected. Two embryonic shells were syringed from another specimen. Practically all specimens of *C. conoides* were taken under leaf trash on the ground.

***Celticola* (*Nesonoica*) *conoides*, new species (fig. 65, a-d).**

*Shell* conic, isabella color in dead state, thin, semi-translucent, somewhat dull, distinctly striate, striae regular, distantly spaced, extending to base of shell though somewhat weaker below periphery. *Spire* conic, with nearly straight outlines, diminishing regularly to slightly flattened apex. *Suture* indistinctly crenulate, well impressed. Whorls 7+, convex; initial whorl slightly flattened; upper post-embryonic whorls slightly flattened; last two whorls convex, the last large. *Aperture* wide. *Parietal* lamella moderate, simple, nearly a whorl long. *Columella* hardly sigmoid, with three subequal, very oblique lamellae; sub-columellar lamella more deeply seated and not visible except when viewed obliquely. *Palatal wall* unarmed at all stages of growth. *Peristome* thin, erect.

Length 5.15 mm., diameter 2.88 (56 percent); apertural axis 1.97, diameter 1.54 (78 percent); last whorl 3.17 (61 percent); parietal lamella 0.21.

A fresh juvenile, the only representative of the species taken alive, had 4.75 whorls and is 2.64 mm. long; shell is clay color, glossy. Under a strong lens, embryonic (2.25) whorls closely spirally striate. Demarcation between embryonic and first postembryonic stage abrupt, the transverse striae developing rapidly soon after or during nepionic stage. Parietal lamella fairly strong, oblique, its free margin not sinuous. Columella calloused and with three lamellae; supra- and columellar lamellae stronger than subcolumellar lamella. No indication of a palatal fold.

Rapa: northwest slope of Mount Tautautu, alt. about 750 ft., Kondo, July

25; holotype 8778 (figured, meta-ananeanic 143313), paratypes 143311 (not dissected).

In the Museum collection are three lots totaling eight specimens. Two lots (138479, 144160), each with a single specimen, were collected on the same slope as were the types but at a slightly lower altitude.

This species is very distinct from *C. pilsbryi* and its subspecies. The more conical form of *C. conoides* and the fewer and more convex whorls, of which the embryonic are spirally striate, easily separate the two species. The juveniles are also distinct, for the columellar lamellae are weaker in *C. conoides* and there is no indication of a palatal fold.

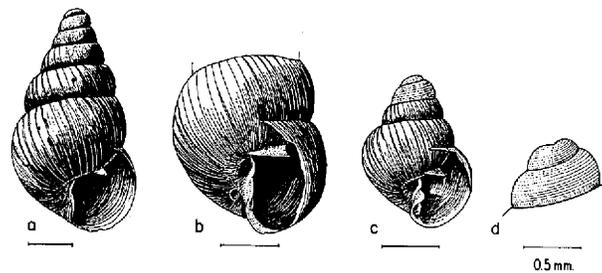


FIGURE 65.—*Celticola (Nesonoica) conoides*: a, adult, holotype; b, adult, columellar view; c, meta-ananeanic; d, meta-ananeanic, embryonic whorls.

***Celticola (Nesonoica) anatonuensis*, new species (fig. 66, a-e).**

*Shell* ovate-turrite, color tawny olive, opaque, rather thick, dull, finely and closely striate, striae not strongly oblique. *Spire* straight, tapering regularly and quite rapidly to apex, upper part weakly and spottily eroded. *Suture* well impressed, whorls not margined. *Whorls* 7; embryonic whorls small, subacute; postembryonic whorls convex, last whorl broad. *Aperture* vertical, ovate, subauriform. *Parietal lamella* strong, high, one whorl, or a fraction over one, in length. *Columella* trilamellate; supracolumellar lamella subvertical, weak, narrow; columellar lamella strongest, quite thick, semilunate, subtransverse; subcolumellar lamella smaller, weak, parallel to columellar lamella, deeply seated. *Palatal folds* absent. *Peristome* thin, not reflected.

Length 5.66 mm., diameter 2.85 (50.4 percent); apertural axis 2.02, diameter 1.45 (72 percent); last whorl 3.42 (60.5 percent); parietal lamella 0.22; whorls 7 (10193).

Large adult 0.75 mm., 0.5 whorl longer than typical adult, spire comparatively more pointed, last whorl more elongate and comparatively narrower, striae slightly weaker.

Length 6.4 mm., diameter 2.98 (46.5 percent); apertural axis 2.2, diameter 1.5 (70 percent); last whorl 3.7 (58 percent); parietal lamella 0.26; whorls 7.5 (10194).

Paraneanic specimen similar to typical adult in all characters except lamellae of columella very slightly weaker, parietal lamella thinner, and striae weak, palatal folds absent.

Length 5.2 mm., diameter 2.76 (53 percent); whorls 6.5 (10195).

Metaneanic specimen with columellar lamellae weaker, parietal lamella thinner. Spire slightly convex. Striae quite strong.

Length 4 mm., diameter 2.28 (55.6 percent); whorls 6.3 (10196).

Anatomy unknown.

Tubuai; Raivavae, back of Anatonu village, hillside below main cliff, under stones and dead leaves, alt. 650-700 ft., Anderson, Aug. 12; holotype 10193; paratypes 10194-10196, 147460 (64 specimens). East of Anatonu village, inland 20 ft., alt. 6 ft. [notebook: fossil in road cutting about one-fourth mile east of temple], Cooke and Kondo, 147146-147148, 22 specimens.

Dead specimens of *C. anatonuensis* were abundant only at Anatonu, where concentrated efforts to locate living examples were futile, indicating that the species inhabits some tree or shrub under a specialized condition. No embryos were recovered from the shells and no young juveniles were collected.

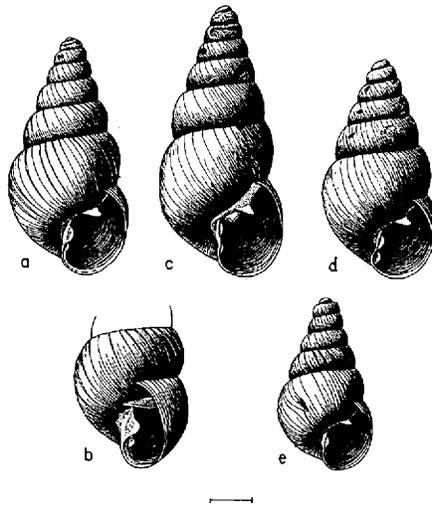


FIGURE 66.—*Celticola (Nesonoica) anatonuensis*: a, adult, holotype; b, adult, columellar view; c, large adult; d, paraneanic; e, metaneanic.

*C. anatonuensis* strongly resembles *C. conoides*, but is differentiated from it by a more turreted spire, a less bulging ultimate whorl, and a well-developed columellar lamella in the adult stage, characters which are weak in *C. conoides*. The parietal lamella of *C. anatonuensis* is stronger and thicker and its sutures are more deeply impressed. It is also a longer shell.

The shells range from about 4.75 to 6.4 mm., with about 70 percent of them between 5 and 5.75 mm. and about 25 percent between 6 and 6.4 mm. (mean 5.47 mm.), of which the largest is illustrated (fig. 66, c). Even from our meager series of juveniles, it is safe to say that the columellar lamellae and parietal lamella probably undergo only a gradual increase in size from the youngest stage, attaining maximum growth in the adult. In some specimens the lower two columellar lamellae are equal in size, but typically the subcolumellar lamella is smaller.

Fossil specimens are without epidermis, are white, and appear more solid than dead specimens. There is the barest possibility that remnants of this species may be found somewhere on Raivavae; but this seems remote, as most of the native forest and lowland flora on Raivavae have been destroyed and indications are that this species is a lowland form.

#### Genus *Tubuaia*, new genus

*Adult shells* small, 2-7 mm. long, oblong-conic with slightly convex outlines to narrowly conic with nearly straight outlines, rather thin, translucent. *Whorls* 5 to 7, flatly convex to slightly convex. *Parietal lamella* rather strong (except in *T. inconstans*), slightly obliquely seated, from one-half to a full whorl in length. *Columella* twisted, without folds (except in *T. gouldi*), forming a projecting obtuse angle at the edge of the columella. *Palatal folds* absent.

*Juvenile*: Parietal lamella proportionately stronger, the free margin simple, or undulate to almost lobed. Columella furnished with two lamellae (three in *T. perplexa* and *T. affinis*), of which the lower is the stronger and more transversely seated. Palatal wall (except in *T. inconstans*, which has none) with two rows of spirally entering denticles, nearly united by a very fine threadlike callus. Denticles most easily seen when shell is viewed from outside.

*Adult genitalia* pauciembrionate (two to five embryos per animal). *Ovotestis* multilobate (three to six lobes); follicles few, short-clavate to ovate. *Hermaphrodite duct* short, slightly swollen, convoluted. *Talon and carrefour* not dissected but presumably similar to those of Pityisini. *Albumin gland* relatively large, well developed; follicles quite numerous, round to ovate. *Prostate* small, inconspicuous; follicles few (four to six), short-clavate. *Spermatheca* small, ovate; stalk long, narrow, inserting into oviduct below lowest embryo. *Oviduct* swollen, diaphanous. *Vagina* short,  $\pm 0.2$  to a little less than oviducal length. *Vas deferens* thin, the same or less than width of spermathecal stalk, adnate to penis, entering it subapically. *Penis* short ( $\pm 0.5$  appendical length or  $\pm 0.25$  oviducal length), small (ratio, width to length, 1:4.3 in an average of eight specimens), oblanceolate, without epiphallus. Interior of penis with modified achatinellid pilaster: narrow, ascending fleshy ridge, recurved at apex into relatively large triangular semi-pendent fleshy papilla, below which vas deferens empties. *Appendix* long (0.3 to nearly oviducal length), proximally and distally narrow, slightly bulging at middle (ratio, width to length 1:14), tip blunt; interior with secretory-ejaculatory apparatus. *Retractor* thin, long, bifid, off nuchal membrane; terminal on penis, subterminal on appendix (0.3 from tip). *Atrium* short or medium, narrow.

*Paraneanic or subadult genitalia* exactly like that of adult Pityisini. Penis large, long, clavate (ratio, width to length 1:4.3); interior with achatinellid pilaster, including transparent velum. Appendix large, long (ratio, width to length, 1:8.7; penial length to appendical length, 1:1.6). Retractors both heavy. Oviduct narrow. Vagina short or long. Uterus correspondingly long or short. Albumin gland minute; follicles minute, ovate or round. Prostate large; follicles large, digitate. Ovotestis compact; follicles as in Pityisini. Atrium short, narrow or wide.

Type species: *Tubuaia perplexa* (Garrett).

*Distribution*: Kermadec Islands (Raoul), Cook Islands (Mauke and Mangaia), Society Islands (Huahine), Tubuai Islands (Rimatara, Rurutu, Tubuai, and Raivavae), Rapa, Tuamotu Archipelago (Mangareva, Henderson, and Pitcairn).

Species of *Tubuaia* have been reported only from the southern islands of the eastern Pacific (map, fig. 67), principally the high islands; no specimens

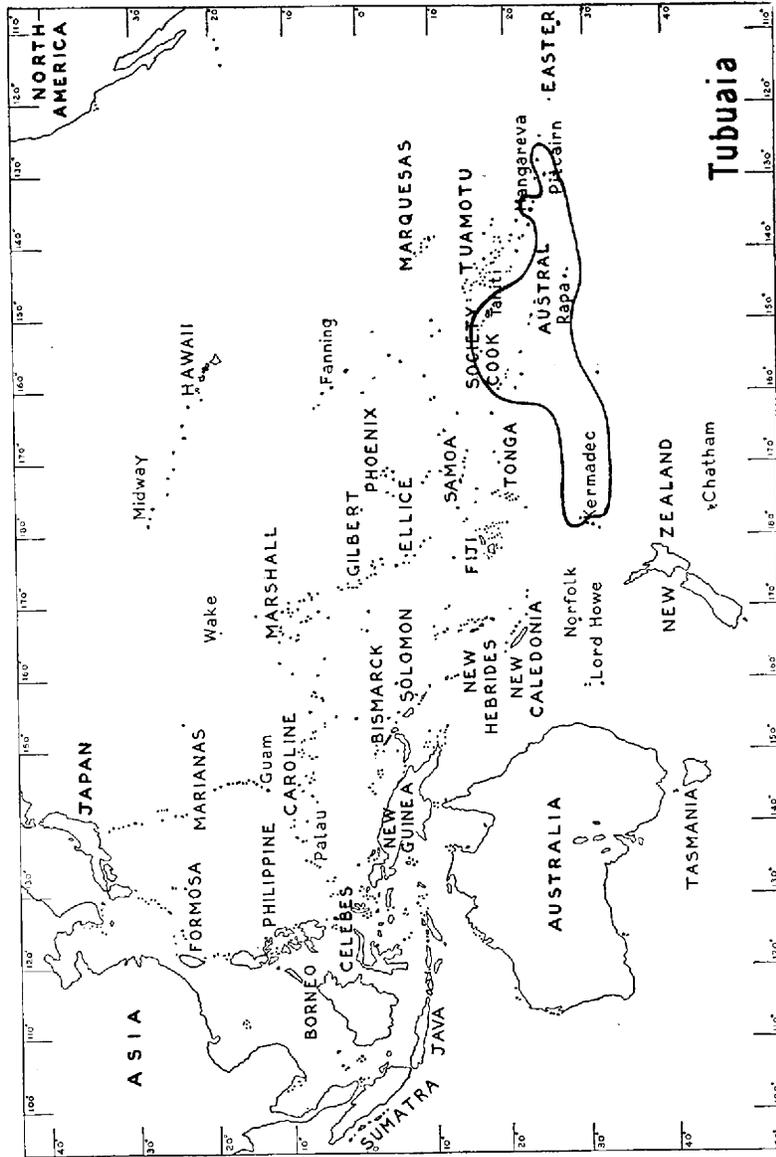


FIGURE 67.—Distribution of genus *Tubuaia*.

have been found on the low coral islets on the reefs surrounding the Mangarevan islets and Raivavae, although they are abundant on the main islands. One species was discovered on Henderson Island, which is neither a high island nor an atoll but an upraised coral island technically known as a *makatea*.

The genus inhabits localities from a few feet to nearly a thousand feet above sea level, in stands of introduced or endemic plants and trees. Nearly all the lots collected by the Mangarevan Expedition were taken on or near the ground, on and under stones and trash. On some of the high volcanic islands specimens were abundant at low altitudes in areas just back of the coral beach under conditions similar to those on the coral islets where not a single specimen was found.

Of the eight species belonging to the genus, as here recognized, six (*affinis*, *raoulensis*, *cylindrata*, *cremnobates*, *inconstans*, and *gouldi*) have been reported only from single islands, one (*perplexa*) from two islands, and one (*voyana*) from the whole range of the genus, excluding the Kermadec Islands. A number of additional species, each of which is limited to a single island, are in the collection of Bishop Museum. These will be treated in a later paper.

Adult specimens of some species of *Tubuaia* are difficult to distinguish from some species of *Lamellidea*, and there seems to be no distinctive conchological character that can be depended upon to separate the adults of the two genera. On the whole, the columella of most species of *Tubuaia* is slightly more twisted and terminates exteriorally in a more extended bluntly angulate process. However, even in this character there is some overlap.

Juveniles of both genera are easily recognized. In all species of *Lamellidea*, except in some specimens of *L. oblonga* and *L. peponum*, juvenile specimens have a vertical palatal rib, the margin of which is either plain or minutely serrate. All species of *Tubuaia* except *T. gouldi* either lack this rib or merely have it indicated by a flat callus (*perplexa*, *affinis*). In juveniles of all species of *Tubuaia*, except *T. inconstans* and some specimens of *T. voyana*, the palatal rib is replaced by one or two rows of spirally entering, oblong denticles which are usually connected by a thin thread. [For further comparative notes see *Lamellidea*, its subgenus (*s.s.*), and *Tornatellinops*.]

The species of the genus *Tubuaia* fall into four more or less natural groups.

(1) *perplexa* (*perplexa*, *affinis*): In these species the shells are small and delicate; the parietal lamella strong. Juveniles have one to three vertical, low, broad calluses on the palatal wall on which are superimposed a lower denticle and an upper denticle, which is always duplicated. The columella has three distinct lamellae. The species are found on Rurutu and Rimatara.

(2) *gouldi* (*gouldi* and *g. nannodes*): This species is larger and thicker than *perplexa* and *affinis*, the whorls more convex, the parietal lamella strong. Juveniles have one to three rather heavy, broad, vertical calluses, on which are superimposed rather heavy denticles similar to those of the *perplexa* group.

The columella has two lamellae, the columellar lamella strong, most often slightly bifid. Found in the Mangarevan islands.

(3) *voyana* (*voyana*, *raoulensis*, *cremnobates*, and *cylindrata*): The shells of these species are small and delicate; the parietal lamella strong. Juveniles lack the vertical palatal callus; and the palatal denticles, of which there are usually two rows (but often one and sometimes none), are low, oblong, and corneous, often difficult to find except when shells are viewed from the outside. The columella has two lamellae, sometimes with the subcolumellar lamella indicated by a minute, deeply seated swelling; but this is never as clearly defined as in the *perplexa* group. Its distribution equals that of the genus.

(4) *inconstans*: The shells of this species are small, delicate, dark-colored; the parietal lamella weak. Juveniles lack palatal denticles. The columella has two folds of about equal development, the columellar lamella very obliquely seated. Found in Rapa.

#### KEY TO SPECIES OF TUBUAIA

1. Parietal lamella low; juveniles without palatal denticles.....**T. inconstans.**  
Parietal lamella strong, high; juveniles with palatal denticles..... 2
2. Adults with vertical palatal callus, 4 mm. or more long.....**T. gouldi.**  
Adults without palatal rib, less than 3.75 mm. long..... 3
3. Juveniles with low, flat, vertical palatal callus, upper palatal denticle duplicate;  
columella with three distinct lamellae..... 4  
Juveniles without palatal callus, upper palatal denticle simple; columella with  
two distinct lamellae, sometimes with a basal denticle..... 5
4. Adults conic, outlines nearly straight, diameter more than 0.5 length.....**T. affinis.**  
Adults elongate, outlines slightly convex, diameter less than 0.5 length; juve-  
niles with three columellar lamellae.....**T. perplexa.**
5. Upper portion of spire subconical, tapering to a rather acute apex; spire with  
nearly straight outlines..... 6  
Shells subcylindrical; upper portion of spire not conical, apex rather blunt,  
outline slightly convex..... 7
6. Diameter 42 to 45 percent of length.....**T. voyana and subspecies.**  
Diameter more than 50 percent of length.....**T. raoulensis.**
7. Shells larger, over 3.4 mm. in length, parietal lamella about a half whorl  
long.....**T. cremnobates.**  
Shells smaller, less than 2.75 mm. long; parietal lamella a full whorl long.....  
.....**T. cylindrata.**

**Tubuaia perplexa** (Garrett). Figures 68, *a-d*; 69, *a-h*.

*Tornatellina perplexa* Garrett, 1879, Acad. Nat. Sci. Philadelphia, Proc.,  
24; 1881, Acad. Nat. Sci. Philadelphia, Jour. II, 8: 391; 1884, II, 9: 82,  
pl. 2, fig. 23.

*Tornatellina* (*s.s.*) *perplexa*, Pilsbry and Cooke, 1915, Man. Conch. 23: 144,  
pl. 34, figs. 12, 13; pl. 36, fig. 2.

*Adult shells* (fig. 68, *b*) elongate conic, honey yellow in color, quite thin, subtrans-  
lucent, surface shining, under a lens minutely striate with lines of growth; spire elongate,

with slightly convex outlines, narrowly conic above, tapering to a rather acute apex. *Suture* simple, or indistinctly narrowly margined, moderately impressed. *Whorls* nearly 7, slightly convex; postembryonic whorls increasing slowly; last whorl oblong, imperceptibly flattened dorsally. *Aperture* nearly vertical, subquadrate, its outer margin flattened or slightly indented. *Parietal lamella* rather strong, obliquely seated, a little over 0.5 whorl long. *Columella* slightly sigmoid, somewhat calloused, ending at its outer margin in an obtuse rounded angle. (In a few specimens which are apparently fully adult, there is a very minute, deeply seated basal fold, visible only when aperture is viewed very obliquely.) *Palatal fold* absent. *Peristome* thin, erect.

Length 3.2 mm., diameter 1.45 (45 percent); apertural axis 1.13, diameter 0.68; last whorl 1.87 (58 percent); parietal lamella 0.13 (8779). Garrett's paratype (fig. 68, *a*) measures: Length 2.74 mm., diameter 1.3 (47 percent); apertural axis 0.96, diameter 0.7 (72 percent); last whorl 1.64 (59 percent); parietal lamella 0.096 (8781).

Juveniles (figs. 68, *c, d*): Parietal lamella strongly undulate. Columella trilamellate, upper lamella linear-sigmoid, middle lamella broadest, subcolumellar lamella smaller. Palatal wall with vertical callus, on which are two sets of denticles, the lower larger, the upper bifid or twin.

Adult genitalia (fig. 69, *a, b*). *Ovotestis* five- to six-lobate, paucifolliculate; follicles short-clavate. *Duct* small, slightly swollen, convoluted. *Talon and carrefour* not dissected. *Albumin gland* fairly large for this tribe; follicles numerous, ovate or curved-digitate.

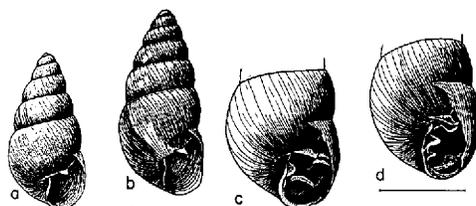


FIGURE 68.—*Tubuaia perplexa*: *a*, subadult from Garrett's paratypes, "Rurutu, Austral Isles"; *b*, adult, Rurutu, Mato Naa; *c*, juvenile, apertural view, Garrett's specimen; *d*, juvenile, latero-oblique view.

*Prostate* not seen. *Uterus* distended, diaphanous, with five embryos, the two earlier embryos enclosed in yolk mass and apparently without shells, or shells minute, the three later embryos free or mostly so. *Vagina* short ( $\pm 0.2$  oviducal length). *Spermatheca* small, ovate, lying on albumin gland; stalk long, narrow, X below lowest embryo. *Vas deferens* thin, difficult to find; Y subapical. *Penis* oblanceolate, small, short. Interior of penis wall smooth; pilaster modified, ascending ridge narrow, low, recurved at apex and enlarging into triangular tongue of flesh (P Pap); papilla thin, flat, adhering at base, apex not adherent but free; orifice of vas deferens (VDO) under papilla. *Appendix* about twice penial length, with median bulge, apex blunt. *Retractor* bifid, thin, long; penial retractor apical; appendical retractor subapical (0.3 below tip). *Atrium* short, narrow.

*Central nervous system*. Similar to that of *Lamellovum auriculella* but cerebral nerve with two frontal nerves; nuchal nerve combined with labio-tentacular nerve. *Teeth* of usual type (see *Celticola pilsbryi*).

Paraneanic or subadult genitalia (fig. 69, *c, d*) pitysinid. *Ovotestis* five- to six-lobate, heavier than in adult; follicles tightly compact. *Duct* convoluted, distended, larger than in adult. *Carrefour* simple. *Albumin gland* minute, attached to carrefour; follicles numerous, minute, round. *Prostate* large, paucifolliculate; follicles few, digitate. *Spermatheca* large, ovate; stalk very short (as in Pitysini), entering oviduct immediately. *Vas deferens* as broad as oviduct, adherent to inner curvature of penis; Y subapical. *Vagina* narrow, long, gently tapering below. *Penis* large, clavate, curved, as long as vagina. Interior of penis

pitysinid. Wall smooth; pilaster differing from that of adult. Ascending pilaster combining with lower end of descending pilaster making rather wide grooved ridge, with both edges high. Penial papilla (P Pap) rooted at apex, the greater part free, connected to ascending pilaster by thin filmy velum; pendent portion not adherent to penial wall, with thin transparent triangular membrane; VDO under papilla. Appendix as large as penis below its retractor; apex small, curved, bluntly pointed, narrow in middle. Retractor quite heavy; penial retractor smaller than appendical retractor. Atrium short, wide.

Dissected 148362 (adult and paraneanic genitalia, interior adult penis), five specimens; 148363, 148364 (juveniles), three specimens of each; 148795 (interior paraneanic genitalia, nervous system), two specimens.

Tubuai: Rurutu (type locality), eastern side of the island, north of Moerai village, at base of Mato Naa, 50-100 yards inland, under stones and dead leaves, alt. about 10 ft., Kondo and Cooke, Aug. 26. (Figured specimen 8779.)

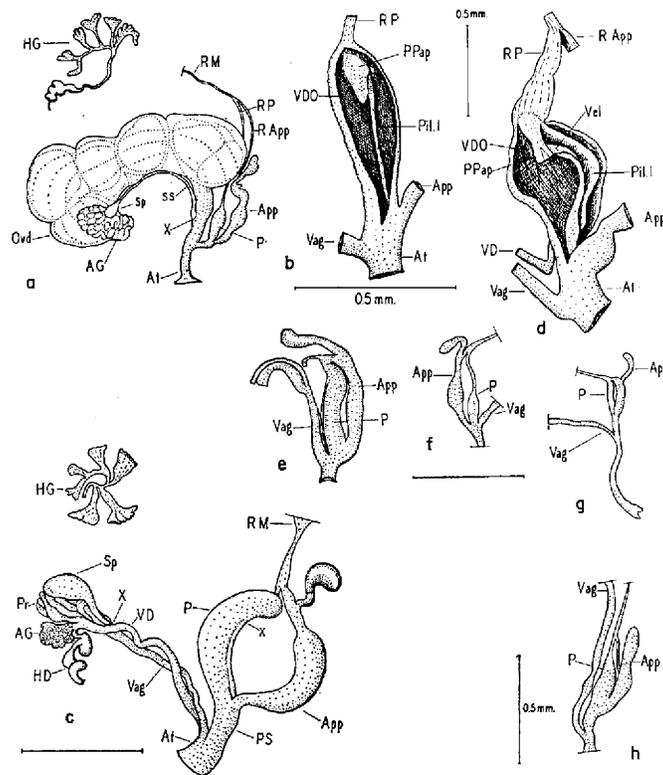


FIGURE 69.—*Tubuaia perplexa*: a, adult genitalia; b, interior of penis, adult; c, paraneanic genitalia; d, interior of penis, paraneanic; e, subparaneanic penial complex; f, metaneanic penial complex; g, ananeanic penial complex; h, ananeanic penial complex, resembling that of *Tornatellinops*.

Also collected on Mato Arei, Mato Arapia, Mato Tea, and on an unnamed *mato* (raised coral ridge) near Vitaria. "Rurutu, Austral Isles" (Garrett, 8780) (figured paraneanic, 8781; figured subadult, from Garrett's paratypes, 1376).

This species is abundant on Rurutu and Rimatara in the Tubuai group and present knowledge indicates that it is limited to these two islands. However, according to Garrett, it occurs on all of the Cook and Society Islands. Typical specimens are found only on the sides and at the foot of raised coral ridges from a few feet above sea level to the ridge tops, on and under trash and stones. None were found on trash lying on volcanic soil.

Of the many typical lots from Rurutu in the Museum's collection, one (8779) has been chosen to represent the adult stage of the species. In this lot the juvenile specimens agree very closely with those of Garrett's collection.

For several younger juveniles (fig. 69, *e-h*) the stages of the penial complexes were dissected to determine the macroscopic ontogeny of the tribe. The subparaneanic stage was found to be similar to the paraneanic stage except for its smaller size and lesser development. The metaneanic stage closely resembled the adult of *Tubuaia* and, somewhat, the adult of *Tornatellinops*. In the ananeanic stage the penial complex of one specimen showed a strong resemblance to the adult penial complex of *Tornatellinops* (penis rather broad, pointed; appendix slightly longer than penis, and stout).

Unfortunately, Garrett described this species from immature specimens. His original lot (1376) consists of five specimens, the largest of which (fig. 68, *a*) has nearly six whorls and is almost adult. This specimen agrees closely with Garrett's measurements (length 2.75, diameter 1 mm.), but it is efflorescent. The remaining four are younger, 4.75 to 5.5 whorls, and 2-2.75 mm. long. The aperture of one of these is figured (fig. 68, *c, d*). This specimen has about 5.5 whorls and is 2.64 mm. long. When viewed obliquely, all of Garrett's specimens have three columellar lamellae, a vertical palatal rib and two rows of denticles, the upper of which is duplicate. Garrett mentions only two columellar lamellae, omitting the supracolumellar lamella, which is usually weaker than the subcolumellar lamella. (Corrected in *Manual of Conchology*, 1915, vol. 23, p. 145.)

***Tubuaia affinis*** (Garrett). Figure 70, *a-d*.

*Tornatellina affinis* Garrett, 1879, Acad. Nat. Sci. Philadelphia, Proc., 23.

*Tornatellina* (*Tornatellinops*) *affinis*, Pilsbry and Cooke, 1915, Man. Conch. 23: 177.

*Tornatellina micans* Garrett, 1879, Acad. Nat. Sci. Philadelphia, Proc., 23.

*Tornatellina* (*s.s.*) *micans* Pilsbry and Cooke, 1915, Man. Conch. 23: 147 [juvenile of *affinis*].

Holotype: Length 3.12 mm., diameter 1.64 (52 percent); apertural axis 1.29, diameter 0.74 (57 percent), last whorl 2.0 (64 percent); parietal lamella 0.097 (8684).

Figured adult: Length 3.42 mm., diameter 1.72 (50 percent); apertural axis 1.3, diameter 0.84 (65 percent); last whorl 2.16 (63 percent); parietal lamella 0.113 (8794).

Rurutu: Mato Arei, southeast of Moerai village, alt. 5 to 50 ft., Anderson and Kondo, Aug. 27 (figured adult 8794, 148521-148523; not dissected).

This species is rare on Rurutu. The Expedition took only five lots containing 21 specimens in 11 days of collecting on the island. All specimens came from near Moerai village and from Mato Arei, just south of the village on the eastern side of the island.

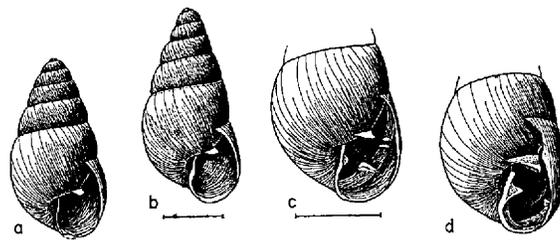


FIGURE 70.—*Tubuaia affinis*: a, adult, holotype from Garrett ("South Australia," obviously an error for Austral Islands); b, adult, Rurutu, Mato Arei; c, juvenile, aperture (type of "*T. micans*" Garrett), BBM 1276, "Rurutu, Austral Isles"; d, juvenile, columellar view.

This species is closely related to *T. perplexa*. Adults of *T. affinis* are most easily recognized because they are broader than those of *T. perplexa* and have more conical spires, which have straight outlines and flatter whorls. Juveniles show that both species are derived from the same stock; they both have a vertical palatal callus and a duplicate upper denticle. However, the juveniles of *T. affinis* are easily recognized not only by their form and flatter whorls but by their much less undulate parietal lamella and the fact that they have only two lamellae on the columella. In juvenile specimens of *T. affinis*, the columella is normally tri-lamellate, and the upper fold is much weaker and is obliquely seated. In most specimens the subcolumellar lamella is indicated by a minute denticle, visible only in oblique view; a few have only two lamellae, which are never as strongly developed as in the juvenile specimens of *T. perplexa*.

The type specimens of both *T. affinis* and *T. micans* came to Bishop Museum with the Garrett collection, in which *T. affinis* is represented by the type and three other specimens; *T. micans*, by the type. Comparison has proved *T. micans* to be a juvenile specimen of *T. affinis*. The original lot contains a juvenile specimen which agrees with *T. micans*. The later collections of the Mangarevan Expedition substantiate this conclusion.

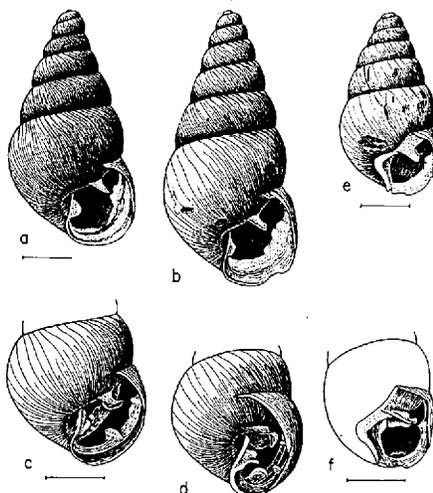


FIGURE 71.—a-d, *Tubuaia gouldi*: a, subadult, paratype of "hidalgoi" Crosse, "Is. Gambier.;" b, large fossil adult, Mangareva, Aukena; c, parametaneanic, apertural view; d, parametaneanic, latero-oblique view. e, f, *Tubuaia gouldi* form *nannodes*: e, adult; f, adult, columellar aspect.

***Tubuaia gouldi* (Pfeiffer). Figure 71, a-d.**

*Tornatellina gouldi* Pfeiffer, 1856, Zool. Soc. London, Proc., 335; 1859, Mon. Hel. Viv. 4: 651.—Pilsbry and Cooke, 1915, Man. Conch. 23: 141.

*Tornatellina ringens* Dohrn, 1863, Malak. Blätt. 10: 161.—Pfeiffer, 1868, Mon. Hel. Viv. 6: 265.—Pilsbry and Cooke, 1915, Man. Conch. 23: 141.

*Tornatellina hidalgoi* Crosse, 1865, Jour. de Conchyl. 13: 219, pl. 6, fig. 6.—Pfeiffer, 1868, Mon. Hel. Viv. 6: 266.—Pilsbry and Cooke, 1915, Man. Conch. 23: 140, pl. 33, figs. 7, 9.

Measurements in Millimeters

CAT. NO.	LENGTH	DIAMETER	APERTURAL AXIS	DIAMETER	LAST WHORL	PARIETAL LAMELLA
8782	5.75	2.78 (49%)	1.83	1.45 (79%)	3.28 (57%)	0.37
115310	4.88	2.63 (54%)	1.79	1.30 (72%)	2.90 (59%)	0.34 (paratype of <i>hidalgoi</i> )

"*Tornatellina Hidalgoi* Crse Is. Gambier co-type (collect Crosse)," 115310 from Dautzenberg, Feb. 3, 1933 (fig. 71, a). "Gambier I" 115405 from Fulton, Feb. 3, 1933 ["This is probably the same lot as represented in Brit. Mus. in lots collected by J. C. Lambert Brit. Mus. No. 86.6.9. 587-591, etc.," according to Cooke]; figured parametaneanic specimen 10745.

? Cuming collection, Philippine Islands (A. Fokkes, coll. Semper). Gambier Islands (Paz).

Mangareva Islands: Aukena, north-central side opposite Koiovao, alt. 6 ft., Cooke and Anderson, May 28, 138720-138722 (figured adult 8782). Other localities: Taravai (138889), Agakauitai (138913), and Mangareva (138985).

No live specimens were taken on any islet of the Mangarevan group, although careful search was made on all but one. The fossil specimens were found in recent, possibly Pleistocene, deposits from a few inches to a foot or more below the surface. The deposit found on Aukena was rich in species belonging to most of the genera inhabiting the islands of the southeast Pacific. This species was not very abundant in any of the deposits, but enough material was taken to identify the species and to show that in size, in form, and in some other characters it is extremely variable.

Bishop Museum is fortunate in having one of the paratypes of *T. hidalgoi* (115310), which was received in exchange from Dr. Ph. Dautzenberg. When this specimen was compared with the type of *T. gouldi* in the British Museum, no specific differences were found. This specimen fits the description of *T. ringens* quite accurately except that the last whorl cannot be considered "sub-angular in the middle." It has not quite reached the adult stage, as can be seen by the size of the columellar lamella and the presence of two vertical palatal ribs. It has nearly seven whorls.

Pfeiffer's type specimen is not fully adult, as there are only six whorls and the shell is 4 mm. long (see Dohrn's description of *T. ringens*). We do not hesitate to place Dohrn's species in the synonymy of *T. gouldi*, as no species of tornatellinid approaching his description has been taken outside of the Mangarevan islands.

Adults of the fossil specimens show considerable variation. There are some differences in size, in the degree of development of the columellar fold and vertical palatal plate, and in the palatal denticles. A representative of the larger specimens with just over seven whorls is illustrated (fig. 71, *b*).

One of the unique characters is the slightly undulate free margin of the parietal lamella, the columellar fold persisting to a greater or lesser degree in adults. The palatal rib is strong, high in back, and gradually diminishing in thickness outward, extends nearly to the margin of the aperture. This character has not been noted in any other tornatellinid. The edge of the only rib is usually slightly uneven to suborbiculate.

In a juvenile specimen with 6 whorls, 4.20 mm. long, the parietal lamella is strong, flaring outward, with a strongly undulate free margin. The columella is invariably bilamellate; the columellar lamella is very strong, its margin deeply forked; the palatal rib is fairly strong and flattened and not as high as that of adult specimens; the lower palatal denticle is strong and elongate; and the upper palatal denticle is bifid and short.

The palatal callus in juvenile specimens is analogous to that found in the species of *Lamellidea*, but it is thicker and heavier and its margin is not serrate

or denticulate. It is probably a further development of the callus thickening found in *T. perplexa* and *T. affinis* from Rurutu.

***Tubuaia gouldi* form *nannodes*** (fig. 71, *e, f*).

Length 3.78 mm., diameter 2.20 (53 percent); apertural axis 1.33, diameter 1.18 (89 percent); last whorl 2.29 (60 percent); parietal lamella 0.30.

Mangareva Islands: Aukena Islet, northern side, near sea level, a few hundred yards from the hamlet, Cooke and Anderson, May 28; holotype 8783; paratypes 138724, 138724A, 138772.

Several specimens of this peculiar form were found on Aukena Islet in the deposit that held the typical specimens. The shells are much smaller than those of the typical form, with more convex outlines and fewer, flatter whorls. The columella is much more heavily calloused along its inner margin and often lacks the median lamella. These specimens have, however, a nearly vertical, deeply seated fold near the upper termination. Intergrades with the typical form occur. Without them, this form might be considered a subspecies or a species.

In a juvenile specimen (138724A) which can be allocated to this form, the parietal lamella is more strongly undulate and has a nearly longitudinal rib along its outer face almost parallel to the free margin; the columella is very heavily calloused and has two nearly parallel and almost equally developed folds.

***Tubuaia cremnobates*, new species** (fig. 72, *a-f*).

*Shell* elongate, between tawny olive and saccardo's umber in color, quite thin, translucent, under a lens minutely and slightly obliquely striate with lines of growth; striae slightly stronger and more widely spaced than in other species from Rapa. *Spire* elongate, with slightly convex outlines, terminating in a rather blunt apex. *Suture* simple, moderately impressed. *Whorls* nearly 7; embryonic whorls eroded in adults, smooth and glossy in juveniles; post-embryonic whorls increasing very slowly, slightly convex; last whorl oblong, indistinctly flattened dorsally. *Aperture* slightly diagonal, its outer margin regularly curved or faintly flattened. *Parietal lamella* rather strong, calloused, obliquely seated, entering for about 0.5 whorl. *Columella* sigmoid, heavily calloused, indistinctly bluntly angled at its outer edge, with an inconspicuous low fold. *Palatal folds* absent. *Peristome* thin, erect.

Length 3.68 mm., diameter 1.61 (44 percent); apertural axis 1.29, diameter 0.84 (65 percent); last whorl 2.09 (57 percent); parietal lamella 0.19.

In a juvenile specimen whorls 5, length 2.42 mm., parietal lamella strong, its free margin sinuous and flaring outward. Columella heavily calloused, especially below lamella, nearly always furnished with two folds (54:62), the upper rapidly ascending, the lower strong, more transversely seated; occasional specimens with vestigial subcolumellar fold (8:62). Palatal wall with two spirally entering rows of rather widely spaced denticles united by a low callus. Denticles of lower row much stronger than those of upper row, three to four denticles in each row.

Adult genitalia similar to that of *T. perplexa*. *Ovotestis* three-lobate, embryos five. *Vagina* slightly longer.

Paraneanic genitalia similar to same stage in *T. perplexa*. *Ovotestis* four- to five-lobate. Duct strongly convoluted and distended. Spermatheca small, elliptical; stalk long ( $\pm 0.5$  oviducal length), wide below. Penis and appendix not as large as is typical.

Dissected 143615 (adult, paraneanic), four specimens.

Rapa: Teutu, northern slope of Mount Tepiahu, along damp fissures of low exposed cliff, alt. about 250 ft.; holotype 8784 (figured juvenile 8785); paratypes 143614-143622, Cooke and Wight, July 27. Maitua, on cliffs, alt. 750 ft., Anderson, July 10, 8786 (figured adult), 140091-140099; also collected at 600-900 ft. on Mount Ororangi, head of Maitua Valley, and the northwestern slope of Mount Tautautu. (All localities on south side of Ahurei Bay.)

The eight lots of this species collected contained more than 1,100 specimens, with all but about 70 in two lots, the type lot and one lot from Mount Tautautu.

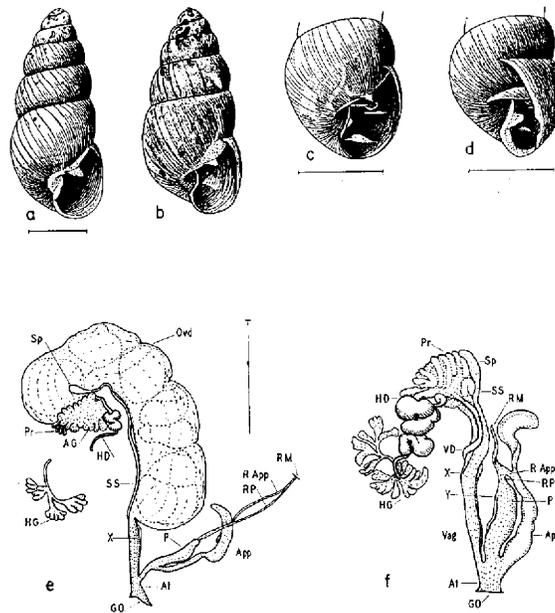


FIGURE 72.—*Tubuaia cremnobates*: a, adult, holotype; b, adult; c, parametaneanic, apertural view; d, parametaneanic, columellar aspect; e, adult genitalia; f, subadult or paraneanic genitalia.

In both colonies, specimens were abundant; but those from Mount Tautautu occurred as a pure colony and those from Teutu were found on a cliff with *T. voyana*. The two species were easily separated before cleaning, as animals of *T. voyana* are of a uniform slate color and those of *T. cremnobates* are almost solid black.

Specimens from Teutu and Mount Tautautu agree closely in all essential characters in both adult and juvenile stages. Shells from Maitua, which is only about 0.5 mile from the Tautautu colony, are proportionately broader and lighter in color than those from the Teutu and Tautautu colonies. In addition,

the aperture is smaller, the columella is more twisted, and the parietal lamella is slightly weaker. The figured specimen (140091) measures: length 3.60 mm., diameter 1.74 (47 percent); apertural axis 1.29, diameter 0.77 (60 percent); last whorl 2.16 (60 percent); parietal lamella 0.13.

In most juvenile specimens the palatal denticles are not strongly developed, and in a few they are entirely absent or represented by a very faint line. The few adult specimens from Mount Ororangi agree with the typical form but are slightly smaller.

*T. cremnobates* was the first species of the tribe in which we found the pitiesinid stage in the paraneanic or subadult animals. This strange phenomenon led us to dissect a dozen other species, totaling about 50 specimens, from Rurutu, Raivavae, Pitcairn, and Mangareva to determine whether or not the pitiesinid stage is universal in the tribe and to certify that no pitiesinid animal had been mixed inadvertently with the tubuaiinids during segregation and extraction in 1935.

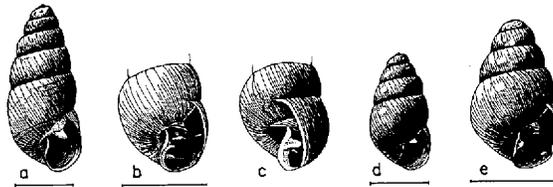


FIGURE 73.—a-c, *Tubuaia cylindrata cylindrata*: a, adult, holotype; b, metaneanic; c, metaneanic, columellar view. d, e, *T. c. philolichen*: d, adult, holotype; e, metaneanic.

***Tubuaia cylindrata cylindrata*, new species (fig. 73, a-c).**

*Shell* subcylindrical, color sayal brown, rather thin, subtranslucent, somewhat glossy, under a strong lens finely striate with growth striae which are slightly stronger just below sutures. *Spire* with slightly convex outlines, tapering gradually to apex. *Suture* simple, moderately impressed. *Whorls* 6-6.25; embryonic whorls comparatively large; postembryonic whorls convex; last whorl indistinctly medially flattened, oblong. *Aperture* vertical, outer margin slightly flattened. *Parietal lamella* strong, oblique seated, a full whorl in length, its outer third high, gradually becoming weaker inwardly. *Columella* slightly sigmoid, inner margin thickened, projecting in a rather prominent obtuse angle at its outer edge. *Palatal wall* without folds. *Peristome* thin, erect.

Length 2.58 mm., diameter 1.26 (49 percent); apertural axis 0.93, diameter 0.61 (65 percent); last whorl 1.74 (67 percent); parietal lamella 0.19.

In a juvenile specimen whorls 4.5, length 1.83 mm., parietal lamella strong, oblique, with a sinuous, slightly upturned free margin; columella less sigmoid than at adult stage, furnished with two to three lamellae (majority three), upper lamella weak, ascending rapidly, columellar lamella strong, more transversely placed; subcolumellar lamella weak, vertical, callus-like, occurring in 21 of 29 specimens. Palatal wall furnished with two spirally entering rows of denticles, each row consisting of four to five longish denticles united by a thin, low indistinct callus; denticles and callus easily visible through shell from exterior.

Rapa: Area, at head of small valley just east of the village (type locality), on cliff and on dead leaves at foot of cliffs, alt. about 350 ft., Cooke and Anderson, July 8; holotype 8795 (figured juvenile 8796), paratypes 135840-135848.

Five additional lots were taken from the vicinity of the village, from near sea level to about 450 feet. Three of the lots were close to the ground on trunks of *Celtis* and *Meryta*, which is quite a departure from the usual habits of the genus, specimens of which are invariably taken on cliffs and on dead leaves, twigs, or under stones.

Seventy specimens in eight lots are in the Museum collection, 43 specimens of which are in the type lot. In addition, five dead and worn specimens collected from sweepings on Mount Ruatara are tentatively assigned to this species.

*T. c. cylindrata* is easily separated from *T. voyana rapaensis* by its smaller size, its lighter color, and its more cylindrical outlines, which taper more slowly toward the apex. In juvenile specimens the palatal denticles of *T. c. cylindrata* are stronger, longer, and more closely spaced than in juveniles of *T. voyana rapaensis*.

***Tubuaia cylindrata philolichen*, new subspecies (fig. 73, d, e).**

*Adult shell* roughly resembles that of young specimens of *T. cylindrata* of same length. It differs from shells of the adults of *T. cylindrata* not only in its smaller size but in its more ovate outlines, more convex whorls, and slightly smoother and glossier surface texture. Whorls about 5.5.

Length 2.03 mm., diameter 1.06 (52 percent); apertural axis 0.71, diameter 0.48 (68 percent); last whorl 1.32 (65 percent); parietal lamella 0.10 (140263).

In a juvenile specimen 4.75 whorls, length 1.96 mm., free margin of parietal lamella slightly more sinuous, lower palatal denticles tuberculate and apparently not connected by a callus, and upper palatal fold longer and very weak. Subcolumellar lamella present in almost all (7:8), absent in one specimen.

Rapa: Tapui Islet, near head of Ahurei Bay (type locality), on and under surface of lichens growing on boulders, alt. about 20 ft., Wight and Kondo, July 13; holotype 140263, figured juvenile 8797, paratypes 140264-140266 (not dissected).

Two lots containing 16 examples were collected.

This subspecies is between *T. c. cylindrata* and *T. voyana rapaensis*. In outline, color, and whorling it seems to be closer to *T. c. cylindrata*, whereas in the form and position of the palatal denticles of the juvenile specimens it resembles *T. v. rapaensis*.

***Tubuaia raoulensis* Pilsbry and Cooke.**

*Tornatellina (Tornatellinops) raoulensis* Pilsbry and Cooke, 1915, Man. Conch. 23: 180, pl. 39, figs. 9, 10, 11.

*Tornatellina (s.s.) kermadecensis* Pilsbry and Cooke, 1915, Man. Conch. 23: 149, pl. 39, figs. 1-5.

Length 3.08 mm., diameter 1.74 (56 percent); apertural axis 1.23, diameter 0.75 (61 percent); last whorl 1.98 (64 percent); parietal lamella 0.22. Whorls 6.

Holotype in Canterbury Museum. Paratype in Bishop Museum (189797, ex ANSP 8313), Kermadecs, Sunday Island (Iredale).

Adults of *T. raoulensis* resemble those of *T. affinis* from Rurutu in size and in general outline. The shells are slender and darker in color than those of *T. affinis*, with slightly more convex outlines and a stronger parietal lamella. The juvenile specimens of *T. raoulensis* are more easily recognized, as they lack the palatal callus and the duplicate upper palatal denticle (Pilsbry and Cooke, 1915, pl. 39, figs. 1-5).

**Tubuaia voyana voyana** (Pilsbry and Cooke). Figure 74, *a, b*.

*Tornatellina (Tornatellinops) voyana* Pilsbry and Cooke, 1915, Man. Conch. 23: 179, pl. 35, figs. 12, 13.

*Tornatellina nitida* Garrett (*nec* Pease), 1879, Acad. Nat. Sci. Philadelphia, Proc., 22, 26; 1881, Acad. Nat. Sci. Philadelphia, Jour., II, 8: 399; 1884, II, 9: 83, pl. 2, fig. 24.

*Tornatellina (s.s.) nitida* Pilsbry and Cooke, 1915, Man. Conch. 23: 145, pl. 34, fig. 11; pl. 36, figs. 3, 7.

*Adult*: Closely resembles paratype (189794, Mauke), slightly longer, and darker; whorls 6.3.

Adults from different islands agree fairly closely in all measurements (in millimeters):

LENGTH	DIAMETER	APERTURAL AXIS	APERTURAL DIAMETER	LAST WHORL	PARIETAL LAMELLA	CAT. No.	LOCALITY
3.28	1.49 (45%)	1.21	0.77 (64%)	2.02 (62%)	0.15	189794, paratype	Mauke
3.38	1.46 (42%)	1.16	0.72 (62%)	2.02 (60%)	0.15	3355 ( <i>nitida</i> Gar.)	Society Is.
3.36	1.57 (46%)	1.21	0.86 (71%)	2.00 (59%)	0.15	97546	Mangaia
3.35	1.55 (46%)	1.21	0.83 (71%)	2.00 (59%)	0.16	143623	Rapa

*Juvenile*: Parietal lamella fairly strong, weakly sinuous, as in typical specimens. Palatal dentition bi-, uni-, or nonplicate, majority biplicate. [In typical specimens (97546-97550, Mangaia) palatal wall all biplicate.] Columella bilamellate.

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

Cook Islands: [Mauke, type locality], C. D. Voy. Mangaia, Oneroa Makatea, under coral stones, alt. 115 ft., P. H. Buck, Feb. 1, 1930, 97546-97550.

Tubuai: Rimatara, taken beating ferns and shrubs, alt. about 250 ft., Zimmerman, Sept. 4, 149122-149123; Rurutu, Mato Naa, on dead banana leaves, alt. 20-30 ft., Anderson, Aug. 29, 148715-148719 (dissected); Rurutu, hanging valley west of Moerai, on dead leaves and ferns and in kukui (*Aleurites*) forest, alt. 500-600 ft., Kondo and Anderson, Aug. 30, 148793-148807 (dissected); Raivavae, Vaiaunauna Point, on dead *Pandanus* leaves, alt. about 150 ft., Fosberg, Aug. 6, 146716-146720.

Rapa: Teutu, on northern slope of Mount Tepiahu, along damp fissure of exposed cliff, alt. about 250 ft., Cooke and Wight, July 27, 8790 (figured adult), 8791 (figured juvenile); 143623-143626 (dissected).

Pitcairn Island: north slope above village, along trail leading to crest of ridge, on dead *Pandanus* leaves, alt. about 700 ft., Cooke and Anderson, June 13, 141902-141912.

Mangareva Islands: Mangareva, south cliff of Mount Mokoto, on low ferns, alt. about 1,000 ft., Anderson, June 6, 141558-141564 (dissected).

Besides a paratype received from the Academy of Natural Sciences, Philadelphia, from Mauke, Cook Islands (189794) and specimens from the Society Islands identified as *T. nitida* by Garrett (3355), Bishop Museum has a large number of shell lots which we have identified as belonging to *T. voyana*. Some specimens of the species (115377) from Mangareva bear the manuscript name *Tornatellina monoliata* Ancey.

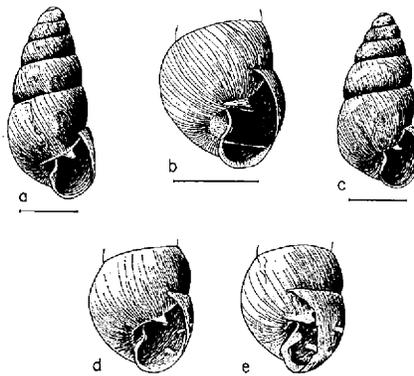


FIGURE 74.—a, b, *Tubuaia voyana voyana*: a, adult; b, metaneanic. c-e, *T. v. rapaensis*: c, adult, holotype; d, paraneanic, apertural view; e, paraneanic, columellar view.

Garrett collected this species on Huahine in the Society Islands; in Rurutu, Tubuai; and in the Cook Islands.

Garrett's identification of *T. nitida* is entirely erroneous, as is obvious by a comparison of his own specimens (*T. voyana* Pilsbry and Cooke, 3355) with paratypes of Pease's specimens (*Lamellidea pusilla* Gould, 189779) from the Museum of Comparative Zoölogy. *L. pusilla* was unknown to either Pease or Garrett.

*T. voyana* is the most widespread species of the genus, though it is not as widely distributed as *Elasmias aperta*, *Lamellidea pusilla* and *L. oblonga*, or *Tornatellides oblongus*. Except in the Kermadec Islands, *T. voyana* appears to be on every island upon which the genus has been found.

Adults of this species cannot be separated from those of *T. perplexa* with any degree of certainty. The two species are here considered distinct on the basis of juvenile apertural characters which are of fairly good specific importance. On Rurutu and Rimatara, the only two islands from which typical

material of *T. perplexa* has been obtained, there did not appear to be any intergrading of the two species. However, an apparently intergrading species has been found on Rurutu since this paper was written. It will be discussed in a later publication.

*T. voyana* shows considerable variability in the apertural characters of juvenile specimens. Specimens from a single colony are rarely consistent in the presence or absence, or in the degree of development, of any one character. As an example, one such colony from Mangareva (141640), in which there are 50 juveniles, contains five with no palatal denticles, 17 with one row, and 28 with two rows.

In only a few of the colonies from which we have examined specimens are the juveniles of the metaneanic substage (4 to 5 whorls) entirely consistent in the development of the palatal denticles, though in most colonies the majority follow a single pattern. Adults do not differ from one another to any such degree. The most noticeable variations are in the sharpness of the apex and the outlines of the spire, sometimes quite noticeable in specimens from a single restricted colony.

Juveniles of *T. perplexa* have 4 to 5 whorls, in which they are uniformly very strong. In juveniles of *T. voyana* the free margin of the parietal lamella ranges from hardly undulate to very strongly so. The subcolumellar lamella is usually absent; rarely, it is indicated by an indistinct swelling on the columellar callus. The low vertical palatal callus is entirely lacking. There is considerable variation in the development of the palatal denticles; these are usually weaker than the palatal denticles of *T. perplexa*. Many specimens have two parallel rows, consisting of one to four denticles, some united by a thin thread, some apparently entirely separated. In some specimens only the basal row is developed, in others, no palatal denticles have been found. The upper denticle is never duplicate (see fig. 68, *c*, *T. perplexa*).

An intensive study of the abundant material collected during the Mangarevan Expedition would undoubtedly lead to recognition of a number of subspecies.

***Tubuaia voyana rapaensis*, new subspecies (fig. 74, *c-e*).**

*Shell* slightly smaller than those of specimens identified as *T. v. voyana*, with sharper apex, more convex outlines, thinner, lighter color. *Whorls* of spire more convex, last whorl more distinctly flattened dorsally, often with a shallow, broad median depression near completion of last whorl.

In juveniles palatal wall biplicate (78 in 81 specimens) or uniplicate (3:81); columella bilamellate (73:81) or trilamellate (8:81), in latter very weak; parietal undulations ranging from weak to strong. In outline, the race always resembles *T. perplexa* rather than *T. voyana*.

Holotype, whorls 6, measures: length 3.06 mm., diameter 1.53 (50 percent); apertural axis 0.97, diameter 0.64 (66 percent); last whorl 1.81 (59 percent); parietal lamella 0.13.

A second specimen (8788), apparently adult, as all juvenile apertural characters lacking, whorls nearly 5.5, measures: length 2.44 mm., diameter 1.25 (51 percent); apertural axis 0.99, diameter 0.57 (58 percent); last whorl 1.63 (67 percent); parietal lamella 0.13.

Rapa: Tapui Islet (type locality), near head of Ahurei Bay, on dead leaves and twigs of *Aleurites moluccana*, Cooke and Wight, July 21; holotype 8787, second measured specimen 8788, figured juvenile 8789, paratypes 142682-142684.

This subspecies is much more widespread than that taken at Teutu, on the northern slope of Mount Tepiahu. Some specimens of *T. v. rapaensis* were collected at Tumu, Mount Tevaitahu, Maitua, Mount Mitiperu, Ahurei, Mount Tepiahu, Mount Tanga, Maomao Point, Rapa Iti Islet, Anatauri Valley, Mount Koara, and Karapo Rahi Islet, all on the eastern and southern sides of the bay. On the northern side of the bay it was found only in a single locality, back of the village of Area and a few feet above sea level.

Thirty-two lots of this subspecies, totaling more than 500 specimens, were collected by the Mangarevan Expedition. Except for the type lot, which includes nearly half of the specimens, the variety was not abundant in any single locality. Most of them held less than 10 specimens. Four other lots were collected by Margaret Stokes, and a single specimen was collected by the St. George Expedition in 1924-1925 (received from Mr. J. R. le B. Tomlin).

#### **Tubuaia inconstans**, new species (fig. 75, a-f).

*Shell* oblong-ovate, color between verona brown and snuff brown, rather thin, sub-transparent, glossy, under a lens minutely striate with slightly oblique lines of growth. *Suture* simple, moderately impressed. *Spire* elongate-ovate, with broadly convex outlines; apex rather blunt. *Whorls* 6; embryonic whorls eroded (smooth and polished in juvenile specimens); post-embryonic whorls increasing rather rapidly, slightly convex; last whorl capacious, occupying more than half of shell. *Aperture* large, its outer margin regularly curved. *Parietal lamella* simple, weak, about one whorl long, continuing at about same height until close to its inner termination. *Columella* twisted, its inner margin calloused, its outer margin only very slightly produced, barely angled. *Palatal* wall without folds or denticles. *Peristome* thin, erect.

Length (holotype) 3.68 mm., diameter 1.93 (53 percent); apertural axis 1.45, diameter 0.87 (60 percent); last whorl 2.26 (61 percent); parietal lamella 0.08 (8792).

A juvenile specimen, whorls 4.75, length 2.74 mm., has a very low, simple parietal lamella which is not proportionately stronger than at adult stage. *Columella* slightly less sigmoid and (viewed obliquely) furnished with two almost equally developed, rather weak, rapidly ascending folds. No indications of palatal folds or denticles in any of the numerous specimens.

Length 3.12 mm., diameter 1.78 (58 percent); apertural axis 1.29, diameter 0.79 (62 percent); last whorl 2.00 (64 percent); parietal lamella 0.06 (8793).

*Adult genitalia.* *Ovotestis* five-lobate. *Oviduct* heavily distended; embryos four. *Penis and appendix* proportionately slightly longer than typical. *Albumin gland* well developed. *Prostate* not seen.

*Paraneanic genitalia* pitysinid. *Ovotestis* five-lobate; not heavily distended, transparent, with yellow globules (ova?) visible. Duct heavily distended, not strongly convoluted. *Albumin gland* large, multifolliculate. *Prostate* small, paucifolliculate. *Spermathecal stalk* very low (0.75 oviducal length).

*Subparaneanic genitalia* (not figured). *Penis and appendix* less developed than in paraneanic stage; stalk of penis long ( $\pm 0.3$  oviducal length). *Spermathecal stalk* short (0.3 oviducal length).

Dissected: 135747 (adult), four specimens; 135750 (paraneanic and subparaneanic), five specimens.

Rapa: head of small valley just east of Area village (type locality), on very damp cliff, alt. about 150 ft., Cooke and Anderson, July 1; holotype, 8792, figured juvenile 8793, paratypes 135747-135759.

Specimens of this species were collected only once and under conditions rather peculiar for a tornatellinid. In an area of 5 to 6 yards on a cliff so damp

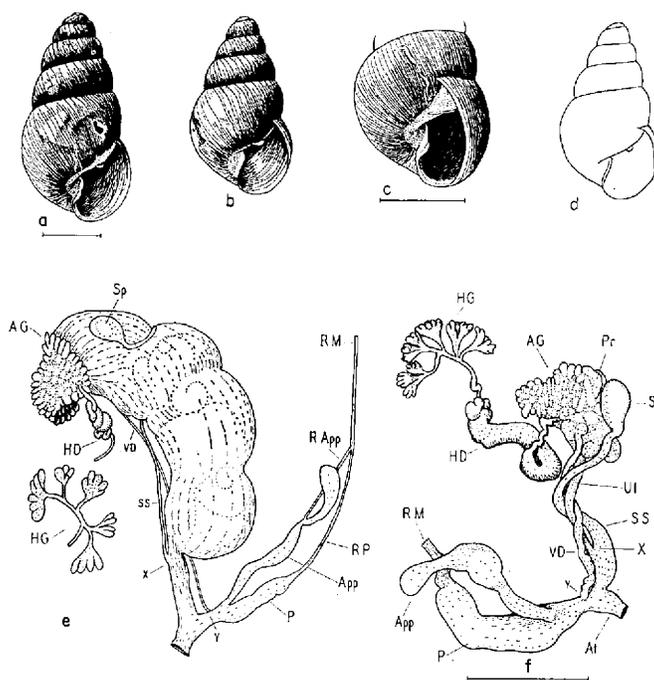


FIGURE 75.—*Tubuaia inconstans*: a, adult shell, holotype; b, parametaneanic; c, parametaneanic, columellar view; d, adult, a form proportionately wider than type; e, adult genitalia; f, paraneanic genitalia.

it was oozing water and was covered with green slime they were so numerous we just scraped them into vials.

