

Lyropupa PILSBRY, 1900. Systematics, evolution and dispersal
(Gastropoda: Pulmonata: Pupilloidea)

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I dedicate this paper to the Hawaiian Malacological Society

ABSTRACT. A Hawaiian endemic genus *Lyropupa* PILSBRY is revised, based on over 68,000 specimens from ca. 250 localities. Identification key, full synonymies, morphological descriptions including variation, distribution maps and figures of each species are provided. Thirty species are recognised, 7 of them known as subfossil only; most species are endemic to particular islands. Fifteen specific and subspecific names are synonymised; the following new taxa are described: *L. societatis*, *ingrata*, *adeps*, *dissimulator*, *hybrida*, *captiosa*, *lualualeiensis*, *micra continua*. Phylogeny reconstruction was based on 23 characters with 49 character states. The genus includes three distinct phylogenetic lineages (*spaldingi* group, *microthauma* group, *ovatula* group) of different morphology, and partly ecology and dispersal abilities. Mean minimum speciation rate, based on the cladogram and age of the islands, ranges from ca. 1.4 to ca. 2.4 event/1 myr, depending on the lineage. Mean speciation frequency in the genus is ca. 8.3 event/1 myr, intra-island speciation (ca. 6) being much more frequent than inter-island (2.2). Island-to-island dispersal is less frequent than speciation: ca. 5.4 event/1 myr, dispersal from NW to SE being much more frequent (ca. 7.4) than from SE to NW (ca. 1.5). All evidence indicates that the genus originated on Oahu; colonisation frequency of the remaining islands decreases with their age: Hawaii - ca. 16.3 event/1 myr, Maui Nui - ca. 4.2 event/1 myr, Kauai ca. 1.1 event/1 myr.

Key words: Malacology, taxonomy, zoogeography, evolution, Hawaii, *Pupilloidea*, *Lyropupa*.

Motto: Everything in order, evolving. [Donovan Leitch "Maya's dance"]

I. INTRODUCTION

Lyropupa PILSBRY, 1900 - a case of monophyletic radiation in the Hawaiian Islands, each of different age and size, and all relatively young - offered a rare opportunity to study a land snail speciation rate and colonisation sequence in an insular situation. This, however, required a thorough revision of the genus, and especially of the abundant material that had accumulated at the Bishop Museum since PILSBRY & COOKE's (1918-1920) monograph, and a re-construction of phylogeny. If my paper appears to be a hybrid between a systematic revision and an evolutionary-biogeographic work, it is only because there are advantages to such a collective approach. Reference to characters and distribution of particular species can be easily made within the limits of the same paper, and phylogenetic or distributional information does not have to be repeated.

II. HISTORICAL ACCOUNT

The first members of *Lyropupa* were described within the genera *Pupa* and *Vertigo* (GOULD 1843, PEASE 1871, ANCEY 1890). In 1900 PILSBRY erected the subgenus