The paraneanic genitalia studied was apparently at the stage where it was metamorphosing into the adult, to judge by the diminution of the ovotestical lobes, the large albumin gland, the small prostate, and the elongation of the spermathecal stalk.

Nearly all adult specimens of *T. inconstans* are heavily pitted or eroded on the surface, and almost all the cuticle is missing in many adults. These specimens show more variability in size and form than any other species that we

have examined. Some of the specimens are proportionately a little narrower than the type, some are wider (135747B).

In many of its characters this is the most distinct species of the genus *Tubuaia*. The adult shells are proportionately wider than those of other species and the parietal lamella decidedly weaker. In young stages (fig. 75, *b*, *c*) the parietal lamella is weaker and simpler and not proportionately stronger than at the adult stage. The columella lacks the strong transverse lamella. There is a complete absence of palatal folds and denticles, which are almost invariably present in *Tubuaia*. (In *T. cremnobates* and *T. voyana* some specimens lack palatal denticles.)

From its shell characters *T. inconstans* might be assigned to *Tornatellinops*. However, it can be placed only in *Tubuaia* after dissection.

#### SUBFAMILY LAMELLIDEINAE

Penis innervated by cerebral ganglion. Right ommatophoral retractor free of peni-oviducal angle. Penis with or without appendix, internally equipped with modified achatinellid pilaster; aphyallic members present. Appendix, when present, with retractor; internally equipped with secretory-ejaculatory organ. Albumin gland small to large, well developed. Prostate small. Spermatheca free. Ovary unilobate.

This subfamily embraces minute to medium, elongate, elongate-conic, turritid, or ovate-conic shells, with or without palatal ribs. It was formerly classified with *Tornatellina*, mostly under sections *Lamellidea* and *Tornatellinops*.

#### TRIBE TORNATELLINOPTINI

With appendix. Viviparous. Conchology as in *Tornatellinops*.

#### Genus *Tornatellinops* Pilsbry and Cooke

*Tornatellina* section *Tornatellinops* Pilsbry and Cooke, 1915, Man. Conch. 23:

169. Type *T. novoseelandica* Pfeiffer (original designation); "Lamellidea Pilsbry, 1910, definition but not the type assigned."

*Pacificella* Odhner, 1922, Natural History of Juan Fernandez and Easter Island 3 (2): 249. Type *P. variabilis* Odhner (monotypic).

*Tornatellinops* Iredale, 1937, Australian Zool. 8 (4): 300.

*Tornelasmias* Iredale, 1944, Australian Zool. 10 (3): 308 (type *T. capricorni* Iredale, original designation); 1945, Australian Zool. 11 (1): 51.

Adult: Shell imperforate, small, 2.2 mm. (*T. hataiana*) to 4 mm. (*T. capricorni*) thin, whorls slightly convex, 3.5 (*hataiana*) to 6 (*philippii*), in most species 5 to 5.5, apex rounded to bluntly pointed, oblong-conic, ovate-conic, to ovate, diameter from a little less than half of length to slightly more than half. Surface nearly shining, nearly smooth, marked with fine lines of growth. Parietal lamella moderate to weak, perpendicularly seated, entering from 0.33 to 0.55 whorl. Columella slightly to strongly twisted, thickened near its middle. Palatal wall unarmed.

Juvenile shells have a much stronger parietal lamella, of which margin is usually simple, sometimes slightly sinuate; columella sometimes equally biplicate, in most species columellar lamella moderately to well developed, much stronger than supracolumellar lamella. In most species palatal wall unarmed. In two species (*T. variabilis*, *T. baldwini*) palatal wall may have one or two low, spirally entering lamellae.

*Ovotestis* unilobate, roughly triangular; follicles few (two to 10), small, usually protruding as points, or "horns," from corners, giving cleft appearance. *Duct* small, slightly swollen and convoluted. *Talon and carrefour* not dissected but presumably similar to those of *Lamellidea*. *Albumin gland* relatively large, multifolliculate; follicles digitate, round, or ovate. *Prostate* small, between albumin gland and uterus; follicles few (five to 12, more or less), digitate or ovate. *Spermatheca* small, ovate, lying on albumin gland or uterus; stalk narrow, thin, entering oviduct below lowest and oldest embryo. *Vagina* short, equal to or shorter than penis. *Vas deferens* same diameter as spermathecal stalk; Y subapical. *Oviduct* distended (embryos two to six, more or less), diaphanous. In general, half of embryos enclosed in white masses, other half free. *Penis* small, short, tapering (average ratio, width to length, 1:6; penial length nearly equal to appendical length; penial length to oviducal, 1:4 in an average of 13 specimens); without epiphallus. Interior with modified achatinellid pilaster: a thick ascending fleshy ridge recurved at apex to long, digitate, semi-pendent papilla, adherent at one edge to penial wall, terminating just below curvature (see *T. concolorans*). *Retractor* thin, bifid, terminal. *Appendix* short, broad (ratio, width to length, 1:5), bluntly pointed, usually bent at a slight angle near middle; retractor near middle, thin; internally with secretory-ejaculatory apparatus. *Atrium* short.

Nervous system: see *T. concolorans*.

Type species: *Tornatellinops novoseelandica* (Pfeiffer).

*Tornatellinops* was first given as a genus by Iredale in 1937. However, Pilsbry and Cooke described their *Tornatellina* section *Tornatellinops* in 1915 as follows:

Tornatellinae with the columella twisted and somewhat calloused, forming an oblique fold above, but not bearing a columellar lamella at any stage; there are no ribs, plicae or denticles within the outer lip at any stage. Shell imperforate, oblong-conic, composed of 5-6 whorls. Type *T. novoseelandica*.

Pilsbry and Cooke added the following note on the same page (169), "Most of the species now placed in *Tornatellinops* are known only in the adult stage, and their systematic place is therefore more or less uncertain. Some of them are likely to turn out to belong to other sections, when series of the young are examined."

As their original description is not applicable to the type species, and as a restudy of abundant additional material has been made, the genus is redefined here.

Odhner separated his genus *Pacificella* from *Tornatellinops* on the presence of a "columellar fold and the palatal plicae and denticles." He considered *Pacificella* a transition between *Tornatellinops* and the *perplexa* group of *Tornatellina* (s.s.), where Pilsbry and Cooke placed the two Hawaiian species *baldwini* and *mcgregori*. Iredale separated his genus *Tornelasmias* on the presence of the columellar fold in juvenile specimens.

When studied separately, the adult specimens of *Tornatellinops* are easily confused with *Lamellidea* or *Tubuaia*; but when species of the three genera are

studied together, they are fairly easily recognized. As a rule *Tornatellinops* is most readily separated by its slightly shorter length, proportionately wider diameter, fewer whorls, blunter apex, larger aperture, and weaker parietal lamella. These characters are not always reliable but will serve to identify the generic position of practically all species of *Tornatellinops*. Most juveniles are more easily recognized by the lack of any palatal armature. In *Lamellidea*, some specimens of *L. oblonga* lack the vertical palatal rib, which as far as we know, is a constant character of all specimens of the metaneanic substage. One or two

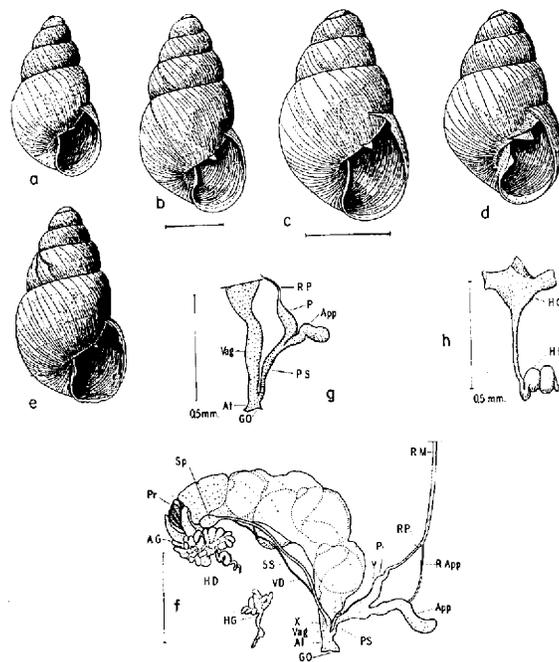


FIGURE 76.—*Tornatellinops variabilis*: a, adult, Rapa Iti; b, adult, Palmyra; c, paraneanic, Palmyra; d, parametaneanic, Palmyra; e, adult, Easter Is.; f, adult genitalia; g, parametaneanic genitalia, in part; h, ovotestis of "*Pacificella variabilis*."

weak spirally entering palatal folds may be present in two species of *Tornatellinops*: *T. baldwini* and *T. variabilis*. Some of the juveniles of most lots of *T. baldwini* have one or two weak palatal folds, a character to be found in about one-half to a majority of the specimens of suitable age.

*T. baldwini* and *T. variabilis* are easily separated from the species of *Tubucaia*, which have similar folds, by their fewer whorls, their blunter apices, and their weaker parietal lamellae. (See figure 76.)

In his description of *variabilis*, Odhner states, ". . . in young specimens sometimes faint traces of 1-2 palatal plicae." These plicae have not been seen

in any of the juvenile specimens from the many other islands of the Pacific which we have referred to *T. variabilis*.

Specimens of *T. variabilis* from Easter Island are very close to some of the Hawaiian forms that we have thought of as *T. baldwini*. The most pronounced difference is in the embryonic whorls. In typical *T. baldwini* the embryonic whorls are considerably wider than in *T. variabilis*, the outlines of the shell are more convex, and the columella is more twisted. However, in some specimens of *T. baldwini* the embryonic whorls approach quite closely to those of *T. variabilis*. Until a large series of Easter Island specimens is available we shall separate the two.

For further discussion on *Tornatellinops* and *Lamellidea* see the discussion of *Lamellidea* and its subgenus (*s.s.*).

Only two species of *Tornatellinops* are treated in this work, *T. variabilis* (Odhner) and *T. concolorans*, new species.

Next to *Elasmias*, *Tornatellinops* is the most widespread genus in the family (map, fig. 6). Species of it have been reported or are in the collection of Bishop Museum from the following islands north of the equator: the Philippines, the Ryukyus, Izu and the Bonin Islands, the Marianas, the Carolines, and the Hawaiian Islands. From south of the equator they have been found in the following islands: Easter Island, Pitcairn, the Tuamotus, Mangareva, the Marquesas, the Australs, the Society Islands, the Line Islands, the Cook Islands, Tonga, Samoa, Fiji, and the Ellice Islands. From the southwestern Pacific, they come from the Kermadecs, New Zealand, Lord Howe Island, New Caledonia, New South Wales and Queensland in Australia, some of the islands in Torres Strait, and Amboina in the East Indies. The genus has not been reported from the New Hebrides, from the Solomons, or from New Guinea; but with further collecting, the distribution will no doubt be extended to include nearly all of the Pacific islands and some of the islands of the East Indies. Undoubtedly, the widespread distribution of the genus is due, in part, to man's agency. This is shown by the very widespread distribution of *T. variabilis* (map, fig. 77).

Specimens in Bishop Museum which show no specific differences from the typical form, are distributed from Easter Island throughout the islands of central Polynesia to as far west as Tonga, Samoa, Lau in Fiji, and the Ellice Islands, all islands inhabited by Polynesians. This distribution compares, though to a lesser extent, with that of *Lamellidea pusilla* and *L. oblonga* (see maps, figs. 81, 85).

*Tornatellinops* seems to be equally at home on both high islands and low coral atolls, differing from *Elasmias*, which seems to be confined almost entirely to high islands. It is a more arboreal genus than *Lamellidea*. In fact, some species are taken almost entirely on the leaves of shrubs and ferns; others seem to be confined to dead leaves on the ground; and still others are found under loose bark and lichens growing on tree trunks.

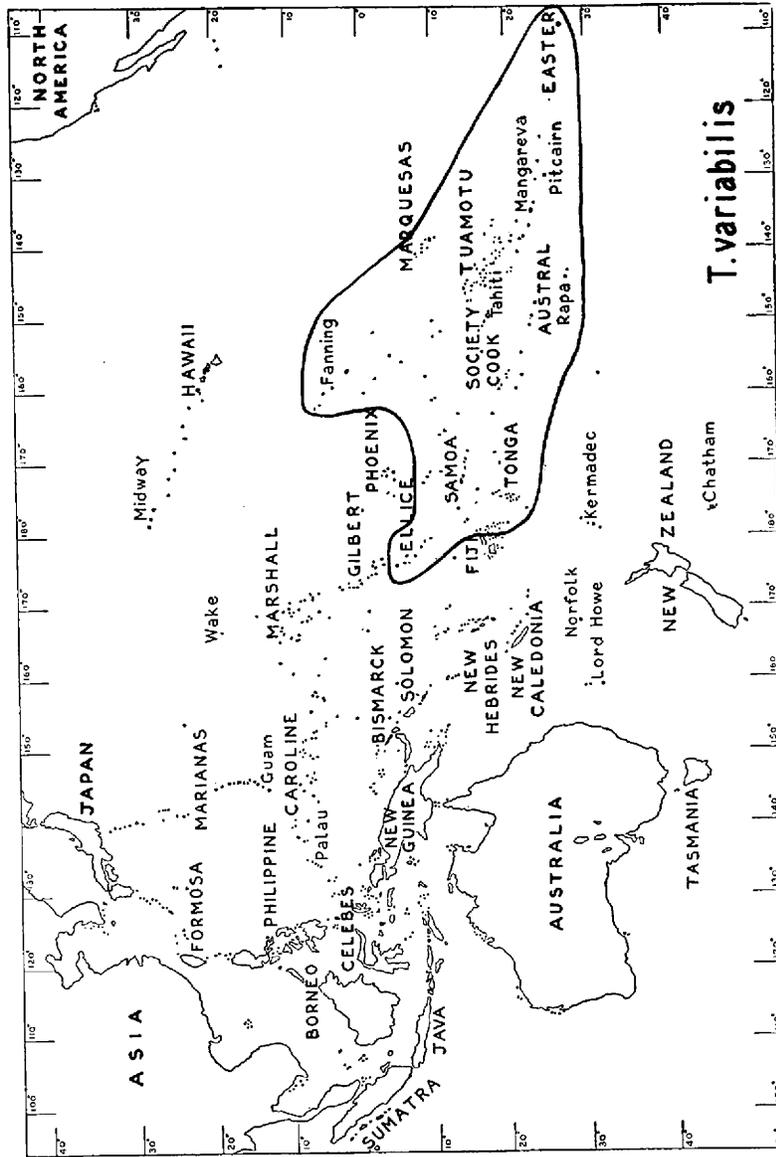


FIGURE 77.—Distribution of *Tornatellinops variabilis*.

Nine species are here removed from the subgenus *Tornatellinops* of Pilsbry and Cooke (1915, Man. Conch., vol. 23, pp. 172-180, 187). Nearly all of the nine have had their generic position fixed by means of a study of their animals as well as their shells. They are transferred as follows:

- Tornatellina* (*Tornatellinops*) *gayi* Pilsbry and Cooke = *Lamellidea*.  
*Tornatellina* (*Tornatellinops*) *tantalus* Pilsbry and Cook = *Lamellidea* (*Elamellidea*).  
*Tornatellina* (*Tornatellinops*) *impressa* Mousson = *Lamellidea* (*pusilla*).  
*Tornatellina* (*Tornatellinops*) *impressa normalis* Pilsbry and Cooke (for *T. conica* Mousson, preoccupied) = *Lamellidea* (*pusilla*).  
*Tornatellina* (*Tornatellinops*) *impressa intuscostata* Pilsbry and Cooke = *Lamellidea* (*pusilla*).  
*Tornatellina* (*Tornatellinops*) *pusilla* (Gould) = *Lamellidea*.  
*Tornatellina* (*Tornatellinops*) *affinis* Garrett = *Tubuaia*.  
*Tornatellina* (*Tornatellinops*) *trochlearis* Pfeiffer = *Antonella*.  
*Tornatellina* (*Tornatellinops*) *voyana* Pilsbry and Cooke = *Tubuaia*.  
*Tornatellina* (*Tornatellinops*) *raoulensis* Pilsbry and Cooke = *Tubuaia*.  
*Tornatellina* (*Tornatellinops*) *minuta* (Anton) = *Tornatellina*.

Transferred from *Tornatellina* (*s.s.*) to *Tornatellinops* are the following (Pilsbry and Cooke, 1915, pp. 142-144):

- Tornatellina* (*s.s.*) *baldwini* Ancey, *Tornatellina* (*s.s.*) *baldwini subrugosa* Pilsbry and Cooke, and *Tornatellina* (*s.s.*) *mcgregori* Pilsbry and Cooke.

Transferred from *Tornatellides* to *Tornatellinops* is *Tornatellides inconspicuus* (Brazier), loc. cit., p. 200.

***Tornatellinops baldwini* (Ancey).**

*Tornatellina baldwini* Ancey, 1889, Soc. Malac. France, Bull. 6: 238; 1903, Jour. de Conchyl. 51: 296.—Sykes, 1900, Fauna Hawaiiensis 2 (4): 380.

*Tornatellina* (*s.s.*) *baldwini* Pilsbry and Cooke, 1915, Man. Conch. 23: 142, pl. 35, figs. 3, 4; pl. 40, fig. 13; pl. 42, figs. 1, 2.

Type in Bishop Museum (18422); Manoa, Oahu.  
 Distribution: Oahu, Kauai, Maui, and Hawaii.

***Tornatellinops baldwini subrugosa* (Pilsbry and Cooke).**

*Tornatellina* (*s.s.*) *baldwini subrugosa* Pilsbry and Cooke, 1915, Man. Conch. 23: 143, pl. 35, figs. 7, 10.

Type in Academy of Natural Sciences, Philadelphia (98050?), Maui.

**Tornatellinops mcgregori** (Pilsbry and Cooke).

*Tornatellina* (*s.s.*) *mcgregori* Pilsbry and Cooke, 1915, Man. Conch. 23 : 144, pl. 35, figs. 14, 15.

“Types” in Academy of Natural Sciences, Philadelphia (86479), Imoto Jima.

Distribution: Bonin Islands, Imoto Jima and Haha Jima.

**Tornatellinops rucuana** (Pilsbry and Hirase).

*Tornatellina rucuana* Pilsbry and Hirase, 1905, Acad. Nat. Sci., Philadelphia, Proc. 57 : 718.

*Tornatellina* (*Tornatellinops*) *rucuana* Pilsbry and Cooke, 1915, Man. Conch. 23 : 170, pl. 37, figs. 4, 5.

Type in Academy of Natural Sciences, Philadelphia (89891); Kerama Jima, Ryukyus.

? **Tornatellinops nakadai** (Pilsbry and Cooke).

*Tornatellina nakadai* Pilsbry, 1902, Nautilus 16 (5) : 57. *Nomen nudum*.

*Tornatellina* (*Tornatellinops*) *nakadai* Pilsbry and Cooke, 1915, Man. Conch. 23 : 170, pl. 37, figs. 8, 9, 10.

Type in Academy of Natural Sciences, Philadelphia (83007); Chichi Jima, Bonin Islands.

**Tornatellinops hataiana** (Pilsbry and Cooke).

*Tornatellina* (*Tornatellinops*) *hataiana* Pilsbry and Cooke, 1915, Man. Conch. 23 : 171, pl. 37, figs. 6, 7.

Type in Academy of Natural Sciences, Philadelphia (84966); Izu, Kita Iwo Jima.

**Tornatellinops ponapensis** (Pilsbry and Cooke).

*Tornatellina pusilla* Möllendorff, 1900, Jour. Malac. 7 : 114. Not *T. pusilla* Gould.

*Tornatellina* (*Tornatellinops*) *ponapensis* Pilsbry and Cooke, 1915, Man. Conch. 23 : 172.

Type whereabouts unknown; Ponape, Caroline Is.

**Tornatellinops philippii** (Pfeiffer).

*Tornatellina philippii* Pfeiffer, 1849, Zeitschr. F. Malak. 6 : 93; 1853, Mon. Hel. Viv. 3 : 524; 1852 (-1859), Conch.-Cab., Pupa 1 (15) : 152, pl. 18, figs. 20, 21.—Pease, 1871, Zool. Soc. London, Proc., 473.—Garrett, 1879, Acad. Nat. Sci. Philadelphia, Proc., 22; 1881, Acad. Nat. Sci. Philadelphia, Jour. 1881 : 397; 1884, II, 9 : 81; 1887, Bull. Soc. Malac. France 4 : 28.

*Tornatellina (Leptinaria) philippii* H. and A. Adams, 1858, *Genera of Mollusca* 2: 141.

*Tornatellina (Tornatellinops) philippii* Pilsbry and Cooke, 1915, *Man. Conch.* 23: 178, pl. 36, fig. 4.

Type whereabouts unknown, Tahiti.

Distribution: Society Islands, Cook Islands, Australs, and the Marquesas.

***Tornatellinops iredalei* (Pilsbry and Cooke).**

*Tornatellina (Tornatellinops) iredalei* Pilsbry and Cooke, 1915, *Man. Conch.* 23: 180, pl. 39, figs. 6-8.

Type in Canterbury Museum, New Zealand; paratypes in Academy of Natural Sciences, Philadelphia (8312), and Bishop Museum (189796); Sunday Island, Kermadec Islands.

***Tornatellinops novoseelandica* (Pfeiffer)**

*Tornatellina novoseelandica* Pfeiffer, 1852, *Zool. Soc. London, Proc.*, 149; 1853, *Mon. Hel. Viv.* 3: 524; 1859, 4: 651; 1868, 6: 263.—Küster, 1852 (-1859), *Conch.-Cab., Pupa*, 1 (15): 149, pl. 18, figs. 10, 11.—Hedley and Suter, 1892, *Linn. Soc. New South Wales, Proc.* II, 6: 660.—Suter, 1893, *Jour. de Conchyl.* 41: 236; 1913, *Manual of New Zealand Mollusca*, 769.

*Tornatellina neozelandica* Pfeiffer, Hutton, 1883 (1884), *New Zealand Inst., Trans.* 16: 191.

*Elasmatina reclusiana* Gray, not of Petit, 1849, *Zool. Soc. London, Proc.*, 167.

*Cionella (Zua) novoseelandica* Albers and von Martens, 1860, *Die Heliceen*, 256.

*Tornatellina (Tornatellinops) novoseelandica* Pilsbry and Cooke, 1915, *Man. Conch.* 23: 181, pl. 38, figs. 1, 2.

Type whereabouts unknown.

Distribution: New Zealand, North Island at Whangarei Heads, near Auckland, Thames, Hunua Range, and Waimarama.

***Tornatellinops jacksonensis* (Cox).**

*Bulimus jacksonensis* Cox, 1864, *Cat. Australian Land Shells*, 25; 1864, *Ann. Mag. Nat. Hist.* III, 14: 185.—Pfeiffer, 1868, *Mon. Hel. Viv.* 6: 149.

*Achatinella jacksonensis* Cox, 1868, *Monogr. Australian Land Shells*, 77, pl. 12, fig. 15.

*Tornatellina jacksonensis* Brazier, 1872, *Zool. Soc. London, Proc.*, 807.—Pease, 1869, *Jour. de Conchyl.* 17: 176.

*Tornatellina (Tornatellinops) jacksonensis* Pilsbry and Cooke, 1915, Man. Conch. 23: 181, pl. 38, figs. 5, 6; pl. 53, figs. 12, 13.

Type whereabouts unknown.

Distribution: Australia, Darling Point and other places about Port Jackson; Wollongong; Botanic Gardens, Sydney.

**Tornatellinops mastersi** (Brazier).

*Tornatellina mastersi* Brazier, 1876, Linn. Soc. New South Wales, Proc. 1: 108.—Hedley, 1901, Linn. Soc. New South Wales, Proc. 26: 705, pl. 34, figs. 13, 14.

*Tornatellina (Tornatellinops) mastersi* Pilsbry and Cooke, 1915, Man. Conch. 23: 182, pl. 38, fig. 8; pl. 53, fig. 11.

Type whereabouts unknown.

Distribution: Darnley Islands, Torres Strait, Northeast Queensland, and islands between it and New Guinea.

**Tornatellinops noumeensis** (Crosse).

*Tornatellina noumeensis* Crosse, 1870, Jour. de Conchyl. 18: 244; 1871, 19: 193, pl. 6, fig. 4; 1894, 42: 305.—Pfeiffer, 1877, Mon. Hel. Viv. 8: 318.—Gassies, 1871, Nouvelle-Caledonie 2: 95.

*Tornatellina (Tornatellinops) noumeensis* Pilsbry and Cooke, 1915, Man. Conch. 23: 184, pl. 38, figs. 3, 4.

Type whereabouts unknown.

Distribution: Ilot Maitre, New Caledonia; Lifu, Loyalty Islands.

**Tornatellinops kochiana** (Möllendorff).

*Tornatellina kochiana* Möllendorff, 1888, Malak. Blätt., new ser. 10: 163, pl. 4, fig. 11.

*Tornatellina (Tornatellinops) kochiana* Pilsbry and Cooke, 1915, Man. Conch. 23: 185, pl. 38, figs. 14, 15; pl. 40, figs. 11, 12.

Type whereabouts unknown, Cebu, Philippines.

**Tornatellinops moluccana** (O. Boettger).

*Tornatellina moluccana* Boettger, 1891, Bericht. Senckenb. Natur. Gesell., 274, pl. 4, fig. 1.

*Tornatellina (Tornatellinops) moluccana* Pilsbry and Cooke, 1915, Man. Conch. 23: 186, pl. 38, figs. 12, 13.

Type whereabouts unknown, Ema, southern Amboina.

**Tornatellinops camarinica** (Möllendorff).

*Tornatellina camarinica* Möllendorff, 1895, Nachrichtenblatt d. Deutschen Malak. Gesell. 27: 117.

*Tornatellina (Tornatellinops) camarinica* Pilsbry and Cooke, 1915, Man. Conch. 23 : 186.

Type whereabouts unknown, Caramuan village, Camarines Province, Luzon, Philippine Islands.

**Tornatellinops inconspicua** (Brazier).

*Tornatellina inconspicua* Brazier, 1872, Zool. Soc. London, Proc., 619; 1889, Australian Mus., Mem. 2 : 27.—Pfeiffer, 1877, Mon. Hel. Viv. 8 : 319.—Hedley, 1891, Australian Mus., Rec. 1 : 142.

*Tornatellides inconspicuus* Pilsbry and Cooke, 1915, Man. Conch. 23 : 200.

*Tornelasmias inconspicuum* Iredale, 1944, Australian Zool. 10 (3) : 308, pl. 18, fig. 4.

Type in Australian Museum (destroyed, Hedley), Lord Howe Island.

**Tornatellinops capricorni** (Iredale).

*Tornelasmias capricorni* Iredale, 1944, Australian Zool. 10 (3) : 308, pl. 18, figs. 6, 6a.

Type in Australian Museum?; Lord Howe, Goat (or Rabbit) Island.

**Tornatellinops lidgbirdense** (Iredale).

*Tornelasmias lidgbirdense* Iredale, 1944, Australian Zool. 10 (3) : 308, pl. 18, fig. 4.

Type in Australian Museum?; Lord Howe, Mount Lidgbird.

**Tornatellinops norfolkensis** (Preston).

*Tornatellina norfolkensis* Preston, 1913, Ann. Mag. Nat. Hist. VIII, 12 : 536.—Pilsbry, 1916, Man. Conch. 23 : 272.

*Tornatellinops norfolkensis* Iredale, 1945, Australian Zool. 11 (1) : 51.

Type whereabouts unknown, Norfolk Island.

**Tornatellinops moohuensis** (Preston).

*Tornatellina norfolkensis moohuensis* Preston, 1913, Ann. Mag. Nat. Hist. VIII, 12 : 537.—Pilsbry, 1916, Man. Conch. 23 : 272.

*Tornelasmias moohuense* Iredale, 1945, Australian Zool. 11 (1) : 51.

Type whereabouts unknown, Moohu Stone, Norfolk Island.

**Tornatellinops nepeanensis** (Preston).

*Tornatellina norfolkensis nepeanensis* Preston, 1913, Ann. Mag. Nat. Hist. VIII, 12 : 537.—Pilsbry, 1916, Man. Conch. 23 : 273.

*Tornelasmias nepeanense* Iredale, 1945, Australian Zool. 11 (1) : 51.

*Tornatellina duplicilamellata* Preston, 1945, Australian Zool. 11 (1): 51.—Pilsbry, 1945, Australian Zool. 11 (1): 51.—Iredale, 1945, Australian Zool. 11 (1): 51.

Type whereabouts unknown, Nepean Island.

The doubtful species in the above list are *T. nakadai* from Chichi Jima and *T. capricorni* from Lord Howe. Judging from the description, figure, and comparison with *T. peponum*, *T. nakadai* may belong to *Lamellidea*. To judge from the figure, *T. capricorni* may be a *Lamellidea*.

***Tornatellinops variabilis*** (Odhner). Figure 76, a-h.

*Pacificella variabilis* Odhner, 1922, Natural History of Juan Fernandez and Easter Island 3 (2): 249, pl. 8, figs. 15-17.

*Tornatellina (Tornatellinops) impressa normalis* Pilsbry and Cooke, 1915, Man. Conch. 23: 175 (in part, specimens from Palmyra Island only).

*Lamellidea (Tornatellinops) variabilis* Pilsbry and Cooke, 1933, Nautilus 47 (2): 60, note 3.—Cooke, 1934, B. P. Bishop Mus., Occ. Papers 10 (11): 9.

"Shell elongate, imperforate, horn-brown, often with pale-brown narrow spiral lines on the last whorl; whorls moderately convex, suture impressed. Aperture narrowly ovate, a third of the total length, with one strong parietal lamella (sometimes a short accessory denticle outside it) entering about a third of a whorl inwardly; columella strongly twisted, convex but without fold in adult stage; outer lip smooth within; in young specimens sometimes faint traces of 1-2 palatal plicae. Dimensions of the shell: height 3.8, breadth 1.5, aperture height 1.3 mm. Whorls  $5\frac{1}{2}$ ." (Odhner.)

Adult genitalia. *Ovotestis* triangular, paucifolliculate; follicles ovate to digitate. *Duct* small, slightly swollen and convoluted. *Talon and carrefour* not dissected. *Albumin gland* small, follicles few, ovate to digitate. *Prostate* small, follicles three to five, digitate. *Oviduct* large, embryos few (five to seven), diaphanous. *Vagina* short. *Spermatheca* small, ovate, lying on albumin gland or between it and uterus; stalk long, narrow, entering oviduct (X) at low level. *Vas deferens* thin, narrow ( $\pm 0.3$  width of SS); Y subapical. *Penis* short, attenuate, narrow near atrium, broadest at origin of appendix, tapering into medium heavy retractor. *Appendix* crooked-clavate, bluntly pointed, projecting somewhat beyond penis, retractor off middle. *Common retractor* twice width of either penial or appendical retractor, long, off nuchal membrane below spermatheca. *Atrium* short, rather narrow.

Parametaneanic genitalia. Penis and appendix varying slightly from adult; penial stalk very long. Change from juvenile to adult gradual.

Dissected 52273 (adult), two specimens; 183701 (para-metaneanic), three specimens, Palmyra; 189707 (ovotestis), one specimen, Easter Island.

Type in Riksmuseum, Stockholm, Sweden; paratype in Bishop Museum (115358).

Rapa: Rapa Iti Islet, just south of entrance of Ahurei Bay, alt. 20 ft., Wight, July 15, 142588, one specimen. Southern Point opposite Karapo Rahi Islet, Wight, July 18, 140590, two specimens. Mount Tepiahu, south side, alt. 550 ft., Kondo, July 23, 143073, one specimen.

Specimens collected by other expeditions: Palmyra, Cooke, July 22, 1913, 52283 (figured 8798, 8799, 8800). Easter Island (type locality), Hanga Roa,

0.5 mile inland, Templeton Crocker Expedition, Dec. 31, 1934, 163206 (figured 28235); Swedish Pacific Expedition, 1916-1917, 189707 (not figured).

This species may be rare on the island of Rapa, as only four specimens were taken from three rather widely separated localities south of the bay. Only one is adult, and none of the juvenile specimens show any sign of palatal folds.

Two juvenile substages are figured: a paraneanic specimen with no columellar lamella and a parametaneanic specimen with broad lamella (fig. 76, *c*, *d*). Neither had a palatal fold. The adult shell (fig. 76, *a*) is considerably smaller than specimens from the nearest islands or from Palmyra and Easter Island. In all other characters it closely resembles the typical form.

#### Dimensions in Millimeters

SPECIMEN	LENGTH	DIAMETER	PERCENT	APERTURAL AXIS (HEIGHT)	DIAMETER	PERCENT	LAST WHORL	PERCENT	PARIETAL LAMELLA	WHORLS
Easter (Odhner)	3.8	1.5	...	1.3	...	...	...	...	...	5.50
Easter	3.45	1.93	53	1.45	0.90	62	2.29	66	0.06	5.50
Rapa	2.8	1.55	55	1.16	0.77	67	1.93	69	0.05	5.00
Palmyra	3.45	1.87	54	1.32	0.81	61	2.29	66	0.096	5.25

This species is represented in Museum collections by specimens from 67 Pacific islands scattered among nearly all of the island groups from Easter Island in the east to Truk in the Carolines in the west (maps, figs. 77, 78). Many of these islands have rather distinct forms or subspecies of *T. variabilis*. Whether the species was dispersed by man or nature cannot be determined. Undoubtedly, man has had a prominent part in dispersal on the low islands and the atolls, both of which are periodically swept almost clean by hurricanes. Furthermore, the close similarity of some specimens on islands in the central Pacific—including Easter Island, the Marquesas, the Tuamotus, the Line Islands, and the Cook and Society Islands—seems to indicate that this species is mainly man-distributed.

On many of the high islands there are distinct species of *Tornatellinops*, showing that the genus has been there for a considerable period of time. No closely related form has been taken in the Hawaiian Islands.

Bishop Museum is fortunate in having three specimens from Odhner's original Easter Island lot (115358, one specimen; 189707, two specimens, including animals for dissection). These are identical with the form collected on Palmyra Island. We also have three specimens from Easter Island collected by the Templeton Crocker Expedition and sent to the Museum by the California Academy of Sciences (CAS 28235). These also agree with the Palmyra form. (See figure 76, *b*, *c*.)

Specimens of different ages (fig. 76, *c*, *d*) from Palmyra were submitted to Odhner for comparison with his type lot. In a letter from him dated March

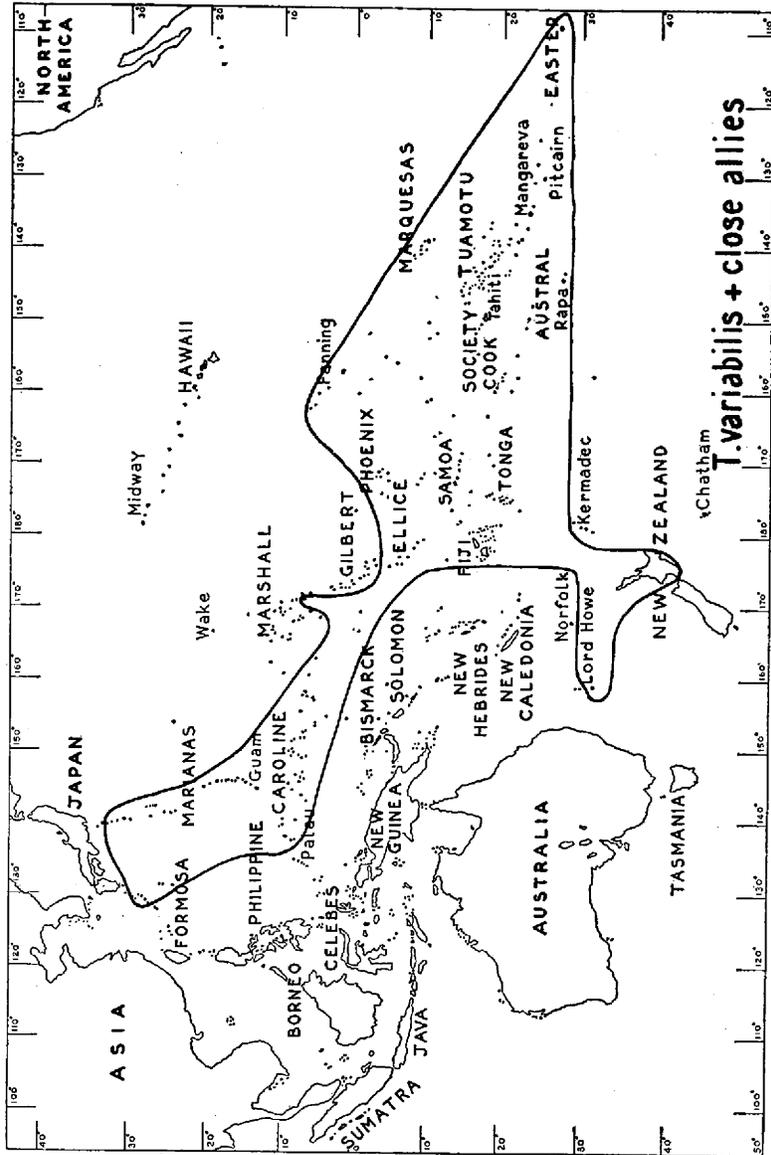


FIGURE 78.—General distributional map of *Tornatellinops variabilis* and close allies.

6, 1943, he states, "I feel convinced that my *Pacificella variabilis* is the same form as your *Tornatellinops impressa* judging from your specimens from Palmyra Isl. so kindly sent me years ago."

Early in this research it was found that the ovotestis was an important aid in classification, especially in the Tubuaiini and the Lamellideini. A study of the two types of genitalia in their adult stages show that they are similar but that (a) the ovotestis of Tubuaiini is multilobate and that of Lamellideini is unilobate, and that (b) there is a subtle difference between the two penial complexes. It was difficult to place Odhner's *Pacificella variabilis* because the figure of the ovotestis (1922, p. 251, fig. 20) indicates it is a member of the Tubuaiini, whereas its meager penial complex places it in the Lamellideini. However, Odhner reexamined his material and sent us a specimen to examine for the position of the species. We found the ovotestis to be unilobate (fig. 76, *h*), the follicles truncate, and the protuberances conical.

***Tornatellinops concolorans*, new species (figs. 79, *a-g*; 80, *a-f*).**

*Shell* (fig. 79, *a*) oblong-ovate, sayal brown, not thin, slightly translucent, finely striate with lines of growth, oily sheen. *Spire* tapering slowly to rather blunt apex, with slightly convex outlines. *Suture* shallow. *Whorls* 5.25; embryonic whorls increasing rapidly, rounded, spirally sculptured (in juvenile specimens), with fine but distinct close striae; post-embryonic whorls increasing regularly, slightly convex; last whorl large, oblong, more than half shell length (54 percent). *Aperture* rather large, nearly as broad as long. *Parietal lamella* moderate to weak, short, about 0.3 whorl long. *Peristome* very thin. *Columella* sigmoid, not strongly twisted, inner face with a weak, indistinct fold.

Length 3.86 mm., diameter 2.1 (54 percent); apertural axis 1.61, diameter 1.0 (62 percent); last whorl 2.55 (66 percent); parietal lamella 0.097.

In juvenile specimens parietal lamella proportionately stronger though actually not as high as in adults (0.088 mm.). Columella with a distinct spiral fold. Spiral striae on embryonic whorls well preserved and distinct. Whorls in figured specimen about 3.75.

Adult genitalia (fig. 79, *d*) typical. *Ovotestis* with three to four blunt square-ended follicles. *Duct* small. *Albumin gland* relatively larger than in *T. variabilis*. *Prostate* not seen. *Vas deferens* and spermathecal stalk narrow, of equal diameter (VD obscured near second embryo). *Oviduct* distended with five to six embryos. *Penis* short-oblongate; interior of penis with typical but modified pilaster. Ascending arm (Pil 1) large, heavy, with subsidiary mediad low, fleshy ridge (Pil 2) recurved at apex and descending ventrad into thin and narrow semi-pendent papilla (P Pap). *Appendix* of secretory-ejaculatory type: distal point hollow, chamber terminating at median crook; proximal ejaculatory mechanism or appendical "verge" (App V) starting at crook, thin, translucent, uncoiled, terminating at muscular wall near junction of appendix with penis.

Central nervous system (fig. 80, *a, b*) typical [compared with *Achatinella* (*s.s.*) *concauospira* Pfeiffer] except for small deviation in left buccal ganglion shown in figure: (2) Lateral buccal nerve off buccal connective instead of ganglion perhaps due to state of contraction. (7) Posterior salivary duct nerve instead of salivary gland nerve (ninth of *Achatinella*). No median oesophageal nerve (fifth of *Achatinella*) but a branch from anterior oesophageal nerve runs posteriad to this position. Twin nerves (third and fourth) as usual.

*Cerebral ganglion*, right: Penial innervation elasmiatinoid, i.e., right inferior frontal (fourth) giving off penial branch. (1) Nuchal nerve long, thin. (2) Ommatophoral and optic nerves off usual angle. (3) Superior frontal nerve from anteroventral surface to superior base of ommatophore. (4) Inferior frontal nerve off nearly same region as 3, adherent to right ommatophoral nerve for short distance, thence making 90-degree turn

anteriad to adhere to superior frontal, then diverging to penis via one branch (4a PN), to ommatophoral base via another branch. (4a) Penial nerve. (5) Labio-tentacular nerve, a very large trunk, off anteroventral surface directly antieriad, dividing into three branches: one to base of mouth, second to labial parts, third to inferior tentacle. (6) Buccal connective off usual point, to buccal ganglion. (7) Buccal retractor nerve off inner caudal surface. Acoustic not seen.

*Pleural ganglion, left*: (8) Subcerebral from just below connective's mergence with pleural ganglion, ventrad to base of cerebro-pedal connective.

*Cerebral ganglion, left*: All nerves the same as in right ganglion, frontals separate and not combined as in *Elasmias*. Seventh also innervating buccal retractor (left).

*Parietal ganglion, left*: (9) Left pallial.

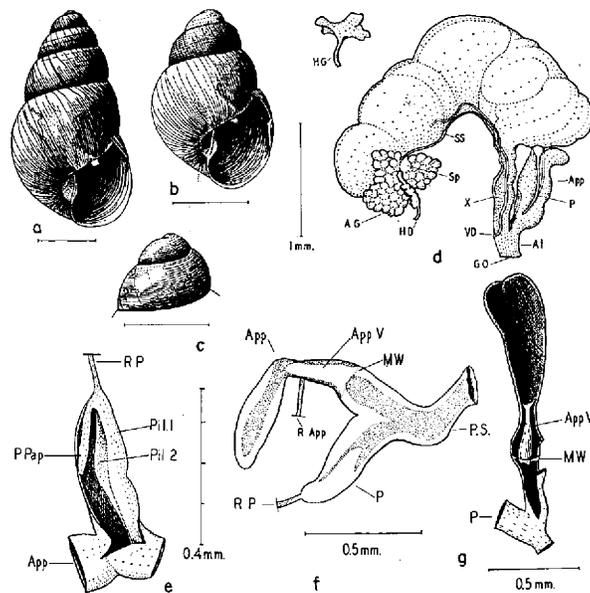


FIGURE 79.—*Tornatellinops concolorans*: a, adult, holotype; b, metaneanic juvenile; c, metaneanic juvenile, embryonic whorls; d, adult genitalia; e, interior of penis; f, penial complex, optical section; g, interior of appendix.

*Right parietal plus abdominal ganglion*: (10) Caudal off upper left angle. (11) Right salivary gland nerve off caudal surface. (12) Intestinal off same surface, to right of 11. (13) Large anal off apex. (14) Large right pallial.

*Pleural ganglion, right*: (15) Right inferior tentacular retractor nerve not off pleural ganglion but off lower end of pleuro-pedal connective.

*Pedal ganglion, right*: Lateral series with one nerve each to the three points, the lateral pedal nerve innervating region of vaginal and penial bases. Ventral series with one nerve each for anterior and median, two for caudal.

*Pedal ganglion, left*: Same as right pedal ganglion.

*Teeth* (fig. 80, c) all similar, small, seven- to eight-dentate. Tooth three-cuspid with three to four fine cusplets. Length 10 microns, width 6 microns.

Paraneanic genitalia with fewer embryos (two in figure 80, d). Prostate small, paucifolliculate. Spermatheca relatively larger than in adult. Penis small.

Metaneanic genitalia (fig. 80, e) without embryos. Oviduct subcylindrical. Hermaphroditic duct not convoluted. Albumin gland relatively large. Prostate and spermatheca not seen. Penis and appendix very short, stalk long.

Ananeanic genitalia: Penis (fig. 80, f) a mere bulge, with retractor. Appendix small, without retractor.

Dissected 135885 (adult genitalia, central nervous system, teeth), six specimens; 135887 (paraneanic), three specimens; 135888 (metaneanic, ananeanic), three specimens.

Rapa: east of Ahurei village, just back of graveyard (type locality), in thick stands of guava shrubs, on half-dead twigs, alt. 50-100 ft., Cooke, July 28;

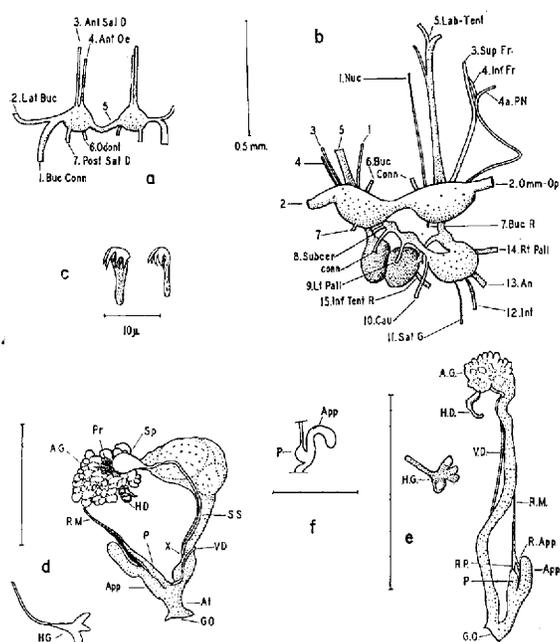


FIGURE 80.—*Tornatellinops concolorans*: a, buccal ganglia and principal nerves; b, central nervous system; c, teeth; d, paraneanic genitalia; e, metaneanic genitalia; f, ananeanic genitalia.

holotype 8802 (figured juvenile 8803), paratypes 135885-135890. Also taken under same conditions along trail to Maitua, just back of village, and on lower northwestern slopes of Mount Ororangi, on trunks of *Celtis* trees; a few specimens found on north side of Anatauri Valley, on dead *Pandanus* leaves. (In some specimens apical whorls somewhat narrower.)

A few specimens were taken by the Templeton Crocker Expedition ("Rapa, Ahurei Bay"), and the Museum has one of these specimens (163207) from the California Academy of Sciences (CAS 28260).

Apparently this species is closely related to *T. variabilis*. It is most easily recognized by its slightly larger size, darker color, slightly more convex outlines, wider and more distinctly spirally striate embryonic whorls, and stronger parietal lamella.

#### TRIBE LAMELLIDEINI

Without appendix. Viviparous. Conchology as in *Lamellidea*.

#### Genus *Lamellidea* Pilsbry

*Lamellidea* Pilsbry, 1910, *Nautilus* 23 (10) : 123. Type by designation *L. pepo-*  
*num* Gould, Pilsbry and Cooke, 1916, *Man. Conch.* 23 : 273 ; 1933, *Nautilus*  
47 (2) : 60.

*Lamellina* Pease, 1860, *Zool. Soc. London, Proc.*, 439. For *L. serrata* Pease  
(*L. pusilla* Gould).

Adult. *Shells* slender, turritate, 2-7+ mm. long, whorls 5 to 9. *Parietal* lamella moderate to strong. *Columella* vertical or somewhat sinuous, with or without distinct lamella. *Palatal* folds absent. (Other characteristics enumerated under subgenera and section.)

Juvenile. *Parietal* lamella usually stronger than in adult, rarely the reverse, sinuous or not. *Columella* with two to three lamellae, columellar lamella generally more prominent than supra- or subcolumellar lamellae. *Palatal* wall with one to three vertical ribs or without ribs; ribs serrate or plain. (Other characteristics under subgenera.)

Adult genitalia. *Ovotestis* unilobate; follicles few, short-clavate to mere stubby protuberances. *Duct* small, with slight median swelling, convoluted. *Albumin gland* usually relatively large; follicles numerous, ovate to short-digitate. *Prostate* small; follicles few, three to ten, usually digitate and rather long but often closely similar to that of albumin gland. *Talon* small, reflexed. *Carrefour* small, saclike, ovate. *Uterus* distended, diaphanous; embryos one to six, upper embryos with coating of yolk masses, lower ones free. *Spermatheca* large to small, round, oval, or elliptical, lying on albumin or prostate glands, sometimes on uterus; stalk long, narrow, entering oviduct below lowest embryo. *Vas deferens* thin, narrow, Y apical or subapical. *Vagina* short. *Penis* short to long (0.3 oviducal length to as long or longer by 0.4), usually linear, cylindrical, or subcylindrical but often with distended head, thus appearing clavate; sometimes without penis. Interior of penis with typical or modified pilaster. *Penial retractor* short to long, thin and weak to stout. *Atrium* short, narrow to fairly wide.

Type species: *L. pepo-num* Gould.

Conchological differences between adult specimens of *Lamellidea* (*s.s.*) and *Tornatellinops* are nebulous. All *Lamellidea* (except *L. gayi* with 4.25 whorls) have at least 5 whorls and some have up to 6.5. About half, or six, of the species of *Tornatellinops* have fewer than 5 whorls, five are described as having 5 whorls, and two species (*concolorans* and *iredalei*) have 5.5 whorls. Embryonic whorls of *Lamellidea* have very weak, very fine spiral lines. With *Tornatellinops* the spiral lines, though fine, are more plainly visible except in *T. baldwini* and *T. mcgregori*.

Juveniles are very easily separated. Most species of *Lamellidea* are furnished with one to three vertical ribs, but in some specimens of *L. oblonga* the ribs are entirely lacking. Juvenile specimens of the subgenera *Elamellidea* and *Atea* of *Lamellidea* have no palatal ribs at any stage of growth.

All of the five species of *Tornatellinops* (*ponapensis*, *variabilis*, *concolorans*, *baldwini*, and *mcgregori*), for which we have sufficient material to open some specimens, have a short (0.33 to 0.5 whorl) rather low, vertically seated parietal lamella. This is apparently true of a few other species that we have examined without opening. A short lamella is characteristic of the subgenus *Elamellidea*, but in this particular subgenus the parietal lamella is strong and obliquely seated.

Specimens of more than half of the species of *Lamellidea* were opened, and in all of them the parietal lamella entered for about the distance of a complete whorl. The parietal lamella is not only longer but stronger than that of *Tornatellinops*.

The subgenus *Atea* has no palatal rib. Specimens are most easily recognized by having seven to nine whorls and by the fact that they have the parietal lamella, which is one to one and a half whorls in length. The shells of *Atea* are more tightly coiled than those of the genus, and the apices are much sharper.

In *Lamellidea* most of the juveniles have about 4 to 4.5 whorls, and the columellar lamella is rather strong and ascends slowly. The upper columellar lamella is much weaker and ascends rapidly, and in most specimens of this age there is a lower columellar lamella, very short and deeply seated, and only visible when viewed obliquely. In many specimens the lower lamella is only indicated, and in a few it is apparently absent.

In *Elamellidea* the columellar fold is rather prominent, ascending slowly, and the upper lamella is weaker and ascends rapidly. There is no lower lamella. Below the columellar lamella the columella is slightly flattened and almost plate-like, as in some species of *Elasmias*.

In *Atea* the columellar and upper lamellae are almost the same size, both ascending obliquely. In only one species, *L. (A.) mumfordi*, could a very weak, lower columellar lamella be distinguished.

The upper and columellar lamellae of *Tornatellinops* are similar in development to those of *Lamellidea*, but columellar lamellae were seen in many examples of the six species examined (*baldwini*, *mcgregori*, *novoseelandica*, *variabilis*, *ponapensis*, and *concolorans*). Some of the juvenile specimens of *T. variabilis*, as reported by Odhner, have one or two entering palatal folds. This character is found to a greater degree in many juvenile specimens of *T. baldwini*.

Further notes on the genus are under *Lamellidea* (*s.s.*) and *Tornatellinops*.

#### KEY TO SUBGENERA OF LAMELLIDEA

- A. Neanic specimens with one to three vertical palatal ribs (Pan-Pacific).... **Lamellidea.**
- AA. Neanic specimens without vertical palatal ribs.
  - B. Adult specimens with 7 to 9 whorls; parietal lamella low to moderate, 1 to 1.5 whorls long; columella with a low rapidly ascending lamella (Marquesas) ..... **Atea.**

- BB. Adult specimens with 4.5 to 6.5 whorls, rarely more than 6; columella without lamella.
- C. Parietal lamella strong, obliquely seated, arcuate in cross section, short, 0.3 to 0.5 whorl in length, neanic specimens with a single columellar lamella, mounted on a narrow nearly vertical plate (Hawaiian Islands) ..... **Lamellidea**.
- CC. Parietal lamella weak to moderate, nearly vertically seated, straight in cross section, about 1 whorl in length. Neanic specimens with two to three columellar lamellae..... **Lamellidea (L. oblonga, in part)**.

The genus, as recognized in this paper, comprises 17 species.

#### KEY TO SPECIES OF LAMELLIDEA

##### Western Pacific: Gilbert to Bonin Islands

- A. Whorls convex to strongly convex, penultimate whorl often swollen (Caroline, Marshalls, and Gilberts)..... **L. pusilla**.
- AA. Whorls moderately convex to somewhat flattened.
- B. Diameter more than half of length, columella of young stages usually biplicate, sometimes triplicate.
- C. Color brown, weakly marked with growth striae, inner lip-rib distinct (Bonins)..... **L. ogasawarana**.
- CC. Color light brownish yellow, almost smooth, without inner lip-rib (Izu Islands)..... **L. biplicata**.
- BB. Diameter about equal to or less than half of length; columella of young stages distinctly triplicate.
- D. Diameter less than half of length.
- E. Lip-rib distinct; last whorl without shallow depression (Bonins)..... **L. ogasawarana longa**.
- EE. Lip-rib absent or indicated only near base of columella; last whorl flattened, with distinct shallow depression about one whorl long (Marianas)..... **L. subcylindrica**.
- DD. Diameter half or slightly more than half of length (Marianas) ..... **L. microstoma**.

##### Polynesian islands: Ellice to the Marquesas

- A. More than 2.5 mm. long, normally 3.5-4.2 mm.
- B. Ovately conic, tapering to a rather sharp apex; whorls convex, penultimate whorl often swollen. Young stages with distinctly serrate palatal ribs; parietal lamella strongly undulate..... **L. pusilla**.
- BB. Elongate, tapering gradually to a rather blunt apex, whorls slightly convex. Young stages with simple or faintly serrate palatal ribs; parietal lamella simple or slightly undulate..... **L. oblonga**.
- AA. Less than 2.2 mm. in length; subcylindrical..... **L. micropleura**.

## Hawaiian Islands

- A. Parietal lamella moderate or low, nearly perpendicular, straight in section.
  - B. Shells more than 2.5 mm. long.
    - C. Whorls flatly convex, last whorl rounded or flattened, without shallow depression on last whorl. Young with simple parietal lamella or slightly undulate margin; palatal ribs when present simple or with slightly serrate margin.....**L. oblonga.**
    - CC. Whorls slightly convex, last whorl flattened, with broad, shallow depression. Young with parietal lamella having a strongly undulate margin; palatal ribs distinctly serrate.....**L. gracilis.**
  - BB. Less than 2 mm. long, young unknown.....**L. gayi.**
- AA. Parietal lamella strong, flaring outward, straight or arcuate in section. Young with parietal lamella having a strongly undulate margin; palatal ribs distinctly serrate.
  - D. Cinnamon color.
    - E. Apex rounded; surface marked with rather distinct growth striae; more than 2.7 mm. long.
      - F. Spire with convex outlines, about 2.3 mm. long.....**L. polygnapta.**
      - FF. Spire with nearly straight outlines, about 3 mm. long.....**L. polygnapta kamaloensis.**
    - EE. Apex sharp; surface marked with indistinct microscopical growth striae; less than 2.2 mm. long.....**L. cylindrica kilohanana.**
  - DD. Lighter in color, cinnamon buff to chamois.
    - G. Narrowly conic.....**L. peponum.**
    - GG. Cylindrical.
      - H. Last whorl proportionately short, flattened, with broad shallow depression.....**L. gracilis.**
      - HH. Last whorl longer, cylindrical, without shallow depression.
        - I. More than 3.5 mm. long.....**L. lanceolata.**
        - II. Less than 3 mm. long.....**L. cylindrica.**

Subgenus **Lamellidea**

Adult shells small, 2 to 4.5 mm. in length, elongate. *Spire* with nearly straight to slightly convex outlines. *Apex* somewhat rounded. *Whorls* 5 to 6.75, slightly flattened to convex, last whorl 0.5 to 0.66 total length, convex or flattened dorsally and sometimes with a broad shallow depression on ultimate half, extending to and modifying outer margin of aperture. *Aperture* rather small, slightly oblique, with simple, thin outer margin. *Parietal lamella* moderate to prominent. *Columella* vertical, from nearly straight to distinctly sigmoid, somewhat thickened near it internally at middle, but without a distinct lamella. *Palatal wall* without folds.

Shells at the metaneanic substage have a proportionately stronger parietal lamella than adult shells, their free margin ranging from simple to strongly sinuous (almost lobed). The columella with two to three lamellae; the columellar lamella strong, entering slightly obliquely. The palatal wall furnished

with one to three vertical palatal ribs; the rib margins serrate in most species, but in one or two the margins are simple or slightly uneven. These ribs are absent in some of the specimens of *L. oblonga*. When there are as many as three ribs the outer and inner ribs are weaker than the central ones. The palatal ribs of juveniles separate *Lamellidea* from practically all other related genera, the only exceptions being some species of *Tubuaia* and specimens of *L. pusilla*. Many adults of *Lamellidea* are confused with those of *Tornatellinops* and *Tubuaia*.

*Lamellidea* is most easily distinguished from *Tornatellinops* by the larger number of whorls, proportionately smaller aperture, and slightly finer embryonic whorls.

There are no discernibly constant characters by which adults of *Lamellidea* and *Tubuaia* may be separated. In juveniles, the distinguishing characteristic is the absence of palatal ribs in most species of *Tubuaia*. Where ribs are present (*T. perplexa* and *T. gouldi*) the margin is not serrate but has two sets of denticles, the lower set single and the upper set bifid. In species of *Tubuaia*, which lack ribs, two spiral rows of plicae are general, solid or interrupted (beaded).

The three genera are almost universally found on the same island throughout the southern rim of islands in the Pacific: The Cook Islands, the Australs, Pitcairn, and Mangareva. *Tubuaia* is almost entirely terrestrial in habit, whereas *Tornatellinops* is most commonly found on leaves of low shrubs and ferns. *Lamellidea* is both terrestrial and arboreal. It is taken under bark and lichens, but rarely, if ever, is it found on leaves.

Anatomically, the three genera are distinct. A few undescribed species in the Museum collection from some of the south Pacific islands will be dealt with in a paper on this genus.

***Lamellidea (Lamellidea) ogasawarana* (Pilsbry and Cooke).**

*Tornatellina ogasawarana* Pilsbry, 1902, *Nautilus* 16 (5): 57. *Nomen nudum*.

*Tornatellina ogasawarana* Pilsbry and Cooke, 1915, *Man. Conch.* 23: 151, pl. 32, figs. 1-4, 11, 12.

"Types" in Academy of Natural Sciences, Philadelphia (85760).

Distribution: Bonin Islands (Minami Jima, Chichi Jima, Anijima, Nakano Shima, and Imoto Jima, Hirase collection).

***Lamellidea (Lamellidea) ogasawarana* var. *longa* Pilsbry, 1915, *Man. Conch.* 23: 152, pl. 32, figs. 5-10.**

Type in Academy of Natural Sciences, Philadelphia.

Distribution: Bonin Islands (Chichi Jima and Imoto Jima).

**Lamellidea (Lamellidea) biplicata** (Pilsbry.)

*Tornatellina biplicata* Pilsbry, 1902, *Nautilus* **16** (5): 57.

*Tornatellina (Lamellina) biplicata*, Pilsbry and Cooke, 1915, *Man. Conch.* **23**: 152, pl. 37, fig. 3.

Type in Academy of Natural Sciences, Philadelphia (83380).

Distribution: Japan (Izu Islands, Hachijo Jima, Hirase collection).

**Lamellidea (Lamellidea) subcylindrica** (Quodras and Möllendorff).

*Tornatellina (Lamellina) subcylindrica* Quodras and Möllendorff, 1894, *Nachrichtsblatt d. Deutschen Malak., Gesell.* **26**: 16.—Pilsbry and Cooke, 1915, *Man. Conch.* **23**: 166, pl. 33, figs. 10, 11.

Type in Senckenberg; paratypes in Bishop Museum (86200).

Distribution: Mariana Islands, Guam, coll. Quodras.

Since the publication of the Manual of Conchology the Museum has received a few lots from Guam and several lots from Rota collected by Hans Hornbostel from 1923 to 1925. Hornbostel collected none on Saipan or Tinian. The number of specimens in our collections indicates that the species is abundant in a few localities.

**Lamellidea (Lamellidea) microstoma** (Quodras and Möllendorff).

*Tornatellina (Lamellina) microstoma* Quodras and Möllendorff, 1894, *Nachrichtsblatt d. Deutschen Malak., Gesell.* **26**: 16.—Pilsbry and Cooke, 1915, *Man. Conch.* **23**: 167, pl. 33, figs. 8, 12.

Type in Senckenberg; paratype in Bishop Museum (86199).

Distribution: Guam, coll. Quodras.

Abundant material from Guam and Rota have come to the Museum through Hornbostel, who found fewer and smaller lots on Saipan and Tinian. Under suitable conditions this species will undoubtedly prove to be abundant on all four islands. Most of our lots were taken from low land, a few yards to about 0.5 mile inland. Two lots were taken between 200 and 300 feet and 1 to 2 miles inland. *L. (L.) microstoma* and *L. (L.) subcylindrica* occur either as pure colonies or mixed lots. Except for very young shells, the two species are easily separated.

**Lamellidea (Lamellidea) microstoma form moellendorffiana** Pilsbry.

*Tornatellina (Lamellina) moellendorffiana* Pilsbry and Cooke, 1915, *Man. Conch.* **23**: 168, pl. 38, figs. 7, 10, 11.

Type in Academy of Natural Sciences, Philadelphia; paratype in Bishop Museum (10094 ex 86199).

Distribution: Guam, coll. Quodras.

Both lots of *L. microstoma* sent by the Senckenbergische Naturforschende

Gesellschaft to the Academy of Natural Sciences of Philadelphia and to Bishop Museum contain this form. It is more or less abundant in lots containing *L. microstoma* from Guam, Rota, Tinian, and Saipan. It has not been taken in a pure lot, so far as Museum material shows. In young stages, up to 4.5 whorls, specimens of *L. microstoma* and form *moellendorffiana* are indistinguishable. However, just before and just after the adult stages form *moellendorffiana* is easily recognized by the formation of the palatal callosity (Pilsbry and Cooke, 1915, pl. 38, fig. 10). This callosity is nearly nodular in some specimens; in others it extends into the aperture under the spiral impression of the last whorl. The basal callus mentioned as characteristic for both *L. (L.) microstoma* and form *moellendorffiana* is more strongly developed in *L. ogasawarana* and *L. o. longa*.

These four western Pacific species, with the addition of *T. pusilla*, constitute a rather tight group of related species. A sixth, recently described species, *Lamellidea solomonensis* Dell, may now be added here.

\* **Lamellidea (Lamellidea) solomonensis** Dell, 1955, Pacific Science 9 (3) : 357, fig. 1.

Holotype (M.F. 2506) in Dominion Museum, Wellington, New Zealand; two paratypes in Bishop Museum (212365).

Solomon Islands, Savo.

**Lamellidea (Lamellidea) pusilla** (Gould). Figures 81; 82, a-p; 83, a-e.

*Partula pusilla* Gould, 1847, Boston Soc. Nat. Hist., Proc. 2: 197; 1852, U. S. Expl. Exped. 12: 83, pl. 7, figs. 90, 90a.—Pfeiffer, 1853, Mon. Hel. Viv. 3: 454.—Gould, 1862, Otia Conch., 33.

*Partula [Auriculella] pusilla* Gould, 1862, Otia Conch., 244.

*Achatinella (Auriculella) pusilla* Pfeiffer, 1859, Mon. Hel. Viv. 4: 570; 1868, 6: 187.

*Auriculella pusilla* Pfeiffer, 1877, Mon. Hel. Viv. 8: 213.—Ancy, 1889, Soc. Malac. France, Bull. 6: 220.

*Tornatellina (Tornatellinops) pusilla* Pilsbry and Cooke, 1915, Man. Conch. 23: 176, pl. 34, figs. 1-4.

*Tornatellina nitida* Pease, 1860, Zool. Soc. London, Proc., 439, Ebon Island (not *Tornatellina nitida* Garrett, 1879, Acad. Nat. Sci. Philadelphia, Proc., 22).—Pilsbry and Cooke, 1915, Man. Conch. 23: 145, pl. 34, fig. 11; pl. 36, figs. 3, 7. Equals *Tubuaia voyana* (Pilsbry and Cooke).

*Lamellina serrata* Pease, 1860, Zool. Soc. London, Proc., 439. Immature stage of *T. nitida*.

*Lamellina laevis* Pease, 1864, Zool. Soc. London, Proc., 672 (according to Garrett, *T. serrata* Pease).

*Tornatellina conica* Mousson, 1869, Jour. de Conchyl. 9 (3) : 342, pl. 14, fig. 8.

- Tornatellina conica* var. *impressa* Mousson, 1870, Jour. de Conchyl. 10 (3) : 128.
- Tornatellina columellaris* Mousson, 1870, Jour. de Conchyl. 10 (3) : 129 (immature stage of *T. conica impressa*).
- Lamellaria perforata* Liardet, 1876, Zool. Soc. London, Proc., 101, pl. 5, figs. 8, 8a.
- Tornatellina impressa* Mousson, 1915, Man. Conch. 23 : 175, pl. 34, fig. 8.
- Tornatellina impressa intuscostata* Pilsbry and Cooke, 1915, Man. Conch. 23 : 175, pl. 34, fig. 7.
- Lamellidea pusilla* Cooke, 1934, B. P. Bishop Mus., Occ. Papers 10 (11) : 8.

For more complete lists of references see the Manual of Conchology, volume 23, pages 146 (*nitida*), 148 (*columellaris*), 164 (*serrata* and *laevis*), and 174 (*conica*).

Genitalia (fig. 83, *e*) typical (see *L. oblonga* Pease) except in the following characters: *Ovotestis* not cleft, follicles few, protruding from both corners and middle like horns and warts; more embryos (five to seven); *penis* comparatively larger (ratio penial width to length, 1 : 1.75), nearly as long (length, oviduct to penis 1 : 1.40); *vagina* longer; *atrium* shorter, broader. *Spermatheca* small. *Prostate* fairly large; follicles few, large, digitate. *Albumin gland* imperfectly preserved.

Dissected 145883 (adult, five specimens), Tahiti, Tautira, Cooke and W. Anderson, Sept. 15.

The "type specimen is no longer to be found in the National Museum," according to Pilsbry and Cooke.

Of the 64 islands on which *L. pusilla* has been found, 38 are mentioned for the first time. These are designated by an asterisk (\*). Bishop Museum has specimens from 56 of them, as designated by the Museum's catalog numbers.

Marquesas Islands: Under the name *T. conica*, Garrett reports this species as rare. No specimens in Bishop Museum.

Tuamotu Islands: Makatea (type locality), Couthouy, U. S. Expl. Exped., 1839; 97706, 97707, K. P. Emory, 1930; 115782, Mrs. G. P. (Lillian) Wilder, 1932. Anaa as "*T. nitida*" Pease, Garrett; 136522, 136523, Mangarevan Exped. \*Toau, 98799, and \*Fakarava, 98801, Pilsbry, Pinchot Exped., 1929. \*Fakahina, 104607, Emory, 1930. \*Hao, 136549, 136550, Mangarevan Exped.

Mangareva Islands: \*Mangareva 115374, collector not known.

Austral Islands: Rurutu, as "*T. conica* and *T. serrata*" Garrett, C. de Gage.

Society Islands: Moorea, Garrett; 151063-151064, Mangarevan Exped. Tahiti, Garrett; 145883-145888, Mangarevan Exped. \*Meetia, 136416-136417, Mangarevan Exped. Huahine, Garrett; 151598-151608, Mangarevan Exped. Raiatea, Garrett; 151649-151656, Mangarevan Exped. Tahaa, Garrett. Borabora, Garrett; 152428-152430, Mangarevan Exped. Maupiti, Garrett, whose identifications include *T. conica* and *T. serrata*.

Line Islands: \*Penrhyn, 79519-79524, S. C. Ball, Kellum [Kaimiloa] Exped., 1924. \*Rakahanga, 95478-95479, Buck, 1929.

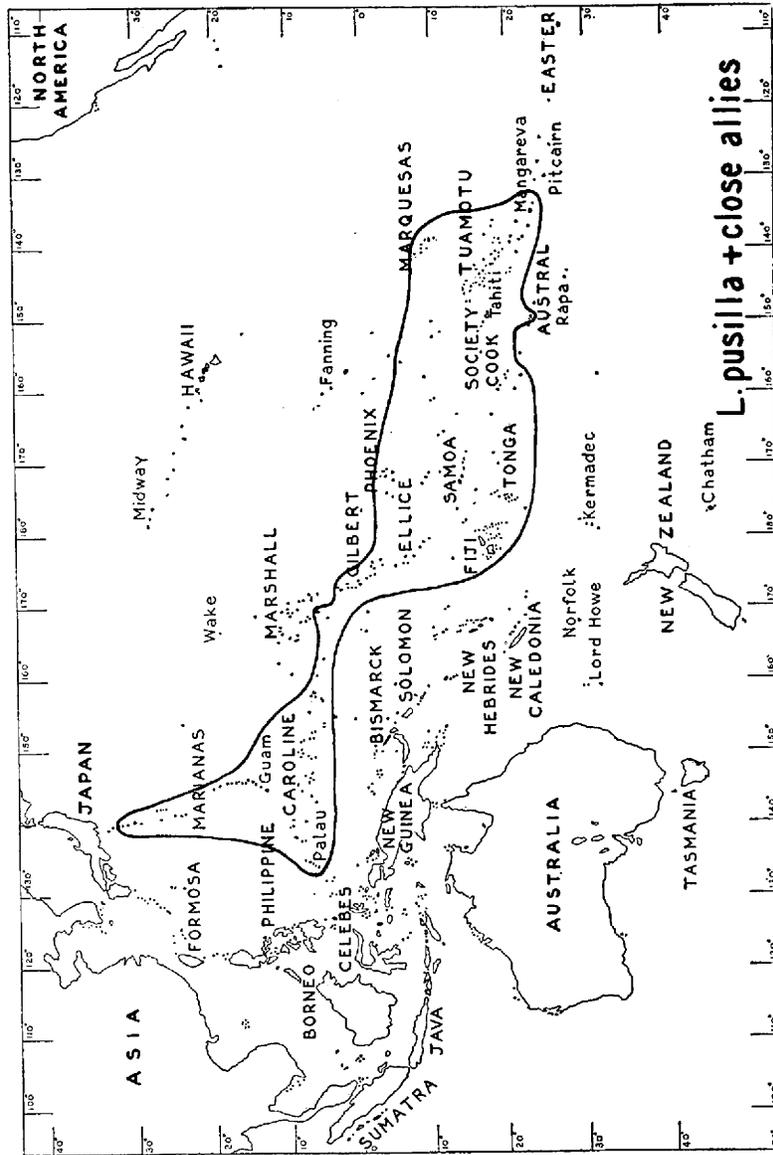


FIGURE 81.—General distributional map of *Lamellidea pusilla* and close allies.

Cook Islands: Rarotonga, 98804, Garrett from Acad. Nat. Sci., Philadelphia. Atiu, Garrett; 95066-95067, Buck, 1929. Aitutaki, Garrett; 95652, Buck, 1929. \*Mauke, 95287, Buck, 1929. Mangaia, Garrett; 97629-97631, Buck, 1930. Garrett's identifications are for both *T. conica* and *T. serrata*.

\*Niue Island: about 200 miles east of Tonga, 185779-185780, T. G. Yuncker, 1940.

Tonga: Ha'apai, E. Graeffe. \*Vava'u, 87862, J. E. Hoffmeister, 1928.

Fiji Islands: \*Makuluva Islet, about 2 miles east of Suva Point, 85988, Dranga (for *T. perforata*), 1926; Taveuni, Liardet (for *T. perforata*). Kana-thea, Graeffe (for *T. conica* and *T. columellaris*); Vanua Mbalavu, Graeffe, 179405-179408, Kondo, Lapham Exped., 1938; \*Karoni, 78611-78612; \*Kimbombo, 79106; \*Komo, 78667; Tavunasithi, 78806, and \*Yavutha, 78492 (all by E. H. Bryan, Jr., Whitney Exped., 1924); \*Aiwa, 167213; \*Namuka Ilau, 166775-166776; \*Navutu Iloma, 167061; \*Wangava, 166956, and \*Yangasa, 167143 (all by H. S. Ladd, 1934); \*Naiau, 180242-180244, Kondo, Lapham Exped., 1938.

\*Niuafoou Island: about 175 miles east of northern Fiji, 104121-104124, T. A. Jagger, 1930.

Samoa Islands: Upolu, Graeffe (for *T. conica*); 185885, Wray Harris, 1937. Tutuila, Graeffe. \*Ofu, 94441-94443, Harris, 1928. \*Olosega, 174662, Harris, 1937. \*Tau, 83027-83029, Cooke, 1926.

Swains Island: 186670, Zimmerman, 1940.

Pukapuka (Danger) Islands: about 390 miles northeast of Samoa. \*Pukapuka, 77269 and \*Nassau, 77228, both by Bryan, Whitney Exped., 1924.

Ellice Islands: \*Nukulaelae, 189661-189662, L. Verrier, 1943. Funafuti, Graeffe; 189656, Verrier, 1941. Nukufetau, Graeffe; 189674, Verrier, 1941. Vaitupu, Graeffe; 189684, Verrier, 1941. Nui, Graeffe, 189676, Verrier, 1941. Niutao, Graeffe. Graeffe's specimens were identified as *T. conica* by Mousson.

Gilbert Islands: \*Tarawa, Abuokoro Islet, 189007, Verrier, 1941.

Marshall Islands: Ebon, Garrett, 189779, "cotypes" of *T. nitida* Pease and 189781 "cotypes" of *T. serrata* Pease, from Museum of Comparative Zoölogy.

Caroline Islands: \*Kusaie, 156086-156095, Kondo, 1936. \*Ponape, 156588-156594, Kondo, 1936. Truk: \*Moen Islet, 155222-155227, Kondo, 1936; \*Param Islet, 155750, Kondo, 1936; \*Falo Islet, 189221, K. Atoda, 1940; \*Fefan Islet, 189170-189171, Atoda, 1940 (all collected by the Micronesian Expedition, 1935-1936, 1940).

*Lamellidea pusilla* heads a group of six species which are distributed from the Marquesas and Tuamotus in the east to the Izu (Japan), Bonin, Marianas, and Caroline Islands in the west. (See map, figure 81.) In its eastern distribution it has been taken only on islands south of the equator, whereas in its western distribution it has been taken from the Gilberts and from islands north of the equator. With further collecting, species belonging to this group may be

found as far west as the Ryukyu Islands and Formosa, from which a few tornatellinids have been reported. South of the equator, representatives of this group may inhabit the New Hebrides and Solomon Islands from which few minute species have been reported.

From the time of its original description in 1847 *L. pusilla* was not again recognized until 1915, when Pilsbry and Cooke identified and figured it (1915, p. 176). The fact that it was not identified by Garrett, Pease, or Mousson, who did describe several species of tornatellinids from the central Pacific, may account for the large number of synonyms. Furthermore, all three authors believed the immature specimens to belong to distinct species.

Though the Museum does not have representatives from nine islands on which this species has been collected under other specific names (the Marquesas; Rurutu, Tubuai Islands; Tahaa and Maupiti, Society Islands; Ha'apai, Tonga Islands; Taveuni and Kanathea, Fiji; Tutuila, Samoa; and Niutao, Ellice Islands), the collection covers most of the distribution (56 islands) and is large enough to permit an adequate future study.

The great variability and intergradation of this species, even among individuals from colonies taken under identical conditions within a few square yards, make it impossible to recognize distinct varieties or subspecies. If some forms were isolated on islands or in island groups they would rightly be considered local subspecies, but one form, representing a more or less distinct type, may be a nearly pure lot on one island and belong to a variable colony on an island several hundred miles away. In this work no attempt is made to divide the species into varieties or geographical subspecies.

There is little doubt that the wide distribution of *L. pusilla* is due to human agency. It was probably transported from island to island during the Polynesian migrations. As the *pusilla* group shows more diversity in the west, it is probable that it originated west of the Marshalls and that one species, *L. pusilla*, was carried eastward and was undoubtedly introduced on nearly every island in the Pacific. It has been found on nearly every island on which thorough collecting has been done.

The wide distribution of this species and its variability, the marked difference between immature specimens, insufficient material, and unfamiliarity with the literature have led various workers to assign a number of specific titles to *L. pusilla*, as listed below.

*Lamellidea pusilla* (Gould): type locality Metia [Makatea]. None of the specimens collected by K. P. Emory or by Lillian Wilder exactly equal Gould's description and figure. The shells (fig. 82, *a*) are slightly smaller than Gould's measurements, the whorls less convex, the outline straighter, and the depression on the last whorl weaker than those in the figure. A single dead specimen in the collection is more typical than our figured specimen, but it is slightly damaged. However, the differences between our figured specimen and that of Gould

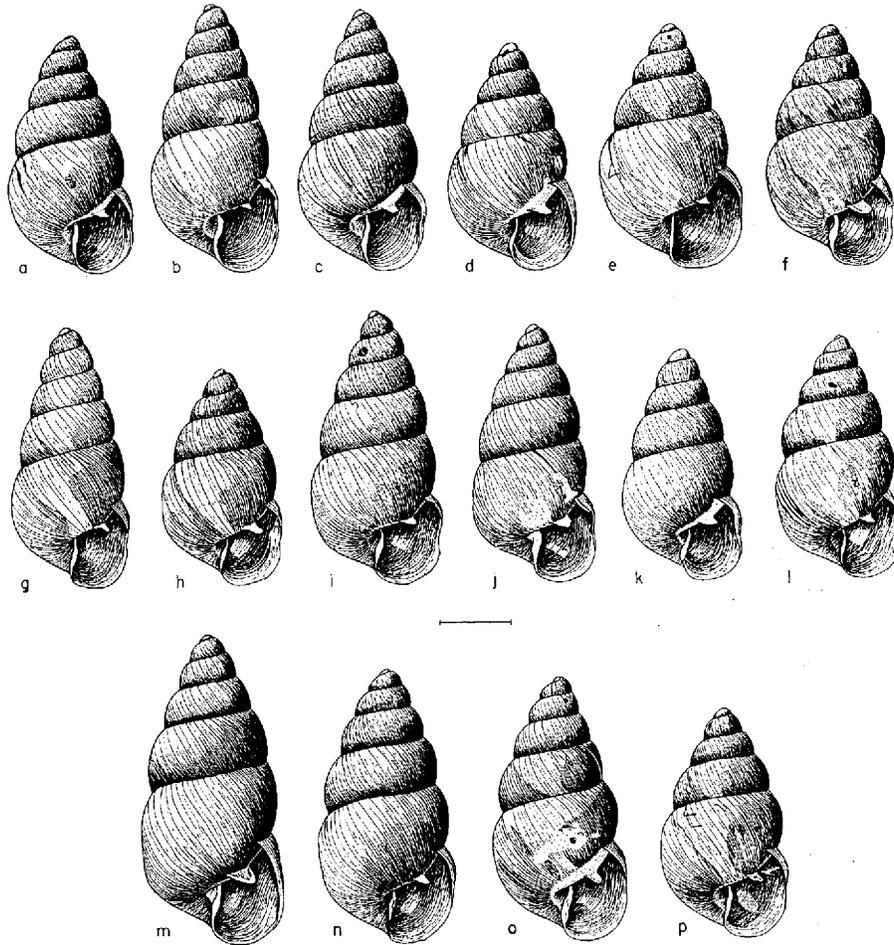


FIGURE 82.—Adult *Lamellidea* (*Lamellidea*) *pusilla* (measurements in table 4): a, Makatea, type locality, average specimen; b, Anaa, Tukahora Islet, unusual specimen; c, Hao, average specimen; d, Huahine, most common form; e, Borabora; f, Penrhyn, most abundant form; g, Penrhyn, same lot as f, unusual specimen; h, Niue, average specimen; i, Vanua Mbalavu, proportionately narrower than average; j, Navutu Iloma, large, uncommon form; k, Navutu Iloma, same lot as j, small form, abundant; l, Tau, average specimen; m, Ebon, paratype of *Tornatellina nitida* Pease, an exceptionally large specimen; n, Ebon, same lot as m, another paratype of Pease; o, Kusaie, large form, common; p, Kusaie, small form.

are less marked than those found in a single restricted colony. Gould's specimen is fairly close in outline but slightly larger than our figured specimen from Penrhyn (fig. 82, f). In a specimen taken alive (115782, Wilder, Makatea) the body whorl is chamois in color and the apical whorl is only slightly darker. This is much lighter than usual.

*Tornatellina nitida* Pease: Pease described his species from specimens collected by Garrett on Ebon in the Marshall Islands. Later, Pilsbry and Cooke (1915, p. 176) redescribed and figured an Ebon specimen from the Pease collection and considered it a pure synonym of Gould's species. Their conclusion is borne out by paratypes from the Pease collection in Bishop Museum (189779, five specimens; 189787, three specimens, from MCZ, 28921). *L. nitida* Pease is not related to Garrett's identification of the species. Figure 82, m, n is after two paratypes from the Pease collection (189787).

*Lamellidea serrata* Pease: Ebon Island. This is a juvenile stage of Pease's *L. nitida*, as our complete paratype series illustrating all stages of growth confirms. (Shell with 4 whorls, length 1.6 mm., to adults in which are shown gradual loss of the columellar fold and palatal ribs as specimens approach maturity.) Figure 83, b is drawn from one of Pease's paratypes. Under this name Garrett recognized the juvenile stages of the shells he identified as *conica* from the Marquesas, Society, Cook, and Tubuai Islands.

*Lamellina laevis* Pease: Garrett and Pilsbry and Cooke consider this synonymous with *T. serrata* Pease.

*Tornatellina conica* Mousson: Originally described from Samoan specimens. The description is based on a shell that had just reached maturity but had not completed its growth. Mousson afterwards identified the species from Fiji and called the mature stage variety *impressa* (fig. 82, i), but in his account of *T. conica* from the Ellice Islands he said that *impressa* was an "individual variation" (fig. 82, k).

*Tornatellina columellaris* Mousson: Described from Fijian specimens. This is an immature stage of *conica*,  $2.8 \times 1.6$  mm., with 5 whorls.

*Lamellaria perforata* Liardet: None of the six specimens which Cooke studied in the British Museum is perforate. These specimens are identical with those of *L. pusilla* from Vanua Mbalavu, Fiji (fig. 82, i).

*Tornatellina impressa* var. *intuscostata* Pilsbry and Cooke: This variety commonly occurs with *pusilla*. In Bishop Museum are specimens from many of the Society Islands, as well as from Penrhyn in the Line Islands and Mauke in the Cook Islands. It represents a stage that has not quite reached maturity or that has done so but has not completed its full growth. This conclusion is reached after a study of a paratype in Bishop Museum (fig. 82, d).

Shells vary in outline, from elongate through ovate-conic to broad-conic (fig. 82, b, g, h, p). This occurs in many specimens from the same colony (fig. 82, f, g, j, k, o, p). The apex ranges from acute to subacute. Specimens

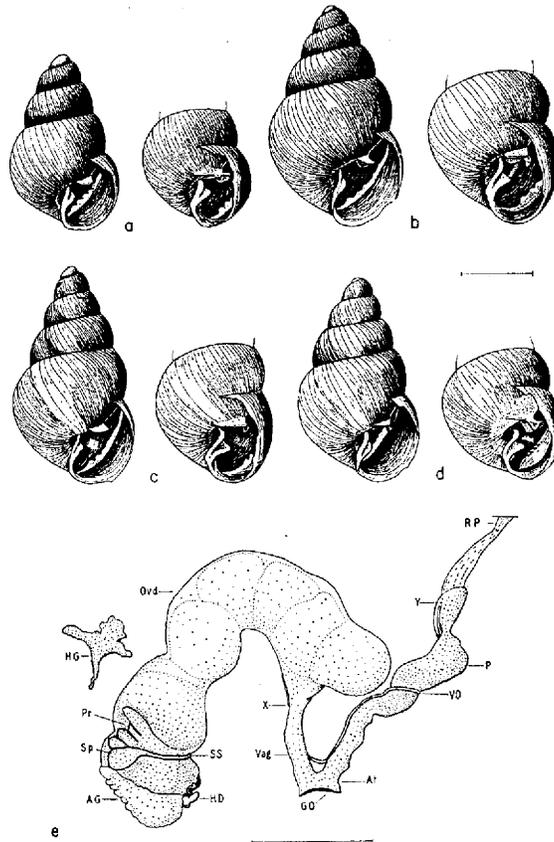


FIGURE 83.—*Lamellidea (Lamellidea) pusilla* (Gould). a-d, juvenile shells: a, *L. pusilla* (Gould), Makatea, length 2.08 mm., diameter 1.32 mm., whorl 4.25, frontal and oblique views; b, *L. serrata* (Pease), Ebon, paratype, length 3.12 mm., diameter 1.90 mm., whorls 5.1; c, *L. columellaris* (Mousson), Vanua Mbalavu, length 3.10 mm., diameter 1.71 mm., whorls 5.25; d, Hao, length 2.44 mm., diameter 1.45 mm., whorls 5. e, adult genitalia.

that have evidently reached their complete growth are 3-4.4 mm. long. They range from comparatively thin, subtransparent or translucent, to opaque. The initial embryonic whorl is microscopically granulose; the second whorl is marked with very minute, slightly wavy striae; the postembryonic whorls are somewhat irregularly, finely striate with lines of growth (151600, Huahine). The surfaces of some adult specimens from Hao are marked with very minute, closely or widely spaced spiral lines. Similar lines were observed on only two specimens from Niue. The color ranges from chamois through cinnamon buff to clay. In some specimens the color is uniform, but in most of

them the upper whorls are darker than the lower whorls. In most specimens the whorls are uniformly convex; but they are more so in some than in others, even from the same colony. In several lots the penultimate whorl is somewhat swollen (fig. 82, *l, n*), but this is not a constant character. Nearly all shells that have completed their growth after maturity have a rather broad, shallow depression on the last half of the ultimate whorl.

The aperture ranges from subquadrate to elongate-oval (fig. 82, *l, n*). Its outer margin is more or less modified by the depression. The parietal lamella is fairly strong, slightly obliquely seated, 0.09-0.26 mm. in height. In opened specimens its length is about one whorl long. The outer half is of nearly equal height, descending gradually and extending inward as a low, hardly discernible thread. The columella is slightly sigmoid to nearly straight, is somewhat heavily calloused near the middle of its length, and tapers gradually at each end. It is slightly arched outward, forming a rather blunt-angled projection. Mature shells have no distinct columellar fold, though sometimes there is a slight median depression (fig. 82, *g, n*).

*L. pusilla* may mature when the shells have acquired about 5.5 whorls. Maturity is indicated by the absence of a distinct columellar fold and palatal ribs. From this stage onward embryos in the uterus are common. In most lots we found many of the mature shells gravid. In a few lots separated as to gravid and nongravid we found few gravid specimens in which the columellar fold and the palatal ribs had not been completely absorbed. It may, therefore, be assumed that until the folds are eliminated the young cannot pass out of the aperture unhampered. A gravid specimen from Ponape (156591A), 5.25 whorls, length nearly 3 mm., has a distinct but much reduced columellar lamella and three low, unserrated palatal ribs with two embryos caught between them. Another specimen, from Huahine (151319A), nearly 5.5 whorls, length almost 3 mm., has a well-developed columellar fold and two strong, serrated palatal ribs, and the embryo is lodged behind the inner rib.

The juveniles of this species which Pease named *serrata* and *laevis* and which Mousson called *columellaris* were described from shells with 5 whorls and were 0.5 whorl short of what might have been the mature stage. Immature specimens differ slightly in form and in sharpness of apex. The parietal lamella is strong and flares outward—its free margin strongly undulate, almost lobed—and is nearly one whorl in length (Hao and Penrhyn specimens). The extreme height of the lamella is carried back farther in juvenile specimens than in the adult stage and descends much more regularly. The columella is thickened and always has two folds. The supracolumellar lamella is low, very oblique; the columellar lamella much stronger, more transversely seated, entering for about 0.5 whorl. A few specimens from several islands have an indistinct and very deep-seated swelling below the columellar lamella, but in only a few can this swelling be called a fold (fig. 83, *d*). This is, apparently, an aberrant

character. There are always one to three vertical palatal ribs, the margins of which are serrate or smooth. The smooth-margined ribs are either at an early stage of development or at a later stage where they are being absorbed. As Pilsbry and Cooke observed, the ribs (one or two) are low, their margins even just before the shells reach maturity.

TABLE 4.—COMPARATIVE MEASUREMENTS OF SHELLS OF LAMELLIDEA (LAMELLIDEA) PUSILLA

Figure 82, a-p	SHELL			APERTURE			LAST WHORL		Height Par. Lam.	No. Whorls	
	Length	Diameter	Percent	Axis	Diameter	Percent	Length	Pct. Total Length			
a	Makatea	3.38	1.74	51	1.17	0.83	71	2.00	59	0.12	6.00
	Makatea	3.52	1.77	50	1.06	0.93	87	2.30	58	0.13	6.33
b	Anaa	3.80	1.79	47	1.30	0.88	68	2.18	57	0.09	6.33
c	Hao	3.70	1.81	49	1.22	0.80	66	2.08	56	0.10	6.33
d	Huahine	3.22	1.81	57	1.24	0.86	69	2.00	62	0.13	5.66
e	Borabora	3.45	2.20	64	1.43	0.99	69	2.26	65	0.10	5.50
f	Penrhyn	3.40	1.79	53	1.19	0.91	76	2.13	62	0.21	5.66
g	Penrhyn	3.70	1.66	45	1.19	0.78	65	2.08	56	0.16	6.50
h	Niue	3.06	1.68	55	1.19	0.86	72	2.00	65	0.18	5.50
i	Vanua Mbalavu	3.87	1.87	48	1.27	0.91	71	2.13	55	0.10	6.25
j	Namuka Ilau	3.64	1.74	48	1.19	0.88	74	2.00	55	0.16	6.33
k	Namuka Ilau	3.27	1.68	51	1.12	0.83	74	1.95	60	0.10	5.66
l	Tau	3.43	1.74	51	1.19	0.83	69	2.05	60	0.13	6.00
m	Ebon	4.40	2.00	45	1.45	0.93	64	2.60	59	0.26	6.33
n	Ebon	3.87	1.95	50	1.40	0.88	63	2.23	57	0.16	6 +
o	Kusaie	3.74	1.90	51	1.30	0.91	70	2.26	60	0.18	6.00
p	Kusaie	3.25	1.81	56	1.24	0.83	66	2.08	64	0.16	5.50

**Lamellidea (Lamellidea) micropleura**, new species (fig. 84, a-f).

*Shell* very small, cylindrical, chamois color, thin, not transparent, faintly marked with growth lines. *Spire* with indistinctly convex outlines, tapering gradually to rather blunt apex. *Suture* barely impressed. *Whorls* 5; embryonic whorls increasing rapidly; post-embryonic whorls slowly and evenly, flatly convex, last whorl long, nearly 0.33 total length, cylindrical, flattened dorsally. *Aperture* nearly vertical, subovate. *Parietal lamella* well developed, simple, obliquely seated, more than 0.5 whorl long. *Columella* vertical, imperceptibly sigmoid, very slightly thickened. Outer margin of aperture slightly broken in holotype, very thin and delicate.

Length 2.07 mm., diameter 0.88 (42 percent); apertural axis 0.72, diameter  $\pm 0.44$  ( $\pm 60$  percent); last whorl 1.30 (63 percent); parietal lamella 0.11.

Juvenile with little more than 3.5 whorls, 1.25 mm. in length, with well-developed parietal lamella. *Columella* slightly calloused, with a strong, spirally entering lamella, a very oblique weak upper lamella extending to outer margin. Palatal wall furnished with a weak, basally situated vertical rib.

Many genitalia lack penis; minute. *Ovotestis* unilobate, and shallowly bi-cleft. *Duct* small, slightly swollen and convoluted. *Talon* and *carrefour* not dissected. *Albumin gland* very large; follicles numerous, large, globular. *Prostate* minute. *Oviduct* diaphanous, with

one mature embryo. *Spermatheca* small, ovate; duct short. *Vas deferens* of abnormal animals entering vagina at atrium. One normal parametaneanic specimen (condition poor) dissected, penis 0.5 oviducal length.

Dissected 150531 (three specimens without penis, adult); 150532 (one without penis, parametaneanic); 151053 (one normal, adult).

Society Islands: Moorea, Faatoai Valley, near head of southeast branch (type locality), on bark of upper branches of tree, 30 ft. from ground, alt. 700 ft., Kondo, Sept. 24; holotype 150531 (figured meta-ananeanic 8866);

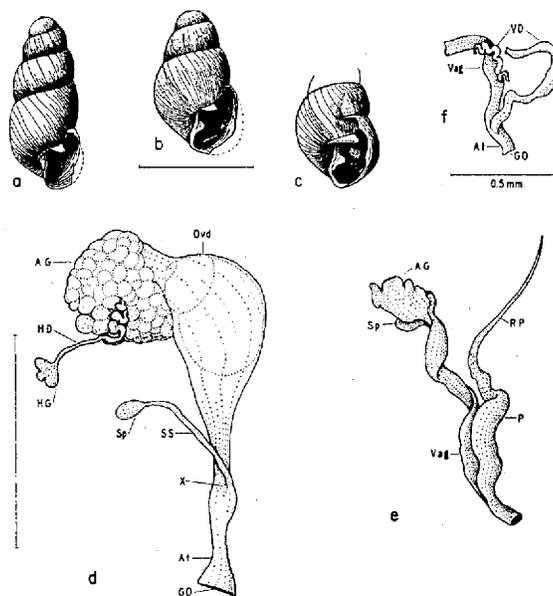


FIGURE 84.—*Lamellidea (Lamellidea) micropleura*: a, adult, holotype; b, meta-ananeanic juvenile; c, meta-ananeanic, oblique apertural view; d, adult aphallic reproductive organs; e, phallic adult genitalia, poorly preserved; f, aphallic parametaneanic, in part, penis absent.

paratypes 150532-150534 (150532 dissected). Taken also at two localities in Faatoai Valley, 200-300 ft. and on Mount Teaharoa, alt. 1,800 ft.

This species is quite rare; only a few examples were taken in the four localities. Apparently it is widely distributed on the island, to judge by the range of altitudes. All were taken under loose bark or lichens growing on trees.

*L. micropleura* somewhat resembles *L. cylindrica* Sykes from the Hawaiian Islands, but it is easily recognized by its smaller size and weaker parietal lamella. The juveniles of *L. cylindrica* have a stronger parietal lamella, the columella has three folds, and the palatal ribs are longer, stronger, and have a serrate margin.

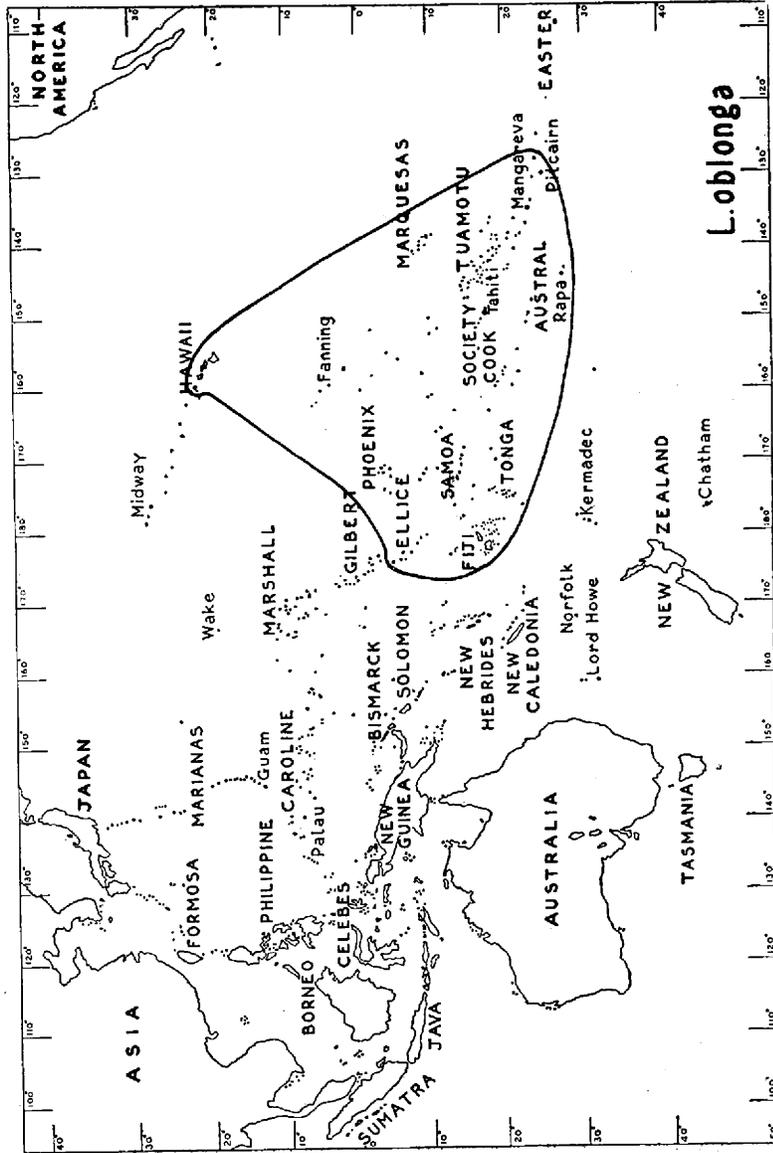


FIGURE 85.—Distribution of *Lamellidea oblonga*.

Four out of five dissected specimens were without penis. However, it is questionable whether this character, unaccompanied by differential shell characters, should be considered of generic or subgeneric importance.

The size, form, and columellar fold of the juveniles indicate that this species is intermediate between *Lamellidea* (*s.s.*) and *Elamellidea*; and it is placed provisionally in *Lamellidea sensu stricto*.

**Lamellidea (Lamellidea) oblonga** (Pease). Figures 85; 86, *a-m*; 87, *a-l*; 88, *a-l*; 89, *a-f*; 90, *a-h*; 91, *a-e*.

*Tornatellina oblonga* Pease, 1864, Zool. Soc. London, Proc., 673.

*Tornatellina (Lamellina) oblonga*, Pilsbry and Cooke, 1915, Man. Conch.

23: 160-165, pl. 36, figs. 5, 6, 8-11; pl. 41, figs. 6, 9; pl. 42, figs. 7-10.<sup>4</sup>

*Tornatellina bacillaris* Mousson, 1871, Jour. de Conchyl. III, 19 (11): 16, pl. 3, fig. 5.

*Tornatellina dentata* Pease, 1871, Zool. Soc. London, Proc., 460.

*Lamellidea oblonga* Cooke, 1934, B. P. Bishop Mus., Occ. Papers 10 (11): 9.

"Shell long, turritate, thin, the sides straight, apex rather obtuse; brownish yellow, glossy, very lightly marked with growth wrinkles. Whorls 6, convex. Aperture very small, oblique, ovate; outer lip simple. Columella lightly thickened, nearly straight and vertical, or only slightly sinuous, in front view, but in profile view it is seen to arch forward at the base. Parietal lamella small, a half-whorl long. Length 3.5, diameter 1.5 mm., aperture 1.3 mm." (Pilsbry and Cooke; Huahine, Society Islands.)

Adult genitalia (fig. 91, *a-e*). *Ovotestis* unilobate, deeply cleft; follicles few, fused to one another, ends distinguishable as mere papillae on distal surface. *Duct* small, slightly swollen, convoluted. *Talon* sigmoid, small. *Carrefour* small, shape indefinite, with small prostate gland attached to origin of vas deferens. *Albumin gland* quite large; follicles numerous, ovate. *Prostate* small follicles fairly large, distended (about nine counted). *Spermatheca* large, oval, with sperm mass; stalk large, long. *Oviduct* distended, diaphanous, with two embryos, one yolk-covered, the other free. *Vas deferens* narrow (0.5 diameter of spermathecal stalk), twisting around penis 1.5 times, entrance into penis (Y) almost apical. *Vagina* short. *Penis* longer than oviduct (penial to oviducal length, 1.45:1), club-shaped. Interior of penis with short but strong fleshy recurved pilaster (Pil 1); principal pilaster terminating in small muscular cord below; papilla (P Pap) short, pointed; remainder of penis a mixture of thin portions plus irregular hardened areas. *Retractor* short, stout, off diaphragm. Individual without penis (only one found) and with vas deferens attached to atrium; one embryo. *Atrium* short, broad or narrow.

Paraneanic genitalia (fig. 91, *d*). *Ovotestis* without deep cleft; follicles protruding farther than in adult, short-clavate. *Duct* swollen, convoluted. *Albumin gland* with numerous ovate follicles. *Prostate* follicles few, clavate. *Oviduct* empty, shrunken; uterus short; vagina very long. *Spermathecal* stalk about half length of adult, joining oviduct midway instead of at usual point farther below. *Penis* broader than in adult but comparatively shorter. *Retractor* longer, narrower.

Metaneanic genitalia (not figured) with narrowly cylindrical, apically tapering penis; no embryo.

To judge by the paucity of embryos in the oviduct (usually one or two), this species does not appear to be prolific. Therefore it is difficult to explain why the adults and juveniles are found in large numbers whenever collected. Where single, the embryo is either heavily covered by yolk mass or is free. Where double, one is free, the other covered.

<sup>4</sup> For synonymy and a more complete list of references, see Man. Conch. 23: 161-163.

Dissected 151469 (adult, paraneanic, carrefour complex, interior of penis, specimen lacking penis), eight specimens; 151470 (adult, paraneanic), two specimens; 151571 (metaneanic), four specimens.

Type in Museum of Comparative Zoölogy. (The description of the shell is based on a specimen received from Pease.)

In the following locality citations an asterisk denotes islands from which *L. oblonga* is being reported for the first time.

#### Islands east of 165th meridian

Hawaiian Islands: Hawaii, Niulii, 59703, Marie C. Neal, 1922. Maui, Wailua, 49542, Cooke, 1920. \*Molokai, Mapulehu, 47699, C. F. Mant, 1919. Oahu, Manoa, 15001, Cooke, 1906; Moanalua, 19168, I. Spalding, 1909; Kalihi, 40557, A. Gouveia, 1915; Kahana, 42899, Spalding, 1916; Hakipuu, 98967-98972, Cora McAllister, 1930; Kaneohe, 184965, Anderson, 1940. Kauai, Lihue, 36296, Cooke, 1914; Nounou Mountains, 80869-80870, Dranga and Cooke, 1925; Hanapepe, 129725, Anderson, 1933.

Marquesas Islands: Garrett. \*Hatutaa, 105145-105147, 1931; \*Eiao, 105131-105136, 1931; \*Nukuhiva 95967, 1929; \*Uahuka, 95483, 1929; \*Uapou, 98404-98406, 1929; Hivaoa, 95853, 1929; \*Mohotani, 104784, 104785, 1931 (all collected by Pacific Entomological Survey).

Tuamotu Islands: Makatea, 97709-97713, Emory, 1930. \*Fakarava, 118527, Pilsbry, Pinchot Exped., 1929. \*Toau, 118513, Pilsbry, 1929. Anaa, Garrett. \*Tenaararo, 164561, Emory, 1934. \*Tepoto, 136532-136533; \*Hao, 136600-136603; \*South Marutea, 136612-136613; \*Oeno, 150087-150091; \*Timoe, 150159-150160; and \*Henderson, 149463-149465 (collected by Mangarevan Expedition).

Mangareva Islands: \*Mangareva, 136663-136673, 140699-140701, 140738-140740, 140785-140786, 141277-141281, 141307-147312; \*Aukena, 140977-140980; \*Akamaru, 140926-140930; \*Taravai, 141105-141110; \*Agakauitai, 141761-141762; \*Kamaka, 141005-141007; \*Makaroa, 141021; \*Tauna, 140887, 141039-141040; \*Tarauroa, 140878-140880; \*Vaiatekena, 141482-141483; coral islet No. 2, 141520-141524 (all collected by Mangarevan Expedition).

\*Pitcairn, 141898-141901, Mangarevan Expedition.

Austral Islands: Rurutu, Garrett. \*Raivavae, 146300-146306, 146669-146672; \*Tubuai, 147643-147644 (dissected), 147771-147781, 148031-148042, 148361; \*Rimatara, 149103-149104, 149181. \*Maria 149316-149321 (all collected by Mangarevan Expedition).

Rapa: 140644-140645, 142583-142585, Mangarevan Expedition.

Society Islands: Garrett, 3351. Moorea, Garrett; 150648-140652, Mangarevan Expedition. Tahiti, Garrett; 145772-145776, Mangarevan Expedition. \*Meetia, 136426-136427, 136437-136440, Mangarevan Expedition. Huahine,

Garrett; 151466-151473, Mangarevan Expedition. Raiatea, Garrett; 151815-151818, 152047-152048, Mangarevan Expedition. Tahaa, Garrett; 152215-152217, Mangarevan Expedition. Borabora, Garrett. Maupiti, Garrett.

Line Islands: Palmyra, 52301-52302, Cooke, 1913. \*Washington, 77790, Dranga, 1924. \*Flint, 152597-152600, Mangarevan Expedition.

Cook Islands: Rarotonga, Garrett; 95415-95417, Buck, 1929. Atiu, Garrett; 95020-95022, Buck, 1929. Aitutaki, Garrett; 95653-95654, Buck, 1929. \*Mauke, 95276, 95624, Buck, 1929. Mangaia, Garrett; 97457, Buck, 1929.

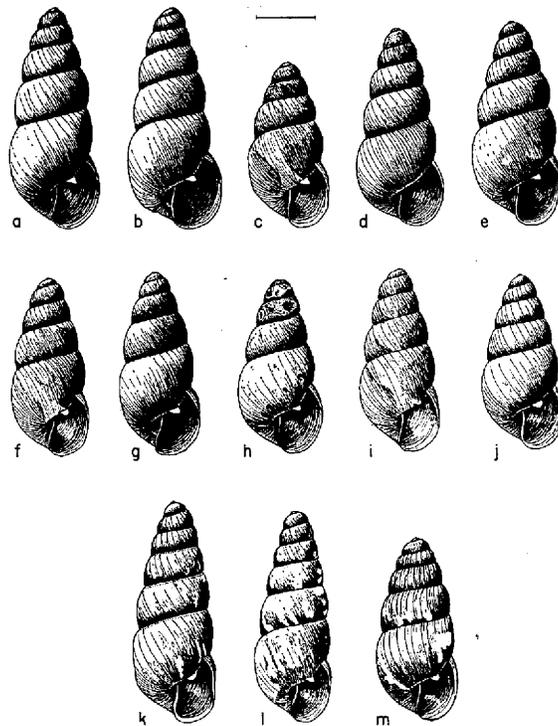


FIGURE 86.—*Lamellidca (Lamellidca) oblonga*: a, Oahu, average form; b, Oahu, slightly broader form with more ample aperture; c, Kalihi, Oahu, average form of dwarf race; d, Moanalua, Oahu, unique specimen with much reduced parietal lamella; e, Hakipuu, Oahu, largest specimen of a somewhat small, very light-colored (chamois) race; f, Kaneohe, Oahu, largest specimen of small, subtransparent race; g, Hanapepe Valley, Kauai, smaller than average adults, close to figures a and b; h, Lihue, Kilo-hana, and Kukaua Valley, Kauai, short, conical form, merging into typical Hawaiian form represented by a and b; i, Uahuka, average specimen; j, Makatea, slightly shorter than average adults, merging gradually into more typical form approximating 88, g, Huahine; k, Tekotika Islet, Hao, average adult; l, Tekotika Islet, narrow form; m, Tekotika Islet.

## Islands west of the 165th meridian

Tonga: \*Tongatabu, 87811, Hoffmeister and Ladd, 1928, a single juvenile specimen.

Fiji: Garrett says of *L. oblonga* (1879, p. 21), "perhaps extends further west to the Fiji group"; later (1887, p. 187) he includes the species in the Fijian fauna. The Museum's extensive collection from Fijian islands contains no specimen of *L. oblonga*. If Garrett's identification is correct, it should be in the Lau Islands.

Horne Islands: Futuna, Graeffe. [Mousson places this island in the Tonga group (1871, p. 6); Garrett, in Samoa (1879, p. 21).]

Samoa: Garrett. Tutuila (1874, Schmeltz, p. 89 for *T. bacillaris*). \*Tau, 83054, Cooke, 1926; 173469, Harris, 1937. \*Olosega, 174573-174575, 174676, Anna and Wray Harris, 1937.

Pukapuka (Danger) Islands: \*Nassau, 77229, Bryan, Whitney Exped., 1924.

Ellice Islands: Funafuti, Hedley. \*Vaitupu, 189686, Verrier, 1941.

The above list represents proportionately few of the hundreds of lots in the Bishop Museum collection. We have selected for appraisal at least one lot from each island represented in our collection. When more than one lot is quoted, each of the lots may contain variants.

Of the 65 islands on which *L. oblonga* has been found, 43 are mentioned here for the first time (designated by an asterisk). Bishop Museum has specimens from 58 of the islands from which the species has been reported and these islands are designated by Museum catalog numbers.

Fifty-seven of the 65 islands on which *L. oblonga* is known to occur lie to the east of the 165th meridian (map, fig. 85). Undoubtedly it is on most of the Polynesian Islands within this area, as more intensive collecting should prove. On only a few of the fairly well investigated islands have no specimens been found. Among these islands are Necker, Nihoa, Niihau, Lanai, and Kahoolawe in the Hawaiian Islands and Fanning, Christmas, Penrhyn, and Rakahanga, in the Line Islands. Since *L. oblonga* has been collected on 11 of the 16 Tuamotu Islands, it is reasonable to assume that it should be on almost all the atolls of the group. It is already known from nearly all of the high islands in the Marquesas, Society, Mangareva, Austral, and Cook Islands in the south-central Pacific. *L. oblonga* has been found on only eight islands west of the 165th meridian.

Shells have been collected on 84 of the islands shown on the map of *L. oblonga*'s range of distribution (fig. 85). The Fijian islands are included on the authority of Garrett, though none of the 52 Fijian islands from which the Museum has shells affords examples of this species, despite the fact that the Museum has very large and supposedly representative collections of other species from some of these islands. *L. pusilla* is represented in the collections

from 12 of the islands, and *L. pusilla* is commonly associated with *L. oblonga* on islands east of the 165th meridian. Its absence, therefore, is not due to unsuitable ecological conditions.

None of the lots from islands west of the 165th meridian contains more than a few specimens, and these fail to show the great variability characteristic of lots found toward the east.

This species is more or less confined to the lowlands. Garrett states that it occurs up to 2,000 feet, but few of the Museum lots are from the 1,000-foot contour. The species is most abundant from just back of the beaches to altitudes

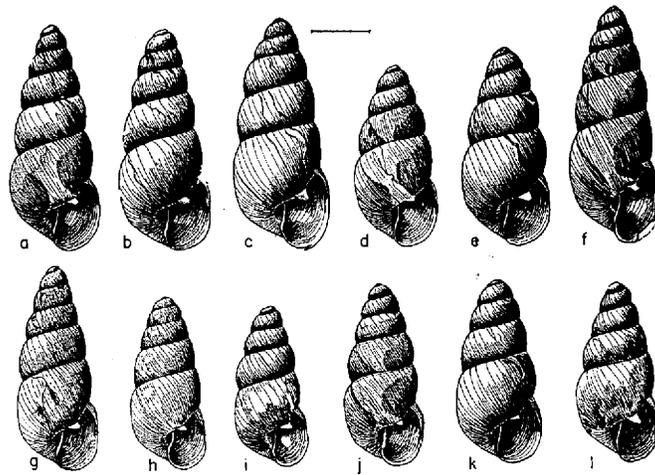


FIGURE 87.—*Lamellidea (Lamellidea) oblonga*: a, Gatawake, Mangareva, form with tapering spire and pointed apex; b, Rikitea, Mangareva, typical Mangarevan form; c, Gatawake, Mangareva, form with swollen upper whorls; d, Gatawake, Mangareva, small, broad form of *b*; e, Gatawake, Mangareva, form with larger embryonic whorls, more convex spire, and stronger parietal lamella than *d*; f, Makaroa Islet, Mangareva, form with slightly convex spire and somewhat flattened whorls; g, Rapa Iti, Rapa, small cylindrical form; h, Karapo Rahi, small cylindrical form; i, Tuitui Islet, Rai-vavae, average form of a small race; j, Tapapataui Islet, Tubuai, average form; k, near Matura, Tubuai; l, near Matura, Tubuai.

of a few hundred feet. It is very abundant on and under dead leaves of coconut, pandanus, breadfruit, and other plants lying on the ground. It is often taken on stones but rarely found near the bases of tree trunks and even less often on the leaves of growing shrubs and ferns. As far as can be ascertained from Museum specimens, few, if any, of them were taken in endemic native forests.

*L. oblonga* is usually found under moist conditions, near or at no great distance from occupied or deserted human habitations; and many of the lots in the Museum collection were taken from the leaves of economic plants. Under

especially favorable conditions, colonies of thousands occur. More than 100 were taken from the under surface of a single dead breadfruit leaf on the island of Kauai, and hundreds of immature specimens were found there. The species seems to be equally at home on high islands and low coral atolls.

The islands on which *L. oblonga* is known are in the north-central and south-central Pacific. They are enclosed in a nearly equilateral triangle, extending from Henderson Island ( $128^{\circ} 19' W.$ ) on the east to Vaitupu ( $178^{\circ} 41' E.$ ) on the west—a distance of a little more than 3,100 nautical miles—and from Kauai ( $22^{\circ} 13' N.$ ) to Rapa ( $27^{\circ} 36' S.$ ) in a north-south direction, or

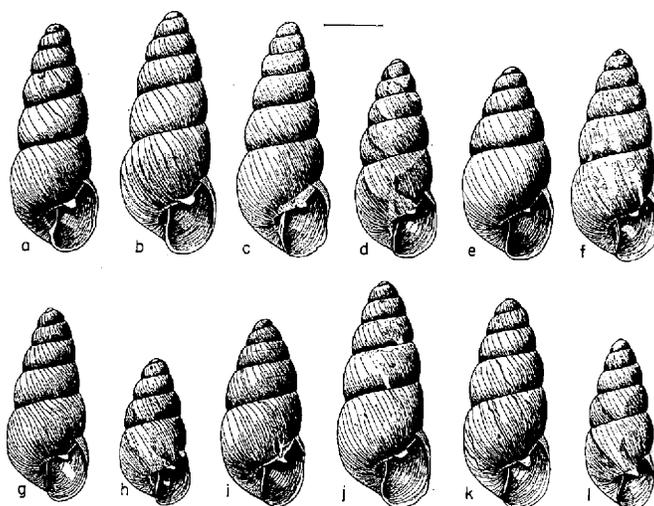


FIGURE 88.—*Lamellidea (Lamellidea) oblonga*: a, near Moerai, Rurutu; Rurutu forms approximate those from Mangareva, figure 87, a, b. b, Society Islands [Garrett]; the largest specimen in collection 4.26 mm. long. c, Paaroa, near Maraa Point, Tahiti. d, Paaroa, near Maraa Point, small adult. e, Paaroa, near Maraa Point. f, Vaiorea Islet, Huahine. g, Vaiorea Islet. h, Horea Islet, Raiatea. i, Toahiva Valley, Raiatea; a rare form occurring as a pure race, approximating the Tahitian specimen (e). j, Home Islet, Palmyra; a common form. k, Home Islet. l, Mauke.

slightly less than 3,000 nautical miles. There is little doubt that the wide distribution of this species is due, mainly to the frequent voyages of the Polynesians, who transported food plants on their travels, especially between islands only a few hundred miles apart. The fact that the species occurs much less frequently west of the 165th meridian may be due to the fact that migrations between the Cook and Society Islands and to the islands of Samoa and Tonga were infrequent.

The distribution of *L. oblonga* is quite different from that of *L. pusilla*, which originated in the western Pacific and was carried eastward to the

eastern islands by the native voyagers. *L. oblonga*, originating in eastern Polynesia, was taken westward only occasionally.

*L. oblonga* undoubtedly originated on one of the groups of high islands south of the equator, which one we cannot determine at present. The species is equally abundant on all of the groups and shows about the same amount of diversity in each. Its nearest relative is *L. peponum* (Gould) from Hawaii and Maui, Hawaiian Islands, where there seems to be no evidence that *L. oblonga* shows more endemism than it does in the Society, Cook, or Austral Islands.

*L. oblonga* is evidently a newcomer to the Hawaiian Islands, as no specimen has been found in any of the Pleistocene or early post-Pleistocene fossil beds. Though the Museum has six lots classified as fossils, these are either dead surface or subsurface shells recently covered over. None of the beds that were evidently formed prior to the coming of the Hawaiians contains *L. oblonga*. Further evidence that this species was probably introduced in comparatively recent time is that *L. oblonga* is unrepresented in more than 450 lots of *Lamellidea* from the Waianae Mountains, Oahu. But undoubtedly, the species will be found in some of the valleys when suitable investigations are made. Specimens have been taken from within 5 miles of the southern end of the Koolau Range, Oahu, to nearly the northernmost end. It is abundant both on the windward and leeward sides of the range.

*L. oblonga*, as recognized in this paper, shows great variation. At the beginning of this study, some of the rather diverse forms were thought to be representatives of distinct subspecies or at least varieties, but further study indicated that it was more logical to lump them all into one species and figure some of the most diverse forms. Very few of the more distinct forms were taken in pure colonies; and practically all of these, according to our collecting notes, are associated with more or less typical specimens.

In numerous lots of a hundred to several hundred examples the amount of variation is quite marked, though in a few lots the specimens are more or less uniform, consisting of examples approaching the typical form. Usually in lots of 10 specimens or fewer there is more uniformity. This may be due to wide-area collecting for the larger lots of two or more adjacent colonies. Smaller lots probably came from areas restricted to a few square feet. Unfortunately, most of our collecting notes fail to state the area covered by each colony.

This species in many of our lots is more or less dimorphic, sometimes polymorphic. The most notable differences are in the size of the embryonic whorls, in the convexity of the upper portion of the spire, and in the strength of the parietal lamella. In a number of lots there are intergrades between the different forms, and in a very few lots there are apparently no intergrades. Examples from single colonies illustrate the range of variability on the following islands: Oahu; Hao, Tuamotus; Mangareva, Mangareva Islands; Tubuai, Australs;

Tahiti and Huahine, Society Islands; Palmyra, Line Islands (figs. 85-90). Similar ranges of variability in a single colony might be given for specimens from nearly every island on which fair series have been taken.

A short, broad form with either narrow or wide embryonic whorls has been noted from Oahu, Mangareva, Tubuai, Tahiti, and Raiatea (figs. 86, *c*; 87, *d, e, k, l*; 88, *e, i*).

One of the specimens figured by Pilsbry and Cooke (1915, pl. 36, figs. 9, 10) should be considered the type of *L. oblonga* because it was probably selected from the original lot sent by Garrett to Pease (Academy of Natural Sciences,

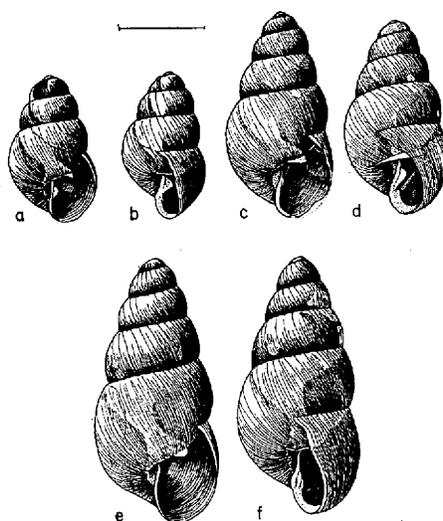


FIGURE 89.—*Lamellidea (Lamellidea) oblonga*, Vaioarea Islet, Huahine, same colony as figure 88, *f, g*; juvenile apertural characters illustrated at three stages of growth: *a, b*, whorls, slightly over 4, length 1.76 mm.; *c, d*, whorls 5, length 2.46 mm.; *e, f*, whorls 5.5, length 3.17 mm.

Philadelphia, 59888). It is not exactly matched by any of the Museum specimens from Huahine. Figure 88, *f* represents an average specimen but has slightly more convex outlines than Pilsbry's figure and has a weaker parietal lamella. Figure 88, *g* agrees fairly closely with Pilsbry's figure in size and number of whorls, but the spire is not as finely tapered.

Specimens approximating the typical form illustrated in the Manual of Conchology are found throughout the range of the species. Some of these are figured to illustrate minor variations for Oahu, Hao, Mangareva, Rurutu, Tahiti, "Society Islands," and Palmyra (figs. 86, *a-k*; 87, *a, b*; 88, *a-c, j*).

*L. oblonga* appears to be rare west of the 165th meridian. The Museum has specimens from only five islands: from Olosega and Tau in Samoa, from

the island of Tonga, from Nassau in Pukapuka (Danger Islands), and from Vaitupu in the Ellice Islands. Graeffe collected the species on Futuna in the Horne Islands and on Tutuila in Samoa, and Hedley reports the species from Funafuti, Ellice Islands. However, *L. oblonga* seems to be much fewer in number and less frequently collected than *L. pusilla* on most of these islands. All the lots from these islands are remarkably uniform in appearance and show little variation. They are rather small, ranging from 3.00 mm. to 3.75 mm., most being about 3 mm. (average of 18, 3.18 mm.).

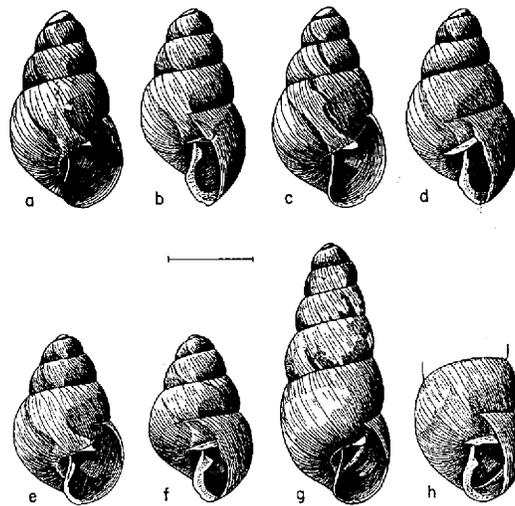


FIGURE 90.—Juveniles of four of the forms of *L. oblonga*: a, b, Palmyra; juvenile of form shown in figure 88, j; whorls 4.25, length 2.35 mm. c, d, Mangareva; juvenile of form shown in figure 87, d, e; whorls 4.25, length 2.40 mm. e, f, Toahiva, Raiatea; juvenile of form shown in figure 88, i; whorls slightly over 4, length 2.04 mm. g, h, Hao, juvenile of form shown in figure 86, k; whorl 6, length 3.13 mm.

In outline the shell may be turrete to ovate (figs. 86, l; 88, e). The diameter is 37 to 51 percent of the total length. The outlines of the spire are nearly straight to somewhat convex. The width of the embryonic whorls is variable even in a single colony (fig. 87, k, l). The embryonic whorls increase rapidly, the later whorls slowly and regularly. The last whorl is ample and is about 50 to nearly 65 percent of the total length. The whorls are flatly convex to slightly convex. Adult specimens (those which have passed through the juvenile stages, as indicated by the complete absence of columellar lamellae) may have 5.25 to nearly 7 whorls (fig. 88, h, c).

The shells are thin, in most specimens translucent; but some are subtransparent, the outlines of the columella and internal whorling being more or less

visible through the shell (figs. 86, *c, i* and 87, *a*, for instance). The surface is glossy and faintly but quite regularly marked with fine lines of growth. The embryonic whorls in very young specimens are glossy with microscopically very fine lines of growth (151472, Huahine). No trace of spiral sculpture is visible under a high power lens.

The color of most of the figured specimens ranges from clay to honey yellow. Fewer specimens are lighter shades of cinnamon buff to chamois. Quite a number of the shells are marked with hydrophanous blotches (figs. 86, *f, l*; 87, *a, i, l*). In figures 87, *g* and 88, *i* this takes the form of spiral lines, which are not associated with the surface sculpture. This hydrophanous condition is undoubtedly due to preservation in too weak alcohol.

The aperture is relatively small in most forms, more or less vertical, its outer margin regularly curved to slightly flattened. Adult specimens, except for the parietal lamella, lack all apertural armature.

The parietal lamella may be very low (fig. 86, *d*), weak (figs. 87, *d*; 88, *e, i*) to faintly strong (fig. 87, *c, l*). In these partly opened specimens (15001) the parietal lamella is from just under to just over a whorl in length. The outer third is quite high and slightly thickened; it then descends gradually in height and continues into the shell as a very low spiral thread.

The columella is vertical, slightly sigmoid, or nearly straight. In most specimens it is only slightly thickened, rarely terminating outwardly in a narrow lobe (Pilsbry and Cooke, 1915, p. 151, *T. ogasawarana*).

The length of adult specimens is 2.5-4.3 mm. The smaller examples may not have reached their full growth, but they are very much smaller than specimens from many of the colonies showing juvenile characters (fig. 90, *g*; 3.13 mm.).

Embryonic specimens (136630, Mangareva) are globose, transparent, glossy, the initial 1.5 whorls with very fine raised lines, the parietal lamella well developed, about half a whorl in length; the columella is thickened, indistinctly bidentate (Pilsbry and Cooke, 1915, pl. 42, fig. 7).

The apertural teeth are built up to a certain point in the early stages, then are resorbed in the later neanic stages. At about 4 whorls (fig. 89, *a, b*) the parietal lamella is well developed, its margin slightly sinuous; the columellar lamella is strong and platelike, having a threadlike subcolumellar fold; and the palatal ribs are absent. At about 5 whorls (fig. 89, *c, d*) the parietal lamella is still strongly developed, but the columellar lamella begins to weaken and weak transverse palatal ribs are deposited. At about 5.5 whorls (fig. 89, *e, f*) all apertural teeth have become greatly reduced; the parietal lamella has become weaker, the columella thickening and often showing mere traces of the columellar lamellae; and, usually, the palatal folds have disappeared completely.

Juveniles from various geographic localities show perceptible differences in their apertural armature from place to place, as shown by examples of forms

within the same age groups from Palmyra, Mangareva, and Raiatea. Juveniles from Palmyra (fig. 90, *a, b*), whorls 4.25, are larger than those of the same age from Huahine (fig. 89, *a, b*). Furthermore, the margin of the parietal lamella is not sinuous, the columellar lamella is weak, and the palatal rib (not figured) is merely indicated by a faint line. Juveniles from Mangareva (fig. 90, *c, d*), whorls 4.25, are broader and more conical than those from Huahine;

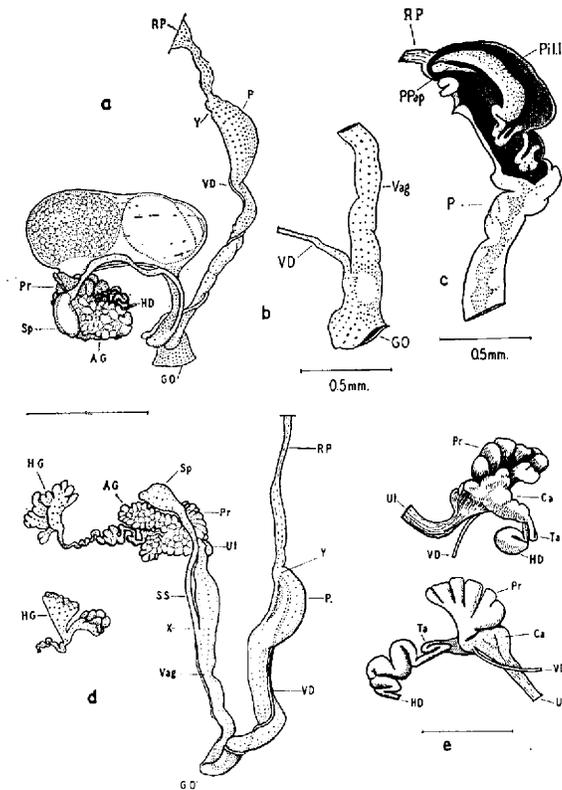


FIGURE 91.—*Lamellidea (Lamellidea) oblonga*: a, adult genitalia; b, aphyllid individual; c, interior of penis, distal part only; d, paraneanic genitalia; e, carrefour complex, reverse above, obverse below.

the margin of the parietal lamella is not sinuous; the columellar lamella is weak; and the parietal folds, if present, are merely indicated. Juveniles from Raiatea (fig. 90, *e, f*), whorls slightly over 4, are much wider than those from Huahine; the parietal lamella is only slightly sinuous; the columellar lamella is well developed and extends to the outer margin; and the palatal folds are absent. In some specimens from an older age group, exemplified by a subadult

from Hao (fig. 90, *g, h*), whorls 6, the palatal rib is retained to a late juvenile stage, an uncommon characteristic in this species.

In almost all of the species of *Lamellidea* the presence of palatal ribs is a constant character of juvenile specimens. However, in a number of the neanic specimens of *L. oblonga* this rib is entirely lacking. In many other specimens the ribs are not visible when viewed through the aperture but, when examined through the shell, appear as fine white lines. From 57 lots, juvenile specimens of the appropriate age and covering nearly the whole distribution of the species were examined. In 29 of these lots, or 184 specimens, all the juveniles had one or two palatal ribs. In three lots—one each from Oahu, Uahuka, and Rimatara—totaling only 10 specimens, no palatal ribs could be seen. But, because of the few specimens in these lots, too much importance cannot be placed upon them. The juvenile specimens of all the larger lots were chosen at random, selected on the basis of age and well-cleaned specimens. Only a few of the thousands of young specimens in the collection were critically examined, with the following results (table 5).

TABLE 5

ISLAND GROUPS	NO. OF LOTS	WITH PALATAL RIB	WITHOUT PALATAL RIB	TOTAL	PERCENT
Hawaiian Islands .....	11	181	44	225	80
Marquesas .....	7	36	5	41	88
Palmyra, Flint, Tuamotus, Mangareva, Pitcairn.....	13	86	22	108	80
Tubuai .....	7	71	17	88	81
Cook .....	3	4	33	37	11
Society Islands .....	5	35	56	91	38
Islands west of 165th meridian.....	11	30	0	30	100
	57	443	177	620	71

From table 5 it is evident that the loss of the palatal rib in juvenile specimens, an evolutionary character in the retrogression of the species to a more simplified form, has progressed more in the Cook and Society Islands than in any of the other islands of the Pacific. In fact, the species may have originated on one of these islands. Conversely, the continued presence of the palatal rib in all the specimens from islands west of the 165th meridian seems to indicate that the species has been somewhat recently introduced into these islands. This agrees with the lack of variation in the adults. However, the comparatively small amount of material in the Museum's collection from the Cook Islands and the western Pacific does not allow for a conclusive theory. The Museum has ample material from a few of the islands for a detailed study, but from most of the islands juvenile specimens are too few for a definite conclusion.

TABLE 6.—COMPARATIVE MEASUREMENTS OF SHELLS OF LAMELLIDEA  
(LAMELLIDEA) OBLONGA

Figure 86, a-m	SHELL			APERTURE			LAST WHORL		Height Par. Lam.	No. Whorls
	Length	Diameter	Percent	Axis	Diameter	Percent	Length	Pct. Total Length		
a Oahu, Manoa	3.87	1.58	41	1.19	0.74	62	2.13	55	0.13	6.25
b Oahu, Manoa	3.87	1.65	43	1.26	0.87	69	2.40	52	0.13	6.50
c Oahu, Kalihi	2.80	1.42	51	1.10	0.71	65	1.87	67	0.10	5.00+
d Oahu, Moanalua	3.45	1.52	44	1.13	0.74	65	1.87	54	0.03	6.00
e Oahu, Hakipuu	3.42	1.55	45	1.19	0.74	62	2.06	60	0.11	6.00
f Oahu, Kaneohe	3.13	1.36	43	1.07	0.65	60	1.87	60	0.10	5.75
g Kauai, Hanapepe	3.20	1.42	46	1.00	0.68	68	1.94	60	0.10	5.75
h Kauai, Lihue	3.04	1.43	48	1.16	0.74	64	1.94	64	0.10	5.75±
i Uahuka	3.20	1.39	43	1.10	0.68	62	1.94	59	0.06	5.50
j Makatea	3.07	1.42	46	1.10	0.68	62	1.87	59	0.10	5.75
k Hao	3.88	1.45	37	1.16	0.65	56	1.97	51	0.10	6.75
l Hao	3.70	1.36	37	1.07	0.61	57	1.80	49	0.10	6.75
m Hao	3.23	1.45	45	1.10	0.65	61	1.87	58	0.10	5.75

The amount of variation of the adults and juveniles of this species on several of the islands included in its known distribution furnish evidence that *L. oblonga* offers an important problem in the study of evolution. Such a comparative study must be based on a large collection, however.

TABLE 7.—COMPARATIVE MEASUREMENTS OF SHELLS OF LAMELLIDEA  
(LAMELLIDEA) OBLONGA

Figure 87, a-l	SHELL			APERTURE			LAST WHORL		Height Par. Lam.	No. Whorls
	Length	Diameter	Percent	Axis	Diameter	Percent	Length	Pct. Total Length		
a Mangareva	3.97	1.58	40	1.23	0.74	60	2.06	52	0.10	6.50+
b Mangareva	3.88	1.61	41	1.29	0.74	57	2.13	55	0.13	6.50
c Mangareva	4.07	1.68	41	1.33	0.81	61	2.23	55	0.19	6.25
d Mangareva	3.20	1.48	46	1.23	0.71	58	1.97	61	0.06	5.50
e Mangareva	3.45	1.55	44	1.19	0.77	65	2.06	59	0.16	5.50+
f Makarua	4.15	1.61	38	1.42	0.74	52	2.31	56	0.13	6.50
g Rapa	3.58	1.40	39	1.13	0.67	60	1.93	54	0.11	6.50
h Rapa	3.03	1.29	42	1.00	0.64	64	1.77	58	0.10	5.75
i Raivavae	2.84	1.29	45	0.97	0.61	63	1.68	59	0.10	5.50
j Tubuai	3.20	1.39	43	1.03	0.68	66	1.77	55	0.06	6.00
k Tubuai	3.20	1.52	47	1.16	0.74	64	1.94	60	0.06	5.50
l Tubuai	3.16	1.48	47	1.10	0.77	70	1.90	60	0.19	5.75

TABLE 8.—COMPARATIVE MEASUREMENTS OF SHELLS OF LAMELLIDEA  
(LAMELLIDEA) OBLONGA

Figure 88, a-l	SHELL			APERTURE			LAST WHORL		Height Par. Lam.	No. Whorls
	Length	Diameter	Percent	Axis	Diameter	Percent	Length	Pct. Total Length		
a Rurutu	4.00	1.55	38	1.26	0.74	59	2.06	51	0.16	6.75
b Society Islands	4.26	1.68	39	1.33	0.81	61	2.29	54	0.13	6.50
c Tahiti	4.15	1.65	40	1.29	0.81	62	2.13	51	0.10	7.00
d Tahiti	3.49	1.42	41	1.19	0.71	60	1.94	56	0.06	6.25
e Tahiti	3.40	1.61	47	1.26	0.71	56	2.10	62	0.06	5.50
f Huahine	3.71	1.55	42	1.19	0.91	59	2.03	55	0.10	6.50
g Huahine	3.40	1.45	43	1.10	0.71	64	1.90	56	0.10	6.00+
h Raiatea	2.58	1.26	49	0.93	0.58	62	1.55	60	0.10	5.25
i Raiatea	3.30	1.48	45	1.22	0.74	61	2.00	60	0.13	5.50
j Palmyra	3.97	1.65	41	1.33	0.81	61	2.23	56	0.10	6.25
k Palmyra	3.71	1.55	42	1.26	0.74	59	2.16	58	0.16	6.00
l Mauke	3.00	1.22	41	0.97	0.58	60	1.70	57	0.13	6.00

**Lamellidea (Lamellidea) cylindrica** (Sykes).

*Tornatellina cylindrica* Sykes, 1900, Fauna Hawaiiensis 2 (4): 381, pl. 11, fig. 28.—Ancey, 1903, Jour. de Conchyl. 51: 301, pl. 12, figs. 11, 12.

*Tornatellina (Lamellina) cylindrica*, Pilsbry and Cooke, 1915, Man. Conch. 23: 153, pl. 43, figs. 1-3; pl. 40, figs. 1, 2.

Cotypes in Academy of Natural Sciences, Philadelphia, and Bishop Museum (13426).

Typical specimens of this species have been taken only in the Waianae Mountains on Oahu.

**Lamellidea (Lamellidea) cylindrica** var. **kilohanana** (Pilsbry and Cooke).

*Lamellidea cylindrica kilohanana* Pilsbry and Cooke, 1915, Man. Conch. 23: 154, pl. 40, figs. 3, 6.

“Types 108587 ANSP, cotypes No. 33587 BPB Mus.” (Pilsbry and Cooke); Molokai, Kilohana, near leper settlement.

**Lamellidea (Lamellidea) polygnapta** (Pilsbry and Cooke).

*Tornatellina (Lamellina) polygnapta* Pilsbry and Cooke, 1915, Man. Conch. 23: 155, pl. 41, figs. 1-5, 7, 8.

Type in Academy of Natural Sciences, Philadelphia; Maui, Makawao and Kaupakalua.

Since the publication of the Manual of Conchology, the typical form has been taken from several localities on east and west Maui.

**Lamellidea (Lamellidea) polygnapta** var. **kamaloensis** (Pilsbry and Cooke).

*Tornatellina (Lamellina) polygnapta* var. *kamaloensis* Pilsbry and Cooke, 1915, Man. Conch. 23: 156, pl. 40, figs. 4, 5.

Type in Academy of Natural Sciences, Philadelphia; Molokai, Kamalo.

**Lamellidea (Lamellidea) peponum** (Gould).

*Pupa peponum* Gould, 1847, Boston Soc. Nat. Hist., Proc. 2: 197; 1852,

U. S. Expl. Exped. 12: 93, pl. 7, figs. 104, 104 d; 1862, Otia Conch., 34.

*Tornatellina? peponum* Pfeiffer, 1853, Mon. Hel. Viv. 3: 527.

*Achatina (Leptinaria) peponum* Pfeiffer, 1856, Malak. Blätt. 2: 170.

*Tornatellina peponum* Pfeiffer, 1859, Mon. Hel. Viv. 4: 651.

*Leptinaria peponum* Frauenfeld, 1869, Zool.-bot. Ges. Wien, Verh. 19: 874.

*Cionella (Tornatellina) peponum* Paetel, 1873, Catalogue, 107.

*Tornatellina peponum* Paetel, 1889, Catalogue 2: 291.

*Tornatellina peponum* Sykes, 1900, Fauna Hawaiiensis 2 (4): 382. (Sykes selected Gould's figures 104 and 104 d to represent the species.)

*Tornatellina (Lamellina) peponum* Pilsbry and Cooke, 1915, Man. Conch. 23: 156, pl. 35, figs. 1, 2, 5, 6; pl. 42, figs. 4-6.

Not *Tornatellina peponum* Ancey, 1889, Soc. Malac. France, Bull. 6: 240; 1903, Jour. de Conchyl. 51: 301, 302.

Type in U. S. National Museum (5506); Hawaii, Hilo (type locality?).

Distribution: Hawaii (Olaa, Okala, Kohala), Oahu.

Ancey's specimens from Kauai, Oahu, Maui, and Hawaii belong to the genus *Tornatellides* and are closely related to his *Tornatellides procerulus*. They do not represent Sykes' *Tornatellides confusus* which Sykes selected for Gould's figures 104 a-c.

**Lamellidea (Lamellidea) lanceolata** (Pilsbry and Cooke).

*Tornatellina (Lamellina) lanceolata* Pilsbry and Cooke, 1915, Man. Conch. 23: 158, pl. 43, figs. 4-6.

Type in Bishop Museum (13442); paratypes in Academy of Natural Sciences, Philadelphia, and Bishop Museum (13622).

Since this species was proposed it has been found to inhabit nearly the whole length of the Koolau Range and a large part of the Waianae Mountains, Oahu. Only a few are found in any one locality.

**Lamellidea (Lamellidea) gracilis** (Pease).

*Tornatellina gracilis* Pease, 1871, Zool. Soc. London, Proc., 460.—Sykes, 1900, Fauna Hawaiiensis 2 (4): 381.

*Tornatellina (Lamellina) gracilis*, Pilsbry and Cooke, 1915, Man. Conch. 23: 159, pl. 42, fig. 11; pl. 43, figs. 7-9.

*Tornatellina extincta* Ancey, 1890, Soc. Malac. France, Bull. 7: 341.—Ancey, 1904, Jour. Malac. 11: 70.—Henshaw, 1904, Jour. Malac. 11: 64.

Type whereabouts unknown; paratypes in Bishop Museum (59028).

Since *L. gracilis* was treated in the Manual of Conchology it has been found on the following eight islands: Wake, Ocean, Lisianski, Nihoa, Niihau, Molokai, Lanai, and Kahoolawe; but the Tanager Expedition did not take *L. gracilis* on Necker, Pearl and Hermes, Midway, or Johnston, although a very few species of other tornatellinids were found in abundance.

Laysan 1915  
Longation

To find *L. gracilis* on Wake Island is surprising. Its presence cannot be attributed to man's agency, as there is no evidence that this island was ever inhabited by Polynesians. The nearest islands on which the species occurs is the small, low island of Lisianski, slightly more than 1,000 miles to the northeast.

This species is now known to inhabit all of the main Hawaiian islands. It is extremely abundant in the Pleistocene and more recent fossil deposits at low altitudes. In many such deposits individual specimens range from the typical form to a much more slender form with much flatter whorls and a fine, tapering upper spire.

From the abundance of the specimens in lowland deposits and the known fact that it occurs on low coral islands, it may be inferred that the species is primarily a lowland form. No specimens represented in the Museum collection were taken alive above 1,000 feet.

#### **Lamellidea (Lamellidea) gayi** (Pilsbry and Cooke).

*Tornatellina (Tornatellinops) gayi* Pilsbry and Cooke, 1915, Man. Conch. 23: 172, pl. 42, fig. 3.

Type in Bishop Museum (13444); paratypes in Bishop Museum (13476) and perhaps in Academy of Natural Sciences, Philadelphia; Kauai, Makaweli.

On reexamination of the original material, we have placed this species in *Lamellidea* rather than in *Tornatellinops*, where it was tentatively placed in the Manual of Conchology. Lacking juvenile specimens, our decision is based solely on adult characters. *L. gayi* looks like a diminutive *L. oblonga*. Its nearest relative is undoubtedly *L. cylindrica*.

#### Subgenus **Elamellidea**

Shells slightly smaller than most species of *Lamellidea* with proportionately much stronger, more obliquely seated parietal lamella, which is not much more than half a whorl in length.

In juveniles free margin of parietal lamella not undulate, columella thickened, almost platelike, as in some species of *Elasmias*, and furnished with a strong, slowly ascending lamella. No distinct upper columellar fold noted. No palatal ribs at any stage of growth.

Type species *Lamellidea tantalus* Pilsbry and Cooke.

At the time volume 23 of the Manual of Conchology was written, this species was known only from a single colony on Mount Tantalus, Oahu; but in

recent years specimens have been taken from a number of localities on the Koolau Range from Palolo to Helemano. Some specimens referable to this species have also been found on Kauai and Molokai.

**Lamellidea (Elamellidea) tantalus** (Pilsbry and Cooke). Figure 92, a-d.

*Tornatellina (Tornatellinops) tantalus* Pilsbry and Cooke, 1915, Man. Conch. 23: 172, pl. 40, figs. 8-10.

"The shell is oblong, slender, cinnamon, distinctly but irregularly striate; outlines of spire slightly convex; last whorl somewhat compressed laterally. Parietal lamella very broad, subhorizontal, about a half-whorl long. Columella spirally twisted.

"Length 3, diam. 1.2, aperture 1 mm.; 5 whorls.

"Length 2.4, diam. 0.9, aperture 0.8 mm.;  $4\frac{2}{3}$  whorls.

"In the neanic stage the parietal lamella is broader but not sinuated; the columella has a stout median lamella; there are no palatal ribs or plicae." (Pilsbry and Cooke.)

Adult genitalia. *Ovotestis* unilobate, roughly triangular, follicles few, visible as rounded tips; round white objects (ova?) visible within. *Duct* small, slightly swollen, convoluted. *Talon and carrefour* not dissected. *Albumin gland* large; follicles numerous, large, ovate to oblong, translucent, fatty globules visible within. *Prostate* small; follicles few, large,

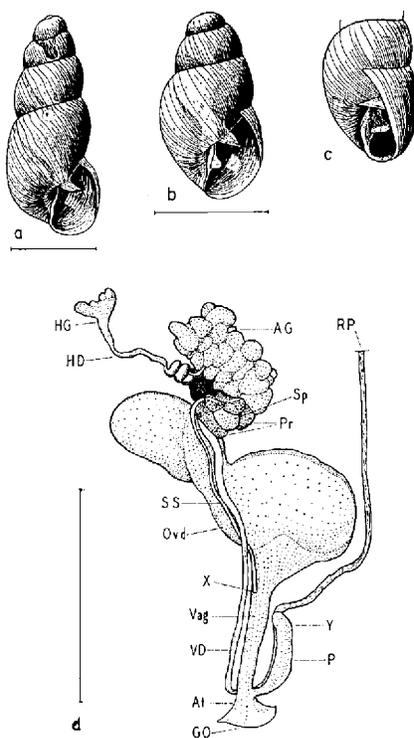


FIGURE 92.—*Lamellidea (Elamellidea) tantalus*: a, adult; b, metaneanic; c, metaneanic, oblique view; d, adult genitalia.

distended, ovate to short-digitate. *Spermatheca* fairly large, ovate, lying among prostatic follicles; stalk small, medium long, insertion into oviduct (X) quite high. *Oviduct* distended with embryos (two in figured specimen). Embryos large for size of genitalia, all embryos except lowest encased in heavy, hard coating of yellow translucent matter. *Vagina* long (0.3 oviducal length), subcylindrical. *Vas deferens* broad (twice width of SS), Y apical. *Penis* short (0.25 oviducal length), subcylindrical, thick (ratio of length to width, 5:1). *Penial retractor* long, heavy.

Dissected 16160, five specimens.

Type in Academy of Natural Sciences, Philadelphia.

Hawaiian Islands: Oahu, Mount Tantalus (type locality), south, low rim, Cooke, Feb. 3, 1911.

Though *Lamellidea tantalus* resembles *L. cylindrica*, the systematic position of *L. tantalus* in 1915 was uncertain, owing to its stronger striations and to characters of the neanic stage.

Three new species from Ponape, Truk, and Fiji that are classifiable under *Elamellidea* will be described in a subsequent publication.

*Elamellidea* is similar to *Lamellidea* (*s.s.*) with the following differences: The animal is very small, often lacking a penis. The penis does not exceed the oviducal length (0.25 to 0.6 oviducal length; average, 0.3 oviducal length); the interior of the penis has a modified achatinellid pilaster; the pilaster is small and short, ascending and recurving at the apex, the descending arm shorter, without the typical pendent arm or velum. The vas deferens enters the atrium directly or not at all when the penis is lacking. If it does not enter at all, the vas deferens is suspended in the coelom with, apparently, a closed end. Abnormal specimens which have no penis are generally without embryos or have only one. The spermathecal stalk enters the oviduct about midway, hence the vagina is long.

The lack of a penis in the Pupillidae is fully discussed by Boycott (1917, pp. 223-226) and Watson (1920, pp. 17-18; 1923, pp. 275-280). In our dissections most specimens lacking the penis were non-gravid and gravid specimens had no more than one embryo. We also found that the terminus of the vas deferens at the vagina, when attached, was a plain tube with no intromittent organ. In many specimens the prostate was minute and hidden from view within the albumin gland follicles.

#### Subgenus *Atea* = *Aubea*

*Atea* Pilsbry and Cooke, new subgenus of *Lamellidea*. Type *L. adamsoni* [Pilsbry and Cooke, 1933, *Nautilus* 47 (2): 62].

"Shell slender, of numerous (7 to 9) slowly increasing whorls, the apertural armature as in *Tornatellinops*. Type *L. adamsoni*." (Marquesas, Pilsbry and Cooke.)

The shells of the subgenus *Atea* differ from those of *Lamellidea* (*s.s.*) in having at least 0.5 more whorl. [The species nearest to *adamsoni* (9 whorls), *mumfordi* (7.5 whorls), and *uahukana* (7-7.5 whorls) are *microstoma* (6.5

#### Nomenklatorische Bemerkungen. Arch. f. moll. 91:125, 1962

*Aubea* KONDO n. nom. pro *Atea* PILSBRY & COOKE 1933 (*Nautilus*, 47: 62)

non *Atea* KOCH 1837 (Uebers. Arachnidensyst., 1: 3) [Arachn.].

YOSHIO KONDO, Honolulu.

whorls) and *subcylindrica* (6.5 whorls) from the Marianas.] In *Atea* the parietal lamella is longer (one and a half whorls) and extends exteriorly of the apertural area farther than in any other group in the family; so much so that instead of a triangular profile in the frontal view a semi-lunate aspect is strongly evident. The columella of juveniles has two equal, rapidly ascending lamellae. No palatal ribs are found in any stage of growth.

Morphologically, the genitalia are closely similar to those of *Lamellidea* except for the following characters: animal larger; penis not exceeding oviducal length nor receding below 0.5 oviducal length, averaging 0.35, shorter than oviduct; width of penis relatively narrower (ratio of penial length to penial width, 14.4:1). Interior of penis with ascending fleshy pilaster, recurving at apex and descending as a narrower non-pendent pilaster; without velum. Embryos more numerous (six to 12 in adult).

The anatomical description is necessarily based on only two species and will probably prove to be inadequate. However, until a good series is collected and studied, the above must suffice.

**Lamellidea (*Atea*) adamsoni** Pilsbry and Cooke, 1933, *Nautilus* 47 (2): 62 (fig. 93, *a-e*).

"The shell is slender, pale brown, somewhat transparent, glossy, of 9 convex whorls, the apex acute; smooth, with some irregularly spaced growth marks. Aperture narrowly oblong, the parietal lamella large, columella thickened, sinuous, bearing a small, somewhat receding, steeply oblique lamella; outer lip thin. Length 7.2, diam. 2.4 mm. Hakahetau, Uapou. Cotypes 108448 Bishop Museum and 161691 A.N.S.P." (Pilsbry and Cooke.)

In adult last whorl conspicuously pointed, making shoulder prominent. A small remnant of columellar lamella present. Parietal lamella strongest in adult. (See figure 93, *a*.) Lectotype (8867): Length 7.04, diameter 2.47 (35 percent); apertural axis 2.17, diameter 1.3 (59 percent); last whorl 3.39 (48 percent); parietal lamella 0.17 mm. Whorls 9.25.

Genitalia. *Ovotestis* unilobate, deeply cleft once; lobelets small; follicles few, small, clavate or short-clavate. *Duct* strongly convoluted, swollen. *Talon and carrefour* not dissected but presumably similar to those of *Lamellidea* (*s.s.*). *Albumin gland* quite large; follicles numerous, small, ovate or round. *Prostate* small; follicles fairly numerous, oblong to ovate. *Spermatheca* small, ovate; stalk narrow. *Oviduct* distended (figured specimen not fully developed, only four embryos), diaphanous. *Vagina* short. *Vas deferens* as narrow as spermathecal stalk, looping around penis two to three times; Y apical. *Penis* long (0.6-0.7 oviducal length), cylindrical; interior of penis with modified achatinellid pilaster: thick fleshy ascending pilaster (Pil 1) recurved at apex, descending a short distance as smaller non-pendent pilaster (P Pap), soon fading into penial wall. *Retractor* (RP) quite long, rather heavy. *Atrium* (At) short.

Dissected 108448, four specimens; 108516 (interior penis), one specimen.

Marquesas Islands: Uapou, Hakahetau, Vaihakaatiki, hillside valley, inland 4 km., on *Musa* and *Freycinetia*, alt. 2,500 ft., Pacific Entomological Survey, Nov. 18, 1931; lectotype 8867; paratypes 108448, 108449; figured metaneanic specimen 8868. Other paratypes: Hakahetau 98392, 98394, 98395; Kohepu 108516. Uapou, Hakahetau, ridge of Teavatuhai, 98395, 3,000 ft., Pacific Entomological Survey, Dec. 11, 1929.

Of the four specimens dissected, only one was in sufficiently good condition to be illustrated (fig. 93, *d, e*) and it was not fully mature. A metaneanic specimen (fig. 93, *b, c*) is also illustrated (length 4.04, diameter 1.9, whorls 6.75). At this stage the last whorl is rounded, the parietal lamella is strong, and the columellar lamella flares slightly.

Subgenus *Atea* appears to be more prolific than subgenus *Lamellidea*, one specimen containing 12 embryos. The ovotestis, though deeply cleft and appearing bilobate, is really unilobate.

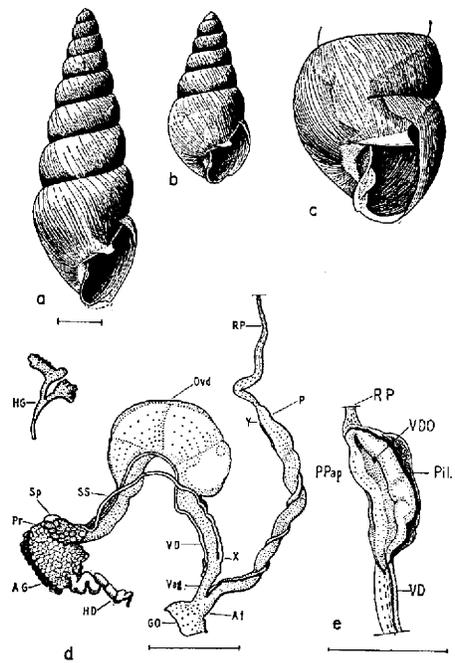


FIGURE 93.—*Lamellidea (Atea) adamsoni*: *a*, subadult, lectotype; *b*, metaneanic juvenile; *c*, metaneanic, magnified, oblique columellar view; *d*, near-adult genitalia; *e*, interior of penis, distal part.

***Lamellidea (Atea) mumfordi*** Pilsbry and Cooke, 1933, *Nautilus* 47 (2): 62 (fig. 94, *a-e*).

"Similar [to *adamsoni*] but smaller, of  $7\frac{1}{2}$  less convex whorls, the apex rather obtuse, striation more developed, especially below the suture. Aperture wider. Length 5.2, diam. 1.9 mm.; length 4.7, diam. 1.75 mm. Ponaohumu, Hivaoa. Cotypes 94877 B. M. and 161692 A.N.S.P." (Pilsbry and Cooke.)

Most conspicuous is the weak parietal lamella, in many specimens much weaker than in figured specimens or even absent (98615). Columellar lamella persists until late in adolescence and remains in most adults as vague callus.

Lectotype (8869): Length 4.21, diameter 1.82 (43 percent); apertural axis 1.39, diameter 0.91 (65 percent); last whorl 2.08 (49 percent); parietal lamella 0.086 mm. Whorls 7.3.

Perfect specimen (94800) close to description: Length 4.95, diameter 2.00 (40.4 percent); apertural axis 1.60, diameter 1.08 (67.5 percent); last whorl 2.52 (50.9 percent); parietal lamella 0.086 mm. Whorls 7.5.

Genitalia similar to those of *adamsoni* except more mature (six embryos). Ovotestis bi-cleft, each arm shallowly cleft once. Duct smaller. Albumin and prostate glands smaller. Penis about same length.

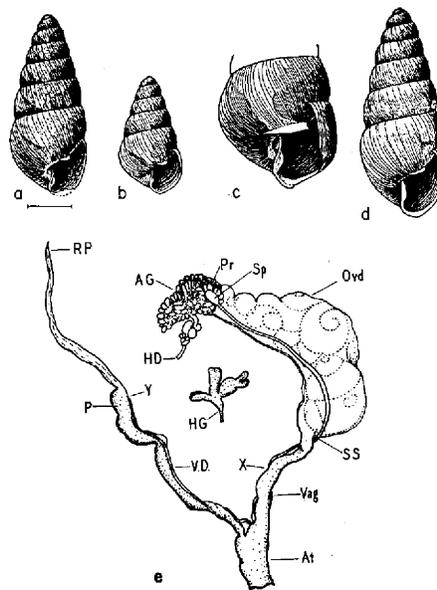


FIGURE 94.—*Lamellidea (Atea) mumfordi*: a, subadult, lectotype; b, metaneanic juvenile; c, metaneanic, oblique columellar view; d, adult, perfect specimen, closest to original description; e, adult genitalia.

Dissected 98636, one specimen only.

Marquesas Islands: Hivaoa, Ponaohumu, alt. 3,100 ft., Pacific Entomological Survey, Aug. 3, 1929; lectotype 8869, paratypes 94877, metaneanic specimen 8870, perfect specimen 94800. Hivaoa, Tenatinaei, ridge north of summit, 3,760 ft., Pacific Entomological Survey, Aug. 1, 1929. Mount Temetiu, 1,000 ft., Pacific Entomological Survey, Dec. 12, 1929 (98636).

In the perfect specimen (fig. 94, d) the columella is thickened, but a vague remnant of the columellar lamella is perceptible and the greater part of the shell is hydrophanous. The juvenile (fig. 94, b, c) has a slight angle to the periphery, and the columellar lamella is a weak fold (length 2.78, diameter 1.51, whorls 6).

**Lamellidea (Atea) uahukana** Pilsbry and Cooke, 1933, *Nautilus* 47 (2) : 62 (fig. 95, a-c).

"Shell more slender, of 7 to 7½ moderately convex whorls, which are finely *costulate* below the suture. Apex somewhat obtuse. Length 4.5, diam. 1.45 mm.; length 4.4 mm., diam. 1.4 mm. Hane, Uahuka. Cotypes 161693 A.N.S.P. and 104972 B.M." (Pilsbry and Cooke.)

Conspicuously *costulate*. Parietal lamella strongest in adult. Lectotype (8871) : Length 4.08, diameter 1.47 (36 percent); apertural axis 1.17, diameter 0.73 (62 percent); last whorl 2.00 (49 percent); parietal lamella 0.086 mm. Whorls 7.5.

Metaneanic juvenile with weak columellar lamella (length 2.34, diameter 1.3 mm., whorls 5).

Marquesas Islands : Uahuka, Hane ridge, on ferns ("Oaha leaves," or *Asplenium nidus*) and shrubs, 2 to 3 miles inland, alt. 2,170 ft., Pacific Entomological Survey, Mar. 3, 1931; lectotype 8871; figured metaneanic specimen 104973; paratypes 104972, 104973-104975. Additional paratype 104989, Uahuka, Hitikau, crest of Hane, on ferns, *Freycinetia*, dead leaves, 3 km. inland, alt. 2,500 ft., Pacific Entomological Survey, Mar. 3, 1931.

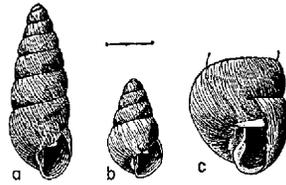


FIGURE 95.—*Lamellidea (Atea) uahukana*: a, subadult, lectotype; b, metaneanic juvenile; c, metaneanic, oblique columellar view.

**Tornatellina globulosa** Quadras and Möllendorff, 1898, *Naturf. Ges., Abh. [zu Görlitz?]* 22 : 128 (*vide* Faustino).—Faustino, 1930, *Philippine Jour. Sci.* 42 (1) : 148. (Position uncertain.)

*Tornatellina varicifera* Pilsbry, 1902, *Nautilus* 16 (5) : 57. *Nomen nudum*.

#### SUBFAMILY TORNATELLININAE

*Tornatellinidae* Pilsbry (in part), 1910, *Nautilus* 23 (10) : 122.—Pilsbry and Cooke (in part), 1915, *Manual of Conchology* 23 : 66.—Odhner, 1922, *Natural History of Juan Fernandez and Easter Island* 3 (2) : 234.—Pilsbry and Cooke, 1933, *Nautilus* 47 (2) : 59.

Penis innervated by cerebral ganglion (in *Elasmiatini*; unknown in *Tornatellinini*). Right ommatophoral retractor free of peni-oviducal angle. Penis vestigial, with or without pilaster. Appendix present, either with secretory-ejaculatory apparatus or with complex copulatory mechanism composed of rugae

and pilasters. Both penial and appendical retractors present. Albumin gland small to relatively large, well developed, dominant. Prostate small, recessive. Spermatheca free. Carrefour with small and short or long and large carrefour vesicle distally attached to columellar muscle. Ovotestis unilobate or multilobate. Viviparous.

The subfamily Tornatellinae includes the widely dispersed genus *Elasmias* and the Juan Fernandez genera *Tornatellina* and *Fernandezia*.

#### TRIBE ELASMIATINI

Conchology as in genus.

Ovotestis unilobate. Appendix with internal secretory-ejaculatory apparatus, without the complex copulatory mechanism of *Fernandezia*. Penis without interior musculature. Carrefour vesicle small.

#### Genus *Elasmias* Pilsbry

*Elasmias* Pilsbry, 1910, *Nautilus* 23 (10) : 122. Type *Tornatellina aperta* Pease.

*Elasmias* Pilsbry and Cooke, 1915, *Man. Conch.* 23 : 113.

*Elasmias* Iredale, 1937, *Australian Zool.* 8 (4) : 299; 1941, 10 (1) : 63; 1944, 10 (3) : 307.

*Elasmias* Faustino, 1930, *Philippine Jour. Sci.* 42 (1) : 148.

"The shell is imperforate, globose-conic or rotund-ovate, composed of few (3 to 5½)<sup>5</sup> whorls, usually striate spirally. Aperture large, the columella calloused, in form of a wide or narrow vertical plate, bilobed or angular, but without deeply entering lamellae, truncate or excavated below the plate; parietal lamella as usual in the family. Viviparous or ovoviviparous. Radula as in *Tornatellina*.

"Type: *E. apertum* (Pease). Distribution: islands of the central and western Pacific and Indian Ocean; Australia. Living on the leaves of plants." (Pilsbry.)

Adult genitalia. *Ovotestis* unilobate, with or without clefts; clefts shallow or deep, few to numerous, forming digitate to blunt follicular points; or clefts rarely deep, causing bilobate appearance. *Hermaphrodite duct* short, small, with median bulge, convoluted. *Albumin gland* rather small, well developed, multifolliculate; follicles digitate, ovoid, or round. *Prostate* small to fairly large, paucifolliculate, two to eight follicles, usually broad, short, bluntly pointed. *Carrefour* small, ovate. *Carrefour vesicle* small, off floor of carrefour below exit of vas deferens, short, thin, the distal end embedded in columellar muscle. *Talon* either non-existent or modified. *Spermatheca* small, ovate, free, lying on albumin gland or between it and uterus; stalk thin, narrow, long. *Oviduct* sac-shaped, transparent, distended with embryos (four to 15 per gravid adult). *Vagina* short (0.2 to 0.25 oviducal length in adult). *Vas deferens* about same diameter as spermathecal stalk, emptying at base of penis. *Penis* vestigial, in size from minute papilla to small conical mound at the largest, with appendix. *Appendix* large (ratio of width to length, ±1:9), long (0.5 to as long as oviduct or longer), broader at base, with bulge above penis, tapering very gradually to blunt, slightly wider point; rarely, with appendical diverticulum at bulge; internally with secretory-ejaculatory apparatus obviously used as stimulator during copulatory act. *Common retractor* thin bifid; penial retractor also thin, terminal; appendical retractor thin, insertion median. *Atrium* short.

The following *Elasmias* species were dissected but not described or figured: *amphodon* Cooke and Kondo (148235), Rurutu; *anceyanum* Pilsbry and Cooke

<sup>5</sup> Originally 4½, a typographical error.

(92460), Maui, two specimens (21429); *fuscum* (Ancey), Hawaii (22777), two specimens, (92826) three specimens, and Molokai (33723), three specimens; *luakahaense* Pilsbry and Cooke, Oahu (37865), three specimens; *ovatum* (Möllendorff), Ponape (157707), four specimens, (156995) two specimens; *Elasmias* sp. Oahu (90235), three specimens, and Molokai (129407), one specimen.

*Elasmias* is a rather compact genus. All of the species are similar in form, specific differences being based, for the most part, on the thickness and color of the shell and on the form and degree of development of the apertural armature. The globose-conic outlines, the few whorls, and the flattened columellar plate of most species easily distinguish the genus. Of the 12 species represented in our collection, all except *E. simplicimum* from Rapa have the embryonic whorls marked with fine microscopical lines. In most species the adult specimens have these closely placed spiral lines on the last whorl, but they are visible only under a strong lens with reflected light.

*Elasmias* is the most widespread of the tornatellinid genera (map, fig. 96). Species of the genus *Elasmias* have been reported from the Hawaiian, Marquesan, and Mangarevan islands to the east; from Australia, Java, the Philippines and from the Izu (Japan) Islands to the west. Two species occur on islands in the Indian Ocean: The Maldive Islands and Reunion and Mauritius. Undoubtedly, the widespread distribution of this genus is due partly to man's agency, as the species might well be carried on garden plants. The northernmost point at which *Elasmias* has been taken is in the Izu Islands just south of Japan, about 33° north; the southernmost points are Grafton, New South Wales, nearly 30° south, and the Kermadec Islands at about the same latitude.

Bishop Museum has examples of *Elasmias* from 59 of the Pacific islands between, and including, the Marquesas Islands on the east and the Palau Islands on the west. The genus has been collected mostly on high volcanic islands, and further collecting will undoubtedly show that it occurs on nearly all of the volcanic islands of the Pacific. A number of the older raised coral islands also have representatives of the genus. Henderson and Makatea in the Tuamotus, Niue in the central Pacific, Mitiaro in the Cook Islands, and Pukapuka in the Pukapuka (Danger) Islands. Bishop Museum also has representatives from three low coral islands: Oeno, one of the southernmost of the Tuamotus, one specimen; Maria, the westernmost of the Austral Islands; and Kayangel, the northernmost of the Palau Islands. No specimens were taken on low coral islets on the reefs of Mangareva, Raivavae, Tubuai, or Raiatea, although these islets are only 0.75 to 3.5 miles from the shores of the high islands on which *Elasmias* were abundant. However, during the Mangarevan Expedition abundant collections of land shells were made on 11 islets of this type, providing a comparison of the endemicity of faunas of satellite islets with their main islands. A single specimen was collected on Arno, Marshall Islands,

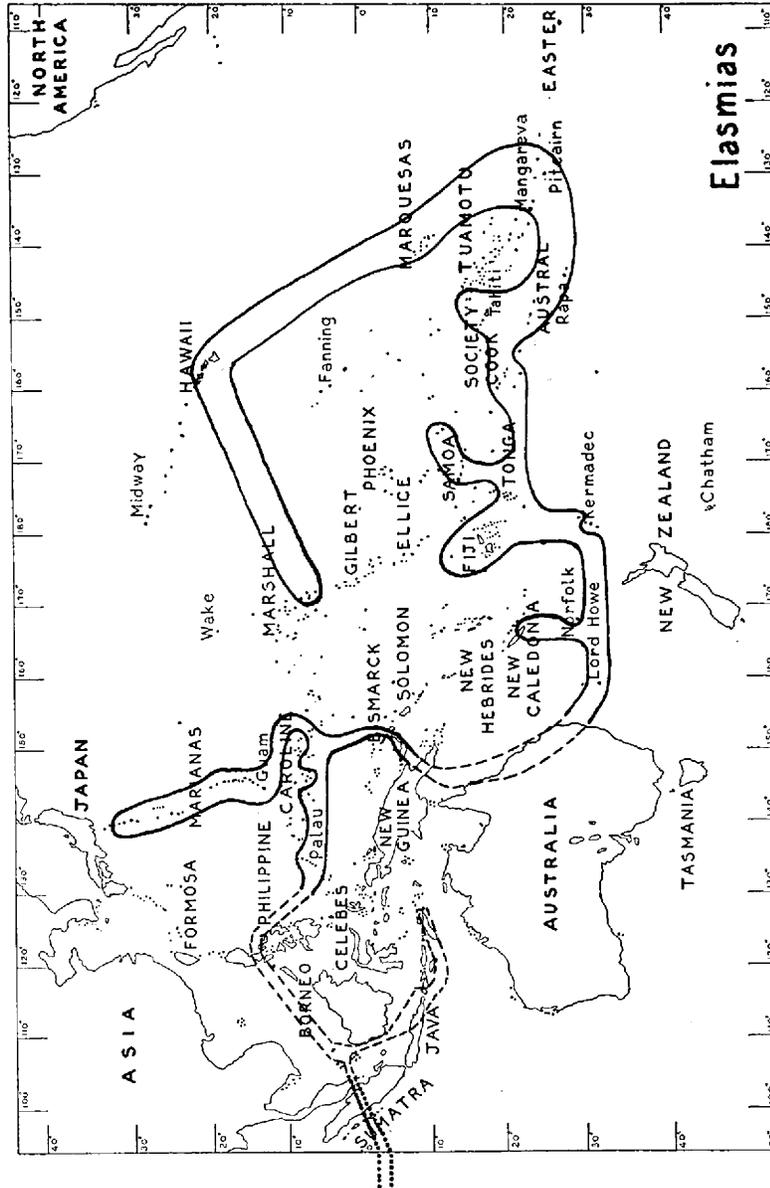


FIGURE 96.—Distribution of genus *Elasmias*; broken lines (----), extralimital distribution; dotted lines (....) point to Mauritius and Maldive Islands in the Indian Ocean.

by W. H. Hathaway, July 15, 1952. On May 28, 1958, R. P. Owen collected 17 specimens of *Elasmias apertum*? from a citrus plant on Majuro, Marshall Islands.

The species of this genus are almost exclusively arboreal in habit, being found on leaves of ferns, shrubs, and occasionally on trunks and twigs of small trees with smooth bark. But at Rurutu the Expedition took six lots on the ground, five of these lots consisting of one to four specimens. Though they may have been accidentally shaken from plants, the nine individuals in one lot (148951) might indicate natural conditions. Brazier (1915, p. 124) states that *E. terrestris* was "found on the ground under leaves" on Yule Island.

Semper (1870, p. 140) writes that *E. manilense* lives among and on the leaves and stems of water plants and often crawls to quite high on the trunks of mangroves, a statement which has been corroborated. Bishop Museum has two lots that were taken on leaves of mangroves. The first lot, from the islet of Param, off Truk (155744), were abundant on leaves of mangroves standing in water a few inches deep. The second lot came from the base of Laimi Ridge, about five miles west of Suva, where a nearby inlet was bordered with mangrove and other shrubs. *Elasmias* (178493) was not abundant in Fiji but specimens were taken on the leaves of mangrove and other shrubs.

Under favorable conditions on eastern and southeastern Pacific islands *Elasmias* may be abundant on native and cultivated plants just back of the strand and at altitudes of only a few feet, or inland up to a few hundred feet. The lowland species, usually *E. apertum* or one of its closely allied forms, have undoubtedly been disseminated by man.

*Elasmias* have been taken alive in the Hawaiian Islands only at altitudes of several hundred to 4,000 or 5,000 feet, most frequently along the edges of native forests. They are rare in the lowland fossil deposits, and at no place in Hawaii are they as abundant as in the islands farther south.

In the south seas some forms occur at high altitudes; up to about 6,000 feet on the island of Tahiti, for instance. A number of these high altitude forms may constitute distinct species. They differ in many characters from the lowland form of *E. aperta*.

Preliminary studies indicate that the most distinct speciation occurs in the Hawaiian Islands, in Tahiti and Moorea, and in Rapa and Rurutu. From all other Pacific islands most of the specimens at hand seem to follow closely only three to five types in specific characters. (See figures in Manual of Conchology, vol. 23, pls. 30, 31.) In only three species—*E. fusca* and *E. luakahaense* from the Hawaiian Islands and *E. amphodon* from Rurutu—do juveniles have palatal plicae. It is remarkable that this character has developed, apparently independently, in two widely separated localities. Specimens of *E. ovatum* (Rapa, 135680) with barely three whorls have been found to contain embryos.

We have added species and synonyms to those recognized in the Manual of Conchology as follows: *E. amphodon* Cooke and Kondo, Rurutu; *E. schola* Iredale, Lord Howe Island; *E. connisum* Iredale [= *apertum* (Pease)], Kermadecs.

A doubtful species is ?*E. jauffreti* Madge, Mascarene Islands, Rodriguez.

New species and subspecies are *E. simplicimum*, Rapa and Raivavae, and *E. ovatum exiguum*, Rapa.

**Elasmias amphodon** Cooke and Kondo, 1943, B. P. Bishop Mus., Occ. Papers 17 (21): 263, fig. 1, *a, b*.

Holotype in Bishop Museum (10116); Austral Islands, Rurutu, Mount Manureva.

*E. amphodon*, *E. fuscum*, and *E. luakahaense* are the only species of the genus with palatal plicae in the neanic stage. The genitalia are as in other species.

**Elasmias anceyanum** Pilsbry and Cooke, 1915, Man. Conch. 23: 118, pl. 31, figs. 7, 8.

Holotype in Bishop Museum (14147), west Maui, Maunahooma.

**Elasmias apertum** (Pease). Figure 97, *a-d*.

*Tornatellina aperta* Pease, 1864, Zool. Soc., London, Proc., 673; 1871, 473.  
—Pfeiffer, 1868, Mon. Hel. Viv. 6: 264.—Schmeltz, 1874, Cat. Mus. Godeffroy 5: 90.—Garrett, 1884, Acad. Nat. Sci. Philadelphia, Jour. II, 9: 83, pl. 2, fig. 20.—Binney, 1884, New York Acad. Sci., Ann. 3: 99, pl. 3, fig. F (teeth).—Smith, 1897, Ann. Mag. Nat. Hist. VI, 20: 521.

*Elasmias apertum* Pilsbry, 1910, Nautilus 23 (10): 122.

*Elasmias ovatum apertum* Pilsbry and Cooke, 1915, Man. Conch. 23: 120, pl. 30, figs. 2-5.—Cooke, 1934, B. P. Bishop Mus., Occ. Papers 10 (11): 8.

*Elasmias connisum* Iredale, 1944, Australian Zool. 10 (3): 308.

Measurements of figured specimen: Length 3.70 mm., diameter 2.68 (72 percent); apertural axis 2.1, diameter 1.5 (70 percent); last whorl 3.1 (83 percent); parietal lamella 0.13.

Genitalia simple. *Ovotestis* unilobate, medially and shallowly cleft, forming two truncated follicles. *Duct* small, convoluted and swollen medially. *Talon and carrefour* as in *E. peasianum*. *Carrefour vesicle* (VS) medially enlarged, tapering toward both ends, 0.3 oviducal length, tip strongly adherent to columellar muscle. *Albumin gland* quite small, ovate, follicles numerous. *Prostate* fairly large, trilobate; follicles (or lobes) heavily distended. *Spermatheca* ovate; stalk thin, long, narrow. *Upper uterus* narrow, inflated below, embryos four to eight. *Vagina* long ( $\pm 0.25$  oviducal length). *Vas deferens* off right side of carrefour, same diameter as spermathecal stalk, emptying into penis at base (Y). *Penis* vestigial, minute, interior plain. *Appendix* large, quite long ( $\pm 0.5$  oviducal length), broad; interior as in *E. peasianum*. *Appendical retractor* heavier than penial retractor, which is very thin. *Atrium* short.

Teeth delicate, all alike, head broad, seven-dentate. One ecto-, one ento-, and one mesocone plus three to four fine cusplets below principal cusps; formula about 98-1-98. Length  $\pm 12$  microns, width  $\pm 6$  microns.

Dissected 141180 (genitalia, teeth), five specimens.

Type in Museum of Comparative Zoölogy?; type locality, Tahiti?

Society Islands: Tahiti, Tairapu, Vaipoe, on ferns and shrubs, alt. 5-30 ft., Cooke and others, Sept. 20 (figured specimen 8874).

Mangareva Islands: Mangareva, south side of Mount Makoto, on leaves of *Asplenium nidus*, coffee, banana, and *Passiflora*, alt. about 1,000 ft., Anderson, June 2 (dissected 141180).

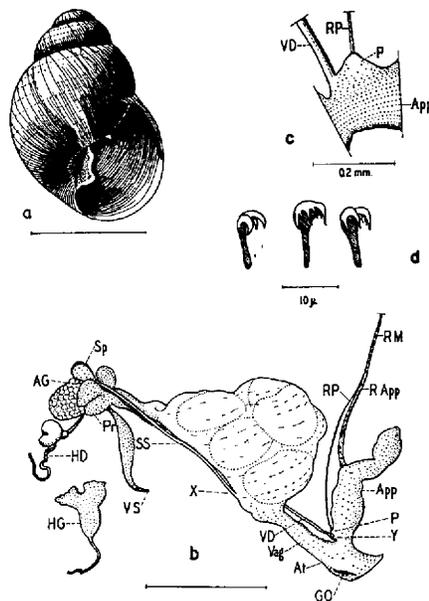


FIGURE 97.—*Elasmias apertum*: a, shell; b, genitalia; c, closeup of vestigial penis; d, teeth.

This species (fig. 97, a) is widely distributed in the islands of the south Pacific. Typical specimens in the Museum collections are from several of the Marquesas Islands, Society Islands, Mangareva, the Cook Islands, Tubuai, and Makatea in the Tuamotus. It is also reported from Rotuma, Tongatabu, and the Kermadec (Sunday) Islands. Undoubtedly, early Polynesian voyagers account for the wide distribution of this species. Pease's specimens probably came from Tahiti.

Specimens from Mangareva were selected for dissection, as they are somewhat larger than any in the collection from Tahiti.

**Elasmias cernicum** (Benson).

- Tornatellina cernica* Benson, 1850, Ann. Mag. Nat. Hist., II, 6: 254.—Pfeiffer, 1853, Mon. Hel. Viv. 3: 526.—Küster, 1852 (-1859), Conch.-Cab., Pupa, 1 (15): 155, pl. 18, figs. 30, 31.—von Martens, 1880, in Möbius, Beiträge zur Meeresfauna der Insel Mauritius u. der Seychellen, 199.—Viader, 1937, Mauritius Inst., Bull. 1(2): 88.
- Tornatellina (Septinaria) cernica* Benson, Nevill, 1870, Asiatic Soc. Bengal, Jour. 39 (2): 413.
- Tornatellina mauritiana* Pfeiffer, 1852, Zool. Soc., London, Proc., 150.
- Achatina minutissima* Barclay (*vide* Pfeiffer).
- Elasmias cernicum* Pilsbry and Cooke, 1915, Man. Conch. 23: 127, pl. 31, figs. 1-4.

Type whereabouts unknown.  
Mauritius.

**Elasmias citreum** (Smith).

- Tornatellina citrea* E. A. Smith, 1898, Malac. Soc., London, Proc. 3 (1): 30, pl. 2, fig. 17.
- Elasmias citreum* Pilsbry and Cooke, 1915, Man. Conch. 23: 126, pl. 30, figs. 6, 7.—Rensch, 1935, Sitzungsb. Gesell. naturf. Freunde, 1 April, 323.

Type in British Museum?  
Lombok (type locality), Timor, Rensch.

**Elasmias eucharis** (Brazier).

- Tornatellina eucharis* Brazier, 1876, Linn. Soc. New South Wales, Proc. 1: 110.—Hedley, 1901, Linn. Soc. New South Wales, Proc. 26: 705, pl. 34, fig. 12.—Pilsbry and Cooke, 1915, Man. Conch. 23: 123.
- Elasmias eucharis* Iredale, 1937, Australian Zool. 8 (4): 299.

Type whereabouts unknown.  
Barnard Islands, No. 3, northeastern Australia, North Queensland.  
The statuses of *E. eucharis* and *E. terrestris* have not been clarified since 1915 (Pilsbry and Cooke, pp. 123-124). They are, however, given provisional specific rank here, after Iredale.

**Elasmias fuscum** (Ancey).

- Tornatellina fusca* Ancey, 1903, Jour. de Conchyl. 51: 306, pl. 12, figs. 23, 24.—Henshaw, 1904, Jour. Malac. 11: 64.
- Elasmias fuscum* Pilsbry and Cooke, 1915, Man. Conch. 23: 115, pl. 29, figs. 1-6.
- Elasmias fuscum obtusum* Pilsbry and Cooke, 1915, Man. Conch. 23: 117, pl. 28, fig. 5.

Holotype in Bishop Museum (18434); Hawaii, Puna, Oloa, Thaanum.  
Distribution: Hawaiian Islands (Hawaii, Maui, Molokai, and Oahu).

? **Elasmias jaffreti** Madge, 1946, Mauritius Inst., Bull. 2 (4): 221, text fig. 1, a, b, pl. 7, fig. 12.

Type in British Museum.

Mascarene Islands, Rodriguez.

To judge from the description and figures, *E. jaffreti* may belong to the genus *Tornatellinops*.

**Elasmias kitaiwojimanum** (Pilsbry and Hirase).

*Tornatellina kitaiwojimana* Pilsbry and Hirase, 1903, Nautilus 17 (5): 53.

*Elasmias kitaiwojimanum* Pilsbry and Cooke, 1915, Man. Conch. 23: 130, pl. 31, figs. 9, 11.

Type in Academy of Natural Sciences, Philadelphia (84965), Kita Iwo Jima.

Distribution: Sulphur Islands, Hachijo, Izu Islands, and Bonins (British Museum, two specimens).

**Elasmias luakahaense** Pilsbry and Cooke, 1915, Man. Conch. 23: 117, pl. 29, figs. 7-10.

*Tornatellina aperta* Ancey, 1903, Jour. de Conchyl. 51: 295 (not of Pease).

Type in Bishop Museum (41224); Ancey's type (18467) also in Bishop Museum.

Hawaiian Islands: Oahu, Nuuanu, Luakaha (type locality); collected also in Manoa, Punaluu, Kaliuuaa, Waialua, and various other localities.

**Elasmias manilense** (Dohrn).

*Tornatellina manilensis* Dohrn, 1863, Malak. Blätt. 10: 160.—Pfeiffer, 1868, Mon. Hel. Viv. 6: 264.—Semper, 1870, Reisen im Archipel der Philippinen 3 (2): 133, 140, pl. 16, fig. 13 (tooth).—E. A. Smith, 1902, Gardiner's Fauna and Geography Maldivo-Laccadive Archipel. 1 (2): 144.

? *Tornatellina natunensis* E. A. Smith, 1894, Ann. Mag. Nat. Hist. VI, 13: 458, pl. 16, fig. 7.

*Elasmias manilense* Pilsbry and Cooke, 1915, Man. Conch. 23: 125, pl. 31, fig. 6 [?].—Faustino, 1930, Philippine Jour. Sci. 42 (1): 148.

Type whereabouts unknown.

Distribution: Philippine Islands (Manila, Luzon, Ubay, Bohol), Semper; Maldivo Islands (Hulule, north Male Atoll), Gardiner; Natuna Island (Bunguran), A. Everett.

Pilsbry and Cooke (1915, p. 126) write: "The specimens seen from Manila (pl. 31, fig. 6, length 2.7 mm.) do not agree well with Dohrn's description, and

their identity with his type must be regarded as doubtful . . . The Maldive and Natuna records are from E. A. Smith, who states that he cannot distinguish the Maldive specimens from the Philippine form, and that the shells described as *T. natunensis* are the same."

**Elasmias mariei** (Crosse).

*Tornatellina mariei* Crosse, 1874, Jour. de Conchyl. 22: 109, 393, pl. 12, fig. 7; 1894, 42: 306.—Pfeiffer, 1877, Mon. Hel. Viv. 8: 319.—Gassies, 1880, Faune Conchyl. Nouv. Caledonie 3: 48, pl. 2, fig. 22 (in Actes de la Société Linnéene de Bordeaux).

*Elasmias mariei* Pilsbry and Cooke, 1915, Man. Conch. 23: 124, pl. 30, figs. 11, 12.

Type with Jour. de Conchyl., Paris.

New Caledonia: Baie du Sud.

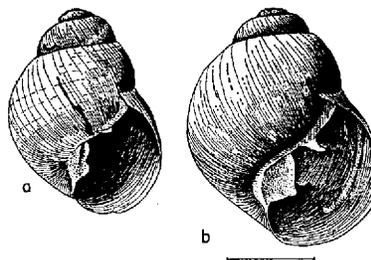


FIGURE 98.—a, *Elasmias ovatulum*, "cotype" (paratype); b, *E. quadrasi*.

**Elasmias ovatulum** (Möllendorff). Figure 98, a.

*Tornatellina ovatula* Möllendorff, 1900, Jour. Malac. 7 (5): 114.

*Elasmias ovatulum* Pilsbry and Cooke, 1915, Man. Conch. 23: 129.

Paratype (86248) measures: Length 2.41 mm., diameter 1.80 (75 percent); apertural axis 1.20, diameter 1.03 (86 percent); last whorl 2.04 (80 percent); parietal lamella 0.04.

Type in Frankfurt am Main; Ponape.

A cotype [paratype] received from Senckenbergische Naturforschende Gesellschaft as an exchange is illustrated (fig. 98, a). Its measurement is shorter than that of Möllendorff's specimen, which is 3 mm., is weatherworn, shows distinct spiral lines, and has 4 whorls.

*E. ovatulum* is very close to *E. apertum*, and a specialized study of the genus may place *E. apertum* as a subspecies of *E. ovatulum*. Specimens referable to *ovatulum* were collected on Kusaie, Ponape, Truk, and Palau, in the Caroline Islands by the Micronesian Expedition, 1935-1936.

**Elasmias ovatum ovatum** (Anton). Figure 99, *a, b*.

*Strobilus ovatus* Anton, 1839, Verzeichniss der Conchylien, 46, no. 1697.

*Achatina ovata* Pfeiffer, 1841, Symbolae 1: 29.

*Achatina (Leptinaria) ovata* Pfeiffer, 1856, Malak. Blätt. 2: 170.

*Tornatellina ovata* Pfeiffer, 1848, Mon. Hel. Viv. 2: 394.—Küster, 1852 (-1859), Conch.-Cab. 1 (15): 150, pl. 18, figs. 12, 13.

*Tornatellina (Leptinaria) ovata* H. and A. Adams, 1858, Genera of Mollusca 2: 141.

*Cionella (Tornatellina) ovata* von Martens, 1860, Albers Die Heliceen, 259.

*Elasmias ovatum* Pilsbry and Cooke, 1915, Man. Conch. 23: 119, pl. 30, fig. 1.—Rensch, 1937, Archiv für Naturgesch., new ser. 6 (4): 582.

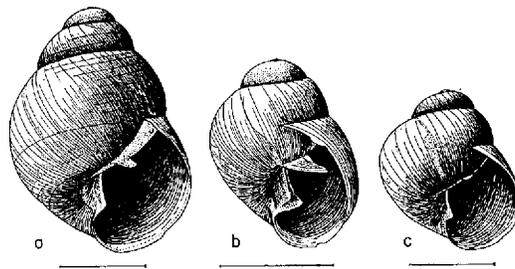


FIGURE 99.—*a, b*, *Elasmias ovatum ovatum*: *a*, adult; *b*, metaneanic. *c*, *E. o. exiguum*, adult, holotype.

“Ovate ventricose; 3 ventricose whorls, with deep suture, the last whorl  $\frac{2}{3}$  of the whole; apex obtuse; aperture oval, with two lamellae on the columella, the lower broadly recurved. Diam. 1”, length  $1\frac{1}{2}$ ” [ $2 \times 3$  mm.]” (Anton)

Illustrated specimen. *Shell* cinnamon buff, with darker embryonic whorls. *Whorls* 4, increasing rapidly, apex blunt, rounded; surface somewhat glossy, marked with weak lines of growth and, under a strong lens, with indistinct, very fine and closely spaced spiral lines (not shown in figure). *Parietal lamella* well developed, about a third of a whorl in length, very slightly arched outward. *Columellar plate* long, narrow, its free margin slightly thickened, nearly straight, not toothed.

Length 2.94 mm., diameter 2.15 (73 percent); apertural axis 1.54, diameter 1.16 (75 percent); last whorl 2.41 (82 percent); parietal lamella 0.13.

Juvenile specimen (figured), whorls 3, parietal lamella strong and high, nearly 0.5 whorl in length, and arched outward. Columellar plate narrowly triangular, truncated below, and margined with a rather strong, nearly horizontal lamella.

Opana [Opara, or Rapa] (Anton): Mount Ororangi, easternmost south-east valley, on shrubs and ferns, alt. 550-700 ft., Cooke and Anderson, July 3, 8875 (figured adult, 8876; figured metaneanic specimen), 135680-135682; back of Ahurei village, along trail to Maitua, on guava shrubs, alt. 50-100 ft., Cooke, July 28, 135884; Mount Perahu, eastern ridge, on leaves of shrubs, alt. 1,200-1,500 ft., Zimmerman and Anderson, July 21, 142722; Area, about 200 yards east of village, on leaves of coffee and *Piper*, a few feet above sea level

to 150 ft., Cooke and Anderson, July 1, 135737; Karapo Rahi Islet, on leaves of shrubs, alt. 250 ft., Anderson, July 18, 140672-140674.

Additional lots were taken from 25 other colonies on different parts of the island. Apparently the species is distributed over the whole island from near sea-level to the highest altitudes, as a specimen in fair condition was taken from the crop of *Microcystis perahui* Baker which was collected on the top of Mount Perahu at an altitude of more than 2,000 feet. Most of the lots consist of one to fewer than six specimens.

Measurements of adult specimens of *E. ovatum* collected by the Expedition on Rapa correspond closely with those given by Anton, whereas Pfeiffer's specimen ( $3.5 \times 2.5$  mm.) is larger than any of our material.

*E. apertum* (Pease) was treated as a subspecies of *E. ovatum* in the Manual of Conchology, for at that time no material from Rapa was available for comparison. However, with sufficient material of both forms collected by the Mangarevan Expedition, we have found them to be closely related and hold them to be distinct species. No intermediates connect the two forms.

The shells of *E. apertum* are larger than those of *E. ovatum* with the same number of whorls, the surface is more strongly marked with fine, close spiral striae, the parietal lamella is weaker and shorter, and the columellar plate is wider, its inner margin bidentate.

***Elasmias ovatum exiguum*, new subspecies (fig. 99, c).**

*Shell* smaller than that of type form, broader in proportion to its length, slightly lighter in color, surface texture similar to that of the species but with weaker growth striae and finer spiral lines. *Whorls* nearly 4, increasing rapidly. *Parietal lamella* very weak. *Columellar plate* narrow.

Length 1.19 mm., diameter 1.67 (87 percent); apertural axis 1.14, diameter 0.86 (75 percent); last whorl 1.69 (88 percent); parietal lamella 0.04.

Metaneanic juvenile (138478A) with very strong parietal lamella, pointing more ventrally than in *E. o. ovatum*. Columella more vertical, the lateral plate more clearcut than in parent species. Both lamellae diminishing in size with age, parietal lamella becoming especially weak.

Rapa: northwest slope of Mount Tautautu (type locality), at edge of forest, on leaves of coffee trees, alt. 600-700 ft., Cooke, July 9; holotype 8877, paratypes 138477-138478.

The only colony of this dwarf form which was found consisted of 15 specimens, 11 of which were gravid. As no other specimens of *Elasmias* were found in the immediate neighborhood, they are probably subspecies. All of the adults agree closely in size and other characteristics. Because of its weak parietal lamella and narrow columellar plate this form might fall between *E. ovatum* and *E. simplicimum*. However, it shows no relationship with *E. simplicimum*, whereas its color, surface texture, and blunt apex point to *E. ovatum* as the parent species.

**Elasmias peasianum** (Garrett). Figure 100, a-g.

*Tornatellina peasiana* Garrett, 1884, Acad. Nat. Sci. Philadelphia, Jour. II, 9: 83, pl. 2, fig. 19.

*Elasmias peasianum* Pilsbry and Cooke, 1915, Man. Conch. 23: 122, pl. 31, fig. 5.

Shell oblong-ovate.

Adult genitalia. *Ovotestis* bi-cleft, follicles strongly evident. *Carrefour* small, giving vesicle off ventrum (VS), vas deferens off right lateral wall; uterus above vas deferens. *Carrefour vesicle* short, thin, narrow, semi-transparent, with slight terminal swelling; most of vesicle lying upon columellar muscle, the distal pouch strongly and intimately adherent to muscular tissues, containing fibrous material (sperm?). *Talon* absent. *Albumin gland* small but well developed, multifolliculate. *Prostate* small, paucifolliculate; follicles

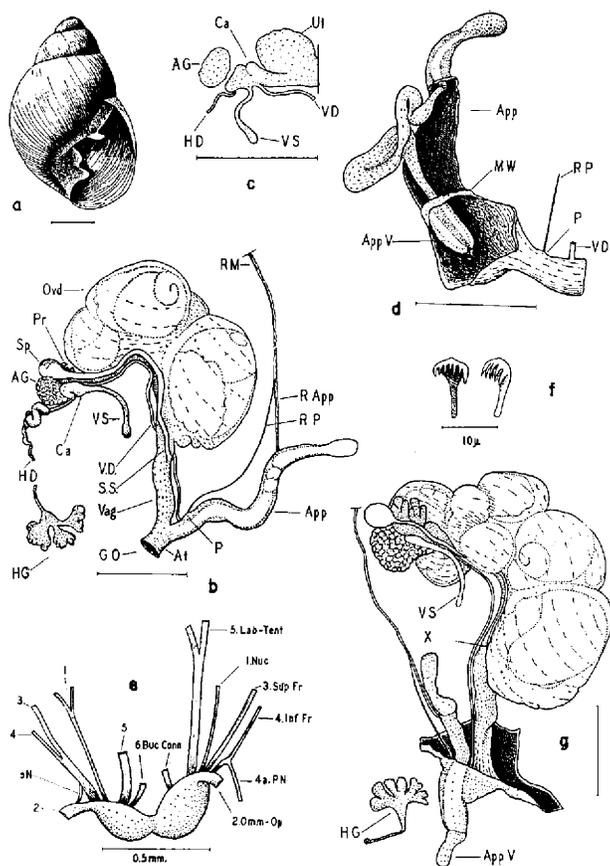


FIGURE 100.—*Elasmias peasianum*: a, adult shell; b, genitalia; c, carrefour complex; d, interior of appendix; e, central nervous system, in part; f, teeth; g, genitalia with appendical verge extruded.

branched-digitate, stout. *Spermatheca* small, ovate; stalk narrow, long. *Vas deferens* thin, narrow. *Oviduct* inflated, embryos numerous. *Penis* vestigial, a minute papilla; interior plain. *Appendix* long (nearly oviducal length), subcylindrical; interior of appendix with long tube, proximally shaped into eversible "verge" (App V), held there by muscular wall; midbody tubular, tapering distally after looping 1 to 1.5 times, uniting with sheath at apical constriction and opening into apical bulb. *Retractors* thin. [One specimen with appendix partially extruded was dissected. "Verge" (App V) emerging from genital orifice.]

Meta- and ananeanic juveniles similar to adult, appendix slightly smaller. Embryos produced at all stages down to ananeanic stage, where two to four are found, the oldest quite well developed.

Central nervous system (shown in figure 100, e) as follows:

*Cerebral ganglion*, right: (1) Small nuchal nerve from left side of frontal nerve directly anterior, branching once near termination. (2) Ommatophoral and optic nerves off usual angle of ganglion. (3) Superior frontal nerve from anteroventral surface to superior base of ommatophore. (4) Inferior frontal nerve off ventrolateral surface, giving off penial (4a) nerve branch lateroposteriad to penis, thence continuing anteriorly to inferior base of ommatophore. Small innominate nerve connects penial to ventral base of ommatophoral nerve (not figured). (5) Large labio-tentacular nerve from left to nuchal nerve with two heavy branches at tip, one to inferior tentacle, the other to labial parts. (6) Buccal connective nerve off inner anteroventral surface to buccal ganglion.

*Cerebral ganglion*, left: All nerves similar to right except two frontals combined into heavy trunk (3 and 4), and small innominate nerve (sN) connects frontal trunk with ommatophoral nerve, as in *Lamellovum auriculella*.

*Teeth* (fig. 100, f) all alike, as small as in *E. apertum*. Head broad, eight- to nine-dentate, all cusps and cusplets nearly alike at first glance but ecto-, ento-, and mesocones visibly larger on close examination. Length 11 microns, width 6.3 microns.

Dissected 150450 (adult genitalia, interior of appendix, central nervous system, teeth), nine or more specimens; paraneanic stage, carrefour (150451), three specimens; metaneanic (150452), two specimens; ananeanic (150454), two specimens.

Type in Academy of Natural Sciences, Philadelphia; Moorea.

Society Islands: Moorea, Uafara Valley, alt. 10-50 ft., Gessler, Cooke, and Kondo, Sept. 22, 150230 (shell figured); Faatoai Valley, on ferns and shrubs, alt. 300-800 ft., Gessler and Cooke, Sept. 24, 150450-150454 (anatomy). More specimens were collected at Tepatu, Maramu, and Mount Teaharoa.

***Elasmias quadrasi*** (Möllendorff). Figure 98, b.

*Tornatellina quadrasi* Möllendorff, 1894, *Nachrichtsblatt d. Deutschen Malak. Gesell.* 26 (1, 2): 16.

*Elasmias quadrasi* Pilsbry and Cooke, 1915, *Man. Conch.* 23: 129.

Figured specimen: Length 2.81 mm., diameter 2.29 (81 percent); apertural axis 1.8, diameter 1.32 (73 percent); last whorl 2.51 (89 percent); parietal lamella 0.2.

Type whereabouts unknown; Mariana Islands.

Mariana Islands: Guam, Paasan, valley side, on fern and shrubs, alt. 300 ft., R. L. Usinger, June 15, 1936 (figured specimen 8880).

The illustrated specimen is from Guam: whorls 4, slightly longer than Möllendorff's (length 2.5 mm., diameter 2 mm.). Bishop Museum also has speci-

mens from Saipan, Tinian, and Rota; and the species extends northward into the smaller Mariana Islands.

**Elasmias schola** Iredale, 1944, Australian Zool. 10 (3): 307, pl. 18, fig. 5.

Type in Australian Museum; Lord Howe Island.

**Elasmias simplicimum**, new species (fig. 101, a-f).

Shell globosely conic, paler than ivory yellow, apical 1.5 whorls tinged with brown, very thin, delicate, translucent, surface dull, nearly smooth, marked with very faint lines of growth, interstices microscopically wrinkled, without indications of spiral lines. *Spire* broadly conic, with nearly straight outlines, apex somewhat blunt. *Suture* simple, well impressed. *Whorls* 4.25, convex, increasing very rapidly; embryonic whorl microscopically wrinkled, with very fine close transverse lines; last whorl rotundate, very large, equal to about 80 percent of shell bulk. *Aperture* large, its outer margin convex, very thin, delicate. *Parietal lamella* very low, threadlike, about 0.25 whorl long. *Columella* simple, sigmoid, with slightly thickened margin, without columellar fold or plate.

Length 4.06 mm., diameter 3.06 (75 percent); apertural axis 2.45, diameter 1.68 (68 percent); last whorl 3.68 (90 percent); parietal lamella not measurable.

Juvenile specimen with 3 whorls, aperture more than 0.5 length of shell. Parietal lamella well developed, about 0.3 whorl long. Columella nearly straight, and truncated at base by fairly strong, spirally ascending fold.

Genitalia typical, with slight variations: *albumin gland* small; *prostate* small, with very small lobes; appendix more slender distally, expanded at base; *carrefour vesicle* almost like that of *E. apertum*. Embryos eight to 15. Closeup of ovotestis illustrated for comparison with *E. apertum* and *E. peasianum*.

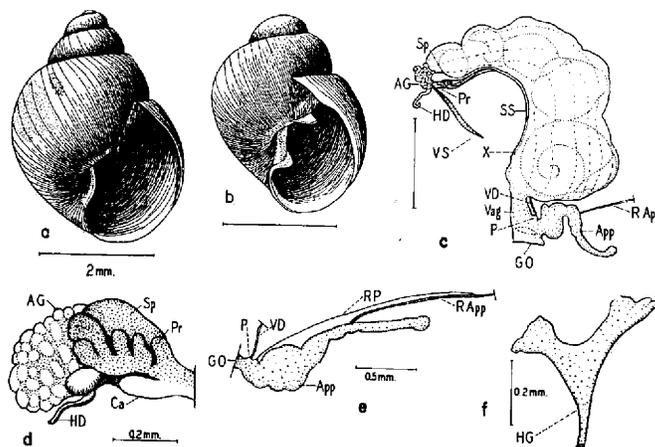


FIGURE 101.—*Elasmias simplicimum*: a, adult shell, holotype; b, meta-ananeanic juvenile; c, genitalia; d, upper organs, magnified; e, penis, closeup; f, ovotestis, closeup.

Dissected 140352, two to three specimens; 137693, five specimens.

Distribution: Rapa, Raivavae.

Rapa: back of Area village (type locality), on *Piper excelsium*, alt. 300-400 ft., Cooke, July 15; holotype 8878, figured meta-ananeanic stage 8879;

paratypes 140352, 140353. East of Area village, mostly on coffee, alt. a few feet above sea level to 150 ft., Cooke and Anderson, July 1, 135738-135742. Maitua, on ferns and shrubs, alt. 600 ft., Cooke and Anderson, July 2, 137693, 137694. Also collected from 20 additional colonies.

Raivavae: southern slope of Mount Turivao, near eastern end of island, alt. 500 ft., W. Anderson, Aug. 11, 147360-147361; southern slope of Mount Muanui, near center of island, on shrubs and trees, alt. 600 ft., Kondo and Anderson, Aug. 8, 146899, 147003.

This species is well distributed over the island of Rapa up to 1,000 feet, and one colony was found on the islet of Karapo Rahi, south of the main island. *E. simplicimum* was more abundant than *E. ovatum* in some colonies. In five colonies both species were taken, but whether they occurred on the same individual plants was not noted.

This species was much more rare on the island of Raivavae, where only five specimens were taken from two localities in native forests separated by about half the length of the island.

*E. simplicimum* is easily separated from *E. ovatum* by its larger size, lighter color, more pointed apex, and lack of fine microscopical spiral striation. The parietal lamella and columellar plate are either lacking or much weaker at all stages of growth than those of *E. ovatum*. In fact, none of the other species of the genus have so weak a columellar plate as that of *E. simplicimum*, although in some both characters are much weaker than in *E. ovatum*.

**Elasmias sundanum** (Möllendorff).

*Tornatellina sundana* Möllendorff, 1897, *Nachrichtsblatt d. Deutschen Malak. Gesell.* 29: 90.

*Elasmias sundanum* Pilsbry and Cooke, 1915, *Man. Conch.* 23: 127.

Type whereabouts unknown; Java.

**Elasmias terrestris** (Brazier).

*Tornatellina terrestris* Brazier, 1876, *Linn. Soc. New South Wales, Proc.* 1: 109.—Pilsbry and Cooke, 1915, *Man. Conch.* 23: 124.

*Elasmias terrestris* Iredale, 1941, *Australian Zool.* 10 (1): 63.

Type whereabouts unknown; New Guinea, Yule Island.

See comment under *E. eucharis*.

**Elasmias wakefieldiae** (Cox).

*Achatinella wakefieldiae* Cox, 1868, *Monogr. Australian Land Shells*, 78.

*Tornatellina wakefieldiae* Petterd, 1877, *Jour. de Conchyl.* 25: 361.—Pfeiffer, 1877, *Mon. Hel. Viv.* 8: 318.

*Elasmias wakefieldiae* Pilsbry and Cooke, 1915, *Man. Conch.* 23: 122, pl. 30, figs. 9, 10.—Iredale, 1937, *Australian Zool.* 8 (4): 300.

Type whereabouts unknown; Australia, C. R. Grafton.

## TRIBE TORNATELLININI

Ovotestis multilobate. Appendix complexly plicose for copulation. Penis with vestigial pilaster. Carrefour vesicle large, conspicuous. (After *Fernandezia bulimoides*.)

Pauci- ( $\pm 5$ ) to multiwhorled ( $\pm 11.5$ ) shells of Juan Fernandez range from those in which apertural armature is completely absent in all growth stages to those having armature during some growth stages. Height approximately 2.8-12 mm. Shapes from ovate-conic through bulimoid and conic to turrite-cylindric.

Odhner (1922) gives a full account of the species of land shells collected by the Swedish Pacific Expedition on the Juan Fernandez Islands and a summary of the relationships of the tribe. The earliest descriptions—by Anton, Férussac, King, Pfeiffer, and Reeve—were undoubtedly based on collections made by Cuming when he visited the islands on November 1 to 12, 1827 (St. John, 1940). About 20 species were described from the Cuming material, and an additional four species, described by King, may also have been Cuming's. After the Challenger Expedition visited these islands during November 13 to 15, 1875, 10 species were enumerated by E. A. Smith, one of which was described as new. However, our greatest knowledge of the fauna of Juan Fernandez comes from the Swedish Pacific Expedition conducted by Carl Skottsberg, whose party was on the islands from December 1, 1916 to April 30, 1917. The material was identified by Odhner, who enumerated 31 species, of which six were introduced. The collectors of six species of *Fernandezia* described by Pilsbry are unknown; but the specimens came to the Academy of Natural Sciences, Philadelphia, through T. B. Wilson. Only one of these species was re-collected by the Swedish Pacific Expedition.

About 50 species of Juan Fernandez land mollusks have been enumerated. Allowing for synonymy, for wrong localization, and for introduced forms, the number of endemic species should total about 35 to 40. Most endemic species are known only from Masatierra; six are from Masafuera; and one is from both islands.

A most interesting fact, and one which may prove of utmost importance, is that no land operculates have been reported from these islands. In most faunas of Pacific islands the land operculates represent a fair proportion of the known species.

The genera *Tornatellina* (*s.s.*) and *Fernandezia* differ markedly from the genera found on other Pacific islands not only in anatomical but, to a smaller extent, in conchological characters.

*Tornatellina* is represented by seven species, if we accept the localities of Cuming. (*T. minuta* Anton and *T. reclusiana* Petit were re-collected by the Challenger or Swedish expeditions.) In the conformation and apertural characters the five species collected by the Swedish expedition represent distinct

forms, according to Odhner. Only one of these (*T. bilamellata* Anton) has been dissected. In two of these species (*T. bilamellata* and *T. conica*) the palatal wall has a broad vertical callus, not as prominent as that in *Lamellidea* but similar to that of some species of *Tubuaia*.

Juvenile specimens of four of the five Swedish expedition species, excepting *T. aperta*, have exceptionally strong, subhorizontal columellar lamellae. *T. aperta* also differs from the others, in that it has no palatal folds during the neanic stage. In some ways it appears to be an intermediate form between *Tornatellina* and *Fernandezia*. In three of the species the parietal lamella is lacking in the adult stage but is present in different degrees of development during the neanic stage. One species, *T. plicosa*, is absolutely unique among all the species of the family which have a parietal lamella, in that a number of juvenile specimens have an additional minute lamella between the parietal lamella and the insertion of the aperture. Altogether, these five species of *Tornatellina* display much more diversification than is exhibited in any other genus of the family.

The species of *Fernandezia* (except *F. cylindrella*) form a much more compact group than those of *Tornatellina* and are separated on much fewer conchological characters. All species of *Fernandezia* lack the parietal lamella at all stages of growth, the columella is greatly simplified, and there are no palatal folds. To some extent, *Fernandezia* also differs from *Tornatellina* in its anatomy. *F. cylindrella* is apparently an intermediate form linking *Fernandezia* with *Tornatellina*. In the number of whorls and in the conformation of the spire *F. cylindrella* approaches some of the species of *Tornatellina*; and in these characters it is absolutely unlike any of the species of the genus.

Undoubtedly a more extensive survey of Juan Fernandez would yield many more such interesting species.

#### Genus *Tornatellina* Pfeiffer

*Tornatellina* Beck (in part), 1837, Index Molluscorum, 80. *Nomen nudum*.

*Strobilus* Anton (in part), 1839, Verzeichniss der Conchylien, 46.

?*Tornatellina* Gray, 1847, Zool. Soc. London, Proc., 175. Type *Tornatellina clausa* = *T. bilamellata*.

*Tornatellina* Beck, Pfeiffer (in part), 1881, Nomenclator Hel. Viv., 341.

*Tornatellina* Pilsbry (in part), 1910, Nautilus 23 (10): 123.

*Tornatellina* Pilsbry and Cooke (in part), 1915, Man. Conch. 23: 132.

*Tornatellina* Odhner, 1922, Natural History of Juan Fernandez and Easter Island 3 (2): 235.

*Tornatellina* Pilsbry and Cooke, 1933, Nautilus 47 (2): 60.

Elongate-conic to ovate-conic shells (Juan Fernandez)  $\pm 2.8-7.2$  mm.,  $\pm 5$  to 10 whorls, having parietal or palatal folds (or both) at some stage of growth, columellar lamellae well developed.

Genitalia with large "carrefour vesicle" depending from carrefour, penis vestigial, appendix well developed, ommatophoral retractor free of peni-oviducal angle. Viviparous.

Type species: *T. bilamellata* (Anton).

Pilsbry and Cooke thoroughly covered the history of the genus *Tornatellina* (*s.l.*) in the Manual of Conchology (1915, pp. 132-134). Later, following Odhner's excellent work on the Juan Fernandez tornatellinids (1922), they brought it up to date (1933, pp. 59, 60).

In brief, from Beck's first mention of *Tornatellina* (1837) to Pilsbry's initial attempt at the classification of its multifarious species (1910), the genus had grown into a large heterogeneous group. Pilsbry's article was a preliminary to volume 3 of the Manual of Conchology, in which he and Cooke defined the genus to include four sections: *Tornatellina*, 12 species; *Lamellina* = *Lamellidea* (p. 273), 12 species; *Tornatellinops*, 23 species; and *Elasmatina*, four species. Appended to the same volume (pp. 272-273) are two additional species of *Tornatellina* (section ?): *T. norfolkensis* Preston (subspecies *moohuensis* and *nepeanensis*) and *T. duplicilamellata*, which we have here listed under Lamellideinae.

Odhner restricted *Tornatellina* to the Juan Fernandez species, and this was accepted by Pilsbry and Cooke in 1933. No change in the status of *Tornatellina* has been made in the present work.

Exact localities given for each species are by Odhner and Cuming. Otherwise, the broad term Juan Fernandez applies.

*Tornatellina* <sup>= *skottsbergi*</sup> *aperta* Odhner, 1922, Natural History of Juan Fernandez and Easter Island 3 (2): 238, pl. 9, figs. 45, 46.

Type in Göteborg Museum (*vide* Odhner).  
Masatierra (Odhner).

***Tornatellina bilamellata*** (Anton).

*Strobilus bilamellatus* Anton, 1839, Verzeichniss der Conchylien, 46. Subgenus of *Clausilia*.

*Tornatellina clausa* Beck, 1837, Index Molluscorum, 80. *Nomen nudum*, subgenus of *Achatina*.

*Tornatellina clausa* Pfeiffer, 1842, Symbolae 2: 55.

*Tornatellina* (*Strobilus*) *bilamellata* Pfeiffer, 1848, Mon. Hel. Viv. 2: 393.

*Tornatellina bilamellata* Küster, 1852 (-1859), Conch.-Cab., Pupa, 1 (15): 147, pl. 18, figs. 3-5.

*Tornatellina bilamellata* Pfeiffer, 1853, Mon. Hel. Viv. 3: 527.

*Tornatellina bilamellata* Pfeiffer, 1856, Malak. Blätt. 2: 170. Subgenus of *Achatina*.

*Tornatellina skottsbergi* ODHNER n. nom. pro *Tornatellina aperta* ODHNER 1922 (Nat. Hist. of Juan Fernandez and Easter Island, 3: 238) non *Tornatellina aperta* ANCEY 1903 (J. de Conch., 51: 295) [= *luakabaense* PILSBRY & COOKE 1915] non *Tornatellina aperta* PEASE 1864 (Proc. zool. Soc. London, 1864: 673 [= *Elasmias aperta* (PEASE)]).

Archiv f. Moll. 91:125, 1962 NILS HJALMAR ODHNER, Stockholm.

*Tornatellina bilamellata* Albers, 1860, Die Heliceen, 259. Subgenus of *Cionella*.

*Tornatellina bilamellata* Pfeiffer, 1868, Mon. Hel. Viv. 6: 265.

Not *Tornatellina* (*Strobilus*) *bilamellata* Schmeltz, 1874, Cat. Mus. Godefroy 5: 90.

*Tornatellina bilamellata* Pfeiffer, 1877, Mon. Hel. Viv. 8: 319.

*Tornatellina* (*s.s.*) *bilamellata* Pilsbry and Cooke, 1915, Man. Conch. 23: 139, pl. 34, figs. 9, 10.

*Tornatellina bilamellata* Odhner, 1922, Natural History of Juan Fernandez and Easter Island 3 (2): 235, pl. 9, fig. 36.

Type whereabouts unknown.

Masatierra (Odhner).

***Tornatellina callosa*** Odhner, 1922, Natural History of Juan Fernandez and Easter Island 3 (2): 238, pl. 9, figs. 43, 44.

Type in Riksmuseum, Stockholm (*vide* Odhner).

Masatierra (Odhner).

***Tornatellina conica*** Anton.

*Tornatellina trochiformis* Beck, 1837, Index Molluscorum, 80. *Nomen nudum*, subgenus of *Achatina*.

*Strobilus conicus* Anton, 1839, Verzeichniss der Conchylien, 46. Subgenus of *Clausilia*.

*Tornatellina trochiformis* Pfeiffer, 1842, Symbolae 2: 55. Subgenus of *Achatina*.

*Elasmatina cumingiana* Petit, 1843, Zool. Soc., London, Proc., 2.

*Tornatellina trochiformis* Pfeiffer, 1848, Mon. Hel. Viv. 2: 392; 1853, 3: 525; 1859, 4: 651; 1868, 6: 263.—Küster, 1852 (-1859), Conch.-Cab., Pupa, 1 (15): 154, pl. 18, figs. 28, 29.—E. A. Smith, 1884, Zool. Soc., London, Proc., 280.

*Tornatellina* (*Elasmatina*) *conica* Pilsbry and Cooke, 1915, Man. Conch. 23: 189.

*Tornatellina* (*Elasmatina*) *trochiformis* Pilsbry and Cooke, 1915, Man. Conch. 23: 190, pl. 53, fig. 14.

Type whereabouts unknown.

Masatierra (Odhner).

***Tornatellina minuta*** (Anton).

*Achatina minuta* Anton, 1839, Verzeichniss der Conchylien, 44. Subgenus of *Bulimus*.

*Tornatellina minuta* Pfeiffer, 1842, Symbolae 2: 130; 1848, Mon. Hel. Viv. 2: 392.—Küster, 1852, Conch. Cab., Pupa, 1 (15): 150, pl. 18, figs. 14, 15.

*Tornatellina (Tornatellinops) minuta* Pilsbry and Cooke, 1915, Man. Conch. 23: 187, pl. 40, fig. 7.

Type whereabouts unknown.

***Tornatellina plicosa*** Odhner, 1922, Natural History of Juan Fernandez and Easter Island 3 (2): 237, pl. 9, figs. 38-42.

Type in Riksmuseum, Stockholm.

Masatierra (Odhner).

***Tornatellina reclusiana*** (Petit).

*Elasmatina reclusiana* Petit, 1843, Zool. Soc. London, Proc., 2.

*Tornatellina (Elasmatina) reclusiana*, Pilsbry and Cooke, 1915, Man. Conch. 23: 189.

Type whereabouts unknown.

Masafuera (Cuming).

#### Genus **Fernandezia** Pilsbry

*Fernandezia* Pilsbry, 1911, Man. Conch. 21: 93.—Odhner, 1922, Natural History of Juan Fernandez and Easter Island 3 (2): 240.

Type species *F. wilsoni* in Academy of Natural Sciences, Philadelphia (10166).

"Shell imperforate, varying from ovate to oblong-turrite, thin, yellow or pale-brown, glossy, striate or weakly plicate. Initial  $1\frac{1}{2}$  to  $1\frac{3}{4}$  whorls smooth or very delicately striate spirally, semiglobose, forming an obtuse summit. Aperture irregularly ovate, subvertical, the outer lip a little thickened, having a smooth finish when adult; the columella short, bearing a more or less prominent, spirally entering fold or lamella. Soft anatomy unknown. Type: *F. wilsoni*." (Pilsbry.)

Since discovery of new species *F. cylindrella* Odhner, above diagnosis may be expanded to include "turrite-conic." Shells  $\pm 3.5$ -12 mm.,  $\pm 5$ -11.5 whorls, no parietal or palatal folds in any stage of growth, columella usually simple; viviparous.

Genitalia. *Ovotestis* multilobate; lobes  $\pm 10$ -12, all efferent ducts focusing to a single point; follicles evident only as terminal knoblets, tightly packed. *Hermaphrodite duct* swollen, convoluted. *Albumin gland* rather large, well developed (see Odhner, fig. 17, p. 243). *Prostate* well developed, multifolliculate. *Spermatheca* quite small, ovate; stalk long. *Vas deferens* narrow, terminating at base of penis. *Penis* vestigial; interior with vestigial pilaster or muscular tissue. *Appendix* large, copulatory; interior complexly rugose, with muscular cords. *Retractor* bifid; penial retractor terminal, appendical at upper 0.25; both thin. *Carrefour* with long muscular vesicle descending to, and terminally embedded in, columellar muscle. Penial innervation unknown.

Pilsbry (1911) states that "These shells resemble species of *Glessula* and *Leptachatina* so closely that only their geographical remoteness gives reason for belief that they will prove generically distinct, when the soft parts can be examined." Cooke concurs with Pilsbry regarding the resemblance to species of *Leptachatina*.

Exact localities are by Odhner. Otherwise, the broad term Juan Fernandez applies.

**Fernandezia bulimoides** (Pfeiffer). Figures 102, a-g; 103, a-i.

*Achatina bulimoides* Pfeiffer, 1846, Zool. Soc. London, Proc. 14: 116; 1848, Mon. Hel. Viv. 2: 271.—Reeve, 1849, Conch. Icon., 5, pl. 19, fig. 103, (*vide* Pilsbry).

*Spiraxis bulimoides* Pfeiffer, 1852, Mon. Hel. Viv 3: 472.

*Stenogyra (Nothus) bulimoides* E. A. Smith, 1884, Zool. Soc. London, Proc., 280.

*Fernandezia bulimoides* Pilsbry 1911, Man. Conch. 21: 94, pl. 14, fig. 4.—Odhner, 1922, Natural History of Juan Fernandez and Easter Island 3 (2): 241, pl. 9, fig. 47.

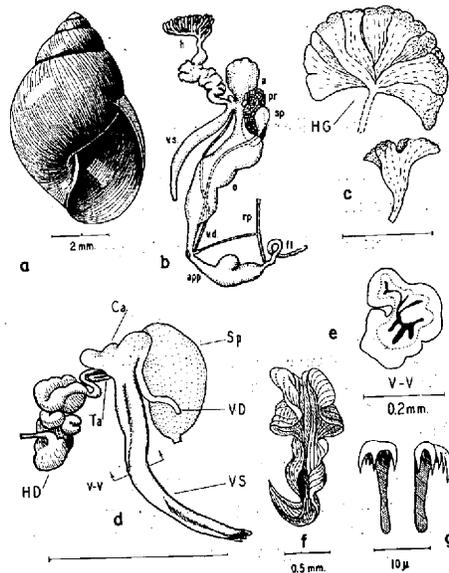


FIGURE 102.—*Fernandezia bulimoides*: a, shell; b, genitalia, after Odhner; c, oovestis (HG), one follicle shown below; d, seminal vesicle; e, cross section of seminal vesicle at V-V in d; f, radula; g, teeth.

"Shell [fig. 102, a] ovate-conic, thin, striatulate, covered with a pellucid corneous-buff epidermis. Spire conic, acute; whorls  $5\frac{1}{2}$ , scarcely convex, the last more swollen, as long as the spire. Columella twisted above, thread-like very obsoletely truncated above the base of the broad, semioval aperture, provided with a thin callus covering the ventral part of the preceding whorl. Peristome simple, thin. Length 11, diameter 6, aperture  $6 \times 3.5$  mm." (Pfeiffer, Pilsbry trans.)

Genitalia. *Oovestis* (fig. 102, c) multilobate; lobes  $\pm 10$  to 12, their efferent ends converging at a common point, appearing stringy as in *Pityisini*, the distal ends showing tips of numerous compactly bundled follicles. *Carrefour vesicle* stemming off lower part of *carrefour*, extending ventrad to columellar muscle, strongly embedded therein; strongly

muscular, hollow, chamber empty in dissected specimen, internally strongly folded longitudinally. (This confirms H. B. Baker's statement to Cooke in 1943 that the *vesicula seminalis* of Odhner was an expansion of the carrefour.) *Albumin gland* below carrefour, composed of small digitate follicles stemming erectly from central core. *Prostate* lying upon carrefour; follicles of various sizes and shapes, lying flat, not erect as in albumin gland. This single specimen contained 20 to 22 embryos.

Appendix. *Gross anatomy* (fig. 103, a). Three principal parts apparent: Odhner's "flagellum" (A) at very apex, distad of appendical retractor; large and broad midbody containing principal stimulator (B); and narrow twisted stalk arising above atrium (C), terminating at narrowed lower part of B, giving off penis near middle (P), internally muscular. *Internal anatomy* (fig. 103, b-i). Stalk (fig. 103, b); wall vertically wrinkled with low folds (Fo); muscular cord (MC-1) arising below penis (P) to give branch cords to vestigial penis, a vertically rising cord (MC-3), and the principal knotty cord (MC-2) which is enlarged and which divides into two branches (MC-4, MC-4), these latter, together with MC-3, fusing with muscular wall above. Penis reinforced by two opposing hard muscular plates, not unlike the two cotyledons of a bean seed, the whole of which, in conjunction with principal muscle cord, probably act as stimulators. Dorsad stalk leads into a simple chamber (Ch) where folds of stalk terminate (Fo). Midbody

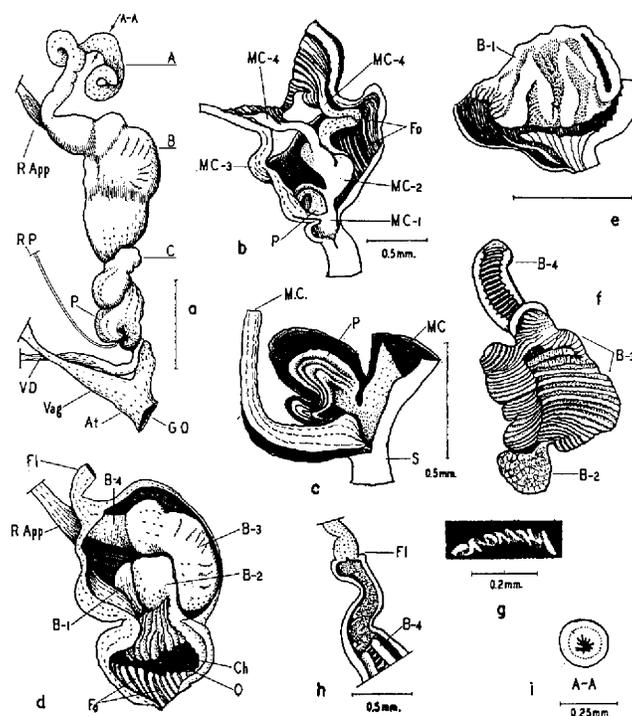


FIGURE 103.—*Fernandezia bulimoides*: a, penis and appendix (A, B, and C are three divisions of male organ); b, penio-appendical stalk at penis and just above it at C; c, interior of vestigial penis; d, interior of principal portion of appendix at B; e, interior of appendix at B-1; f, interior of appendix at B-2, B-3, B-4; g, single ruga (in part) at B-3, magnified; h, interior of flagellum, in part; i, cross section of flagellum at A-A.

contains muscular convoluted tube with large orifice below (O) and connecting with flagellum at apex. Portion B-1 appears to be lowest part of principal copulatory stimulator. B-1 hollow or double-walled, internally heavily rugose, rugae sparse, heavy, inverted V-shaped. B-2 appears to be antechamber to B-3, connecting orifice with B-1, wall simple, faintly papillose, rough. B-3 strongly, circularly trabeculate with numerous transparent rugae (highly magnified), individual ruga much twisted, appearing as a curtain when stretched. B-4 narrow, short, tubular, heavily trabeculate, rugae harder than those of B-3. Flagellum simple, tubular, pebbled throughout. [Order of chambers from below to above: O, B-2, B-1, B-3, B-4, Fl.]

*Radula* (fig. 102, *f*) not different from that of *Achatinella* and other genera of family. Teeth (fig. 102, *g*) about the size of that of *Auriculella auricula*; head quite broad, seven- to eight-dentate; one ecto-, one ento-, and one mesocone plus (usually) four fine cusplets at the usual position. Length 17 microns, width 6.6 microns.

Dissected 189700, one specimen only.

Type whereabouts unknown.

Masatierra (Odhner).

The internal structure of the *Fernandezia* appendix is unique and finds no counterpart in any other tornatellid genus. The appendix has not only taken over the function of the penis but has become complex. It also has a flagellum which probably functions as an ordinary appendix. The vestigial penis still contains the remains of a muscular intromittent organ (pilaster). This muscular structure may be homologous to the achatinellid pilaster.

As classification of the groups of Achatinellidae depends a good deal on the type of ovotestis, it was deemed desirable to dissect and figure the ovotestis of *F. bulimoides*, the animal of which was sent us by Odhner. A comparison between our figure and Odhner's shows that what at first appear to be follicles in Odhner's figure are, in reality, immature lobes (fig. 102, *b*), and it is our belief that he may have figured a subadult or paraneanic specimen. The *Fernandezia* ovotestis is truly multilobate in type, although it is unique. It thus appears that the Elasmiatini and Tornatellinini are much farther apart than the related tribes Tornatellinoptini and Lamellideini.

The single specimen of *Fernandezia bulimoides* which Odhner generously sent to us in 1942 had evidently been dropped into a strong alcohol solution or into formalin in the field, for it was strongly contracted and hard. Fortunately, it was only slightly dehydrated, and we were able to dissect it after hydrating it.

#### ***Fernandezia conifera* (Reeve).**

*Achatina conifera* Reeve, 1849, Conch. Icon., 5, pl. 18, fig. 98 (*vide* Pilsbry).

—Pfeiffer, 1853, Mon. Hel. Viv. 3: 495; 1868, 6: 225.

*Fernandezia conifera* Pilsbry, 1911, Man. Conch. 21: 98, pl. 14, fig. 5.

Type whereabouts unknown.

#### ***Fernandezia consimilis* (Reeve).**

*Achatina consimilis* Reeve, 1849, Conch. Icon., 5, pl. 19, fig. 104 (*vide* Pilsbry).

*Spiraxis consimilis* Pfeiffer, 1853, Mon. Hel. Viv. 3: 471; 1859, 4: 574; 1868, 6: 192.

*Stenogyra (Euspiraxis) consimilis* Pfeiffer, 1881, Nomenclator Hel. Viv., 324.

*Fernandezia consimilis* Pilsbry, 1911, Man. Conch. 21: 94, pl. 14, fig. 11.  
Type whereabouts unknown.

**Fernandezia cylindrella** Odhner, 1922, Natural History of Juan Fernandez and Easter Island 3 (2): 242, pl. 9, fig. 49.

Type in Riksmuseum, Stockholm.  
Masatierra (Odhner).

**Fernandezia diaphana** (King).

*Achatina diaphana* King, 1830-1831, Zool. Jour. 4: 342 (*vide* Pilsbry).

*Fernandezia diaphana* Pilsbry, 1916, Man. Conch. 23: 272.

Type whereabouts unknown.

**Fernandezia expansa** Pilsbry, 1911, Man. Conch. 21: 95, pl. 14, fig. 1.

Type in Academy of Natural Sciences, Philadelphia (10164).

**Fernandezia inornata** Pilsbry, 1911, Man. Conch. 21: 97, pl. 14, figs. 14, 15.

Type in Academy of Natural Sciences, Philadelphia (10168).

**Fernandezia longa** Pilsbry, 1911, Man. Conch. 21: 99, pl. 14, fig. 6.

Type in Academy of Natural Sciences, Philadelphia (10168).

**Fernandezia philippiana** Pilsbry, 1911, Man. Conch. 21: 96, pl. 14, figs. 2, 3.

Type in Academy of Natural Sciences, Philadelphia (10165).

**Fernandezia splendida** (Anton).

*Bulimus (Achatina) splendida* Anton, 1839, Verzeichniss der Conchylien, 44.

?*Achatina splendida* Anton, 1847, Pfeiffer, in Philippi, Abbild. u. Beschreib. neuer Conch. 2: 214, pl. 1, fig. 11 (*vide* Pilsbry).—Küster, 1845 (-1855), Conch. Cab., *Bulimus*, 1 (13): 339, pl. 37, figs. 10-12.—Pfeiffer, 1848, Mon. Hel. Viv. 2: 271.—Reeve, 1849, Conch. Icon. 5: pl. 19, fig. 100 (*vide* Pilsbry).

*Spiraxis splendida* Pfeiffer, 1853, Mon. Hel. Viv. 3: 472; 1859, 4: 575; 1868, 6: 193.

*Spiraxis (Nothus) splendida* Pfeiffer, 1856, Malak. Blätt. 2: 167.

*Oleacina (Nothus) splendida* H. and A. Adams, 1858, Genera of Mollusca 2: 105.

*Stenogyra (Nothus) splendidula*, E. A. Smith, 1884, Zool. Soc. London, Proc., 280.

*Fernandezia splendida* Pilsbry, 1911, Man. Conch. 21: 98, pl. 14, figs. 9, 10.  
—Odhner, 1922, Natural History of Juan Fernandez and Easter Island 3 (2): 241, pl. 9, fig. 48.

Type whereabouts unknown.

Masatierra (Odhner).

***Fernandezia tryoni*** Pilsbry, 1911, Man. Conch. 21: 97, pl. 14, figs. 12, 13.—  
Odhner, 1922, Natural History of Juan Fernandez and Easter Island 3 (2): 242.

Type in Academy of Natural Sciences, Philadelphia (10167).

Masatierra (Odhner).

***Fernandezia wilsoni*** Pilsbry, 1911, Man. Conch. 21: 96, pl. 14, figs. 7, 8.

Type in Academy of Natural Sciences, Philadelphia (10166).

#### SUBFAMILY TORNATELLIDINAE

Shells small, dextral, perforate or umbilicate, the perforation nearly always extending through axis to initial whorls; ovate, ovate-conic, oblong, or pyramidal-conic; whorls 3.5 to 9.5, flat to convex. Parietal lamella weak to strong. Palatal folds or callus absent in all but two species of *Tornatellides* (*waianaensis*, *rudicostatus*). Columella with no folds, or one or two folds in adult; usually with two folds in juveniles.

Oviparous or viviparous.

Penis innervated by cerebral ganglion. Right ommatophoral retractor usually free of peni-oviducal angle but sometimes passing through. Penis with or without appendix; with either reflexed or modified not recurved achatinellid pilaster. Appendix, when present, without retractor; internally without secretory-ejaculatory apparatus, the cavity simple, plain. Albumin gland relatively large, well-developed. Prostate small, fan-shaped. Spermatheca free or partially hidden among albumin or prostate follicles, stalk entering oviduct either above youngest embryo at junction of oviduct and carrefour or below oldest embryo or egg. Ovotestis bi- and tri-lobate to five- to seven-lobate.

#### TRIBE TORNATELLIDINI

Shells small, 2.1 × 1.1 mm. (*Tornatellides leptospira*) to 4 × 1.8 mm. (*T. productus*), mostly about 2.5 to 3 mm. Whorls 3.75 (*T. subperforatus kermadecensis*) to 8 (*T. productus*), mostly about 6, generally convex. Periphery not angular. Base usually convex or saccate.

Viviparous.

With appendix. Right ommatophoral retractor passing or not passing through peni-oviducal angle. Spermathecal stalk entering oviduct above earliest embryo at carrefoural-oviducal junction.

#### Genus *Tornatellides* Pilsbry

*Tornatellides* Pilsbry, 1910, *Nautilus* 23 (10) : 123. Type *T. simplex* Pease [= *T. oblongus* (Anton)].—Pilsbry and Cooke, 1915, *Man. Conch.* 23 : 192.

"The shell is small, dextral, ovate-conic or oblong, *perforate* or *umbilicate* in all post-embryonic stages; thin. Aperture ovate, armed with a parietal lamella and one or two columellar lamellae (often wanting in the adult stage); palatal wall simple. *Reproduction viviparous*. Mantle maculate with black." (Pilsbry and Cooke.)

Genitalia. *Ovotestis* bilobate, rarely trilobate. *Duct* fairly large, convoluted, distended in middle. *Albumin gland* relatively large; follicles numerous, ovate to digitate. *Prostate* small, follicles few, digitate. *Talon and carrefour* small. *Spermatheca* small, ovate to oblong, lying on albumin gland, its stalk hidden by follicles, very short, entering oviduct at its junction with carrefour above embryos. *Oviduct* large, diaphanous; lower oviduct narrow, medium in length; embryos two to eight, all except lowest encased in thick yolk masses. *Penis* slender, narrow below, slightly enlarged above,  $\pm 0.5$  oviducal length; interior of penis with only ascending pilaster; retractor terminal. *Appendix* subterminal, short,  $\pm 0.5$  penial length, subcylindrical, apex blunt or vestigial with small terminal papilla; interior without internal tubular structure, simple, plain; retractor lacking. *Vas deferens* thin, narrow, Y subapical. *Atrium* short, narrow.

Nervous system (see *T. oblongus*).

The following 10 species of *Tornatellides*, which fall into five groups, were dissected but not described or figured except for those dissected for the ommatophoral retractor.

(1) *compactus*: *compactus* (171600), Hawaii, six specimens; *procerulus* (38739), Maui, two; and *subangulatus* (38637), Maui, four. (2) *oblongus*: *tryoni* (89742), Bonins, three. (3) *perkinsi*: *macromphala* (38830), Maui, three; and *perkinsi* (48581), Kauai, one. (4) *euryomphala*: *euryomphala* (38468), Maui, one; *leptospira* (34833), Oahu, four; and *pyramidatus* (189784), Hawaii, two. (5) *terebra*: *drepanophora* (48584), Kauai, three.

*Tornatellides* differs from most of the other genera of the family in having an umbilicus. The only other genera with this character are *Tornatellaria*, restricted to the Hawaiian Islands, and *Pitys* from Rapa. However, since this report was written the genus *Philopoa*, formerly considered a *Tornatellides*, has been erected. It is subumbilicate, has the anatomy of *Tornatellaria*, and is viviparous.

*Tornatellides* is viviparous, whereas *Tornatellaria* and *Pitys* are oviparous. *Tornatellides* and *Tornatellaria* are perforate at all stages of growth, and *Pitys* is perforate in only the ephebic stage. In embryonic specimens of *Tornatellides* the perforation is represented by a cleftlike slit.

Little can be added to the description and discussion of *Tornatellides* in the *Manual of Conchology* (Pilsbry and Cooke, 1915, p. 192). The only additional

observation concerns the parietal lamella. Two to five specimens of 13 species have been partly opened to determine the length of the parietal lamella. These are representative species from each of the following seven groups of species.

(1) *oblongus*: *oblongus*; (2) *compactus*: *subangulatus*, *confusus*; (3) *idae*: *idae*, *stokesi*; (4) *cyphostyla*: *cyphostyla*, *moomomiensis*; (5) *perkinsi*: *perkinsi*, *macromphala*; (6) *euryomphala*: *euryomphala*, *ronaldi*, *brunneus*; (7) *terebra*: *serrarius*.

The adult shells of all species of *Tornatellides* have a very short parietal lamella, ranging from 0.33 to 0.50 whorl long. In a few examples this lamella continues as a faintly indicated line to a total length of about one whorl. With most juvenile specimens, this continuation consists of a distinct, raised, thread-like line.

The distribution of this genus differs completely from that of any other genus of the family, in that it occupies most of the high islands forming the northern, eastern, and southern peripheries of the islands of the Pacific Ocean. Beginning at the northwest (see map, fig. 104), the genus has representatives from Hongkong, Formosa, the Ryukyus, and the Izu and Ogasawara (Bonin) Islands. In the Hawaiian chain it extends from Ocean Island (Kure) to Hawaii, to Johnston Island on the north. On the east it is in the Revillagigedos, Galapagos, and Marquesas. On the south it extends from Pitcairn and Henderson through the Mangarevan islands to Rapa and through all of the high islands of the Australs, Society Islands, Cook Islands, and the Kermadecs to New Zealand.

Bishop Museum has representative collections from scores of islands in the Pacific, a number of which are complete enough to form a fairly good idea of which genera inhabit the various islands. It is remarkable that not a single specimen of *Tornatellides* has been taken on a single coral island in the south-central Pacific, although the genus is abundant on the six low islands of Laysan, Lisianski, Pearl and Hermes, Midway, and Ocean to the northwest of Hawaii and Johnston to the southwest.

No specimens of this genus have been reported from any of the Tuamotu Islands or from the Line Islands (Flint to Palmyra) although fairly complete shell collections from Timoe, Oeno, South Marutea, Hao, Anaa, Tepoto, and Makatea are in the Museum, as well as smaller collections from half a dozen other islands in the Tuamotu Archipelago and good collections from Flint, Tongareva, Christmas, Fanning, Washington, and Palmyra. Other groups of low islands from which we have fair to good collections, but on which no *Tornatellides* have been found, are the Phoenix, Pukapuka (Danger), Tonga, Ellice, and Marshall Islands and the low Caroline Islands. Of the high islands well represented in the Museum collection, Fiji, Tonga, and Palau have no known representatives of *Tornatellides*.

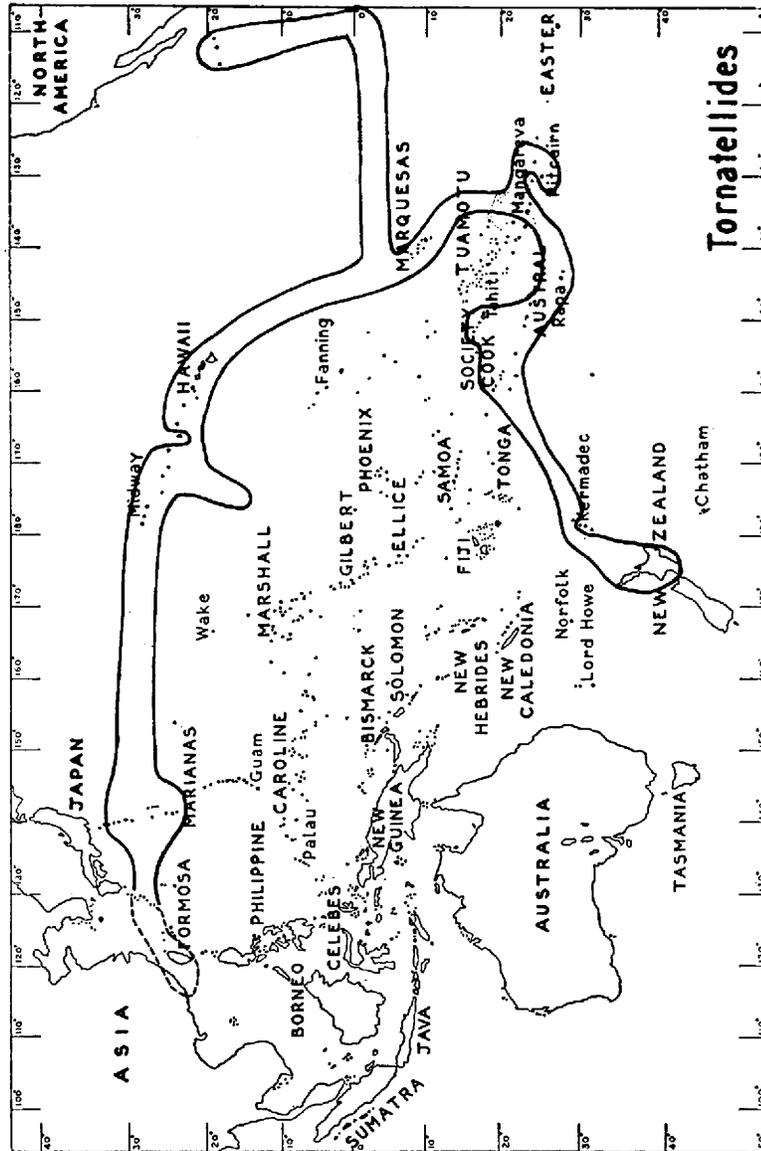


FIGURE 104.—Distribution of genus *Tornatellides*; broken lines indicate extralimital distribution. (Ebon record, Pease collection, not confirmed.)

The significance of this distribution is not clear. Though species of *Tornatellides* are absent from many low coral islands of the central Pacific, these islands are not unsuited to the genus. Examples of it are abundant on the coral islands of Johnston and the western islands of the Hawaiian group (Laysan to Kure). Nor can the absence of the genus from the southern coral islands be due to climate, as a large number of these islands are farther from the equator than is Johnston Island.

The Mangarevan Expedition found no *Tornatellides* on 11 low coral islets on reefs surrounding the high islands of Mangareva, Raivavae, Tubuai, and Raiatea at various distances (0.75-3.5 miles) from the shores of the main islands. This despite the fact that on most of the islets land snails were plentiful and despite the fact that *Tornatellides* were abundant on the four main islands just back of the beach under vegetative and soil conditions similar to those on the coral islets.

Two "lots" of *Tornatellides* in the Museum are of doubtful authenticity. The first (115298), received in exchange, is labeled "*garreti* Pease Mss." from Ebon Island. However, this species is not mentioned by Pease in his paper on Ebon Island landshells (1860, p. 439) and W. J. Clench says that there are no *Tornatellides* from Ebon Island in the Pease Collection, now in the Museum of Comparative Zoölogy. The second (188256) is a single dead juvenile specimen from sweepings presumed to have been collected on the island of Tau, Samoa, by Wray Harris, who took numerous sweepings there; but it is obviously a Hawaiian species with the characteristic form, columellar folds, and parietal lamella of a species related to, if it isn't actually, *Tornatellides procerulus*. It must have been accidentally mixed with the Tau lot when the material was sorted at Bishop Museum. We feel sure that if *Tornatellides* occurred on the island at all, additional specimens would have been taken.

The only species needing special mention is *Tornatellides chathamensis* (Dall) from the Galapagos Islands which is unlike any of the forms of *T. oblongus* from the eastern and southern Pacific islands. Bishop Museum is fortunate in having two series of this species collected by Dr. Pilsbry in 1929 (115299 from Chatham Island and 115300 from Albermarle Island).

In its rather wide embryonic whorls, convex outlines, and the one or two moderately to well-developed columellar folds in juvenile specimens, this species approximates some of the Hawaiian forms though it does not closely match any one species. None of the specimens at hand are as conical as the one figured by Dall (1896, pl. 16, fig. 9) but have more convex outlines and slightly flatter whorls. Undoubtedly, the more or less long isolation of the Galapagos species has caused it to develop its own type of shell.

*T. chathamensis* is of about the same size and outline as *T. oahuensis*, but it has a slightly stronger parietal lamella. Immature stages of *T. oahuensis* have no columellar lamellae, whereas *T. chathamensis* has lamellae. There is

a close resemblance between *T. kahoolavensis* and *T. chathamensis* the outlines of which are slightly flatter, the parietal lamella a little stronger, and the columellar lamellae stronger in the juveniles.

Recently acquired knowledge indicates that the following generic changes should be made in the earlier classification (Pilsbry and Cooke, 1915).

*Tornatellides simplex* (Pease) and *T. oblongus* (Anton) are the same species, the name *oblongus* having priority.

*Tornatellides perforatus* Liardet should be *Lamellidea pusilla* Gould, based on the type material in the British Museum.

*Tornatellides inconspicuus* Brazier should be *Tornatellinops inconspicuus*, based on our examination of Iredale's figure of *Tornelasmias inconspicuus* from Lord Howe Island (1944, pl. 18, fig. 7).

*Tornatellides thaanumi* Cooke and Pilsbry should be *Tornatellaria thaanumi*, based on its genitalia, oviparity, and a reexamination of its shell characters. *Tornatellides idae* Pilsbry and Cooke is now selected to head that group of related species formerly headed by *T. thaanumi*.

*Tornatellaria stokesi* Pilsbry and Cooke should be *Tornatellides stokesi*, based on its ovoviviparity, an examination of the animals, and a reexamination of newly collected material from the type locality. Its nearest relative is *T. idae*, with which *T. stokesi* is now grouped.

Dall has added two new species of *Tornatellides* from the Revillagigedo Islands off the west coast of Mexico. Both belong to the *T. oblongus* group. They are *Tornatellides clarionensis* Dall (1926, p. 485, pl. 35, fig. 9), Clarion Island, and *Tornatellides mexicana* Dall (1926, p. 484, pl. 35, fig. 6), Socorro Island.

We are adding three new forms: (1) *Tornatellides oblongus parvulus* in the group of *T. oblongus*, (2) *T. oswaldi* in the group of *T. terebra*, and (3) *T. neckeri* in the subgenus *Aedituans*.

The taxonomic picture of the tribe *Tornatellidini* shapes up as follows. To date it contains 58 named species divisible into three provisional subgeneric categories: (1) *Tornatellides s.s.*, containing 56 named species, (2) *Aedituans*, containing one species, and (3) *Waimea*, containing one species. *Tornatellides s.s.* can be divided into six superspecific categories: (1) group of *T. oblongus*, containing 22 species, subdivided geographically for convenience into *T. oblongus* with 10 extra-Hawaiian species and *T. compactus* with 12 Hawaiian species; (2) group of *T. idae*, three species, Hawaiian; (3) group of *T. cyphostyla*, six species, Hawaiian; (4) group of *T. perkinsi*, seven species, Hawaiian; (5) group of *T. euryomphala*, 12 species, Hawaiian; and (6) group of *T. terebra*, six species, Hawaiian.

To summarize, *Tornatellides* contains to date a total of 58 species comprising 10 (17 percent) extra-Hawaiian species and 48 (83 percent) Hawaiian species.

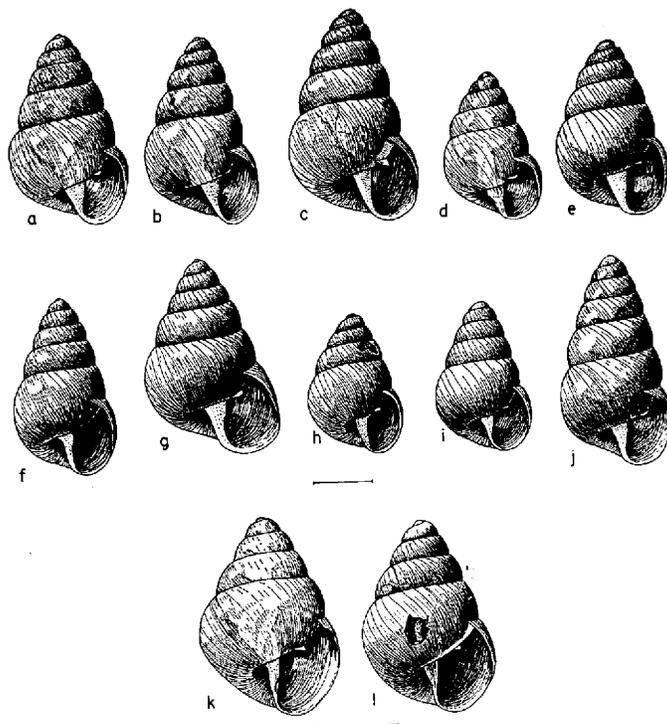


FIGURE 105.—*Tornatellides (Tornatellides) oblongus oblongus*: a, Tahaa, average, typical, "simplex" form, outlines slightly convex, apex quite sharp, parietal lamella very weak; b, Pitcairn; most specimens with more conical spire and finer embryonic whorls than Tahaa specimen (a), few close to it; c, Mount Duff, Mangareva, very close to Tahaa form, figured specimen larger than typical; d, Araua village, Tubuai, shell smaller, proportionately broader than a; e, Maraa Point, Tahiti, smaller than typical, with more convex whorls; f, g, Faatoai Valley, Moorea, average form, close to typical (f), many broader (g), few narrower; h, Rikitea, Mangareva, small form; i, Tahau Point, Moorea, small race; j, Rarotonga, near Raemaru, few specimens close to Tahaa form; most close to Pitcairn (b); k, Moorea, same locality as for f, g, juvenile illustrating very weak columellar fold; l, Rapa Iti, subadult "oblongus" form.

#### Subgenus *Tornatellides*

*Tornatellides (Tornatellides) oblongus oblongus* (Anton). Figures 105, a-l; 106, a-g; 107.

*Strobilus oblongus* Anton, 1839, Verzeichniss der Conchylien, 46.

*Bulimus antoni* Pfeiffer, 1841, Symbolae 1: 24; 1842, 2: 43; 1848, Mon. Hel. Viv. 2: 221.—Reeve, 1849, Conch. Icon., *Bulimus*, pl. 80, fig. 589.

*Tornatellina antoni* Pease, 1871, Zool. Soc. London, Proc., 473 (?*Tornatellina* Clessin, 1878, Nomenclator Hel. Viv., 343).

*Tornatellina simplex* Pease, 1864, Zool. Soc. London, Proc., 673; 1871, 473.—Pfeiffer, 1868, Mon. Hel. Viv. 6: 266.—Garrett, 1879, Acad. Nat. Sci. Philadelphia, Proc., 22; 1881, Acad. Nat. Sci. Philadelphia, Jour. II, 8: 398; 1884, 9: 92, pl. 2, fig. 21; 1887, Soc. Malac. France, Bull. 4: 30.

*Tornatellides simplex* Pilsbry, 1910, Nautilus 23 (10): 124.—Pilsbry and Cooke, 1915, Man. Conch. 23: 198, pl. 44, figs. 8-10.

*Tornatellina newcombi* var. Schmeltz, 1877, Cat. Mus. Godeffroy 6: 80.

*Tornatellides oblongus* Pilsbry and Cooke, 1915, Man. Conch. 23: 198, pl. 44, fig. 13.

"Oval conoidal, moderately long; whorls 5 convex; suture deep; apex sharp; aperture oval, with a flat fold on the columella; glossy, transparent, fragile, brown. H. 1½, diam. ¾" [3 × 1.5 mm.].

"Var. more swollen, shorter." (Anton.)

Adult genitalia (fig. 106, a-d). *Ovotestis* bilobate; follicles merely low projections at distal surfaces. *Duct* small, convoluted, swollen medially. *Talon* absent. *Carrefour* small. *Albumin gland* relatively large, follicles numerous, ovate. *Prostate* small, follicles few, long digitate. *Spermatheca* small, ovate; stalk small, very short, descending immediately into prostate follicles to empty soon into carrefour-oviducal junction well above earliest embryo. *Oviduct* large, inflated, diaphanous, bent into semi-circle by gravidity; embryos six in figured specimen; oviducal stalk quite long, narrow. *Vas deferens* small, thin; Y subapical. *Penis* triangular, upper body flaring, narrow below, short (0.5 oviducal length). Interior of penis simple with small unrecurved pilaster, low, narrow at apex, gradually increasing in size just below midbody, abruptly tapering below and terminating just below middle of penis. *Vas deferens* opening into penis at midpoint of pilaster (VDO). *Appendix* short, 0.5 penial length, subcylindrical. Interior of appendix free of internal tubular apparatus, smooth; vestibule with muscular thickening (MW). *Atrium* short, narrow.

Central nervous system, in part (fig. 106, e). Penial nerve off inferior frontal nerve, not passing through peni-oviducal angle; frontal branch continuing anteriorly to base of ommatophore. Small innominate nerve connecting ommatophoral nerve plus optic nerve to penial nerve. Superior frontal nerve of right cerebral ganglion not seen. Nuchal nerve combined with labio-tentacular nerve (Nuc-Lab-Tent) as in *Tubuaia perplexa* and *Tornatellaria newcombi*.

Paraneanic genitalia (fig. 106, f, in part) similar to that of *Tornatellinops* in external appearance except for absence of appendical retractor. Penis attenuate; appendix long, bluntly pointed; both branches diverging much lower than in adult (that is, penial stalk quite short).

*Teeth* (fig. 106, g) all similar except atypically large teeth sometimes present among normal (middle) teeth. Formula ±78-1-78. Normal teeth three-cuspid plus about two fine cusplets. Atypically large teeth three-to-five-cuspid; one ecto-, one ento-, and three mesocones plus three to four fine cusplets below them. Normal tooth 12.6 microns long, 3.6 microns wide. Atypically large tooth 17 microns long and 5 microns wide. As in *Achatinella concavospira*, atypical teeth follow each other in each subsequent row, one a row in this specimen.

Dissected 152177, Tahaa (adult genitalia, teeth), four specimens plus 10 for ommatophoral retractor; 152221, Tahaa (penial interior, central nervous system), two specimens; 145095, Tahaa (paraneanic juvenile), six specimens plus 10 for ommatophoral retractor; 136633, Mangareva, 10 specimens for ommatophoral retractor.

Rapa: Rapa Iti Islet, just south of entrance to Ahurei Bay, on stones and logs, alt. 20 ft., Wight, July 15, 142589-142590 (three specimens). Also collected above the cemetery just south of Ahurei village, Varniex, W. Anderson, July 28, 143669 (one specimen) and at the north slope of Anatauri Valley, on dead *Pandanus* leaves, alt. 50 ft., Zimmerman, Anderson, Toto, July 30, 143782 (one specimen).

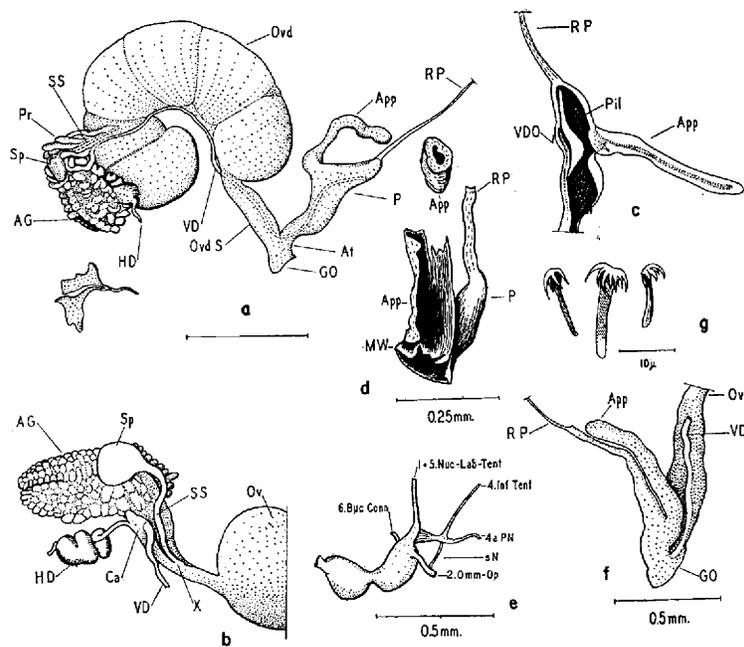


FIGURE 106.—*Tornatellides (Tornatellides) oblongus oblongus*: a, adult genitalia; b, closeup of carrefoural-spermathecal complex; c, interior of penis; optical section of appendix; d, interior (in part) and cross section of appendix; e, central nervous system (in part); f, paraneanic penial complex; g, teeth.

Only five specimens, three living, were taken on Rapa by the Mangarevan Expedition. Undoubtedly, others would have been found if more attention had been paid to the lowland fauna just back of the strand, a position not usually occupied by endemic species. The specimen illustrated (fig. 105, *l*) is not quite adult, but it is the oldest and in the best condition of the five specimens, two of which are dead adults and badly broken.

Under the designation *Tornatellina simplex*, Garrett reported this species from Tahiti, Moorea, Huahine, Raiatea, Tahaa (type locality), Borabora, and

Maupiti in the Society Islands; from Rarotonga, Aitutaki, Atiu, and Mangaia in the Cook Islands; from Rurutu in the Tubuai Islands; and from the Marquesas Islands, where it was collected by Voy.

The Bishop Museum, through the efforts of a number of expeditions and individual collectors, has acquired specimens of this species from the following islands: the Marquesas (Nukuhiva, Uahuka, and Hivaoa), the Mangarevan islands (Mangareva, Aukena, Akamaru, Taravai, Agakauitai, and Makaroa), Pitcairn, the Australs (Raivavae, Tubuai, Rurutu, and Rimatara), the Cook Islands (Mangaia, Rarotonga, Mauke, Atiu, and Mitiaro), and the Society Islands (Tahiti, Moorea, Huahine, Raiatea, Tahaa, Borabora, Maupiti, and Meetic). Except Mitiaro, all of these islands are volcanic and at least a few hundred feet high. Mitiaro, with an altitude of about 50 feet, consists mostly of raised coral rock, but volcanic soil has been reported near its center. The distribution is shown on the map (fig. 107).

There is no doubt that this species will be found on the few remaining high volcanic islands in the southeast Pacific when they have been thoroughly collected. Specimens in Bishop Museum are from most of the high islands on which land shells have been collected: from Nukuhiva (lat.  $8^{\circ} 52'$  S.) in the north to Rapa (lat.  $27^{\circ} 36'$  S.) and from Pitcairn (long.  $130^{\circ} 06'$  W.) in the east to Rarotonga (long.  $159^{\circ} 46'$  W.) in the west. These islands are scattered throughout an area which is more than half the size of Australia, though the total land area of the islands on which the species is known to occur is not much more than 1,300 square miles.

The species is abundant on most of the islands on which it has been found, and most of the specimens taken by the Mangarevan Expedition were found at altitudes of a few feet above high water mark on the flat just back of the beach to about 200 feet. It is especially abundant on dead coconut, breadfruit, and banana leaves in plantations; on dead leaves in rather open spaces or in dense thickets of *Hibiscus tiliaceus* and *Pandanus odoratissimus*; and under native trees and shrubs. A very few specimens were taken on the leaves and stems of plants (see 140832). Only on Tahaa, Society Islands (see 145094), were specimens found above 1,000 feet, and on only a few islands were specimens taken above 500 feet. No specimens have been reported from the highlands of Tahiti, though the Museum has good collections of shells made above 500 feet by five different expeditions.

From the similarity of shells from different islands and from different island groups, some of which are separated by as much as 800 miles, it seems that the distribution from its original home has been comparatively recent, probably since the advent of the Polynesians. It was undoubtedly a lowland species disseminated accidentally with food plants. A study of some of the lots in the Museum collection makes it apparent that there is no consistent variation in the species from island to island or even between island groups.

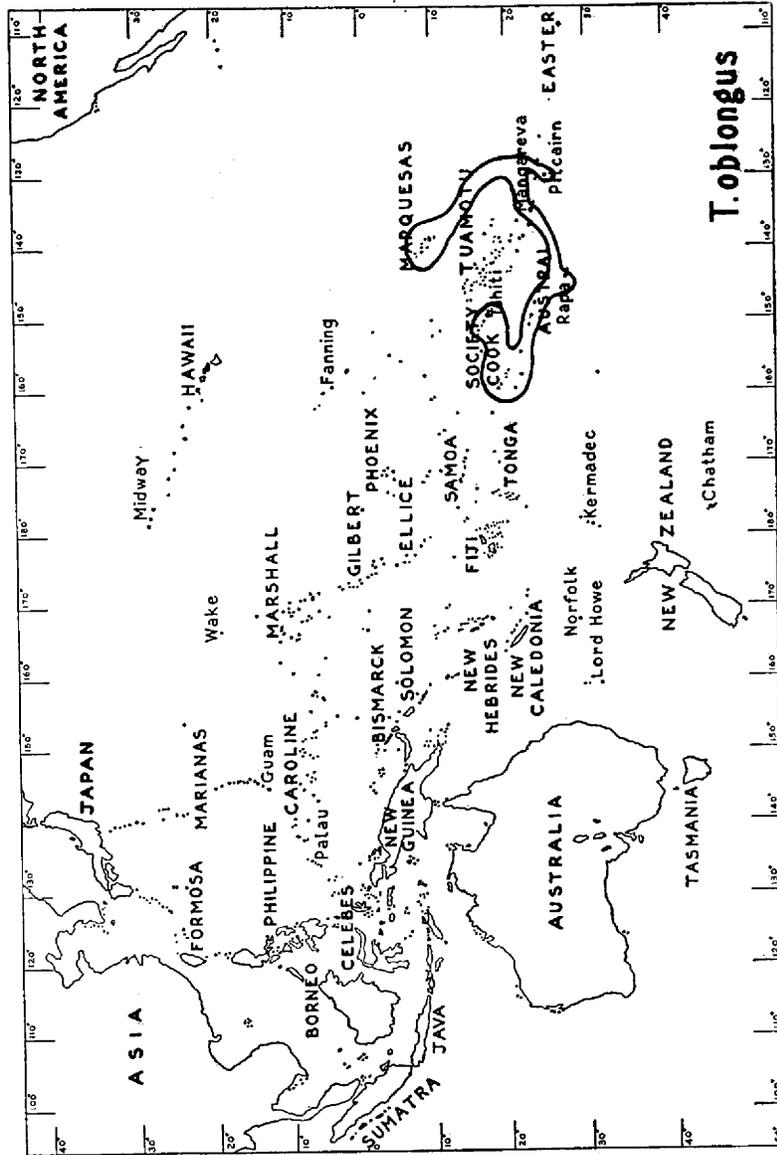


FIGURE 107.—Distribution of *Tornatellides oblongus*.

In form, the shells may be conic (fig. 105, *a*) to conic with slightly convex outlines (fig. 105, *l*). Adult specimens have 5.25 to 6.5 whorls, which range from flat-convex to distinctly convex. There is some variation in the width of the embryonic whorls, for some specimens have a slightly more acute apex than do others. There is also some variation in the height of the parietal lamella, which in most lots is rather low. In other lots some specimens have a very weak parietal lamella. The columellar lamella is apparently absent in all adult specimens.

Some of the colonies can be classed as "tight," in that there is little variation among the individual specimens, exemplified by 140735 from Mangareva (fig. 105, *h*). However, many colonies found on different islands show more or less variation in size, proportion of breadth to length, sharpness of the apex, and development of the parietal lamella (see 150357, fig. 105, *f, g*).

In color the shells range from pinkish buff (Tahiti, 145783, a very light specimen, fig. 105, *e*) to clay color (Mangareva, 136633, fig. 105, *c*). Most, however, range between these two colors in shades close to cinnamon buff. The parietal lamella is slightly less than 0.5 whorl long (Mangareva, 136633, fig. 105, *c*).

One subadult specimen with only 4.75 whorls, taken on Raiatea in the Society Islands, contained an embryo.

The parietal lamella is usually proportionately stronger in juveniles than in adults. However, there may be a good deal of individual variation in the absence or degree of development among the juvenile specimens from a single colony. The juveniles with three to four whorls in some colonies on the different islands have a weak, somewhat oblique, threadlike columellar fold. In the members of some colonies this fold is merely indicated or weakly developed (fig. 105, *k*), whereas in most of the others the fold is entirely absent. There may be no indication of the columellar fold, it may be merely indicated, or it may be low but distinct (see 148335 and 148597, Rurutu, and 150671, Moorea, fig. 105, *k*). There seems to be no correlation between the presence of the columellar fold and its distribution by groups of islands. On Rurutu and Moorea a larger percentage of the juvenile specimens have a low but distinct columellar fold. In specimens from the Marquesas and the Mangarevan islands this columellar fold seems to be almost entirely lacking, though it is slightly indicated in a few individual specimens. However, this fold is lacking in most specimens examined throughout the range of the species.

One of the peculiarities of *T. oblongus* is the fact that the ommatophoral retractor is either free or passes through the peni-oviducal angle. Of 33 specimens dissected, 32 were free, one was not free (this odd specimen from 145095, of which 10 were dissected). The peculiarity ascribed to *T. oblongus* is shared by the genus and discussed in the next two paragraphs.

TABLE 9.—COMPARATIVE MEASUREMENTS OF SHELLS OF  
TORNATELLIDES OBLONGUS

Figure 105, a-l	SHELL			APERTURE			LAST WHORL		
	Length	Diameter	Percent	Axis	Diameter	Percent	Length	Pct. Total Length	Height Par. Lam.
a Tahaa	3.39	2.06	61	1.23	0.97	79	2.0	59	0.065
b Pitcairn	3.30	1.97	60	1.23	0.90	73	2.0	61	0.048
c Mangareva	3.71	2.26	61	1.39	1.00	72	2.2	58	0.130
d Tubuai	2.58	1.71	66	1.03	0.77	75	1.7	65	0.065
e Tahiti	3.06	1.97	64	1.32	0.97	73	1.9	63	0.065
f Moorea	3.10	1.80	57	1.22	0.86	70	1.9	63	0.024
g Moorea	3.45	2.32	67	1.35	1.13	83	2.2	64	0.080
h Mangareva	2.43	1.65	68	1.10	0.77	71	1.6	66	0.065
i Moorea	2.58	1.68	65	1.10	0.81	74	1.6	62	0.030
j Rarotonga	3.68	1.97	54	1.29	0.94	72	2.1	56	0.065
k Moorea	2.37	1.64	69	1.16	0.79	68	1.6	69	0.065
l Rapa	2.29	1.58	68	1.05	0.75	71	1.6	68	0.046

Though the passage or non-passage of the ommatophoral retractor through the peni-oviducal angle is consistent in all genera of the Achatinellidae, no such consistency exists in the genus *Tornatellides*. Of the five groups of species of the genus dissected (table 10), one species in the *terebra* group (*oswaldi*) and one species in the *perkinsi* group (*macromphala*) yielded specimens the ommatophoral retractors of which passed through the peni-oviducal angle. Of three species in the *compactus* group, one (*subangulatus*) was free, and in two (*compactus*, *procerulus*) the retractor passed through the angle. One species each in the *terebra* (*drepanophora*) and *euryomphala* (*leptospira*) groups were undetermined, for lack of good animals. In one species of the *perkinsi* group (*perkinsi*) it apparently passes through the angle, the animal being poorly preserved. In the one specimen out of 33 which in *T. oblongus* was aberrant the retractor definitely passed through the peni-oviducal angle. This odd specimen appeared quite early in our investigations, leading us to examine a large number of animals. We conclude that such aberrancy is rare but can be expected occasionally in a group where this anomaly appears to vary with the species. We also conclude that (a) this character is of no great importance as a factor in generic characterization but (b) may be of great importance as an indication of a transitory stage in the course of evolution in the Achatinellidae.

It was difficult to determine the internal structure of the appendix because of the minute size of that organ, but a fairly good longitudinal section was finally achieved at the lower end of an appendix. This specimen proves the lack of an internal tubular structure, but a more satisfactory picture will be obtained by microtomal sections.

TABLE 10

CATALOG No.	ISLAND	GROUP	SPECIES	No. DIS-SECTED	FREE	NOT FREE	NOT DETERMINABLE
99130	Oahu	terebra	<i>T. oswaldi</i>	3		×	
48584	Kauai	terebra	<i>T. drepanophora</i>	3			
48581	Kauai	perkinsi	<i>T. perkinsi</i>	1		×	×
38830	Maui	perkinsi	<i>T. macromphala</i>	3		×	
189782	Hawaii	perkinsi	<i>T. macromphala</i> ?	2		×	
34833	Oahu	euryomphala	<i>T. leptospira</i>	4		×	
189784	Hawaii	euryomphala	<i>T. pyramidatus</i>	2		×	×
171600	Hawaii	compactus	<i>T. compactus</i>	6		×	
38789	Maui	compactus	<i>T. procerulus</i>	3		×	
189783	Hawaii	compactus	<i>T. compactus</i> ?	3	×	×	
189785	Hawaii	compactus	<i>T. compactus</i> ?	3	×	×	
38637	Maui	compactus	<i>T. subangulatus</i>	4	×		
145095	Tahaa	oblongus	<i>T. oblongus</i>	10	×	×	
145096	Tahaa	oblongus	<i>T. oblongus</i>	5	×	×	
152221	Tahaa	oblongus	<i>T. oblongus</i>	10	×	×	
136633	Mangareva	oblongus	<i>T. oblongus</i>	10	×	×	
89742	Bonin	oblongus	<i>T. tryoni</i>	3	×	×	

\* Apparently passes through peni-oviducal angle; animal poorly preserved.

† One specimen only.

**Tornatellides (Tornatellides) oblongus parvulus**, new subspecies (fig. 108, a, b).

Shell as small as, or even smaller than, the smallest specimens of *T. oblongus* examined from any other island, uniformly lighter colored, conic with almost straight outlines. Whorls 5.5, slightly convex. Aperture nearly as broad as long. Columella unarmed. Parietal lamella stronger than in the parent species, longer, more than 0.6 whorl in length.

Length 2.48 mm., diameter 1.61 (65 percent) apertural axis 1.06, diameter 0.77 (72 percent); last whorl 1.61 (65 percent); parietal lamella 0.06.

In a juvenile specimen, whorls slightly more than 4, length 1.67 mm., parietal lamella strong, rather high, flaring outward, and deeply entering. Columella with a strong sub-horizontal lamella-like fold just below its middle.

Henderson Island: Slopes above cove about 1.25 miles south of northwestern point of island, on dead *Pandanus* leaves, W. Anderson, June 18; holotype 8892 (figured juvenile 8893); paratypes 149669, 149671, 148673.

Additional material was collected from 19 other colonies, within a radius of 0.5 mile of the cove where the Mangarevan Expedition ship *Islander* was stormbound for a week. The species was not abundant in any one locality, since only one to five specimens were found in each of the collecting stations.

Shells of *T. o. parvulus* from Henderson Island, all nearly uniform in size and color, are the only specimens distinct enough to be classed as a subspecies. However, they may represent an ecological development rather than a geographical subspecies. This is the only representative of the genus found on the

non-volcanic Henderson Island south of the equator. *T. o. parvulus* is the third species of land mollusk to be reported from Henderson Island. The others are *Orobophana solidula* (Gray, 1839), and *Diastole (s.s.) glaucina* (Baker, 1939). When studies of the molluscan fauna of this island are completed, there will probably be a total of 18 or more species to be reported among the following genera collected by the Mangarevan Expedition: *Thaumatodon*, *Nesopupa*, *Pupisoma*, *Elasmias*, *Lamellidea*, *Tornatellinops*, *Tubuaia*, *Melampus*, *Syncera*, and *Georissa*.

Most of the widespread southeast Pacific species are represented in the Henderson Island fauna and a number of new forms may be expected to evolve. Geologically, Henderson is much older than the neighboring low atolls.

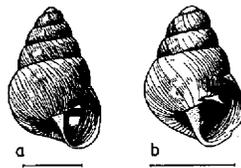


FIGURE 108.—*Tornatellides (Tornatellides) oblongus parvulus*: a, adult, holotype; b, parametaneanic.

In fact, it is almost comparable in age to Makatea, at the opposite end of the archipelago. Time and isolation have aided the process of evolution in mollusks and other forms of life on Henderson, as evidenced by the new forms named above: *T. o. parvulus* and *D. (s.s.) glaucina*. Henderson's estimated 18 species of land snails compares favorably with Makatea's 22 species.

Henderson Island is 5 miles by 2.5 at its widest point and about 90 feet high. It is composed entirely of upraised coral limestone and it has relatively rich bird, insect, and plant populations. Remains of coral platforms indicate that the Polynesians lived here or used this island for various purposes. It is interesting to note that no specimens of *Gastrocopta* and none of the steno-gyrids were found on Henderson, indicating that the Polynesians occupied the island prior to the advent of Europeans, who unwittingly introduced these common snails in the tropical Pacific islands when they introduced plants.

Juveniles of the subspecies differ from *T. o. oblongus* more than do adults. The longer and much stronger parietal lamella and the strong lamella-like columellar fold make it easy to separate the two forms.

***Tornatellides (Tornatellides) stokesi* (Pilsbry and Cooke).**

*Tornatellaria stokesi* Pilsbry and Cooke, 1916, *Man. Conch.* 23: 259, pl. 54, fig. 8.

Type in Academy of Natural Sciences, Philadelphia (112747); Oahu, Nuuanu, Glen Ada.

Specimens of this species from Makiki, Oahu (44220) were compared with the type specimens by both Pilsbry and Cooke who found them to agree exactly. Many of the adult shells contained embryos, which were stuck behind the large parietal lamella. Viviparity is conclusive evidence that the species belongs to *Tornatellides*. The embryonic whorls are less flattened and lack the spiral striae which are characteristic of *Tornatellaria*.

*T. stokesi* is the representative of the *T. idae* group from the Waianae Mountains. It is easily separated from *T. idae* by its shorter length, though with the same number of whorls, by its greater diameter, and by a stronger parietal lamella.

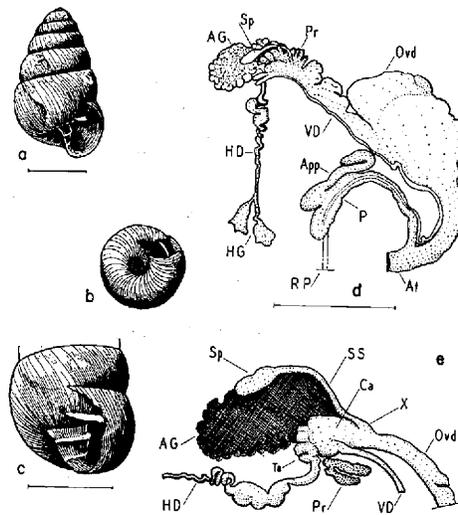


FIGURE 109.—*Tornatellides (Tornatellides) oswaldi*: a, adult shell, holotype; b, adult, umbilical view; c, adult, lateral view, showing columellar lamellae; d, adult genitalia; e, closeup, carrefour-spermathecal complex; prostate (in part); albumin gland in outline only.

***Tornatellides (Tornatellides) oswaldi*, new species (fig. 109, a-e).**

*Shell* widely perforate, ovately conic, thin, subtransparent, color pinkish buff, glossy, very finely striate with lines of growth. *Spire* ovately conic, with very slightly convex outlines, apex blunt. Suture lightly impressed. *Whorls* 6.25; embryonic whorls increasing rapidly, the rest very slowly and regularly, slightly convex; last whorl large with slightly flattened base. *Aperture* medium, truncate, oval. *Parietal lamella* low, erect, its margin slightly uneven, especially inwardly, but not serrate. *Columella* rather broad, slightly swollen above, furnished with two minute, nearly transverse lamellae, of which upper is slightly stronger. Both lamellae extend to outer margin of columella. *Umbilicus* rather large, about 0.33 diameter, its outer third perspective.

Length 2.61 mm., diameter 1.58 (61 percent), apertural axis 0.97, diameter 0.75 (77 percent), last whorl 1.55 (59 percent), parietal lamella 0.06, umbilicus 0.51.

Genitalia typical. *Ovotestis* bilobate. *Albumin gland* well developed, relatively smaller than type. *Prostate* also relatively smaller, follicles shorter, but covering more latitude. *Upper oviduct* contracted, wrinkled; expanded at middle, with two embryos; lower oviduct narrowed. *Spermatheca* oblong, small. *Stalk* very short, descending diagonally and soon emptying into carrefour-oviducal junction (X). *Talon* a mere enlargement of terminal end of hermaphrodite duct. *Carrefour* roughly ovate, hermaphrodite duct entering laterad, *vas deferens* emerging ventrad, oviduct off lateral wall opposite talon. *Penis* as in *T. oblongus*; 0.33 to 0.5 oviducal length. Right ommatophoral retractor passing through peni-oviducal angle.

Dissected 99130 (genitalia, carrefour complex), four specimens.

Hawaiian Islands: Oahu, Moanalua Valley, on spur leading to Puu Kahu-auli (Mauna Kope of earlier collectors), on fronds of *Acrostichum*, alt. two-thirds of way up the mountain ( $\pm 1,600$  ft.), Olaf Oswald; June 1, 1930; holotype 8894, paratypes 99130.

*T. oswaldi* differs from the known species of the *terebra* group in having an entire margin to the parietal lamella without serrations or projections. All its characters, except those of the parietal lamella, place it in this group. Its nearest relative is *T. forbesi* from Maui, from which it differs in outline, relatively larger umbilicus, and simpler parietal lamella. It differs from *T. serrarius* from Oahu in its less conic outlines, wider embryonic whorls, and entire parietal lamella.

This species is named for Olaf Oswald, long a friend of Bishop Museum.

#### Subgenus *Aedituans*

The shell of this subgenus shows no material differences from those of the genus. In outline and apertural characters it most closely resembles some of the species belonging to the group of *T. euryomphala*, especially *T. euryomphala* and *T. irregularis*. It is, however, about 0.66 mm. longer than the longest species (*T. ronaldi*) of this group. In juvenile specimens, the development of the apertural armature closely resembles that of specimens of the same age in the *T. euryomphala* group.

This subgenus is considered distinct solely on its genital characters, especially the very weak development of the penial appendix.

Type species: *Tornatellides neckeri*, Necker (8895).

#### *Tornatellides (Aedituans) neckeri*, new species (fig. 110, a-f).

*Shell* elongate, oblong turreted, perforate (the axial perforation relatively small and circular until the last whorl, where it enlarges rapidly to about three times its original diameter), somewhat thin, semitranslucent, not transparent, glossy, indistinctly and irregularly marked with lines of growth, color nearly uniform tawny olive. *Spire* elongate, subcylindrical, tapering gradually to apex, with slightly convex outlines; apex blunt, base rounded. *Whorls* 7.5; the first whorl increasing rapidly, the rest increasing very slowly and regularly, convex, separated by a distinct shallow suture; last whorl rounded, very slightly flattened at base. *Aperture* truncate-ovate, nearly vertical when viewed from front, somewhat oblique. *Parietal lamella* moderate, about 0.3 whorl in length, continued indistinctly for a short distance, slightly diagonal to parietal wall. *Columella* narrowly triangular, the two folds merely indicated by slight surface swellings.

Length 4.55 mm., diameter 2.29 (50 percent); apertural axis 1.52, diameter 1.26 (83 percent); last whorl 2.45 (54 percent); parietal lamella 0.13.

Embryonic shells globose, indistinctly perforate just before birth (in some younger specimens apparently closed), the surface microscopically and indistinctly spirally striate. Parietal lamella high, long, oblique to parietal wall. Columella heavily calloused along its inner surface, base of truncation oblique, not decidedly truncate in some specimens, in others decidedly so, with lower fold more prominent (embryos younger); in still younger specimens, whorls about 2, columella straight, with narrow, heavy callus along inner face for whole length of columella. Older embryos have a more decided upper columellar fold, which is oblique; in younger specimens position of upper columellar fold only indicated.

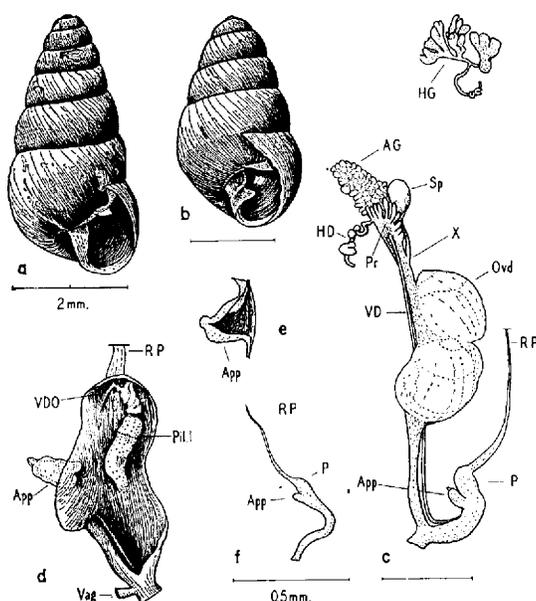


FIGURE 110.—*Tornatellides (Aedituans) neckeri*: a, adult shell, holotype; b, meta-paraneanic juvenile; c, adult genitalia; d, interior of penis; e, interior of appendix; f, metaneanic penis.

All embryos very glossy; in most specimens first 1.5 whorl smooth; some specimens with indistinct spiral lines (these spiral striae only faintly visible in certain light and merely indicated). Just after end of second whorl, surface becomes gradually striate, striae growing stronger with growth of shell.

Nepionic stages. From birth to about 3.75 whorls lower columellar fold becomes much stronger; upper columellar fold does not gain much prominence, being indicated as a low, oblique swelling; it is not distinct as such until shell has completed about five whorls. Juveniles with slightly more than 5 whorls, parietal lamella proportionately stronger than in adults and about one whorl long. Columellar lamellae well developed. From then until about completion of whorl 6 upper fold present as a real fold. During growth of last and seventh whorl second columellar folds as well as parietal lamella diminish in size. Lower

columellar fold diminishes in size rather rapidly to about size of upper columellar fold and is placed more and more obliquely on columella, probably owing to the slight enlargement of the perforation.

Adult genitalia. *Ovotestis* bi- to trilobate, usually trilobate, meager; follicles bluntly terminate, usually branching. *Duct* thin, with small median convoluted bulge. *Talon and carrefour* not dissected. *Albumin gland* fairly large; follicles numerous, ovate to short-digitate. *Prostate* small, paucifolliculate ( $\pm 12$  in figured specimen); follicles clavate or digitate. *Spermatheca* quite large, ovate, nearly spherical; stalk very short, terminating just below carrefour on preuterine tube, above embryos (X). *Oviduct* diaphanous, usually containing one embryo, less frequently two, rarely three (82 specimens inspected: 21 not gravid, 48 with one embryo each, 12 with two each, and one with three). *Vas deferens* off carrefour below prostate, thin, narrow, adherent to penis from base, terminating apically on penis (Y). *Penis* small, short (0.3 oviducal length); interior with small, narrow pilaster (0.5 penial length), with vestiges of recurvature and descending arm, otherwise plain. *Appendix* vestigial, short, stubby, with small terminal papilla, without retractor; interior plain, smooth. *Penial retractor* terminal, heavy below, tapering to fine thread above. *Atrium* short.

Metaneanic substage with penis simple, appendix present.

Dissected 57431 (adults), five specimens; 57437 (metaneanic juveniles), two specimens.

Hawaiian Islands: Necker Island, Summit Hill (type locality), western slope, on ancient stone wall, alt. 225-250 ft., Cooke and Thaanum, June 17, 1923; holotype 8895, figured metaparaneanic 8896; paratypes 57414-57420, 1,423 specimens.

*Tornatellides neckeri*, the only species of land shell found on Necker, is extremely abundant under stones, and was collected in five localities from Annexation Hill to Bowl Hill. As on Nihoa Island, no live specimens were taken under stones in direct contact with the ground, though a few dead ones were found in an exposed ground position. None were found east of Bowl Hill or on the isolated hill at the northwest portion of the island although both localities were searched. Thaanum and Cooke found no specimens except under stones, though Charles S. Judd took a number of specimens on the dried stems of *Portulaca lutea* on the northern slope of Summit Hill at about 160 feet.

Five series, numbering more than 3,800 specimens, were taken by Thaanum and Cooke; and Judd took more than 400 specimens.

*T. neckeri* is fairly uniform in color and outline. Immature specimens are slightly darker in color, thinner (being semitransparent), and glossier than the adults. When fully grown nearly all the specimens are irregularly discolored in patches and are pitted. Whatever variation occurs in color tends to lighter shades. A few specimens are cream color, and a single albino (54546) was taken on Bowl Hill. Very few specimens are proportionately slightly broader than the typical examples (length 4.5 mm., diameter 2.5, whorls 7, 57429A).

Specimens of *T. neckeri*, one of the three outstanding and largest species of the genus, have exceeded 4.1 mm. The other two species are fossil: *T. moomo-miensis* from Molokai ( $\pm 4.5$ -5 mm., 45995) and *T. attenuatus* from Oahu

( $\pm 4.4.25$  mm., 13747). The species closest to *T. neckeri* is a much smaller and proportionately broader unnamed new species found on Nihoa, an island about 175 miles east of Necker. In turn, the Nihoa species (57243-57246, 57365-57370, and others) finds its nearest relationship with *T. procerulus kailuanus* from Oahu (41208-41209).

*T. neckeri* differs from *T. oblongus* (compare with Tahaa 152177) as follows: It is a much longer and larger shell, with a more produced spire, with less tightly coiled and less convex whorls, and with a proportionately smaller body whorl and umbilicus. The parietal lamella is stronger. Juveniles have two strongly developed columellar lamellae, whereas only an occasional vestige is seen in *T. oblongus*.

The abundance of this species in ancient stone walls is probably because it found them acceptable stations, rather than because the species was transported by man.

Compared to Necker, Nihoa has a rich fauna, consisting of *Thaumatodon* (one species), *Endodonta* (one), *Lamellidea* (one), *Tornatellides* (three), and *Philopoa* (one). The almost entire absence on Necker of *Lepturus*, of which only a few dead specimens were found, probably accounts for the absence of other species of *Tornatellides* and other genera, for those collected on Nihoa were almost exclusively confined to this bunch grass.

In view of the vestigial appendix, except for which it is similar in all ways to *Tornatellides* (*s.s.*), this subgenus may be considered either the immediate ancestor of the northwest Hawaiian *Tornatellides* or a degenerate offshoot of it. When a series of juveniles was dissected to determine whether specimens of the earlier stages have the appendix, we found that half-grown animals (metaneanic) still retained a conspicuous appendix. But the genitalia of very young specimens were too difficult to dissect.

The nervous system was investigated only insofar as the penial innervation was concerned. The penis was found to be innervated by the cerebral ganglion.

The right ommatophoral retractor passed through the peni-oviducal angle.

#### Subgenus *Waimea*

*Waimea* Pilsbry and Cooke, 1915, Man. Conch. 23: 250.

"The shell is similar in form to *Tornatellides*. It differs in its *costate* surface and the broad, shallow, dorsal sulcus or depression on the last whorl. In immature specimens there is a rather long, low, palatal fold and two columellar lamellae. The embryonic whorls are spirally striate as in *Tornatellaria*." (Pilsbry and Cooke.)

Embryonic whorls as distinctly spirally striated as those of *Tornatellaria*, somewhat stronger than in any species of *Tornatellides*. These whorls narrower and apex more pointed than in any species of *Tornatellaria*. Embryonic whorls separated by a distinct suture as in *Tornatellides* and more marked than those of *Tornatellaria*.

Parietal lamella about one whorl long, diminishing gradually interiad, not threadlike as in most species of *Tornatellides*.

Palatal fold of neanic specimens long, extending inward for about 0.33 whorl.

Anatomy unknown.

Type species: *Tornatellides rudicostatus* (Ancey).

Holotype in Bishop Museum (18448): "Hawaii, fossil in the Hamakua district (Henshaw, Thaanum)."

Since 1915, fossil specimens from Waimea and Puuwaawaa, Hawaii, have come to the Museum. In recent years David Fleming collected examples at Pulehu, Makawao, Maui, and it has also been collected at Kula, Maui. In 1946 an intensive but unsuccessful search was made on the slopes of Mount Hualalai, Hawaii, in the hope of procuring living specimens for the study of the anatomy.

This subgenus is based on a single species.

#### TRIBE TORNATELLARIINI

Shells generally larger than those of Tornatellidini, from  $2.75 \times 1.65$  mm. in *T. thaanumi* to  $5.8 \times 2.8$  mm. in *T. henshawi*, which is usually about 4 mm. Whorls are from 6.25 in *T. thaanumi* to 9.33 in *T. trochoides*, average about 7, generally flat. Periphery usually angular.

Oviparous or viviparous (*Philopoa*). Without appendix. Ommatophoral retractor passes through peni-oviducal angle.

#### Genus *Philopoa*, new genus

Shell small, elongate-conic, subumbilicate, umbilicus shallow, entering for about 1.5 whorl, enlarging rapidly. Embryonic whorls spirally striate, striae fine, consisting of closely spaced minute points. Parietal lamella strong, about 0.5 whorl in length. Columella triangular, with two lamellae, of which upper is much stronger than lower. Upper portion of free columellar margin bent downward forming a sulcus between upper columellar lamella and parietal wall.

Genitalia generally similar to those of *Tornatellaria*. Ototestis multi-lobate; spermathecal stalk entering oviduct below embryo. Penis without appendix, long. Reproduction viviparous.

Type species: *Philopoa singularis*.

Hawaiian Islands: Nihoa.

Nihoa, 150 nautical miles west-northwest from the island of Kauai, is nearly a mile long with an extreme width of about 0.6 mile. It has an area of 156 acres, and its highest altitude is 895 feet.

*Philopoa* differs conchologically from *Tornatellides* in having spirally striate embryonic whorls, in a stronger parietal lamella, and in a shallow perforation. In *Tornatellides* the perforation is continuous up to an early postembryonic stage, whereas in *Philopoa* it is mostly imperforate in the embryos to apparently minutely perforate in juveniles up to the paraneanic substage, in which the perforation is minute and hardly discernible and ascends spirally under the upper columellar lamella. At adulthood a shallow umbilicus is formed, in which character it approximates some of the species of *Auriculella*. *Philopoa* agrees with *Tornatellides*, in that its reproduction is

viviparous (=ovoviviparous). Anatomically it differs from *Tornatellides* to a greater degree. The penial appendix is lacking and the spermathecal stalk enters the oviduct below the embryo.

*Philopoa* differs conchologically almost as much from *Tornatellaria* as it does from *Tornatellides*. Both *Philopoa* and *Tornatellaria* have spirally striate embryonic whorls, but in *Philopoa* the striae are made up of closely placed minute points whereas they are continuous in *Tornatellaria*. The apex of *Tornatellaria* is slightly rounded; that of *Philopoa*, pointed. Anatomically, there is little superficial difference between the two genera, though *Philopoa* is viviparous and *Tornatellaria* is oviparous. Otherwise the genitalia are similar with the following minor differences: the ovotestis of *Philopoa* is seven-lobate, the follicles closely united, only their tips showing; the lobes of *Tornatellaria* number three to five, and the follicles are protuberant. In the interior of the penis the pilaster of *Philopoa* is simple, the papilla vestigial; the pilaster of *Tornatellaria* is highly developed, with strong crossribs, and the papilla is strongly developed into a lingual process. *Philopoa* probably descended from the same stock as *Tornatellaria* after *Tornatellides* had become separated from this common ancestor.

*Tornatellaria* is not common on Kauai, the nearest island to Nihoa. The single species from Kauai, which has been taken from widely separated localities, is referred to the common *Tornatellaria newcombi* from Oahu by Pilsbry and Cooke (1915, p. 258). There are no apparent specific differences between the Oahu and Kauai specimens.

***Philopoa singularis*, new species (fig. 111, a-h).**

*Shell* shallow perforate, elongate, narrowly conic, rather thin, translucent to subtransparent, lower whorls isabella color, upper whorls tawny, postembryonic whorls somewhat glossy, marked with very fine lines of growth. *Spire* elongate, narrowly conic with slightly convex outlines, apex acute. *Suture* shallow, narrowly margined. *Whorls* 7, slightly convex; postembryonic whorls nearly flat; last whorl tapering regularly and slowly to base, slightly more than 0.5 shell length. *Aperture* obliquely truncate-ovate. *Parietal lamella* strong, obliquely seated, slightly more than 0.5 whorl long, its free margin flaring outward. *Columella* narrowly triangular, the upper portion of its free margin bent downward to form an angle when viewed laterally; two slightly oblique lamellae, the upper strong, riblike, extending nearly to margin; the lower weaker, more deeply seated. *Peristome* erect, indistinctly thickened in some individuals, the upper portion slightly flattened just below its insertion.

Length 3.97 mm., diameter 2.0 (50 percent); apertural axis 1.52, diameter 1.06 (70 percent); last whorl 2.26 (57 percent); parietal lamella 0.26.

*Ovotestis* seven-lobate; lobes triangular, thin; follicles visible only terminally, united below, few in number. *Duct* thin, with small median convoluted bulge. *Talon and carrefour* not dissected. *Albumin gland* large, multifolliculate; follicles round, ovate, or short-digitate. *Prostate* large, multifolliculate ( $\pm 20$  in figured specimen); follicles digitate, usually distended. *Spermatheca* large, ovate; stalk quite large, passing through prostatic follicles, joining oviduct shortly below embryo (X). *Vas deferens* off lower part of carrefour below prostate, loosely adnate to penis, entering penis terminally. *Oviduct* with narrow neck, diaphanous at bulge, containing one embryo (41 inspected: 22 non-gravid, 19 with single embryos). *Vagina* fairly long. *Penis* large, long (0.75 oviducal length); interior

with small recurved pilaster (Pil 1), papilla (P Pap) not pendent, very weak, low. Atrium short.

Central nervous system studied only for penial innervation. Penis innervated by cerebral ganglion.

A juvenile specimen, whorls 5.5, length 3.06 mm., is indistinctly angled at periphery. Parietal lamella proportionately stronger than in adults, its free margin distinctly flaring upward, slightly thickened for a short distance, with a row of denticles just above edge. Columella with two strong, nearly equally developed lamellae; narrow above upper lamella, heavily calloused below. (This type of columella occurs in no other genus of the family.)

The embryos in *P. singularis* have a much heavier calloused columella than in any species of *Tornatellides*, and the two columellar lamellae are more distinctly developed. Spiral striae are always present in the embryonic whorls (2.5 to 2.75 whorls), consisting of microscopic granules. In younger embryos the columellar lamellae are weaker.

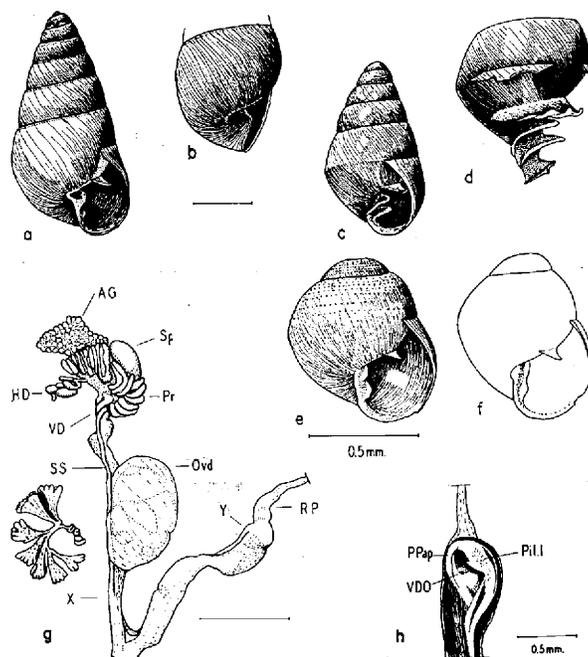


FIGURE 111.—*Philopoa singularis*: a, adult, holotype; b, adult, profile; c, parametaneic; d, closeup of parietal and columellar lamellae; e, embryo; f, younger embryo; g, adult genitalia; h, interior of penis, distal portion.

Dissected 57248 (adults), three specimens.

Hawaiian Islands: Nihoa, northwest part of island, just below highest peak, dry open ridge, on *Eragrostis variabilis*, alt. about 900 ft., Thaanum and Cooke, June 13, 1923; holotype 8897, 8898 (figured parametaneic stage); 57265A (figured apertural armature), 8899 and 8900 (figured embryos); paratypes 57262-57269, 699 specimens.

This species is very abundant wherever *Eragrostis variabilis* grows, and no specimens were taken on any other plant. Several thousand specimens were taken at different altitudes and on different parts of the island. Of these, only five specimens, all juveniles, were found under stones.

#### Genus *Tornatellaria* Pilsbry

*Tornatellaria* Pilsbry, 1910, *Nautilus* 23 (10): 123 (type *T. newcombi*).—  
Pilsbry and Cooke, 1915, *Man. Conch.* 23: 251.

"*Tornatellinidae* with the shell perforate or umbilicate, thin, dextral; shape from ovate to pyramidal-conic, the outlines of the spire nearly straight; whorls  $6\frac{1}{2}$  to  $9\frac{1}{2}$ , flattened or not convex; apex minute striate spirally, surface smoothish. Parietal lamella from two-thirds to an entire whorl long. Two columellar lamellae in the young stages, one or both emerging in the adult. Peristome thin, unexpanded and acute. Mantle marked with narrow black splotches and lines transverse to the whorls. Oviparous." (Pilsbry and Cooke.)

*Ovotestis* three- to five-lobed, lobe consisting of two to six basally con crescent follicles; follicles globular, clavate, or short-digitate, semi-transparent, globules (ova ?) visible within. *Hermaphrodite duct* greatly distended in middle, convoluted. *Talon and carrefour* not studied. *Albumin gland* large, multifolliculate; follicles ovate to digitate. *Prostate* small to large; follicles comparatively numerous (12 to 30), well developed in most specimens dissected, ovate to digitate. *Spermatheca* large, ovate, lying on albumin gland or between it and prostate or uterus; stalk medium long, stout, entering oviduct 0.25 to 0.5 way down oviduct. *Oviduct* narrow. *Vas deferens* wide, entering penis subapically, but strongly adherent to penial stalk from near its origin. *Vagina* short to long, depending on insertion of spermathecal stalk. *Penis* large (ratio, width to length, 1:6), robust, crooked-clavate, short, as long as oviduct or longer (0.4, 1.0, 1.25, to 1.75 times oviducal length); internally equipped with typical recurved pilaster. *Retractor* terminal, short and robust or long and thin.

Paraneanic genitalia with botryoidal ovotestis; larger albumin gland; smaller prostate; cylindrical, smaller, and shorter penis.

The genus *Tornatellaria* resembles *Tornatellides* very closely. Adult specimens have 6.5 to 9.5 whorls (*Tornatellaria trochoides*). The shells are more brittle, the embryonic whorls more rounded and with stronger spiral lines, and the whorls are, as a rule, flatter than those of *Tornatellides*. This is the only genus in the tribe in which the animal is oviparous.

The removal of *Tornatellaria stokesi* into *Tornatellides* and of *Tornatellides thaanumi* into *Tornatellaria* has already been discussed in this paper. Further study of the abundant material now in the Museum may necessitate the reduction of a few of the forms now considered species (Pilsbry and Cooke, 1915). Practically no new species of the genus have been found since 1915.

The following *Tornatellaria* species were dissected but not described or illustrated: *adelinae* (119147), Oahu, three specimens; *cincta* (38507, two specimens; 38836, one specimen), Maui, three specimens; *sykesi* (161862-161863), Hawaii, three specimens; *sykesi illibata* (36576), Molokai, two specimens; *thaanumi* (36572), Molokai, one specimen.

***Tornatellaria newcombi*** (Pfeiffer). Figure 112, *a-e*.

*Tornatellina newcombi* Pfeiffer, 1856, *Zool. Soc. London, Proc.*, 335; 1859, *Mon. Hel. Viv.* 4: 653.

*Tornatellina (Tornatellaria) newcombi* Pilsbry, 1910, *Nautilus* 23 (10): 124.

*Tornatellina newcombi* Pilsbry and Cooke, 1916, *Man. Conch.* 23: 258, pl. 54, figs. 9, 10.

Shell ovate-turrite and approximately  $4 \times 2.3$  mm., about 7 whorls.

Adult genitalia. *Ovotestis* five-lobed; follicles fairly numerous, large, clavate, semi-transparent, globules (ova ?) visible. *Duct* large, distended, strongly convoluted. *Talon and carrefour* not studied. *Albumin gland* fairly large; follicles short-clavate, heavily distended. *Spermatheca* large, heavily distended; stalk approximately 0.5 oviducal length, large. *Vas deferens* quite large, emptying into penis at midbody (Y) or just above it (fig. 112, c; VDO). *Oviduct* subcylindrical. *Uterus and vagina* nearly equal in length. *Penis* large (ratio of width to length, 1:5.4), as long as oviduct or slightly longer, crooked-clavate, larger in the middle and above, narrower below. Interior of penis with typical achatinellid pilaster, slightly modified; ascending or principal pilaster (Pil 1) giving off several lateral ribs connecting or not with descending arm; apex enlarged, without velum; descending pilaster terminating as large pendent lingual papilla (P Pap) which lies over orifice of vas deferens; wall of penis otherwise plain. *Retractor* short, stout. *Atrium* short, narrow.

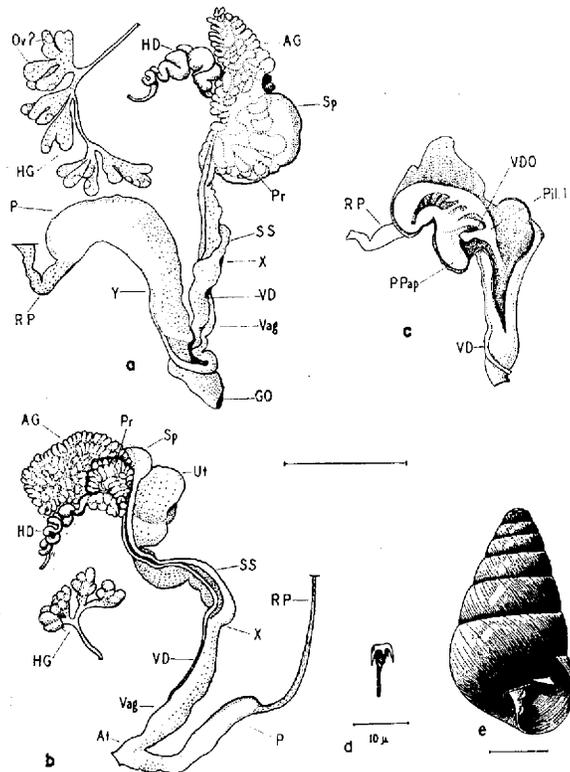


FIGURE 112.—*Tornatellaria newcombi*: a, adult genitalia; b, paraneanic genitalia; c, interior of penis; d, tooth; e, shell.

Central nervous system (not figured). Inferior frontal nerve passes through penioviducal angle, giving off strong penial nerve attaching to base of penis. Left ganglion with two frontals, the superior nerve larger. Superior frontal of right ganglion bifurcates near terminus, the right branch innervating base of ommatophore, the left branch inserting in wall above lower tentacle. Labio-tentaculo-nuchal nerve very large, giving off respective nerves at distal points as in *Tornatellides oblongus* and *Tubuaia perplexa*.

*Teeth.* All alike, small delicate, five-dentate, with three cusps plus two fine cusplets below. Length 10 microns; width 3.3 microns. Formula  $\pm 65-1-65$ .

Subadult or paraneanic juvenile genitalia similar to those of adult except as follows: Ootestis trilobate, botryoidal; follicles more globular than clavate. Albumin gland relatively much larger, with more follicles. Prostate more reduced; follicles small, more numerous. Uterus with large distension above. Penis small, cylindrical, short ( $\pm 0.3$  oviducal length).

Dissected 91061 (adult and juvenile genitalia, nervous system, teeth), five specimens.

Type in British Museum.

Distribution: Kauai and Oahu.

The differences between adults and juveniles in regard to the albumin and prostate glands, and correlated by penial size, are reminiscent of an identical phenomenon in *Pityisini* and *Tubuaia*. The large size of the prostate and the diminution of the albumin gland in the adult may possibly indicate that the adult of *Tornatellaria* is a functional male and, conversely, that the subadult or paraneanic is a functional female.

Four other *tornatellarias* were dissected: *T. sykesi*, which is very close to *T. newcombi*; *T. sykesi illibata*, which has a more cylindrical and longer penis than *T. newcombi*, a larger prostate with longer follicles, and a somewhat shorter spermathecal stalk; and *T. thaanumi*, which was too poorly preserved for satisfactory study.

#### ***Tornatellaria thaanumi* (Pilsbry and Cooke).**

*Tornatellides thaanumi* Pilsbry and Cooke, 1915, *Man. Conch.* 23: 215, pl. 47, figs. 1, 2, 4.

Holotype in <sup>Bishop</sup>British Museum (36243); cotypes in Academy of Natural Sciences, Philadelphia (111847). *Thaanum* collection, type locality Mapulehu, Molokai.

This species was transferred from *Tornatellides* to *Tornatellaria* after examination of a typical lot (36572) from Kalamaula, Molokai, led to a re-examination of the type and paratypes. The blunt apex and the texture of the surface, together with the spiral striation of the embryonic whorls, confirm this separation.

*Tornatellaria thaanumi* is the smallest species of the genus (2.75 mm. long). The smallest species found previously was *T. sharpi* (3.3 mm. long), from Kilauea, Hawaii.

Since all animals in the Museum collection are in poor shape, the genitalia are not illustrated.

## SUBFAMILY AURICULELLINAE

Hawaiian shells of the genera *Auriculella* and *Gulickia*,  $\pm 3.5$ -12 mm. long, whorls  $\pm 5$  to 9.5, sinistral or dextral, perforate, minutely perforate, or closed, with well-developed parietal lamella, one or two columellar lamellae, no palatal folds, reproducing oviparously.

Penis innervated by cerebral ganglion. Right ommatophoral retractor (left in sinistral) passing through peni-oviducal angle. Penis with appendix, without achatinellid pilaster, with small epiphallus. Epiphallus with small verge or papilla. Appendix without retractor, interior with straight tubular secretory-ejaculatory apparatus. Albumin gland fairly large, well developed. Prostate large, fan-shaped. Ovotestis multilobate.

Auriculellinae differs from the other five subfamilies in that it has an epiphallus on the penis which has a verge (or papilla) and in that the penis lacks an achatinellid pilaster.

## TRIBE AURICULELLINI

With penial appendix; without appendical retractor.

Genus *Auriculella* Pfeiffer

- Auriculella* Pfeiffer, 1855, Zool. Soc., London, Proc., 1 [for *Helix auricula* Férussac, *Tornatellina petitiiana* Pfeiffer, *Partula pusilla* Gould?, *Achatinella (Auriculella) cerea* Pfeiffer].—Pfeiffer, 1877, Mon. Hel. Viv. 8: 209.  
—Pease, 1868, Jour. de Conchyl., 342; 1869, Zool. Soc. London, Proc., 649.  
—Pilsbry and Cooke, 1915, Man. Conch. 23: 71.
- Frickella* Pfeiffer, 1855, Zool. Soc. London, Proc., 2. Monotype *A. amoena* Pfeiffer.
- Trickella* Pfeiffer, Nevill, 1878, Indian Mus., Handlist, 159 (*vide* Pilsbry and Cooke).

"The shell is oblong-conic or ovate-pyramidal, perforate or closed; the internal axis is slender, imperforate, unarmed except in the last whorl; surface highly polished; aperture ovate, the outer lip somewhat expanding, blunt, usually thickened; there is a well-developed parietal lamella and often one or two columellar lamellae or folds, the latter always present in the young stages. Animal oviparous, the eye-tentacles swollen at their tips.

"Type *A. auricula* (Fér.). Distribution, Hawaiian Islands (except Niihau, Kauai, and Kahoolawe); station, on bushes and other plants." (Pilsbry and Cooke.)

*Ovotestis* multilobate; lobes five to seven; follicles numerous, tips well defined, ordinarily branched. *Duct* distended, convoluted. *Albumin gland* ordinarily small, occasionally larger than prostate; follicles minute, numerous, erect, apparently radiating from central core. *Prostate* ordinarily large, usually fan-shaped; follicles large, digitate, usually quite numerous, sometimes scarce. *Talon* small, recurved. *Carrefour* small. *Spermatheca* large, ovate or oblong, lying on prostate; stalk 0.25 to 0.75 times oviducal length, usually the

latter. *Oviduct* long, narrow; uterus occasionally saccate near prostate. *Vas deferens* free, quite wide, entering penis through small epiphallus. *Penis* large, long, with epiphallus and appendix; length in relation to oviduct, 0.5 to 1.5 times oviducal length (average ratio, oviduct to penis, 1.25:1; ratio, penial length to width, 3.5:1); interior of penis without achatinellid pilaster, with low vertical secondary pilasters; with small apical epiphallus, with small verge within epiphallus. *Appendix* small, fairly long, 0.7 to 2.4 penial length (ratio, penis to appendix, 1:1.4; ratio, appendical length to width, 24:1), without retractor; interior with inner tubular secretory-ejaculatory apparatus. *Atrium* short.

Four groups of species of *Auriculella* totaling 22 species were dissected. From these were derived the rough measurements given in the preceding description. Basically, all the species are similar, differing in minor details. Sectional differences are not apparent.

For a discussion of this genus, see the Manual of Conchology (Pilsbry and Cooke, 1915). Little has been added to our knowledge since 1915, except in regard to the distribution of the different species and descriptions of a few new forms.

Shells of two to four specimens of nine representative species from each of the four groups of species from the different islands were partly opened to determine the length of the parietal lamella. In every specimen the parietal lamella was at least one whorl long and quite uniform: divided into two parts, the front (0.33-0.50), rather high, the back decreasing either abruptly or gradually and continuing for the rest of its length as a low threadlike line. In juvenile specimens the parietal lamella (*A. westerlundiana*) is of nearly even height for almost its whole length; in another species (*A. straminea*) the high portion occupies about two-thirds of the length.

The following 22 species of *Auriculella*, which fall into four groups, were dissected but not described or illustrated. Unless otherwise indicated, they were collected on Oahu.

(1) *auricula: ambusta* (33790), two specimens; *auricula* (23127), two specimens; *diaphana* (16101), one specimen; *diaphana cacuminis* (41322), one specimen; *montana* (23119, 20163), three specimens of each number; *olivacea* (17741), five specimens; *pulchra* (19299), two specimens; *straminea* (19685), two specimens, (43835), four specimens, and (16195), two specimens; new species (21721), three specimens.

(2) *perpusilla: minuta* (12799), three specimens, (16371), four specimens; *perpusilla* (24943), three specimens; *perversa* (12798), four specimens; new species (24989), four specimens.

(3) *castanea: castanea* (16370), one specimen; *tantalus* (16191), three specimens; *tenella* (21869), one specimen; *turritella* (17621), one specimen.

(4) *cerea: crassula* (21617), Maui, two specimens; *brunnea* (47093), Molokai, three specimens; *lanaiensis* (34254), Lanai, two specimens; *newcombi* (24500), Molokai, two specimens; *uniplicata* (21031), Maui, two specimens; *westerlundiana* (39672), Hawaii, two specimens.

**Auriculella auricula** (Férussac). Figures 113, *a-e*; 114, *a-c*.

*Partula auricula* Férussac, 1821, Prodrôme, 66.

*Auriculella auricula* Pilsbry and Cooke, 1915, Man. Conch. 23: 78, pl. 24, figs. 1-10.

For complete synonymy, see Pilsbry and Cooke (1915).

"Shell ovately-acute, imperforate, slightly thickened, somewhat striate, yellowish; spire conical, apex obtuse. Whorls 5, contiguous, the last ventricose, subcarinate. Aperture subquadrangular; lip acute, thickened within, with flexuous outer margin; columella unidentate. Furnished, in the depth of the aperture, with an elevated strongly marked lamella. Length 3, diam.  $1\frac{3}{4}$  lines ( $6.8 \times 4.0$  mm.)." (Férussac, Pilsbry and Cooke's translation.)

*Adult genitalia* (animal dextral; figs. 113, *b*; 114, *a-c*). *Ovotestis* multilobate, lobes seven, follicles somewhat loosely packed, in contrast to those of *Achatinella*, clefts between

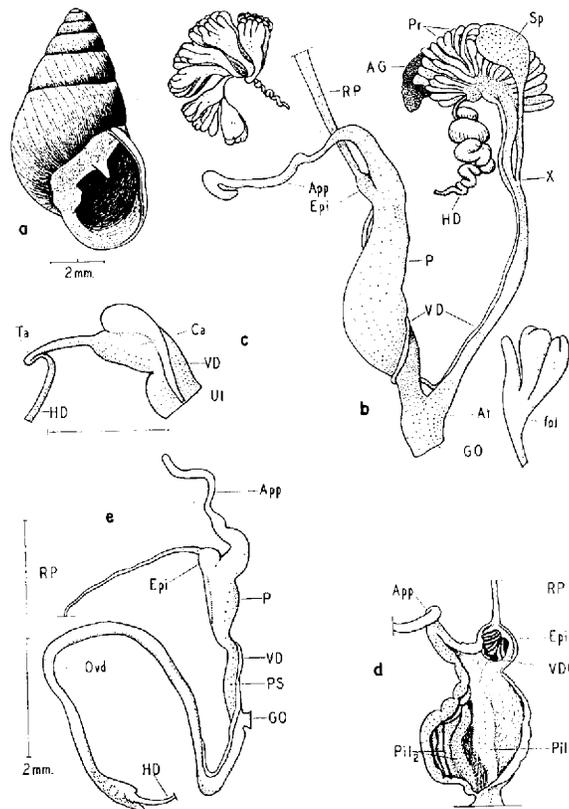


FIGURE 113.—*Auriculella auricula*: a, shell; b, adult genitalia, with closeup of a follicle from ovotestis; c, carrefour complex, closeup; d, interior of penis; e, parametaneanic genitalia, minus ovotestis.

follicular branches deeper, contours of follicles more round. *Duct* strongly convoluted, distended mediad. *Talon* small, hairpin-shaped. *Carrefour* oblong-ovate, embedded within prostatic follicles. *Albumin gland* terminal, fairly large, below prostate; follicles numerous, minute, round or oval, only tips visible. *Prostate* large, fan-shaped; follicles large, numerous, digitate. *Spermatheca* large, oval, lying on prostate; stalk short, 0.3 vaginal length, entering vagina at X. *Vas deferens* free, narrow, long, following oviduct to atrium, thence making a complete turn around penis, entering penis at epiphallus (figs. 113, *d*; 114, *a*). *Uterus* narrow short. *Vagina* long (three times uterine length), narrow (four to five times width of vas deferens), somewhat flaring near atrium. *Penis* nearly as long as oviduct, stalk narrow, middle body expanded, upper body narrow; retractor terminal, large. Interior of penis with low vertical secondary pilasters (figs. 113, *d*; 114, *a*: D-D), pilasters diminishing apicad (fig. 114, *a*: C-C), smooth farther above (fig. 114, *a*: B-B); apex of penis chambered by small epiphallus. *Epiphallus* faintly trabeculate, papilla not seen (seen in *A. castanea*, 16370). *Appendix* (App) also terminal, without retractor, small, short (as long as penis). Interior of appendix (fig. 114, *a*: E-E), smooth below, with low indistinct vertical pilasters; above with "verge" or internal tube of circular muscle tissues (App V) which becomes thinner near tip and appears to consolidate with integument of appendix (fig. 114, *a*: F-F).

Central nervous system (fig. 114, *b*), in sinistral specimens, reversed.

*Buccal ganglion*, left: (1) Buccal connective from cerebral ganglion to postero-lateral corner of buccal ganglion. (2) Lateral buccal nerve off lateral edge next to connective, ventrad and slightly forward. (3 and 4) Anterior oesophageal and anterior salivary duct nerves, very thin twin nerves off anterior face to innervate these ducts at, respectively, their emerging point (oesophageal) and terminal point (salivary ducts). (5) Median oesophageal duct nerve off inner edge directly to oesophagus. (6) Buccal commissure joining buccal ganglia. (7) Odontophoral off postero-latero-ventral surface directly ventrad. (8) Posterior salivary duct nerve off posterior edge to salivary duct.

In right buccal ganglion nerves are identical.

The buccal ganglion of *Auriculella auricula* differs from that of *Achatinella concavospira* in that the accessory nerves are absent (sixth of *Achatinella*); also, the eighth of *Auriculella* (posterior salivary duct) innervates the duct rather than the gland. It is possible that the eighth continues posteriad to the glands, adhering tightly to the duct.

*Cerebral ganglion*, right: (1) Nuchal nerve off medio-ventral surface to head parts. (2) Ommatophoral and optic nerve through peni-oviducal angle to superior tentacle. (3) Superior frontal nerve from near base of ommatophoral, through peni-oviducal angle, to base of ommatophore. (4) Penial nerve off root of nuchal nerve, through peni-oviducal angle, to penial stalk, making left spiral up vas deferens, thence up penis [corresponding nerve on left cerebral ganglion = fourth, inferior frontal]. (5) Labio-tentacular (= *nerf labial median* of Steenberg) a very large trunk off ventral surface, giving off one nervelet to ventrum of mouth, thence trifurcating to (a) inferior tentacle, (b) into lateral integument of mouth anteriorly of mouth retractor, and (c) to base of mouth. (6) Buccal connective off fronto-ventral surface to buccal ganglion. (7) Buccal retractor nerve off posterior inner surface (see inside circumoesophageal ring). (8) Acoustic nerve (not figured) between two pedal connectives, ventrad to otocysts. (9) Subcerebral nerve, seen in part only, off region of cerebro-pedal connective, ventrad, to be lost among arteries (in this specimen).

*Cerebral ganglion*, left: all nerves identical except for substituting inferior frontal (fourth) for penial and left salivary gland lobe nerve (seventh) for buccal retractor.

*Pleural ganglion*, left: (10) Small nerve to left inferior tentacular retractor [to right retractor (16) in right pleural].

*Parietal ganglion*, left: (11) Large left pallial.

*Abdominal and right parietal ganglia*: (12) Caudal nerve to columellar muscle and dorsum of tail. (13) Intestinal nerve off apex, giving off uterine branch (Ut) farther caudad. (14) Anal nerve quite large, over retractor muscles, thence under uterus to integument (not followed farther). (15) Right pallial. (16) Right inferior tentacular retractor nerve (see tenth).

*Pedal ganglion*, right, lateral series: (17) One anterolateral pedal. (18) One trifurcating lateral: (a) one branch through peni-oviducal angle to body wall opposite penis, (b) second branch over vagina to body wall, and (c) third branch going below uterus to body wall (figure shows two main branches). (19) One posterior lateral.

*Ventral series* (in heavy black): (20) One anteroventral pedal. (21) One to two (if one then soon bifurcating) medioventral(s). (22) One to two large caudoventral(s).

*Pedal ganglion*, left, lateral series: (23) One large anterolateral pedal nerve. (24) Two laterals the anterior nerve to retractor of foot, the posterior to body wall. (25) Small posterolaterals.

*Ventral series* (in heavy black): (26) Three anteroventral pedals or none. (27) Apparently no medioventral pedals or two if anteroventral pedals absent (twenty-sixth). (28) Two large caudoventrals.

Total number of nerves 28, in contrast to 29 in *Achatinella concavospira*. *Auriculella* lacks salivary gland nerve, the eleventh on left parietal ganglion in *Achatinella*.

Para- to metaneanic genitalia (fig. 113, e) closely similar to that of adult *Tornatellides oblongus*. Appendix without retractor, epiphallic branch a mere knob with retractor, below tapering gradually to a long stalk. Internally same as in adult, free of principal pilaster, smaller pilasters weak, epiphallus faintly trabeculate. Female portion undeveloped.

*Radula* as in *Achatinella*. Formula  $\pm 88-1-88$ . *Teeth* (fig. 114, c) all alike, seven-dentate, head narrow; one ectocone, one mesocone, one entocone plus four fine cusplets between and below cones. Length 16.6 microns, width 6 microns.

Dissected 189709 (adult genitalia, central nervous system, teeth), seven specimens; 189710 (juvenile genitalia, teeth), two specimens; 34067 (teeth, sections of appendix), two specimens.

*Auriculella* is the only genus in Achatinellidae characterized by a penial epiphallus. *Auriculella* and *Tornatellides* appear to be related, in that the penises of both are externally similar. Both lack the appendical retractor, and the epiphallic and appendical branches of the penises are terminal, not lateral.

External similarity is not confirmed by internal morphology. The penis of *Auriculella* has no achatinellid pilaster, whereas the penis of *Tornatellides* has a modified pilaster. The penis of *Auriculella* has a small but true epiphallus, whereas *Tornatellides* has none. The appendix of *Auriculella* has an internal tubular structure similar to that in Achatinellini, whereas the appendix of *Tornatellides* has none. Therefore, the subfamily Auriculellinae is here placed between Tornatellidinae and Achatinellinae.

#### *Auriculella castanea* Pfeiffer (fig. 114, d).

Animal sinistral. Interior of penis without achatinellid pilaster but with low vertical secondary pilasters (Pil 2). Epiphallus small, with small verge at termination of vas deferens; verge with minute, shallow, vertical slits. Sperm mass at penial orifice; upper half brown, semi-translucent, hard; lower portion white, opaque, soft; without chitinous covering.

Dissected 16370, two specimens.

See 215621 (Sever)  
215573 (1)

Genus *Gulickia* Cooke

*Gulickia* Cooke, 1915, Man. Conch. 23: 112, 228. Type *Gulickia alexandri* Cooke.

This monotypic genus has been taken only on west Maui, Hawaiian Islands, but from three widely separated localities. It is undoubtedly an inhabitant of most of the western part of Maui. The exact position of this genus is open to doubt because only a single animal, too mashed for dissection, is available. It is

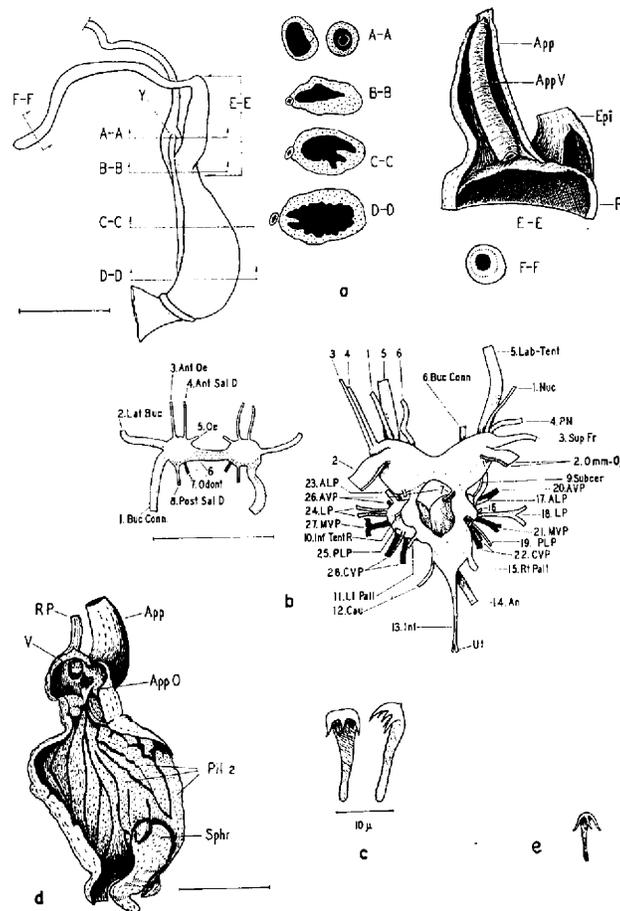


FIGURE 114.—a-c, *Auriculella auricula*: a, cross section of penis and appendix [A-A = a section through both penis (distal) and appendix (proximal); E-E = a longitudinal incision at lower part of appendix; F-F = a cross section near tip of appendix; B-B, C-C, D-D = sections of upper, middle, and lower penis]; b, central nervous system (left = buccal ganglia); c, teeth. d, *Auriculella castanea*, interior of penis. e, *Gulickia alexandri*, tooth.

here tentatively placed in the tribe Auriculellini because of its conchological characters. The shells are sinistral, which agrees with a majority of the species of *Auriculella*; and its habits are arboreal. The subperforate columella and the two very oblique, almost equal, columellar folds are similar to the species of *Auriculella* in the *castanea* group. The most important characters which separate it from *Auriculella* are the unthickened lip and the deeply entering parietal lamella. The margin of the lamella is unevenly, weakly serrate, as in *Auriculella serrula*. The columellar folds in juvenile specimens are nearly equal in development, whereas in *Auriculella* the lower fold is much stronger than the upper.

The anatomy is unknown; oviparous.

The teeth (fig. 114, *e*) are small and three-dentate, and no delicate intermediate cusplets are discernible. They are 8.6 microns long and three microns wide (38975).

#### SUBFAMILY ACHATINELLINAE

*Achatinellidae* Tryon, Pilsbry and Cooke, 1914, Man. Conch. 22: ix.

"The shell is more or less glossy, dextral or sinistral, oblong or ovate, minutely perforate or closed, composed of five to seven whorls, the last convex; aperture ovate; outer lip thickened or simple, sometimes expanding a little; columella usually bearing a strong, obliquely entering lamella in the last whorl; internal axis sinuous. No entering lamella or tooth on the parietal wall. . . . Viviparous.

"Distribution, the Hawaiian Islands (except Kauai, Niihau, and perhaps Kahoolawe). Living on trees and other plants." (Pilsbry and Cooke.)

Penis innervated by cerebral ganglion. Right ommatophoral retractor (left in sinistral) passing through peni-oviducal angle. Penis with appendix; with reflexed pilaster. Appendix with retractor; interior with straight tubular secretory-ejaculatory apparatus. Albumin gland minute or nearly so. Prostate large, multifolliculate; follicles long, slender, bundled, not fanned. Spermatheca not free, buried within prostatic follicles. Ovary multilobate. Viviparous.

#### TRIBE ACHATINELLINI

With appendix; with appendical retractor. Viviparous.

The following description applies to the genera *Newcombia*, *Perdicella*, *Partulina*, and *Achatinella*.

*Ovary* three- to 10-lobed; when three lobes, emaciated, meager, follicles short, tightly packed; when more than three lobes, robust, follicles numerous, long, tightly packed. *Duct* heavily convoluted, with large median distention. *Talon* probably non-existent; at least, no reflexed part seen as yet. *Carrefour* very small, a mere meeting place for ducts and glands. *Albumin gland* minute. *Prostate* large; follicles slender, long, digitate, usually lying parallel (or nearly so) upon each other, enclosing spermatheca in middle. *Spermatheca* rather large, oval; stalk long, quite large, inserting on oviduct below embryo(s). *Vas deferens* fairly large, free, terminating or nearly terminating on penis at apex. *Oviduct* with preuterine chamber next to carrefour, containing one to three very small and immature embryos which are probably more correctly termed eggs. *Median uterus* inflated in adult, usually with one embryo, rarely two, translucent to opaque. *Lower uterus* narrow, 0.3 to 0.5 total length. *Vagina* short. *Penis* quite long ( $\pm 0.3$  to 0.5 oviducal length) large (ratio, width to length,  $\pm 1:5$ ), clavate. Interior of penis with large recurved pilaster, either with semi-pendent fleshy lingual penial papilla or with simple fleshy ridge; pilasters either

beginning and terminating at atrium or beginning and terminating at level of appendical orifice, or some combination of the two types. Termination of vas deferens terminal or nearly so. *Appendix* large, often quite short ( $\pm 1.75$  to 2.0 times penial length), often extremely long ( $\pm 2$  to 6 times penial length). Interior of appendix with secretory-ejaculatory apparatus; apparatus a thin tube, without convolutions upon itself, enclosed by outer tube of circular muscles; outer tube enclosed, in turn, by appendicular sheath of longitudinal muscle. *Retractor* bifurcate; terminal in penial retractor; appendical retractor near base. *Atrium* short, narrow or fairly wide.

Genital characteristics of Achatinellinae follow same fundamental plan. (The parts will be treated below and the minor peculiarities, if any, discussed in detail.)

Ovotestis multilobate, similar in all genera, in that lobes are numerous (up to 10), and richly supplied with follicles (with the exception of *Perdicella*), appearing full; easy to dissect and to mount. In *Perdicella* and *Newcombia cumingi* ovotestis paucilobate (three at most in *Perdicella* and three or four in *N. cumingi*) appearing shriveled, difficult to dissect and mount, and having tightly bunched, very short follicles. Carrefour very small, without definite shape, serving merely as a meeting place for the three ducts (HD, VD, Ut) and two glands (Pr, AG). Talon, as such, not found. Hermaphrodite duct enters directly without contorting (see *Achatinella concavospira*, *Perdicella helena*). Spermatheca always enclosed by the numerous digitate prostatic follicles, fairly large, ovate. Stalk enters lower uterus below embryos. Prostate well developed, with numerous long, digitate follicles in all genera. Albumin gland minute in all genera and on carrefour. Preuterine chamber present in all genera as one small globular or oval sac at carrefour exit of uterus; in some specimens two or three bulges, each bulge containing roundish yolk masses, very immature embryos or shell-less eggs (these have been carefully studied macroscopically and appear to be eggs rather than immature embryos); from preuterine chamber a narrow, short, wrinkled "neck" leads to uterus proper; mature uterus almost always contains one embryo, rarely two; any with three or more have not yet been seen. Penis length and size in relation to length of oviduct nearly constant; penial lengths  $\pm 0.3$  oviducal length to  $\pm 0.5$ , none seen exceeding oviducal length; interior structure of penis basically similar in all genera in that pilaster is achatinelloid, consisting of an ascending and descending fleshy ridge. In *Perdicella*, *Newcombia*, and *Partulina* dissected so far, descending arm of pilaster not semi-pendent and tongue-like, as in some *Achatinella*, but consisting of a (usually) low strip of flesh that either ends at level of appendix origin or continues ventrad as an inconspicuous series of low ridges. Penial papillae of *Achatinella* not all tongue-like, but some simple ridges. Simplest pilasters found in *Perdicella* and *Newcombia*. *Partulina* pilaster more elaborate, with some fleshy ribs radiating laterally from main ridge (except *P. mighelsiana*) and ascending arm folding partially upon itself at least once (three times in *P. dubia*). (For further notes, see discussion in introduction.)

Appendices of two lengths among all genera of Achatinellinae; short appendices  $\pm 1.75$  times to 2.0 times length of penis and long ones ranging from  $\pm 2.0$  times to  $\pm 6$  times penial length and rather distinctly divided into three parts: (a) short, stout proximal root, (b) short median portion which tapers into distal part, and (c) the long tube, wide and bluntly tipped at the end and gradually tapering to a narrow tube mediad (Neal, 1928, p. 37). In short type of appendix distal portion quite short. Internally, the three divisions given by Neal correspondingly divided into the vestibular (just below muscular wall); the "verge," or the portion in which the appendical "verge" is the strongest; and the apical where the "verge" thins out into a weak inner tubular structure.

Macroscopically, the secretory-ejaculatory apparatus consists of two tubular structures; outer tube appears to be composed of circular muscles (a longitudinal slit is very difficult to make, the tube almost always splitting into short sections; fig. 116, *f*, *Perdicella helena*). Inner tube very delicate, not straight-sided but regularly folded, nearly transparent and somewhat resilient. "Verge" enclosed by appendicular wall on outside, thick proximally, thin distally, and composed of longitudinal muscular tissues. Tube lies loosely in proximal part but, as appendix narrows distally, becomes tightly enclosed until at tip (fig. 119, *b*: G-G; *Achatinella concavospira*) inner organ and outer sheath cannot be differentiated; tip of "verge" loses all definite characteristics.

Vergic portion of appendix sealed off from vestibular (or proximal) part by a thin muscular wall like that in Pitysiinae, Lamellideinae, and Auriculellinae.

A peculiarity of the Achatinellinae penial retractor is a small, short split just at the insertion on the penial apex. In some the split is strong, in others it is either not noticeable or is non-existent.

In general, the appendical retractor is distinctly separated from the penial retractor and the bifurcation of the common retractor into the penial and appendical branches occurs at a short distance dorsad of the penial apex (*Newcombia*, *Partulina*, *Achatinella*). However, in *Perdicella* the appendical retractor originates on the penis some distance below the penial apex, being strongly adnate to the upper penis (Neal's term = webbed; 1928, p. 37), and thus not clearly separated from the penial retractor. Neal gives an excellent explanation of this phenomenon, "As the webbed condition was found in juvenile *Achatinella viridans* (fig. 20), it is perhaps a juvenile character, significant of a low position of *Perdicella* in the scale of evolution of the family, a theory borne out by a juvenile feature of the adult shell, the thin unexpanded lip."

In regard to the pilasters found within the penis, the terminology applied to their component parts was originally applied to *Achatinella concavospira* and to the other genera by analogy. Ordinarily, the principal pilaster (Pil 1) consists of a heavy fold of flesh which starts at the lower part of the penis, ascends to the penial apex, thence making a recurvature, and descends to or near the point of origin. Some species, *A. concavospira* for example, have a somewhat modified descending arm which is semi-pendent and which is apparently more specialized for stimulation during the copulatory act than is the thin arm. This usually enlarged descending arm is termed the penial papilla. Unfortunately, not all species follow the genital type (*A. concavospira*) pattern. In some of the species (*A. turgida* and the dissected species of *Partulina*, *Newcombia*, and *Perdicella*) the penial papilla may be indistinguishable from the other arm, in which case we have called the arm toward the appendix the ascending arm and the other arm the papilla. In the few specimens where the principal stimulator was obviously on the opposite arm we labeled this arm the penial papilla.

Pilsbry and Cooke's systematic list (1914, pp. xv-xix) remains the same, with these additions: *Partulina dubia perantiqua* Cooke and Kondo is added to *Partulina* section *Baldwinia*, and *Partulina arnemanni* Cooke and Kondo is added to section *Partulinella*.

The anatomy of the following Achatinellinae is herein discussed.

Genus *Newcombia*: *N. canaliculata*, *N. cumingi*. Genus *Perdicella*: *P. helena*, *P. mauiensis*. Genus *Partulina*: *P. dubia*, *P. virgulata*, *P. redfieldii*, and *P. mighelsiana*. Genus *Achatinella*: *A. viridans*; *A. fuscobasis lyonsiana*, teeth; *A. lehuiensis meineckeii*; *A. concavospira*; and *A. turgida*.

Genus *Newcombia* Pfeiffer

*Newcombia* Pfeiffer, 1854, Malak. Blätt. 1: 117, for *Achatinella helena*, *physa*, *ornata*, *cumingi*, *plicata*, *newcombiana*, *cerealis*, and *elongata*.—Pilsbry and Cooke, 1912, Man. Conch. 22: 1.—Neal, 1928, B. P. Bishop Mus., Bull. 47: 43.

For complete synonymy, see Pilsbry and Cooke.

"Shell sinistral, oblong-turritid, usually coarsely sculptured, the embryonic shell of  $3\frac{1}{8}$  whorls having comparatively coarse spirals (8 to 12 spirals on the second whorl), the last embryonic whorl longitudinally striped. Outer lip slightly expanded or not; columella straight or weakly folded.

"Type *N. plicata* Migh. Distribution Molokai and Maui." (Pilsbry and Cooke.)

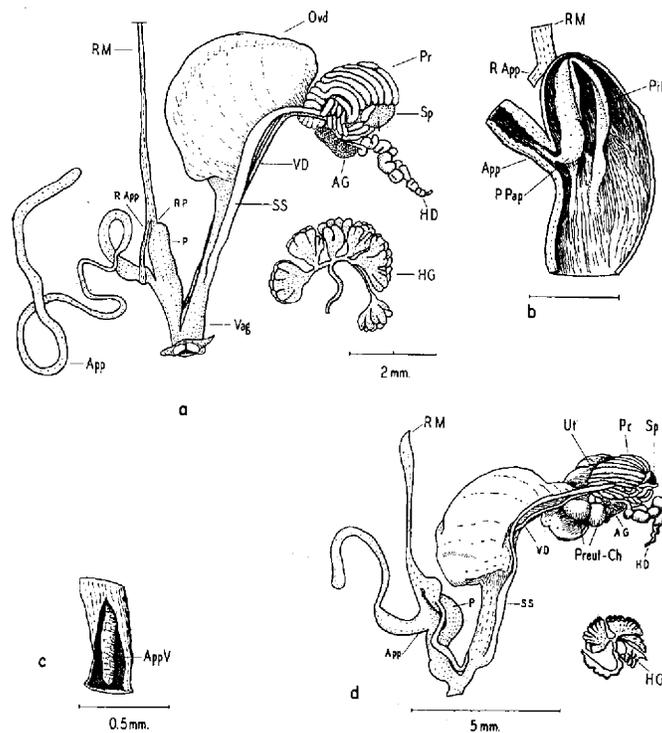


FIGURE 115.—a-c, *Newcombia canaliculata*: a, genitalia; b, interior of penis; c, interior of appendix, lower portion. d, *Newcombia cumingi*, genitalia.

***Newcombia canaliculata* (Baldwin). Figure 115, a-c.**

*Achatinella canaliculata* Baldwin, 1905, Acad. Nat. Sci. Philadelphia, Proc., 226, pl. 10, figs. 28, 29.

*Newcombia canaliculata* Borcharding, 1906, *Zoologica* 19 (48): 96, pl. 9, figs. 3, 3a.—Pilsbry and Cooke, 1912, *Man. Conch.* 22: 6, pl. 2, figs. 5-7.

Animal sinistral. Ovotestis five- to six-lobate, robust; follicles fairly large and few. Oviduct inflated; embryo, one. *Spermathecal stalk* large. *Penis* relatively short,  $\pm 0.3$  oviducal length. Interior of penis simple, with only principal pilaster. Pilaster (Pil 1) starts as low fold at middle, descends as a relatively large fold (P Pap) with one shallow furrow at its upper part, terminating at appendical aperture, continuing into appendix as short branch but also descending to a small, narrow ridge and terminating there. *Appendix* six times penial length; "verge" typical.

Dissected 59834, four specimens.

***Newcombia cumingi*** (Newcomb). Figure 115, *d*.

*Achatinella cumingi* Newcomb, 1853, *Lyceum Nat. Hist. New York, Ann.* 6: 25; 1853, *Zool. Soc. London, Proc.*, 150, pl. 24, fig. 59.—Pfeiffer, 1859, *Mon. Hel. Viv.* 4: 559.—Thwing, 1907, *B. P. Bishop Mus., Occ. Papers* 3 (1): 142, pl. 3, fig. 12.

*Newcombia cumingi* Pilsbry and Cooke, 1912, *Man. Conch.* 22: 10, pl. 3, figs. 1-6.

Animal sinistral. *Ovotestis* small, not robust, three- or four-lobate. *Oviduct* well inflated; one embryo. *Penis*  $\pm 0.5$  oviducal length; pilaster as in *N. canaliculata*. *Appendix* short, 1.75 times penial length; interior not studied.

Dissected 17760, three specimens.

*N. cumingi* resembles *Perdicella helena* closely in a few minor characters. Its appendix is short. Its ovotestis is small, appearing emaciated, and is at the very tip of the animal, as in *P. helena*. In *N. canaliculata* the ovotestis is at the intestinal bend, which is quite low.

#### Genus ***Perdicella*** Pease

*Perdicella* Pease, 1869, *Zool. Soc. London, Proc.*, 648.—Sykes, 1900, *Fauna Hawaiiensis* 2 (4): 329 (type *A. helena* Newcomb).—Pilsbry and Cooke, 1912, *Man. Conch.* 22: 15 (section *Perdicella*).—Neal, 1928, *B. P. Bishop Mus., Bull.* 47: 43 (summary 9).

"Small Partulinae having protracted stripes on the last embryonic whorl, later whorls striped or with a peripheral band; sculpture Partulinoid; columella nearly straight, or if developed the columella fold is moderate, convex, scarcely or not truncate; outer lip thin, not expanded. Type *P. helena* Nc." (Pilsbry and Cooke.)

Distribution: Molokai and Maui.

Because of the peculiar "webbing" of the appendical retractor on the penis, this section is raised to generic rank.

***Perdicella helena*** (Newcomb). Figure 116, *a-f*.

*Achatinella helena* Newcomb, 1853, *Lyceum Nat. Hist. New York, Ann.* 6: 27; 1853, *Zool. Soc. London, Proc.*, 151, pl. 24, fig. 63; 1854, 311.

*Partulina (Perdicella) helena* Pilsbry and Cooke, 1912, Man. Conch. 22: 16, pl. 4, figs. 1-7.

See Pilsbry and Cooke for full synonymy.

Shell as illustrated (fig. 116, a).

Animal sinistral. *Ovotestis* small, not robust, appearing emaciated or shriveled, two- to three-lobate. *Talon* not seen. *Duct* apparently entering carrefour immediately. *Carrefour* tiny, hidden within minute albumin gland. *Albumin gland* minute, multifolliculate; follicles numerous, minute. *Preuterine chamber* inflated, leading to uterus via narrow folded neck. *Oviduct* inflated (one embryo). *Vagina* longer than usual ( $\pm 0.25$  oviducal length). *Penis*  $\pm 0.5$  oviducal length. Interior of penis with simple principal pilaster, secondary pilasters scarce. Principal pilaster (Pil 1) narrow, starting about 0.5 way above penial orifice, gradually enlarging apicad; outer face near apex infolded, with some low, narrow secondary pilasters on outer side. Penial papilla (P Pap) larger and more pendent than ascending

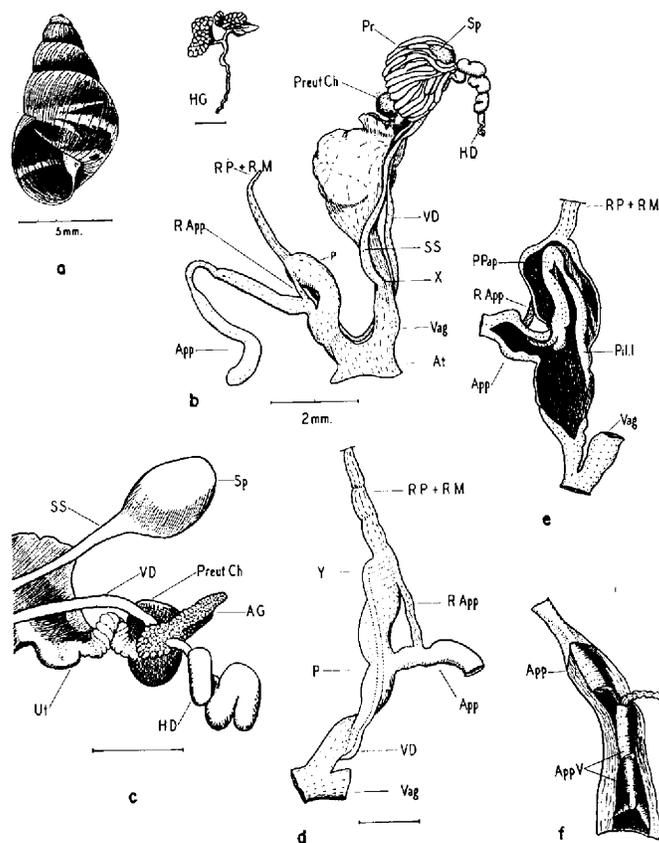


FIGURE 116.—*Perdicella helena*: a, shell; b, genitalia; c, upper female portion showing relationship of HD, AG, preuterine chamber, VD and Ut.; d, penis, illustrating "webbed" appendical retractor which rises off penial head instead of common retractor; e, interior of penis; f, interior of appendix, in part.

arm, terminating at appendical aperture and inserting therein a short distance. *Appendix* 1.75 times penial length; interior with typical "verge." "Verge" thin, narrow, delicate, translucent, regularly wrinkled, covered immediately to its exterior by tough outer tube of circularly arranged muscle tissues which is enclosed by heavy longitudinally arranged muscle tissues of appendix; "verge" strong in proximal part of appendix and loosely enclosed; thin distally and tightly enclosed. Appendical retractor off penial apex, not above it. *Atrium* short, wide.

Nervous system typical (not figured).

Dissected 24576, two specimens; 89047, four specimens.

*Perdicella helena* is unique in two ways: (1) the appendical retractor, instead of diverging some distance above the penial apex (as in all the other genera of this subfamily) is tightly adherent ("webbed") to the penial head at the point surrounded by circular tissues (fig. 116, *d*) and is freed some distance below the apex. Consequently, the common retractor muscle (RP + RM) appears to be a penial retractor. This phenomenon is explained by Neal (1928, p. 37). The "webbed" condition was found in juvenile *Achatinella viridans* and indicates the low position of *Perdicella* in the subfamily. The thin, unexpanded lip of the adult *Perdicella*, a juvenile character, bears out the theory. (2) the ovotestis is peculiar in that it is two- to three-lobate, appears emaciated, is very small, and is difficult to mount for either study or illustration. Its follicles are short, very tightly bunched, and appear meager.

The above characteristics are also applicable to *P. mauiensis* and will, in all probability, hold for the other species of the genus.

#### **Perdicella mauiensis** (Pfeiffer).

*Achatinella mauiensis* Newcomb, Pfeiffer, 1855, Zool. Soc. London, Proc., 207 [typographical error for *mauiensis*].

*Partulina (Perdicella) mauiensis* Pilsbry and Cooke, 1912, Man. Conch. 22: 20, pl. 4, figs. 11-14.

See Pilsbry and Cooke for additional synonymy.

Animal dextral. Genitalia (not figured) same as in *P. helena*. Penis and appendix about the same size and length; interior of appendix identical.

Dissected 87443 (adult, juvenile), three specimens.

#### Genus **Partulina** Pfeiffer

*Partulina* Pfeiffer, 1854, Malak. Blätt. 1: 114 (for *Achatinella virgulata*, *tessellata*, *splendida*, *perdix*, *gouldi*, and *dubia*).—von Martens, 1860, Die Heliceen, 243, type *A. virgulata* Mighels.—Gulick, 1873, Zool. Soc. London, Proc., 90, same type.—Sykes, 1900, Fauna Hawaiiensis 2 (4): 311.—Pilsbry and Cooke, 1912, Man. Conch. 22: 14.

"Shell ovate-conic, usually *perforate*, and having distinct minute sculpture of *spirally descending rippled striae*. Embryonic shell after the first whorl spirally striate. Color pat-

tern of oblique stripes or spiral bands, the last embryonic whorl generally striped. *Lip expanded* more or less; columella folded or almost simple.

"Type *Partulina virgulata* (Migh.). Distribution, Molokai, Lanai, Maui, and Hawaii, one species on Oahu." (Pilsbry and Cooke.)

Excluded is section *Perdicella*; included are sections *Baldwinia*, *Partulina* (*s.s.*), *Partulinella*, and *Eburnella*.

Section **Baldwinia**

**Partulina (Baldwinia) dubia** (Newcomb). Figure 117, *a-c*.

*Achatinella dubia* Newcomb, 1853, Lyceum Nat. Hist. New York, Ann. 6: 23.—1853, Zool. Soc. London, Proc., 152, pl. 24, fig. 65.

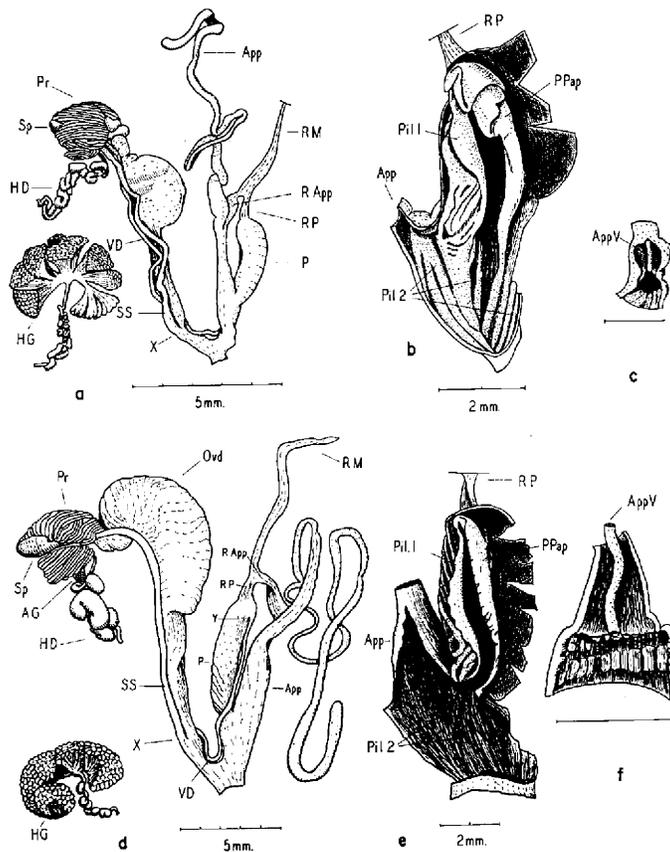


FIGURE 117.—*a-c*, *Partulina (Baldwinia) dubia*: *a*, genitalia; *b*, interior of penis; *c*, interior of appendix, in part. *d-f*, *Partulina (s.s.) virgulata*: *d*, genitalia; *e*, interior of penis; *f*, interior of appendix, in part.

*Partulina (Baldwinia) dubia* Pilsbry and Cooke, 1913, Man. Conch. 22: 113, pl. 26, figs. 7-12.

For additional synonymy see Pilsbry and Cooke.

Animal dextral. *Ovotestis* robust, eight- to 10-lobate. *Penis*  $\pm$  oviducal length. Interior of penis smooth above except for diagonal ribs near middle of penial papilla, heavily ridged below by numerous longitudinal fleshy pilasters. Principal pilaster (Pil 1) flat, wide, starting at penial aperture as a low ridge, widening dorsad, heavily wrinkled at middle, with a free folding mantle on inner face near apex. Penial papilla (P Pap) large above, with a thin fleshy mantle thrice folded upon papilla, gradually lessening in width ventrad, terminating near start of ascending pilaster. *Vas deferens* enters at and below apical recurvature of pilaster. *Appendix*  $\pm$  4.5 times penial length; interior with heavy longitudinal ridges or secondary pilasters. "Verge" typical. *Penial retractor* entire.

Nervous system typical with minor digression: left inferior frontal nerve appears to be consolidated with superior frontal nerve (only one specimen studied, not figured).

Dissected 123769, three specimens.

See the introduction to this paper for further anatomical description.

#### Section *Partulina*

***Partulina (s.s.) virgulata*** (Mighels). Figure 117, *d-f*.

*Partula virgulata* Mighels, 1845, Boston Soc. Nat. Hist., Proc. 2: 20.

*Partulina (s.s.) virgulata* Borcherdig, 1906, Zoologica 19 (48): 50, pl. 1, figs. 1-20.—Pilsbry and Cooke, 1912, Man. Conch. 22: 25, pl. 6, figs. 1-6, 9, 10.

See Pilsbry and Cooke for full synonymy.

Animal dextral or sinistral. *Ovotestis* robust, 10-lobate. *Oviduct* quite long, expanded, containing one embryo. *Vagina* longer than in *P. redfieldii*. *Penis*  $\pm$  0.5 oviducal length, interior diagonal ribs visible from exterior. Interior of penis with very low, indistinct fleshy folds or ridges below; numerous diagonal fleshy ribs above. Principal pilaster (Pil 1) starts at appendical orifice as narrow ridge, gradually widening to middle, and gradually narrowing to reflexure, with undulations on outer free edge, numerous diagonal ribs on outer attached edge. Penial papilla with tiny flap at apex, slightly wider than ascending pilaster, gradually narrowing ventrad into very narrow low ridge, inner face with numerous dents, outer face with some ribs, terminating opposite appendical aperture. *Appendix* more or less six times penial length. Interior of appendix heavily studded with short, fleshy folds or ridges; vergic organ typical. *Penial retractor* split.

Dissected 24762, two specimens.

#### Section *Partulinella*

***Partulina (Partulinella) redfieldii*** (Newcomb). Figure 118, *a-c*.

*Achatinella redfieldii* Newcomb, 1853, Lyceum Nat. Hist. New York, Ann. 6: 22, 325; 1853, Zool. Soc. London, Proc., 131, pl. 22, fig. 5; 1854, 311.

*Partulina (Partulinella) redfieldii* Pilsbry and Cooke, 1912, Man. Conch. 22: 38, pl. 7, figs. 12, 16, 17; pl. 8, figs. 14-20.

See Pilsbry and Cooke for full synonymy.

Animal sinistral. *Ovotestis* (not figured) robust, 10-lobate. *Oviduct* in figured specimen empty. *Vagina* very short. *Penis*  $\pm 0.5$  oviducal length, large, with diagonal interior ribs visible from exterior. Interior of penis with heavy longitudinal folds or secondary pilasters below appendical orifice; above this point diagonal ribs numerous. Principal pilaster (Pil 1) more or less uniformly narrow, starting at appendical orifice. Penial papilla (P Pap) wider, rounder than ascending pilaster, slightly broader near middle, descending as an irregular secondary pilaster from level of appendical aperture. *Vas deferens* enters at and below apical reflexure. *Appendix* more or less twice penial length. Interior of appendix with few indistinct fleshy folds below, smooth above. "Verge" typical. *Penial retractor* entire.

Dissected 76008, two specimens.

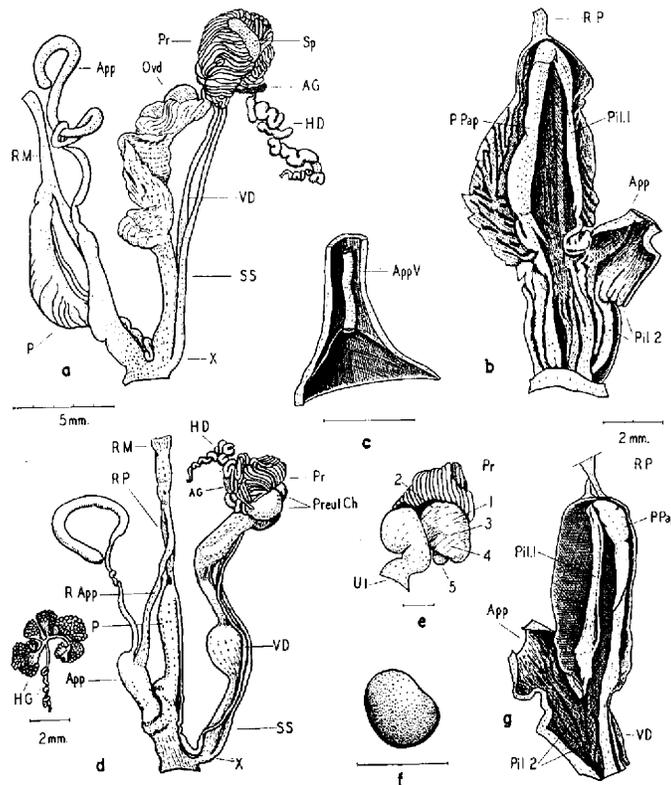


FIGURE 118.—a-c, *Partulina (Partulinella) redfieldii*: a, genitalia (minus ovotestis); b, interior of penis; c, interior of appendix, in part. d-g, *Partulina (Eburnella) mighelsiana*: d, genitalia; e, preuterine chamber with five undeveloped embryos (1 to 5); f, closeup of undeveloped embryo; g, interior of penis.

Section **Eburnella**

**Partulina (Eburnella) mighelsiana** (Pfeiffer). Figure 118, *d-g*.

*Achatinella mighelsiana* Pfeiffer, 1847, Zool. Soc. London, Proc., 231; 1848, Mon. Hel. Viv. 2: 238.

*Partulina (Eburnella) mighelsiana* Pilsbry and Cooke, 1913, Man. Conch. 22: 77, pl. 18, figs. 10-17.

See Pilsbry and Cooke for full synonymy.

Animal dextral. *Ovotestis* about eight-lobate, quite small compared with other species of *Partulina* (specimen probably immature). *Prostate* small, oviduct inflated (both probably the result of immaturity). *Preuterine* chamber with three relatively large bulges, the second bulge containing five undeveloped embryos (technically, probably ova). Undeveloped embryo (fig. 118, *f*: Em 1) composed of spongy substance. *Penis*  $\pm 0.5$  oviducal length, slender; interior smooth above appendical orifice, except for pilaster, with some heavy longitudinal fleshy folds below. Principal ascending pilaster (Pil 1) starting at appendical orifice, thin, flat, with inner edge slightly raised. Penial papilla (P Pap) enlarged above, indented a few times on outer face, narrowing below to a uniform width with one fold which terminates as a sharp point, continuing ventrad to penial orifice as a low but distinct fold. *Appendix*  $\pm 2.5$  times penial length. Appendical "verge" typical. *Penial retractor* split.

Dissected 75992, two specimens.

Genus **Achatinella** Swainson

*Achatinella* Swainson, 1828, Quarterly Jour. Science, Literature and Art II, 3: 83. Type *Monodonta seminigra* Lamarck = *Achatinella apexfulva* Dixon.  
*Achatinella* Pilsbry and Cooke, 1913, Man. Conch. 22: 117.

See Pilsbry and Cooke for full synonymy.

"Shell imperforate or minutely perforate, oblong, ovate, or globose-conic, smooth or longitudinally corrugated, with only minute and weak traces of spiral sculpture; color in spiral bands or streaks in the direction of growth lines, never in forwardly descending stripes; lip simple or thickened within, sometimes slightly expanding; columella bearing a strong callous fold.

"Type *A. apexfulva* (Dixon). Distribution, the island of Oahu." (Pilsbry and Cooke.)

A detailed genital, nervous system, and radula study is given below of *Achatinella* (*s.s.*) *concovospira* to serve as a reference for the entire family. Dentition of *A. fuscobasis lyonsiana* is appended to clarify a minor point in an earlier work by Suter.

**Achatinella (*s.s.*) concavospira** Pfeiffer (figs. 119, *a-d*; 120, *a, b*; 121, *a-e*; 122, *a-l*).

*Achatinella concavospira* Pfeiffer, 1859, Zool. Soc. London, Proc., 30; 1868, Mon. Hel. Viv. 6: 169.

*Apex turbiniformis* Gulick, 1873, Zool. Soc. London, Proc., 81, pl. 10, fig. 7.

*Achatinella* (*s.s.*) *concovospira* Pilsbry and Cooke, 1914, Man. Conch. 22: 351, pl. 52, fig. 16; pl. 61, figs. 12-12d; pl. 62, figs. 24, 25.

Shell as illustrated (fig. 119, a).

Animal dextral. Adult genitalia (fig. 119, b-d; 120, a, b; 121, a-c). *Ovotestis* multi-lobate; lobes nine to 10, composed of numerous tightly packed, branching, truncate follicles, apices broader than stalk. *Duct* strongly convoluted, swollen in middle. *Talon* absent or not seen. *Carrefour* small, of indefinite shape, with or without small protuberances. *Carrefour complex*, on close examination, revealed the following: talon not seen; carrefour a simple sac with a few irregular bulges. Minute albumin gland closely adherent to lower wall of carrefour just below entrance of hermaphrodite duct and exit of uterine duct. *Vas deferens* emerges from upper wall of carrefour, receiving prostatic follicles at the point

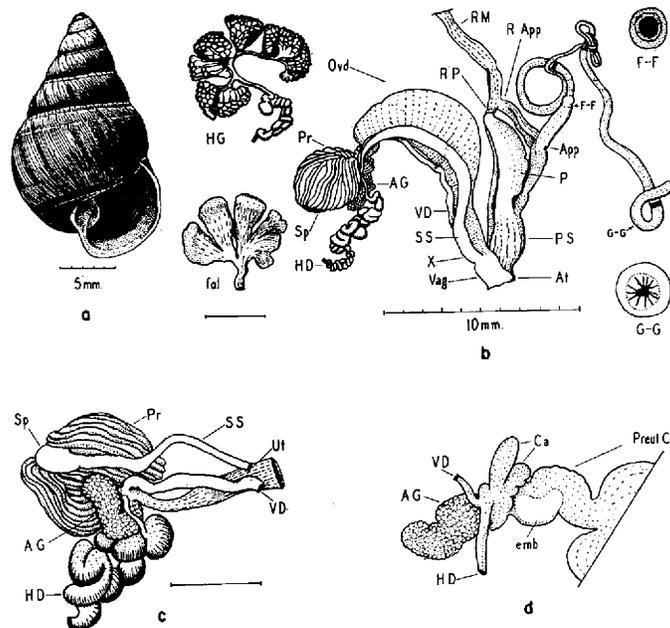


FIGURE 119.—*Achatinella* (*s.s.*) *concavospira*: a, shell; b, genitalia, a follicle of ovotestis magnified, sections F-F and G-G of appendix; c, distal portion of female tube showing entrance of hermaphrodite duct (HD) at carrefour and the efference of vas deferens (VD) and oviduct (Ut); d, carrefour complex and preuterine chamber with a renate protoembryo (emb).

immediately after emerging from carrefour. Narrow preuterine chamber containing one or two renate protoembryos, without visible shells, connects carrefour with expanded portion of uterus. Preuterine chamber characteristic of genera of Achatinellinae. *Albumin gland* minute; follicles numerous, minute, round. *Prostate* large, follicles long, tubular, lying longitudinally, closely packed, enclosing spermatheca tightly within. *Spermatheca* large, ovate, entirely enclosed within prostatic follicles, except tip; stalk large, free, entering vagina a short distance above genital orifice (X). *Vas deferens* free, about 0.3 diameter of spermathecal stalk, entering penis almost apically. *Uterus* with preuterine chamber containing undeveloped renate embryo, somewhat distended in middle with two embryos, narrowing near vagina. *Vagina* very short, narrow. *Penis* large, long (0.5-0.75

oviducal length), clavate above, broad below (ratio of width to length, 1:6); retractor terminal. Interior of penis with large recurved pilaster; pilaster ascending from below as narrow longitudinal ridge of flesh, broadening dorsad to a thick fleshy ridge, recurving at apex, descending as a semi-pendulous penial papilla; papilla with groove formed by free edge curving inward. Vas deferens orifice terminal, without epiphallus. Base of penis strongly, vertically rugose. *Appendix* very long (five to six times penial length, 3.3 times oviducal length), narrow, stemming from penis near middle, broad from root to retractor, thence smaller and cylindrical to knob, thence gradually tapering to small tube at middle, thence gradually enlarging to original size, ending in blunt tip (ratio of width of appendix to length,  $\pm 1:7.5$ ). *Appendix* interior with narrow tubular secretory-ejaculatory apparatus; outer integument coarsely muscular, inner tube thin, double-walled, of circularly arranged muscular tissues (delicate inner "verge" as in *Perdicella helena*, not seen); lower

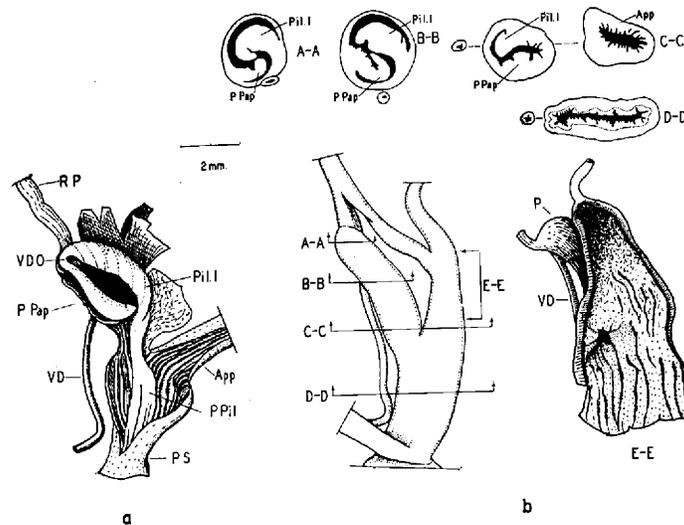


FIGURE 120.—*Achatinella* (s.s.) *concavospira*: a, interior of penis; b, cross sections of penis and interior of appendix, sections magnified in varying degrees.

portion of appendix composed of furry coating of innumerable tightly packed longitudinal rows of minute villi (see also b, section D-D in figure); terminal and flagelliform portion resembling root of appendix but having stronger papillae. *Common retractor* heavy, quite long. *Penial retractor* short. *Appendical retractor* much longer than latter. *Atrium* short, quite wide.

#### Central nervous system.

*Buccal ganglion*, left: (1) Buccal connective (Buc Conn) from cerebral ganglion to posterolateral edge of buccal ganglion. (2) Lateral buccal (Lat Buc) nerve, large, off side, ventrad and anteriad. (3 and 4) Anterior salivary duct plus anterior oesophageal (Ant Sal D, Ant Oe), twin nerves, off anterior face of ganglion, along salivary duct to entrance of duct into pharynx. Oesophageal nerve along oesophagus to exit of oesophagus from pharynx. (5) Median oesophageal (Oe) nerve off anterolateral edge directly laterad to oesophagus. (6) Two small nerves off ventrum, directly ventrad into buccal mass. (7) Buccal commissure. (8) Odontophoral nerve (Odont) off caudal edge, directly ventrad

into radular region. (9) Left salivary gland nerve (Lt Sal G) off root of odontophoral nerve, directly posteriad along left salivary duct to left lobe of gland.

*Buccal ganglion, right*: Nerves identical with left except odontophoral (eighth) off base of right salivary (ninth), probably due to partial contraction of right buccal ganglion.

*Cerebral ganglion, right*: (1) Nuchal (Nuc) nerve from anteroventral surface directly anteriad, bifurcating beyond half-way point to (a) front part of head and (b) lateral mouth parts. (2) Ommatophoral and optic (Omm-Op) off apex, through peni-oviducal angle to ommatophore. (3) Superior frontal (Sup Fr) nerve from below ommatophoral nerve, through peni-oviducal angle to base of ommatophore. (4) Penial nerve (PN) off base of labio-tentacular (fifth) to penis via vas deferens [corresponding nerve on left cerebral ganglion = inferior frontal (fourth) nerve]. (5) Labio-tentacular, large trunk nerve (Lab-Tent) off medioventral surface directly anteriad, trifurcating to (a) side of mouth, (b) inferior tentacle, and (c) lateral labial parts. (6) Buccal connective nerve (Buc Conn) off ventral surface to buccal ganglion. (7) Buccal retractor nerve (Buc R) off caudal surface. (8) Acoustic nerve between pedal connectives to otocysts (not figured). (9) Sub-cerebral nerve not seen but its existence not doubtful.

*Cerebral ganglion, left*. All nerves identical except: (a) inferior frontal (fourth) substituting for penial, (b) an extra nerve connecting ommatophoral to superior frontal, and (c) salivary gland nerve substituting for buccal retractor nerve (seventh).

*Pleural ganglion, left*: (10) Inferior tentacular nerve (not figured).

*Parietal ganglion, left*: (11) Salivary gland nerve (Sal G), bifurcating to left and right salivary lobes. (12) Left pallial (Lt Pall) nerve to body wall.

*Abdominal and right parietal ganglia*: (13) Intestinal (Int) nerve off apex, posteriad along aorta, with small branch to uterus. (14) Large anal nerve (An) below intestinal nerve. (15) Caudal (Cau) nerve from between left parietal and abdominal ganglia to dorsum of tail. (16) Right pallial (Rt Pall) nerve over uterus, to body wall.

*Pleural ganglion*: (17) Inferior tentacular nerve (not figured).

*Pedal ganglion, right, lateral series*: (18) Two anterolateral pedal nerves (ALP) to side of head. (19) A trifurcating lateral trunk (LP) nerve, two branches to body wall opposite penis and vagina via peni-oviducal angle, the third passing under vagina to body wall. (20) One posterolateral (PLP) nerve. Ventral series (in heavy black): (21) Two large anteroventral pedal nerves (AVP) to foot. (22) One large medioventral nerve (MVP). (23) Four caudoventral nerves (CVP), of which three are large, the fourth small and above the third (stippled).

*Pedal ganglion, left*: (24) Two anterolateral pedal (ALP) nerves, the first much larger (latter not figured). (25) One trifurcating lateral (LP) nerve. (26) One posterior lateral (PLP) nerve. Ventral series (in heavy black): (27) One anteroventral pedal nerve (AVP). (28) One medioventral nerve (MVP). (29) Three caudoventral nerves (CVP) two large, one small, the first large nerve bifurcating (two figured).

All nerves similar to those of *Auriculella auricula* except in number of pedals and presence of a salivary gland nerve (eleventh) between left parietal and abdominal ganglia.

For juvenile genitalia see Neal (1928, pp. 44-49), who gives the results of an exhaustive study on juvenile genitalia of *Achatinella viridans*, concluding that the genitalia are not ready-formed but undergo gradual development from simple to complex. Appendix absent in embryos, a condition found also in very young *Lamellovum auriculella*.

*Jaw* not found.

*Radula* short, broad (ratio, length to width, 1:0.70), tooth formula (125-160)-1-(125-160)  $\times$   $\pm$ 130.

*Teeth* (fig. 122, a-l) largest in the entire family. Ectocones and entocones paired, often chelate, curved in or curved out; mesocones one to two, small. Cusplets thin, sharp, needle-like to thornlike, usually two below and between larger cusps. Total cusps plus cusplets, eight to 10 or 12.

Central teeth as large as first marginal (1), remaining teeth (marginals) gradually increasing in size laterad until they attain maximum size (50, 60), thence gradually diminishing to normal or near it (150).

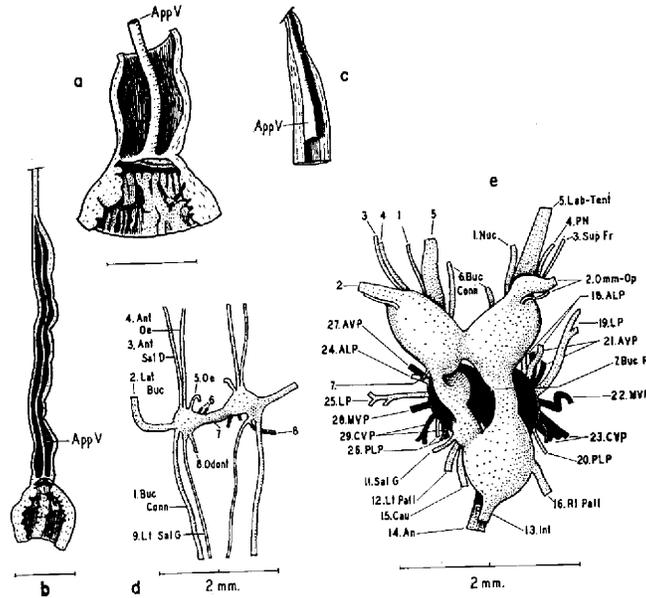


FIGURE 121.—*Achatinella (s.s.) concavospira*: a, interior of appendix, lower part of tubular portion showing "verge" (closeup of section of b); b, interior of appendix to median constriction; c, closeup of inner tube of a portion of appendix; d, buccal ganglia; e, principal ganglia.

Seen in profile, cusps either symmetrically curved or not, depending upon inward curvature or outward curvature of cusps. In natural position and in profile, cusps point posteriad; teeth are so placed that distal third appears to lie beside apical third of following tooth. Teeth chelate, outer pairs of cusps resembling pincers of some crustaceans. Teeth at anterior end of radula well worn from usage; cusps and cusplets blunted or truncate.

Abnormal teeth sometimes found; such teeth duplicated by the following rows indefinitely. In this specimen, teeth 1+2+3 (fig. 122, b) are apparently consolidated into a unit; though base of second is not produced except as slight convexity, close study shows middle portion to be a tooth. Other variants (not abnormal) are crested tooth, broad-headed tooth, and narrow-headed tooth.

Tooth dimensions below are for comparative purposes. Measurements (either average of two or of one, when opposite of pair cannot be measured) are accurate to within 0.5 micron. These dimensions will give some idea as to the gradual increase in size of the teeth to about midway laterad of each half row.

ADULT

TOOTH	LENGTH	WIDTH
Central.....	24	12
No. 1.....	25	13
50.....	33	17
60.....	35	.....
150.....	33	11

## EMBRYO

TOOTH	LENGTH	WIDTH
Central.....	10	3.7
No. 1.....	10.6	4.3
3.....	10.3	5.3
30.....	14.6	7.6
60.....	10.3	5.0

Teeth of embryo shown in figure 122, *k* are fully formed but smaller than those of adult, fewer per row, fewer rows per radula. Formula (60-65)-1-(60-65)  $\times \pm 82$  in this specimen. Central teeth smallest, six- to seven-dentate, ectocone and entocone each paired, mesocone single and small; fine cusplets present below cusps. Other teeth similarly armed; thirtieth or thereabouts the largest, with paired ecto- and entocones plus single mesocone plus three to five cusplets below. Last tooth (No. 60) about size of No. 1. Immature teeth found scattered throughout radula, taking stain very lightly (No. 7), three-cuspid, ecto-, ento-, and mesocone with one cusp each.

Nascent teeth (fig. 122, *l*) non-rigid, non-staining. The earliest ones appear as two out-curving horns (No. 15); the more mature ones acquire jagged edges or incipient denticles (No. 10) which elongate into denticles (No. 7). Bases are difficult to see but do not look like those of mature teeth; that is, upper part of stem is as narrow as that below.

Dissected 38054-38055 (genitalia, nervous system, teeth), 10+ specimens; 186903 (embryo teeth), one specimen.

***Achatinella* (*Bulimella*) *fuscobasis lyonsiana* Baldwin (fig. 122, *m-p*).**

*Achatinella lyonsiana* Baldwin, 1895, Acad. Nat. Sci. Philadelphia, Proc., 218, pl. 10, figs. 9-11.—Suter, 1895, Acad. Nat. Sci. Philadelphia, Proc., 239, pl. 11, fig. 52.

*Achatinella* (*Bulimella*) *fuscobasis lyonsiana* Pilsbry and Cooke, 1913, Man. Conch. 22: 172, pl. 35, figs. 5-7.

Animal sinistral. *Radula* (fig. 122, *o, p*) described in *A. concavospira*. Formula not studied. *Teeth* all alike (fig. 122, *m*), similar to those of *A. concavospira*. Central tooth smaller than marginals, narrower at head. Ecto- and entocone single, mesocone paired and shorter. One or two fine cusplets present below cusps if well stained. Marginals same as in *A. concavospira*, but paired condition of outer cusps not strongly emphasized.

Suter (1895, p. 239) says of this species, "The rachidian tooth is long and slender, with a small reflection and two minute cutting points in *H. lyonsiana*." (*H.* = *Helicter*, now *Achatinella*.) Because one is apt to derive a false impression from Suter's figure (1895, pl. 11, fig. 52), and because Pilsbry contended that the "centrals" were but modifications of the marginals, we decided to restudy the dentition of this species. Under oil immersion the finer cusplets are greatly magnified (fig. 122, *n*) and these show that the centrals more closely resemble the marginals than Suter indicates. Some of the centrals are narrow-headed and appear to have only two large outer cusps plus two small inner ones without cusplets. These are the poorly stained teeth. It is highly probable that, with the microscope of his day, together with a less effective staining technique, Suter was unable to discern the finer cusplets and the mesocones. *Radula* and teeth from 20151-20154.

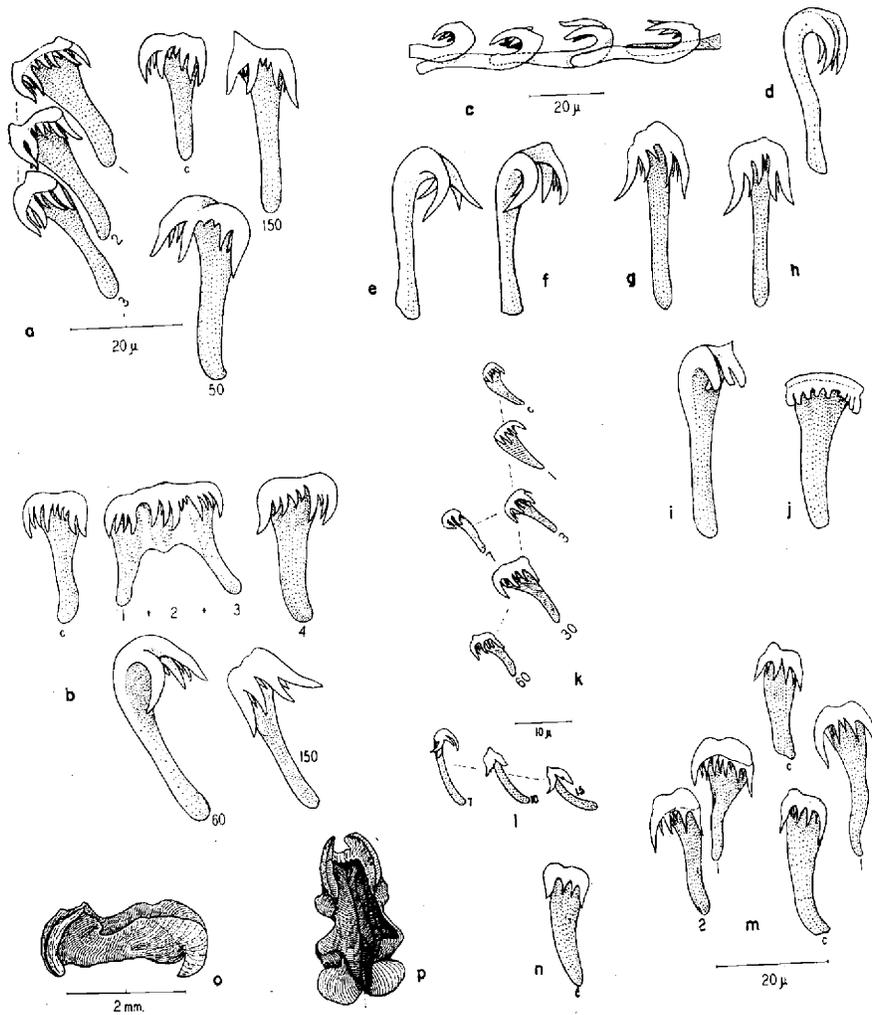


FIGURE 122.—a-l, *Achatinella* (s.s.) *concauospira*: a, teeth, normal (c = central; 1, 2, 3, 50, and 150 teeth laterad of central); b, teeth, fused 1 + 2 + 3; c, profile of a few teeth in natural position; d, tooth with symmetrically curved cusps, incurved; e, f, teeth with unsymmetrically curved cusps, outcurved; g, h, chelate teeth, outer pairs like pincers; i, j, teeth from anterior end of radula, worn, points blunted; k, teeth of embryo; l, nascent teeth of embryo from posterior end of radula. m-p, *Achatinella* (*Bulimella*) *fuscobasis lyonsiana*: m, teeth; n, narrow-headed tooth; o, p, radula, side and dorsal views.

Sections of *Achatinella* (*Bulimella*, *Achatinellastrum*, s.s.)

A cursory survey of the sections of *Achatinella* proves that, as regards the penial papilla, there are no clear-cut differences between genera. The simple pilaster is found in all the sections of *Achatinella*, as well as in all the other genera studied (*Perdicella*, *Newcombia*, *Partulina*). The first *Achatinella* dissected (*A. concavospira*) had a large lingual process (the semi-pendent pilaster or the penial papilla), whereas the remaining representatives of the subfamily revealed only modifications of this lingual type of pilaster.

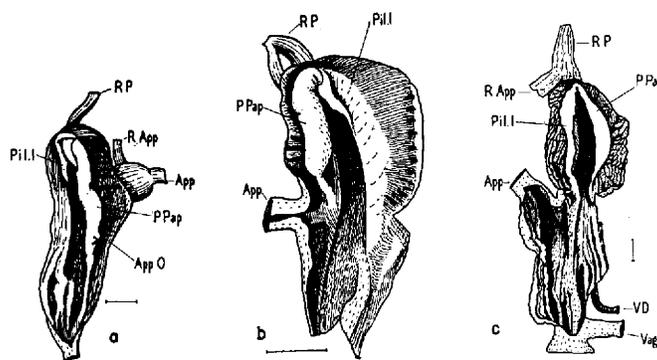


FIGURE 123.—Interior of penis: a, *Achatinella* (*Bulimella*) *viridans*; b, *A. (Achatinellastrum) lehuiensis meineckeii*; c, *A. (s.s.) turgida*.

***Achatinella* (*Bulimella*) *viridans* Mighels (fig. 123, a).**

*Achatinella viridans* Mighels, 1845, Boston Soc. Nat. Hist., Proc. 2: 20.

*Achatinella (Bulimella) viridans*, Pilsbry and Cooke, 1913, Man. Conch. 22: 125, pl. 25, figs. 1-4; pl. 31, figs. 6, 6a.

See Pilsbry and Cooke for full synonymy.

Animal dextral. Interior of penis plain except for principal pilasters plus a few wide ribs formed by inner surface of penis which parted under strain of mounting. Ascending pilaster starts below as low, irregular folds, continues apicad as a low flat ridge. Apex complicated by subsidiary free outgrowth. Penial papilla rounder than ascending arm, decreasing in size below appendical aperture or orifice, thence descending as a narrow fold. Penial retractor split.

Dissected 87424, one specimen.

***Achatinella (Achatinellastrum) lehuiensis meineckeii* Pilsbry and Cooke (fig. 123, b).**

*Achatinella lehuiensis meineckeii* Pilsbry and Cooke, 1921, Nautilus 34 (4): 109, pl. 4, figs. 6-9.

Animal sinistral, Interior of penis plain. Principal pilaster very low, outer boundary barely differentiable from integument of penis, starting below at termination of single low secondary pilaster, with a short, fleshy, ventrally pointed piece at apex. Penial papilla quite large, rounded, semi-pendent, terminating as such at appendical orifice with short branch into appendix and a thin, long, low fold ventrad. Appendicad side of penial integument thickened, having some lateral and short cavities. Penial retractor split.

Dissected 87434, one specimen.

***Achatinella* (s.s.) *turgida* Newcomb (fig. 123, c).**

*Achatinella turgida* Newcomb, 1853, Zool. Soc. London, Proc., 134, pl. 22, figs. 10, 10a.

*Achatinella* (s.s.) *turgida* Pilsbry and Cooke, 1914, Man. Conch. 22: 294, pl. 29, figs. 10, 10a; pl. 56, figs. 1-4.

Animal sinistral. Interior of penis heavily sculptured by secondary pilasters (including interrupted diagonal ribs); principal pilaster relatively inconspicuous, a narrow fleshy ridge, or fold, starting below at penial orifice as a low irregular ridge, taking definite shape at level of appendical aperture, increasing somewhat in width near apex, reflexing at apex thence descending as a somewhat curved-lanceolate fold (P Pap) and ending near the middle as a very narrow fold. Upper penis with numerous low narrow ribs; lower portion with numerous irregular longitudinal low folds. Penial retractor split.

Dissected 76867, one specimen.

## BIBLIOGRAPHY

- ANTON, HERMANN EDUARD  
1839. Verzeichniss der Conchylien welche sich in der Sammlung von Hermann Eduard Anton befinden. Herausgegeben von dem Besitzer. Halle.
- BINNEY, W. G.  
1884. Notes on the jaw and lingual dentition of pulmonate molluscs. *New York Acad. Sci., Ann.* 3: 79-136.  
1873. See Bland, Thomas, and W. G. Binney.
- BLAND, THOMAS, AND W. G. BINNEY  
1873. On the lingual dentition and anatomy of *Achatinella* and other Pulmonata. *Lyceum Nat. Hist. New York, Ann.* 10: 331-351.
- BOYCOTT, A. E.  
1917. The genitalia of *Acanthinula aculeata*. *Malac. Soc., London, Proc.* 12 (5): 221-226.
- COOKE, A. H.  
1895. Molluscs and brachiopods. *Cambridge Natural History* 3. New York, London.
- COOKE, C. M., JR., AND YOSHIO KONDO  
1952. New fossil forms of *Carelia* and *Partulina* (Pulmonata) from the Hawaiian Islands. *B. P. Bishop Mus., Occ. Papers* 20 (20): 329-346.
- DALL, WILLIAM HEALEY  
1896. Insular landshell faunas, . . . *Acad. Nat. Sci., Philadelphia, Proc.*, 395-459.  
1926. Land shells of the Revillagigedo and Tres Marias Islands, Mexico. *California Acad. Sci., Proc. IV*, 15: 467-487.
- DOHRN, H.  
1863. Ueber Tornatellina. *Malakozoologische Blätter* 10: 156-162.
- GARRETT, ANDREW  
1879. List of land shells inhabiting Rurutu . . . with remarks on their synonymy, geographical range, and descriptions of new species. *Acad. Nat. Sci., Philadelphia, Proc.*, 17-30.  
1887. On the terrestrial mollusks of the Viti Islands. Part I. *Zool. Soc. London, Proc.*, 164-189.
- GWATKIN, H. M., HENRY SUTER, AND HENRY A. PILSBRY  
1895. Observations on the dentition of *Achatinellidae*. *Acad. Nat. Sci., Philadelphia, Proc.*, 237-240.
- IREDALE, TOM  
1944. The land Mollusca of Lord Howe Island. *Australian Zoologist* 10 (3): 299-334.
- HEYNEMANN, F. D.  
1867. Die Zungen von *Partula* und *Achatinella*. *Malakozoologische Blätter* 14: 146-150.
- HYATT, ALPHEUS, HENRY A. PILSBRY, AND C. M. COOKE, JR.  
1911. *Achatinellidae* (Amastrinae). *Manual of Conchology* 21.
- KNIGHT, CHARLES  
1859. Observations on the "bitentaculate slug" of New Zealand . . . *Linn. Soc., London, Trans.* 22: 381-382.
- MOUSSON, ALBERT  
1871. Faune malacologique terrestre et fluviatile des Îles Tonga les envois de docteur Ed. Graeffe. *Jour. de Conchyl.* III, 19 (11): 5-33.
- NEAL, MARIE C.  
1928. (See Pilsbry, Cooke, and Neal)
- ODHNER, NILS HJ.  
1922. Mollusca from Juan Fernandez and Easter Island. *The Natural History of Juan Fernandez and Easter Island* 3 (2): 219-265.

- PACIFIC ISLANDS PILOT  
1920. Vol. 2, ed. 2.
- PEASE, W. HARPER  
1860. Descriptions of six new land shells from the Island of Ebon, Marshall's Group, in the collection of H. Cuming.
- PEILE, A. J.  
1929. Notes on radulae. *Malac. Soc., London, Proc.* **18** (6): 268-269.
- PELSENEER, PAUL  
1906. Lankester, E. Ray, ed., *Treatise on zoology, Mollusca* (5). London.
- PFEFFER, GEORG  
1877. Anatomische Untersuchung der *Achatinella vulpina*. *Deutschen Malak. Gesell., Jahrb.* **3**: 330-333.
- PFEIFFER, LUDWIG  
1842. *Symbolae ad Historiam Heliceorum* (2). Casselis.  
1848. *Monographia Heliceorum Viventium* 1, 2. Lipsiae.
- PILSBRY, HENRY A. (see Gwatkin *et al.*)  
1900. On the zoological position of *Partula* and *Achatinella*. *Acad. Nat. Sci., Philadelphia, Proc.*, 561-567.  
1916-1918. Pupillidae (Gastrocoptinae). *Manual of Conchology* **24**.  
1927. Geographic distribution of Pupillidae, Strobilopsidae, Valloniidae and Pleurodiscidae. *Manual of Conchology* **28**.  
1948. Land Mollusca of North America 2 (2). *Acad. Nat. Sci., Philadelphia, Monographs* **3**, 2 (2): 521-1113.
- PILSBRY, HENRY A., AND C. M. COOKE, JR.  
1912-1914. Achatinellidae. *Manual of Conchology* **22**.  
1915-1916. Appendix to Amastridae. Tornatellinidae. *Manual of Conchology* **23**.  
1933. Notes on the land snail family Tornatellinidae. *Nautilus* **47** (2): 59-62.
- PILSBRY, HENRY A., C. M. COOKE, JR., AND MARIE C. NEAL  
1928. Land snails from Hawaii, Christmas Island and Samoa. *B. P. Bishop Mus. Bull.* **47**: 1-49.
- RIDGWAY, ROBERT  
1912. *Color standards and color nomenclature*. Washington, D. C.
- ST. JOHN, HAROLD  
1940. Itinerary of Hugh Cuming in Polynesia. *B. P. Bishop Mus., Occ. Papers* **16** (4): 81-90.
- SCHMELTZ, J. D. E., JR.  
1874. *Cat. Mus. Godeffroy*. Hamburg.
- SEMPER, CARL  
1870-1894. *Landmollusken. Reisen im Archipel der Philippinen* **3** (2). Wiesbaden.
- SIMROTH, H., AND H. HOFFMAN  
1908-1928. *Bronn's Klassen und Ordnungen des Tier-Reichs* **3** (2), Buch 2, Mollusca, Pulmonata. Leipzig.
- STEENBERG, C. M.  
1925. *Etudes sur l'anatomie et la systematique des maillots*. Copenhagen.
- SUTER, HENRY (see Gwatkin *et al.*)  
1913. *Manual of the New Zealand Mollusca*. Wellington.
- THIELE, JOHANNES  
1931. *Handbuch der systematischen Weichtierkunde* **2**. Jena.
- WATSON, HUGH  
1920. The affinities of *Pyramidula*, *Patulastra*, *Acanthinula* and *Vallonia*. *Malac. Soc., London, Proc.* **14** (1): 6-30.  
1923. Masculine deficiencies in British Vertigininae. *Malac. Soc., London, Proc.* **15** (6): 270-280.

## INDEX

Bold-faced type indicates most important references.

- A**
- abbreviata, Achatinella 9
- Achatina: bulimoides 238, conifera 240; consimilis 240; diaphana 241; globosa 104; minuta 236; minutissima 224; ovata 227; peponum 210; splendida 241; trochlearis 118; turrata 57
- Achatinella 8, 9, 10, 12, 13, 14, 15, 16, 18, 24, 30, 31, 38, 41, 175, 240, 270, 274, 275, 276, **284-292**: abbreviata 9; apexfulva 284; byronii 9; bulimoides 13; canaliculata 277; cerealis 277; concavospira 19, 30, 33, 48, 175, 249, 271, 272, 275, 276, **284-289**, 290, 291; cookei 14; cumingi 277, 278; decipiens 10; dolei 6; dubia 280, 281; dunkeri 10; elongata 277; fuscobasis 14, 15, 39, 48, 276, 284, **289**, 290; gouldi 280; helena 277, 278; jacksonensis 169; lehuiensis 8, 10, 48, 276, **291**; lila 9; lorata 9, 10, 11, 13, 15; lyonsiana 14, 15, 39, 48, 276, 284, **289**, 290; maniensis [mauiensis] 280; meineckeii 8, 10, 48, 276, **291**; mighelsiana 284; mustelina 9; newcombiana 277; nobilis 9, 13, 15; ornata 277; perdix 280; physa 277; plicata 277; producta 9, 10, 11; pulchella 10; pusilla 184; redfieldii 282; seminigra 284; simulans 9; splendida 280; stewartii 9, 10, 11, 14; tessellata 280; turgida 10, 14, 48, 276, 291, **292**; virgulata 280; viridans 9, 10, 12, 48, 276, 280, 287, **291**; vulpina 9, 10, 11, 13, 14, 15; wakefieldiae 232
- Achatinellastrum 18, **291**
- Achatinellidae 3, 4, 5, 12, 13, 14, 15, 16, 17, 19, 21, 22, 26, 28, 29, 30, 33, 38, 39, 40, 43, 44, 45, **50**, 272, 274
- Achatinellinae 18, 22, 24, 34, 38, 41, 42, 43, 44, 46, 47, 48, 51, **274-292**
- Achatinellini 18, 19, 30, 35, 36, 38, 41, 43, 46, 51, **274-292**
- acicularis, Strobilus 18, 49, 56, **66**, 67, 69
- acuminatus, Strobilus 49
- acuta, Pukunia 18, 20, 34, 49, 54, **73-75**, 76
- adamsoni, Lamellidea 20, 49, 213, **214-215**, 216
- adelinae, Tornatellaria 265
- Aedituans 18, 19, 20, 247, **258**
- affinis: Tornatellina 149, 167; Tubuaia 143, 145, 146, **149-150**, 153, 157, 167
- alexandri, Gulickia 20, 273
- alpestris, Pitys 19, 54, 95, **103**
- Amastra 14
- Amastriidae 16
- ambusta, Auriculella 269
- amphodon, Elasmias 218, 221, **222**
- anatonuensis, Celticola 19, 79, 132, **141-142**
- anceyanum, Elasmias 218, **222**
- andersoni, Apopitys 19, 20, **92-93**
- Antonella 6, 17, 19, 20, 24, 38, 41, 47, 73, 77, 116, 117-125, 126, 167; fusiforma 19, 121, **122**; nesiotica 19, 121, 122; pellucidus 119, 120; pfeifferi 19, 117, **122**, 123; radícula 19, 121; tenuis 19, 34, 49, 117, **124-125**, 129; trochlearis 19, 20, 33, 49, 117, **118-119**, 124, 125, 167
- Antonellini 17, 19, 22, 33, 34, 35, 36, 41, 42, 44, 51, 53, **116-131**
- antoni: Bulimus 248; Tornatellides 248; Tornatellina 248
- aperta: Elasmias 20, 158, 221, **222**, 225; Tornatellina 222, 225, 234, **235**
- apertum, Elasmias 13, 14, 15, 19, 28, 32, 48, 218, 221, **222-223**, 226, 228, 231
- Apex turbiniformis 284
- apexfulva, Achatinella 284
- Apopitys 17, 19, 20, 24, 38, 41, 54, **92-94**: andersoni 19, 20, **92-93**
- arauana, Taitaa 19, 83, **86**
- arborea, Celticola 19, 20, 132, **138-139**, 140
- archimedes, Tornatellina 57
- arnemanni, Partulina 276
- Atea 17, 18, 20, 30, 178, 179, 213, 214, 215
- Athoracophoridae 13, 15
- attenuatus, Tornatellides 260
- auricula, Auriculella 19, 20, 30, 37, 48, 240, 268, 269, **270-272**, 273, 287; Partula 270
- Auriculella 6, 8, 10, 12, 13, 14, 16, 17, 18, 20, 24, 38, 41, 53, 95, 113, 129, 262, **268-272**, 274; ambusta 269; auricula 19, 20, 30, 37, 48, 240, 268, 269, **270-272**, 273, 287; brunnea 269; cacuminis 269; castanea 48, 269, 272, 273, 274; cerea 9, **268**, 269; crassula 269; diaphana 269; lanaiensis 269; minuta 269; montana 269; newcombi 269; olivacea 48, 269; perpusilla 269; perversa 269; pulchra 9, **269**; pusilla 184; serrula 274; straminea 269; tantalus 269; tenella 269; turritella 269; uniplicata 269; westerlundiana 9, 269
- auriculella, Lamellovum 5, 19, 20, 37, 49, 104, 108, **109-112**, 115, 133, 147, 230, 287
- Auriculellidae 12, 16
- Auriculellinae 18, 20, 24, 34, 40, 41, 42, 43, 44, 45, 46, 47, 48, 51, **268-274**, 276
- Auriculellini 18, 19, 30, 36, 37, 38, 41, 43, 46, 47, 51, **268-274**

- B**
- bacillaris: Lamellidea 196, 199; Tornatellina 196, 199  
 bakeri, Perahua 19, 129-130  
 baldwini, Tornatellinops 48, 163, 164, 165, 167, 178, 179  
 Baldwinia 18, 22, 281  
 Balea turrata 56  
 basalis, Strobilus 18, 56, 60, 66  
 bella, Partulina 10  
 bilamellata: Endodonta 95; Helix 94, 95; Patula 95; Pityx 94, 95; Tornatellina 9, 13, 15, 20, 31, 234, 235-236  
 bilamellatus: Strobilus 235; Tornatellina 235  
 biplicata: Lamellidea 180, 183; Tornatellina 183  
 brevis, Strobilus 18, 20, 55, 56, 70-71  
 brunnea, Auriculella 269  
 brunneus, Tornatellides 244  
 Bulimella 18, 291  
 bulimoides: Achatina 238; Achatinella 13; Fernandezia 4, 9, 11, 13, 15, 16, 19, 31, 32, 38, 48, 233, 238-240; Spiraxis 238; stenogyra 238  
 Bulimus: antoni 248; jacksonensis 169; splendida 241  
 byronii, Achatinella 9
- C**
- cacuminis, Auriculella 269  
 callosa, Tornatellina 236  
 camarinica: Tornatellina 170; Tornatellinops 170  
 canaliculata: Achatinella 277; Newcombia 8, 9, 48, 276, 277-278  
 capricorni: Tornelasmias 162, 171; Tornatellinops 162, 171, 172  
 carinella, Perdicella 9  
 castanea, Auriculella 48, 269, 272, 273, 274  
 Celticola 17, 19, 20, 22, 24, 38, 41, 79, 131-143; anatonuensis 19, 79, 132, 141-142; arborea 19, 20, 132, 138-139, 140; conoides 19, 20, 132, 140-141, 142; incerta 19, 136; latior 19, 136-137; pilsbryi 19, 20, 35, 49, 131, 132-135, 136, 141, 147; proxima 19, 135-136; sororcula 19, 139  
 cerea, Auriculella 9, 268, 269  
 cerealis: Achatinella 277; Newcombia 277  
 cernica, Elasmias 224  
 cernicum, Elasmias 224  
 Charopa 29  
 chathamensis, Tornatellides 13, 15, 26, 246-247  
 Chondrina 11  
 cincta, Tornatellaria 265  
 Cionella: novoseelandica 169; ovata 227; peponum 210; trochlearis 119; turritus 57  
 citrea: Elasmias 224; Tornatellina 224  
 citreum, Elasmias 224  
 clarionensis, Tornatellides 247  
 clausa, Tornatellina 234, 235  
 Clausilia 55: fissidens 105  
 columellaris: Lamellidea 185, 187, 190, 191, 192; Tornatellina 185, 187, 190  
 compactus, Tornatellides 243, 244, 247, 254, 255  
 concavospira, Achatinella 19, 30, 33, 48, 175, 249, 271, 272, 275, 276, 284-289, 290, 291  
 concolorans, Tornatellinops 19, 48, 163, 165, 175-178, 179  
 confusa, Partulina 9  
 confusus, Tornatellides 210, 244  
 conica: Lamellidea, 184, 185, 187, 190; Tornatellina 167, 184, 185, 187, 190, 234, 236  
 conicus: Tornatellina 236; Strobilus 236  
 conifera: Achatina 240; Fernandezia 240  
 connisum, Elasmias 222  
 conoides, Celticola 19, 20, 132, 140-141, 142  
 consimilis: Achatina 240; Fernandezia 240-241; Spiraxis 241; Stenogyra 241  
 convexior, Mitiperua 19, 82
- cookei, Achatinella 14  
 costata, Lamellovum 19, 104, 109, 115-116  
 crassula, Auriculella 269  
 cremnobates, Tubuaia 19, 49, 145, 146, 153-155, 162  
 cumingi: Achatinella 277, 278; Newcombia 9, 33, 48, 275, 276, 277, 278  
 cumingiana: Elasmatina 236; Tornatellina 236  
 cylindrata, Tubuaia 19, 145, 146, 155-156  
 cylindrella, Fernandezia 234, 241  
 cylindrica, Lamellidea 181, 194, 209, 211, 213; Tornatellina 209  
 cyphostyla, Tornatellides 244, 247
- D**
- dacryma, Taitaa 19, 20, 34, 49, 83, 84-86, 89, 91, 92  
 decipiens, Achatinella 10  
 dentata: Lamellidea 196; Tornatellina 196  
 diglyptus 94  
 diaphana: Achatina 241; Auriculella 269; Fernandezia 241  
 Diastole, glaucina 256  
 Diglyptus 94  
 Diplommatininae 29  
 dolei: Achatinella 6; Partulina 8, 9, 10, 12, 14  
 drepanophora, Tornatellides 243, 254, 255  
 dubia: Achatinella 280, 281; Partulina 4, 5, 10, 48, 276, 280, 281-282  
 dunkeri, Achatinella 10  
 duplicilamellata: Tornatellina 172, 235; Tornatellinops 172, 235
- E**
- Eburnella 18, 22, 281, 284  
 Elamellidea 18, 19, 20, 138, 178, 179, 180, 196, 211, 213  
 Elasmatina 16, 55, 235; cumingiana 236; globosa 104; reclusiana 169, 237; subulata 55, 57, 59

- Elasmias 16, 17, 18, 20, 22, 24, 26, 28, 30, 31, 32, 36, 38, 41, 42, 51, 107, 165, 179, **218-232**, 256; amphodon 218, 221, 222; anceyanum 218, 222; aperta 20, 158, 221, 222, 225; apertum 13, 14, 15, 19, 28, 32, 48, 218, 221, **222-223**, 226, 228, 231; cernica 224; cernicum 224; citrea 224; citreum 224; connisum 222; eucharis 224; exiguum 19, 222, 227, 228; fusca 221, 224; fuscum 219, 222, **224**; jauffreti 222, **225**; kitaiwojimanum 225; luakahaense 219, 221, 222, **225**; manilense 221, **225**; manilensis 13, 14, 15, **225**; mariei 226; mauritiana 224; minutissima 224; natunensis 225, 226; obtusum 224; ovata 227; ovatula 226; ovatum 219, 226; ovatum 19, 221, 222, 227, 228, 231; ovatus 227; peasiana 229; peasianum 34, 37, 48, **229**, 231; quadrasi 226, **230**; schola 222, 231; simplicimum 19, 219, 222, 228, **231-232**; sundana, 232; sundanum 232; terrestris 221, 224, 232; wakefieldiae 232
- Elasmiatini 19, 31, 32, 34, 36, 37, 38, 41, 42, 43, 45, 46, 47, 50, **218-232**
- Electrina succinea 106
- elongata: Achatinella 277; Newcambia 277
- Ena 11
- Endodonta 261: bilamellata 95; pagodiformis 96
- Endodontidae 17, 29
- eucharis: Elasmias 224; Tornatellina 224
- eurymphala, Tornatellides 243, 244, 247, 254, 255, 258
- exiguum, Elasmias 19, 222, **227**, **228**
- expansa, Fernandezia 241
- extincta: Lamellidea 211; Tornatellina 211
- F**
- Fernandezia 6, 12, 16, 17, 18, 20, 24, 26, 30, 36, 38, 41, 47, 129, 218, 233, 234, **237-242**; bulimoides 4, 9, 11, 13, 15, 16, 19, 31, 32, 38, 48, 233, **238-240**; conifera 240; consimilis 240-241; cylindrella 234, 241; diaphana 241; expansa 241; inornata 241; longa 241; philippiana 241; splendida 241-242; splendidula 242; tryoni 242; wilsoni 20, 237, **242**
- fissidens: Clausilia 105; Tornatellina 105
- forbesi, Tornatellides 258
- Frickella 268
- fusca, Elasmias 221, 224; Tornatellina 224
- fuscobasis, Achatinella 14, 15, 39, 48, 276, 284, **289**, 290
- fuscum, Elasmias 219, **222**, **224**
- fusiforma, Antonella 19, 121, **122**
- G**
- "garreti," Tornatellides 246
- Gastrocopta 256
- gayi: Lamellidea 167, 178, 181, 211; Tornatellina 167, 211
- Georissa 256
- glauca, Diastole 256
- Glessula 237
- globosa: Achatina 104; Elasmatina 104; Lamellovum 103-104; Tornatellina 103-104
- globosum: Lamellovum 6, 20, 49, 75, **104-108**, 109, 115, 116
- globulosa, Tornatellina 217
- gouldi: Achatinella 280; Partulina 280; Tornatellina 151; Tubuaia 18, 19, 143, 145, 146, **151-153**, 182
- gracilis: Lamellidea 181, **210-211**; Tornatellina 210
- grandis, Perahua 19, 20, 49, 112, 125, **126-128**, 130
- Gulickia 16, 17, 18, 20, 24, 38, 41, 44, 268, **273-274**; alexandri 20, 273
- H**
- hataiana: Tornatellina 168; Tornatellinops 162, **168**
- helena: Achatinella 277, 278; Newcambia 277, 278; Partulina 279; Perdicella 9, 22, 33, 48, 275, 276, **278-280**, 286
- Helicinidae 29
- Helicter lyonsiana 289
- Helix 94: bilamellata 94, 95
- hidalgoi: Tornatellina 151; Tubuaia 151, 152
- horneri, Partulina 8, 10
- I**
- idae, Tornatellides 244, 247, 257
- illibata, Tornatellaria 265
- impressa: Lamellidea 167, 185, 190; Tornatellina 167, 172, 185, 190; Tornatellinops 172, 175
- incerta, Celticola 19, **136**
- inconspicua: Tornatellina 171; Tornatellinops 171
- inconspicuum: Tornelasmias 171; Tornatellinops 171
- inconspicuus: Tornatellides 167, 171, 247; Tornatellinops 167, 171, 247; Tornelasmias 247
- inconstans, Tubuaia 19, 49, 143, 145, 146, **160-162**
- inornata, Fernandezia 241
- intermedius, Strobilus 18, 56, 61, 63, 65
- intuscostata: Lamellidea 167, 185, 190; Tornatellina 167, 185, 190
- iredalei, Tornatellina 169; Tornatellinops 169, 178
- irregularis, Tornatellides 258
- J**
- jacksonensis: Achatinella 169; Bulimus 169; Tornatellina 169; Tornatellinops 169
- Janella 14
- jauffreti, ? Elasmias 222, **225**

## K

- kailuanus, Tornatellides 261  
 kahoolavensis, Tornatellides 247  
 kamaloensis: Lamellidea 181, 210; Partulina 9; Tornatellina 210  
 kermadecensis: Tornatellides 242; Tornatellina 156; Tubuaia 156  
 kilohana, Lamellidea 181, 209  
 kitaiwojimana, Tornatellina 225  
 kitaiwojimanum: Elasmias 225; Tornatellina 225  
 kochiana: Tornatellina 170; Tornatellinops 170

## L

- laevis: Lamellidea 184, 185, 190, 192; Lamellina 184, 190  
 Lamellaria perforata 185, 190  
 Lamellidea 16, 17, 18, 20, 24, 25, 37, 38, 41, 42, 47, 51, 131, 138, 145, 152, 162, 163, 164, 165, 172, 178-217, 235, 256, 261; adamsoni 20, 49, 213, 214-215, 216; bacillaris 196, 199; biplicata 180, 183; columellaris 185, 187, 190, 191, 192; conica 184, 185, 187, 190; cylindrica 181, 194, 209, 211, 213; dentata 196; extincta 211; gayi 167, 178, 181, 211; gracilis 181, 210-211; impressa 167, 185, 190; intuscostata 167, 185, 190; kamaloensis 181, 210; kilohana 181, 209; laevis 184, 185, 190, 192; lanceolata 210; longa 180, 182; micropleura 19, 180, 193-196; microstoma 180, 183, 213; moellendorffiana 183; mumfordi 179, 213, 215-216; nitida 184, 185, 187, 190; normalis 167, oblonga 13, 14, 19, 28, 32, 35, 36, 49, 145, 158, 164, 165, 178, 180, 181,

- 182, 185, 195, 196-209, 211; ogasawarana 180, 182, 205; peponum 20, 145, 178, 181, 202, 210; perforata 185, 187, 190; perforatus 247; polygnapta 181, 209; pusilla 28, 158, 165, 167, 178, 180, 182, 184-192, 193, 199, 200, 201, 204, 247; serrata 178, 184, 185, 187, 190, 191, 192; solomonensis 184; subcylindrica 180, 183, 214; tantalus 20, 140, 167, 211, 212, 213; uahukana 213, 217; variabilis 172

- Lamellideinae 18, 19, 20, 24, 34, 41, 42, 43, 44, 45, 46, 47, 48, 51, 162-217, 235, 276

- Lamellideini 18, 19, 20, 32, 37, 41, 42, 51, 175, 178-217

- Lamellina 16, 178, 235; laevis 184, 190; serrata 184

- Lamellovum, 16, 17, 20, 24, 38, 41, 54, 79, 95, 103-116, 131, 137; auriculella 5, 19, 20, 37, 49, 104, 108, 109-112, 115, 133, 147, 230, 287; costata 10, 104, 109, 115-116; globosa 103-104; globosum 6, 20, 49, 75, 104-108, 109, 115, 116; leptospira 19, 104, 109, 113-114, 116; solitaria 19, 104, 109, 114-115

- Laminella 14

- lanceolata: Lamellidea 210; Tornatellina 210

- lanaiensis, Auriculella 269

- latior, Celticola 19, 136-137

- lehuiensis, Achatinella, 8, 10, 48, 276, 291

- Leptachatina 14, 237

- Leptinaria peponum 210

- leptospira: Lamellovum 19, 104, 109, 113-114, 116; Tornatellides 242, 243, 254, 255

- lidgbirdense: Tornatellinops 171; Tornelasmias 171

- lila, Achatinella 9

- longa: Fernandezia 241; Lamellidea 180, 182

- lorata, Achatinella 9, 10, 11, 13, 15

- luakahaense, Elasmias 219, 221, 222, 225  
 lyonsiana: Achatinella 14, 15, 39, 48, 276, 284, 289-290; Helicter 289

## M

- mcgregori: Tornatellina 167, 168; Tornatellinops 163, 167, 168, 178, 179

- macromphala, Tornatellides 243, 244, 254, 255

- Maitua 17, 19, 20, 104, 108, 137

- Mangaoa 17, 19, 20, 24, 38, 41, 54, 78-79; perissa 19, 20, 49, 75, 78

- maniensis [mauiensis]: Achatinella 280; Perdicella 280

- manilense: Elasmias 221, 225; Tornatellina 225

- manilensis, Elasmias 13, 14, 15, 225

- margaritae, Pukunia 18, 76

- mariei: Elasmias 226; Tornatellina 226

- marmorata, Partulina 22

- mastersi: Tornatellina 170; Tornatellinops 170

- mauiensis: Partulina 8, 280; Perdicella 9, 48, 276, 280

- mauritiana, Elasmias 224

- meinecke, Achatinella 8, 10, 48, 276, 291

- Melampus 256

- Meryticola 17, 19, 20, 131, 132, 137, 138

- mexicana, Tornatellides 247

- micans: Tornatellina 149; Tubuaia 149, 150

- Microcystis perahui 228

- micropleura, Lamellidea 19, 180, 193-196

- microstoma: Lamellidea 180, 183, 213; Tornatellina 183

- mighelsiana: Achatinella 284; Partulina 10, 11, 33, 48, 275, 276, 283, 284

- minuta: Achatina 236; Auriculella 269; Tornatellina 167, 233, 236, 237

- minutissima: Achatina 224; Elasmias 224

- Mitiperua 17, 19, 20, 24, 38, 41, 54, **79-82**: convexior 19, **82**; simplex 19, 20, 49, 79, **80-81**, 82; subcostata 19, **81**, 82  
 moellendorffiana: Lamellidea 183; Tornatellina 183  
 moluccana: Tornatellina 170; Tornatellinops 170  
 Monodonta seminigra 284  
 monoliata, Tornatellina 158  
 montana, Auriculella 269  
 moohuense: Tornelasmias 171; Tornatellinops 171  
 moohuensis: Tornatellina 171, 235; Tornatellinops 171, 235  
 moomomiensis, Tornatellides 244, 260  
 Moussonina 29  
 mumfordi, Lamellidea 179, 213, **215-216**  
 mustelina, Achatinella 9
- N**
- nakadai: Tornatellina 168; Tornatellinops **168**, 172  
 nannodes, Tubuaia 19, 151, 153  
 natti, Partulina 10  
 natunensis, Elasmias 225, 226; ? Tornatellina 225, 226  
 neanica, Taitaa 19, 20, 83, 89, **90-91**  
 neckeri, Tornatellides 19, 20, 48, 247, **258-261**  
 neozealandica: Tornatellina 169; Tornatellinops 169  
 nepeanense: Tornatellinops 171; Tornelasmias 171  
 nepeanensis: Tornatellina 171, 235; Tornatellinops 171, 235  
 nesiotica, Antonella 19, 121, 122  
 Nesonoica 17, 19, 20, 79, 131, 132, 140  
 Nesopupa 256  
 newcombi: Auriculella 269; Tornatellaria 19, 20, 30, 48, 249, 263, **265-267**; Tornatellides 249; Tornatellina 249, 265-266  
 Newcambia 9, 10, 12, 13, 14, 18, 22, 24, 38, 41, 274, 275, 276, **277-278**, 291: canaliculata 8, 9, 48, 276, **277-278**; cerealis 277; cumingi 9, 33, 48, 275, 276, **277**, 278; elongata 277; helena 277; newcombiana 277; ornata 277; pfeifferi 9; philipiana 9; physa 277; piicata 22, 277  
 newcombiana: Achatinella 277; Newcambia 277  
 nitida: Lamellidea 184, 185, 187, 190; Tornatellina 157, 158, 184, 185, 187, 189; Tubuaia 157, 158  
 nobilis, Achatinella 9, 13, 15  
 norfolkensis: Tornatellina 171, 235; Tornatellinops 171, 235  
 normalis: Lamellidea 167; Tornatellina 167, 172; Tornatellinops 172  
 noumeensis: Tornatellina 170; Tornatellinops 170  
 novoseelandica: Cionella 169; Tornatellina 162, 169; Tornatellinops 20, 162, 163, **169**, 179
- O**
- oahuensis, Tornatellides 246  
 oblonga, Lamellidea 13, 14, 19, 28, 32, 35, 36, 49, 145, 158, 164, 165, 178, 180, 181, 182, 185, 195, **196-209**, 211; Tornatellina 196  
 oblongus: Strobilus 248; Tornatellides 19, 20, 28, 30, 35, 45, 48, 158, 224, 243, 244, 246, 247, **248-255**, 258, 261, 267, 272  
 obtusum, Elasmias 224  
 ogasawarana, Lamellidea 180, **182**, 205; Tornatellina 182, 205  
 Oleacina splendida 241  
 olivacea, Auriculella 48, 269  
 Omphalotropis 29  
 oparana, Pitys 95  
 opeas, Strobilus 18, 49, 56, **61-63**, 65, 68  
 ornata: Achatinella 277; Newcambia 277  
 Orobophana solidula 256  
 Orthurethra 10, 17  
 oswaldi, Tornatellides 19, 35, 48, 247, 254, 255, **257-258**  
 ovata: Achatina 227; Cionella 227; Elasmias 227; Tornatellina 227  
 ovatula: Elasmias 226; Tornatellina 226  
 ovatum, Elasmias 219, 226  
 ovatum, Elasmias 19, 221, 222, **227-228**, 231  
 ovatus: Elasmias 227; Strobilus 227
- P**
- Pacificella 6, 8, 12, 16, 162, 163; variabilis 162, 164, 172, 175  
 Pacificellidae 12, 16  
 pagodiformis: Endodonta 96; Patula 95; Pitys 6, 19, 20, 33, 34, 49, 54, 92, 94, **95-97**, 101, 102, 103, 106  
 pagodiformis, Pitys, forms of: A, 97; B, 97; C, 98; D, **98**, 100; E, 101  
 Partula 38: auricula 270; pusilla 184  
 Partulina 9, 10, 12, 13, 14, 18, 22, 24, 38, 41, 274, 275, 276, **280-284**, 291: arnemanni 276; bella 10; confusa 9; dolei 8, 9, 10, 12, 14; dubia 4, 5, 10, 48, 276, 280, **281-282**; gouldi 280; helena 279; horneri 8, 10; kama-loensis 9; marmorata 22; maiensis 8; mighelsiana 10, 11, 33, 48, 275, 276, 283, **284**; natti 10; perantiqua 276; perdix 280; physa 22; proxima 10; redfieldii 8, 9, 10, 11, 48, 276, **282-283**; rufa 10; splendida 280; tessellata 10, 280; variabilis 22; virgulata 8, 10, 22, 48, 276, 280, 281, **282**  
 Partulinella 18, 22, 276, 281, 282

- parvulus, Tornatellides 247, 255-256  
 Patula bilamellata 95;  
   pagodiformis 95  
 peasiana: Elasmias, 229;  
   Tornatellina 229  
 peasianum, Elasmias 34, 37, 48, 229, 231  
 pellucida, Pukunia 19, 76, 77  
 pellucidus: Antonella 119, 120; Strobilus 119, 122  
 peponum: Achatina 210; Ci-onella 210; Lamellidea 20, 145, 178, 181, 202, 210; Leptinaria 210; Pupa 210; Tornatellina 210; Tornatellinops 172  
 Perahua 6, 17, 19, 20, 24, 38, 41, 117, 125-130: bakeri 19, 129-130; grandis 19, 20, 49, 112, 125, 126-128, 130  
 perahui, Microcystis 228  
 perantiqua, Partulina 276  
 Perdicella 9, 12, 18, 22, 24, 38, 41, 274, 275, 276, 278-280, 281, 291: carinella 9; helena 9, 22, 33, 48, 275, 276, 278-280, 286; maniensis 280; mauiensis 9, 48, 276, 280  
 perdis: Achatinella 280; Partulina 280  
 perforata: Lamellaria 185, 190; Lamellidea 185, 187, 190; Tornatellina 187  
 perforatus: Lamellidea 247; Tornatellides 247  
 perfragilis, Strobilus 18, 20, 49, 56, 68-69  
 perissa, Mangaoa 19, 20, 49, 75, 78  
 perkinsi, Tornatellides 243, 244, 247, 254, 255  
 perplexa: Tornatellina 146; Tubuaia 18, 19, 20, 33, 49, 143, 145, 146-149, 150, 153, 158, 159, 163, 182, 249, 267  
 perpusilla, Auriculella 269  
 perversa, Auriculella 269  
 Pfeifferi: Antonella 19, 117, 122, 123; Newcambia 9  
 philippiana: Fernandezia 241; Newcambia 9  
 philippii: Tornatellina 168; Tornatellinops 162, 168  
 philolichen, Tubuaia 19, 155, 156  
 Philopoa 18, 19, 20, 24, 35, 38, 41, 46, 243, 261, 262-265: singularis 19, 20, 48, 262, 263, 264  
 physa: Achatinella 277; Newcambia 277; Partulina 22  
 pilsbryi, Celticola 19, 20, 35, 49, 131, 132-135, 136, 141, 147  
 Pityis 6, 17, 20, 24, 38, 41, 53, 54, 92, 94-103, 243; alpestris 19, 54, 95, 103; bilamellata 94, 95; oparana 95; pagodiformis 6, 19, 20, 33, 34, 49, 54, 92, 94, 95-97, 101, 102, 103, 106 (form A, 97; form B, 97; C, 98; D, 98, 100; E, 101); scalaris 19, 54, 95, 101, 103 (form A, 19, 102)  
 Pitysinae 17, 18, 20, 22, 32, 34, 40, 41, 42, 43, 45, 46, 47, 49, 51-162, 276  
 Pitysini 17, 18, 19, 22, 33, 34, 35, 36, 38, 40, 41, 42, 43, 44, 51, 52, 53-116, 267  
 Pleuropoma 29  
 plicata: Achatinella 277; Newcambia 22, 277  
 plicosa, Tornatellina 234, 237  
 polygnapta: Lamellidea 181, 209; Tornatellina 209  
 ponapensis: Tornatellina 168; Tornatellinops 168, 179  
 procerulus, Tornatellides 210, 243, 246, 254, 255, 261  
 producta, Achatinella 9, 10, 11  
 productus, Tornatellides 242  
 proxima: Celticola 19, 135-136; Partulina 10  
 Pukunia 17, 18, 20, 24, 38, 41, 54, 73-77, 86, 125: acuta 18, 20, 34, 49, 54, 73-75, 76; margaritae 18, 76; pellucida 19, 76, 77  
 pulchella, Achatinella 10  
 pulchra, Auriculella 9, 269  
 Pulmonata 17  
 pumilus, Strobilus 18, 72  
 Pupa peponum 210  
 Pupillidae 39  
 Puposoma 256  
 pusilla: Achatinella 184; Auriculella 184; Lamellidea 28, 158, 165, 167, 178, 180, 182, 184-192, 193, 199, 200, 201, 204, 247; Partula 184; Tornatellina 167, 168, 184  
 pyramidatus, Tornatellides 243, 255
- Q**
- quadrasi: Elasmias 226, 230; Tornatellina 230
- R**
- Rachis 11  
 radícula, Antonella 19, 121  
 raoulensis: Tornatellina 156, 167; Tubuaia 145, 146, 156-157, 167  
 rapaensis, Tubuaia 19, 156, 158, 159-160  
 raphis, Strobilus 18, 49, 56, 66, 67, 68  
 raricifera, Tornatellina 217  
 reclusiana: Elasmatina 169, 237; Tornatellina 233, 237; Tornatellinops 169  
 redfieldii: Achatinella 282; Partulina 8, 9, 10, 11, 48, 276, 282-283  
 ringens: Tornatellina 151; Tubuaia 151, 152  
 ronaldi, Tornatellides 244, 258  
 rucuana: Tornatellina 168; Tornatellinops 168  
 rudicostatus, Tornatellides 20, 242, 262  
 rufa, Partulina 10
- S**
- scalaris, Pityis 19, 54, 95, 101, 103  
 scalaris, Pityis (form A) 19, 102  
 schola, Elasmias 222, 231  
 seminigra: Achatinella 284; Monodonta 284  
 serrarius, Tornatellides 244, 258

- serrata: Lamellidea 178, 184, 185, 187, 190, 191, 192; Lamellina 184; Tornatellina 187, 190
- serrula, Auriculella 274
- sharpi, Tornatellaria 267
- Sigmurethra 10
- similaris, Strobilus 18, 56, 64, **65-66**
- simplex: Mitiperua 19, 20, 49, 79, **80-82**; Tornatellides 26 [=oblongus], 243, 247, 249, 250; Tornatellina 249, 250
- simplicimum, Elasmias 19, 219, 222, 228, **231-232**
- simulans, Achatinella 9
- singularis, Philopoa 19, 20, 48, 262, **263-264**
- solidula, Orobophana 256
- solitaria, Lamellovom 19, 104, 109, **114-115**
- solomonensis, Lamellidea 184
- sororcula, Celticola 19, **139**
- Spiraxis: bulimoides 238; cousimilis 241; splendida 241
- splendida: Achatina 241; Achatinella 280; Bulimus 241; Fernandezia 241-242; Oleacina 241; Partulina 280; Spiraxis 241
- splendidula, Stenogyra 242
- Stenogyra: bulimoides 238; cousimilis 241; splendidula 242
- stewartii, Achatinella 9, 10, 11, 14
- stokesi: Tornatellaria 256, 265; Tornatellides 244, 247, **256, 257, 265**
- straminea, Auriculella 269
- striatula, Taitaa 19, 20, 49, 83, **87-88, 89, 91**
- Strobilus 16, 17, 20, 24, 38, 41, 54, **55-73, 92, 234**; acicularis 18, 49, 56, **66, 67, 69**; acuminatus 49; archimedes 57; basalis 18, 56, **60, 66**; bilamellatus 235; brevis 18, 20, 55, 56, **70-71**; conicus 236; intermedius 18, 56, 61, **63, 65**; oblongus 248; opeas 18, 49, 56, 60, **61-63, 65, 68**; ovatus 227; pellucidus 119, 122; perfragilis 18, 20, 49, 56, **68-69**; raphis 18, 49, 56, 66, 67, 68; similaris 18, 56, 64, **65-66**; strobilis 18, **72**; subsimilis 18, 49, **72**; subtilis 18, 34, 49, 56, **63-65, 66, 67, 70**; subulata 57; turrita 57; turritus 18, 20, 49, 55, **56-60, 63, 65, 92**
- Strombilus 55
- Stylommatophora 17
- subangulatus, Tornatellides 243, 244, 254, 255
- subcostata, Mitiperua 19, **81, 82**
- subcylindrica: Lamellidea 180, **183, 214**; Tornatellina 183
- subperforatus, Tornatellides 242
- subrugosa: Tornatellina 167; Tornatellinops 167
- subsimilis, Strobilus 18, 49, **72**
- subtilis, Strobilus 18, 34, 49, 56, **63-65, 66, 67, 70**
- subulata, Elasmatina 55, 57, 59
- Succinea 14
- succinea, Electrina 106
- sundana: Elasmias 232; Tornatellina 232
- sundanum, Elasmias 232
- sykesi, Tornatellaria 265
- Syncera 256
- T**
- Taireva 17, 19, 20, 83, 87
- Taitaa 17, 19, 20, 22, 24, 38, 41, 53, 54, **82-92, 131**; arauana 19, 83, **86**; dacryma 19, 20, 34, 49, 83, **84-86, 89, 91, 92**; neanica 19, 20, 83, 89, **90-91**; striatula 19, 20, 49, 83, **87-88, 89, 91**; terebriformis 19, 83, **91-92**; zimmermani 19, 83, 87, **89, 91**
- Tanga 17, 18, 20, 70
- tantalus: Auriculella 269; Lamellidea 20, 140, 167, 211, 212, 213; Tornatellina 167, 212
- Taraia 17, 19, 20, 83, 89
- Tautautua 17, 18, 20, 68
- tenella, Auriculella 269
- tenuis, Antonella 19, 34, 49, 117, **124-125, 129**
- terebra, Tornatellides 243, 244, 247, 254, 255, 258
- terebriformis, Taitaa 19, 83, **91-92**
- terrestris: Elasmias 221, 224, **232**; Tornatellina 232
- tesselata: Achatinella 280; Partulina 10, 280
- thaanumi, Tornatellaria 247, 265, **267**; Tornatellides 247, 265, 267
- Thaumatodon 29, 256, 261
- Tornatellaria 8, 10, 16, 18, 20, 24, 38, 41, 46, 95, 243, 257, 261, 262, 263, **265-267**; adelinae 265; cincta 265; illibata 265; newcombi 19, 20, 30, 48, 249, 263, **265-267**; sharpi 267; stokesi 256, 265; sykesi 265; thaanumi 247, 265, **267**; trochoides 265
- Tornatellariini 18, 19, 30, 34, 35, 41, 43, 44, 46, 51, **262-267**
- Tornatellides 16, 17, 18, 20, 24, 26, 30, 31, 37, 38, 41, 50, 95, 210, 242, **243-262, 263, 264, 265, 267, 272**; antoni 248; attenuatus 260; brunneus 244; chathamensis 13, 15, 26, **246-247**; clarionensis 247; compactus 243, 244, 247, 254, 255; confuses 210, 244; cyphostyla 244, 247; drepanophora 243, 254, 255; euryomphala 243, 244, 247, 254, 255, 258; forbesi 258; "garreti" 246; glaucina 256; idae 244, 247, 257; inconspicuum 167, 171, 247; kailuanus 261; kahoolavensis 247; kermadecensis 242; leptospira 242, 243, 254, 255; macromphala 243, 244, 254, 255; mexicana 247; moomomiensis 244, 260; neckeri 19, 20, 48, 247, **258-261**; newcombi 249; oahuensis 246; oblongus 19, 20,

- 28, 30, 35, 45, 48, 158, 224, 243, 244, 246, 247, **248-255**, 258, 261, 267, 272; oswaldi 19, 35, 48, 247, 254, 255, 257, 258; parvulus 247, **255-256**; perforatus 247; perkinsi 243, 244, 247, 254, 255; procerulus 210, 243, 246, 254, 255, 261; productus 242; pyramidatus 243, 255; ronaldi 244, 258; rudicostatus 20, 242, 262; serrarius 244, 258; simplex 243, 247, 249; solidula 256; stokesi 244, 247, **256-257**, 265; subangulatus 243, 244, 254, 255; subperforatus 242; terebra 243, 244, 247, 254, 255, 258; thaanumi 247, 265, 267; tryoni 243, 255; waianaensis 242
- Tornatellidinae 18, 19, 20, 24, 34, 41, 42, 43, 45, 48, 51, **242-267**, 272
- Tornatellidini 18, 19, 30, 35, 37, 38, 41, 43, 44, 45, 46, 47, 51, **242-262**
- Tornatellina 6, 12, 14, 16, 17, 18, 20, 24, 26, 38, 41, 47, 55, 103, 104, 146, 162, 163, 167, 218, 233, **234-237**; affinis 157, 167; antoni 248; aperta 222, 225, 234, **235**; archimedes 57; bacillaris 196, 199; baldwini 167; bilamellata 9, 13, 15, 20, 31, 234, **235-236**; bilamellatus 235; buplicata 183; callosa 236; camarinica 170; cernica 224; citrea 224; clausa 234, 235; columellaris 185, 187, 190; conica 167, 184, 185, 187, 190, 234, 236; conicus 236; cumingiana 236; cylindrica 209; dentata 196; duplicilamellata 172, 235; eucharis 224; extincta 211; fissidens 105; fusca 224; gayi 167, 211; globosa 103, 104; globulosa 217; gouldi 151; gracilis 210; hataiana 168; hidalgoi 151; impressa 167, 172, 185, 190; inconspicua 171; intuscostata 167, 185, 190; iredalei 169; jacksonensis 169; kamalensis 210; kermadecensis 156; kitaiwojimana 225; kochiana 170; lanceolata 210; mcgregori 167, 168; manilensis 225; mariei 226; mastersi 170; mauritiana 224; microstoma 183; minuta 167, 233, **236-237**; moellendorffiana 183; molluccana 170; monoliata 158; moohuensis 171, 235; nakadai 168; natunensis 225, 226; neozealandica 169; nepeanensis 171, 235; newcombi 249, 265, 266; nitida 157, 158, 184, 185, 187, 189, 190; norfolkensis 171, 235; normalis 167, 172; noumeensis 170; novoseelandica 162, 169; oblonga 196; ogasawarana 182, 205; ovata 227; ovacula 226; peasiana 229; peponum 210; perforata 187; perplexa 146; philippii 168; plicosa 234, 237; polygnapta 209; ponapensis 168; pusilla 167, 168, 184; quadrasi 230; raulensis 156, 157, 167; rarificera 217; reclusiana 233, 237; ringens 151; rucuaana 168; serrata 185, 187, 190; simplex 249, 250; subcylindrica 183; subrugosa 167; sundana 232; tantalus 167, 212; terrestris 232; trochiformis 105, 236; trochlearis 118, 167; turrita 57; voyana 157, 158, 167; wakefieldiae 232
- Tornatellinae 163
- Tornatellinidae 3, 9, 12, 13, 15, 16, 17, 29, 40, 45, 50, 217, 265
- Tornatellininae 18, 20, 22, 24, 29, 34, 40, 41, 42, 43, 44, 45, 46, 47, 48, 50, **217-242**
- Tornatellinini 18, 19, 22, 29, 32, 38, 41, 42, 43, 45, 50, **233-242**
- Tornatellinops 12, 16, 17, 18, 20, 24, 26, 27, 29, 38, 41, 42, 51, 99, 112, 131, 145, 148, 149, **162-178**, 179, 182, 211, 225, 235, 256; baldwini 48, 163, 164, 165, 167, 178, 179; camarinica 170; capricorni 162, 171, 172; concolorans 19, 48, 163, 165, **175-178**, 179, 235; duplicilamellata 172; hataiana 162, **168**; impressa 172, 175; inconspicua 171; inconspicuum 171; inconspicuus 167, 171, 247; iredalei 169, 178; irregularis 258; jacksonensis 169; kochiana 170; lidgbirdensis 171; mcgregori 163, 167, **168**, 178, 179; mastersi 170; moluccana 170; moohuense 171; moohuensis 171, 235; nakadai **168**, 172; nannodes 19, 151, **153**; neozealandica 169; nepeanensis 171, 235; norfolkensis 171, 235; normalis 172; noumeensis 170; novoseelandica 20, 162, 163, 169, 179; philippii 162, **168**; ponapensis **168**, 179; reclusiana 169; rucuaana 168; subrugosa 167; variabilis 8, 9, 10, 11, 13, 15, 19, 26, 28, 32, 48, 162, 163, 164, 165, 166, **172-175**, 178, 179
- Tornatellinoptini 18, 19, 32, 36, 38, 41, 43, 51, **162-178**
- Tornelasmias 162, 163; capricorni 162, 171; inconspicuum 171; inconspicuus 247; lidgbirdense 171; moohuense 171; nepeanense 171
- trochiformis, Tornatellina 105, 236
- trochlearis: Achatina 118; Antonella 19, 20, 33, 49, 117, **118-119**, 124, 125, 167; Cionella 119; Tornatellina 118, 122, 167
- trochoides, Tornatellaria 265
- Trochomorphinae 29
- tryoni: Fernandezia 242; Tornatellides 243, 255
- Tubuaia 6, 18, 19, 20, 22, 24, 29, 37, 38, 41, 42, 47, 53, 71, 92, 99, 131, 133, **143-162**, 163, 164, 167, 182, 256: af-

- finis 143, 145, 146, **149-150**,  
 153, 157, 167; cremnobates  
 19, 49, 145, 146, **153-155**,  
 162; cylindrata 19, 145, 146,  
**155-156**; gouldi 18, 19, 143,  
 145, 146 **151-153**, 182; hi-  
 dalgoi 151, 152; inconstans  
 19, 49, 143, 145, 146, **160-**  
**162**; kermadecensis 156,  
 242; micans 149, 150; nitida  
 157, 158; perplexa 18, 19,  
 20, 33, 49, 143, 145, **146-149**,  
 150, 153, 158, 159, 163, 182,  
 249, 267; philolichen 19,  
 155, **156**; raoulensis 145,  
 146, **156-157**, 167; rapaen-  
 sis 19, 156, 158, **159-160**;  
 ringens 151, 152; voyana  
 18, 19, 36, 145, 146, 154,  
 156, **157-159**, 162, 167  
 Tubuaiini 17, 19, 22, 29, 33,  
 34, 36, 37, 38, 40, 41, 42, 43,  
 44, 46, 47, 51, 131-162, 175,  
 267  
 turbiniformis, Apex 284
- turgida, Achatinella 10, 14,  
 48, 276, 291, **292**  
 turrita: Achatina 57; Balea  
 56; Cionella 57; Strobilus  
 57; Tornatellina 55, 56, 57  
 turritella, Auriculella 269  
 turritus, Strobilus 18, 20, 49,  
 55, **56-60**, 63, 65, 92
- U**
- uahukana, Lamellidea 213,  
**217**  
 uniplicata, Auriculella 269
- V**
- variabilis: Lamellidea 172;  
 Pacificella 162, 164, 175;  
 Partulina 22; Tornatelli-  
 nops 8, 9, 10, 11, 13, 15,  
 19, 26, 28, 32, 48, 163, 164,  
 165, 166, **172-175**, 178, 179  
 virgulata: Achatinella 280;  
 Partulina 8, 10, 22, 48, 276,  
 280, 281, **282**
- viridans, Achatinella 9, 10,  
 12, 48, 276, 280, 287, **291**  
 voyana: Tornatellina 157,  
 158, 167; Tubuaia 18, 19,  
 36, 145, 146, 154, 156, **157-**  
**159**, 162, 167  
 vulpina, Achatinella 9, 10, 11,  
 13, 14, 15
- W**
- waianaensis, Tornatellides  
 242  
 Waimea 16, 17, 18, 20, 44,  
 247, **261**  
 wakefieldiae: Achatinella  
 232; Elasmias 232; Tor-  
 natellina 232  
 westerlundiana, Auriculella 9,  
**269**  
 wilsoni, Fernandezia 20, 237,  
**242**
- Z**
- zimmermani, Taitaa 19, 83,  
 87, **89**, 91

1958 Owen 221

1956 Solem to Kondo  
on solomonensis p.  
184.

*L. micropilum*

*L. oblonga*

aphallic 194

aphallic 306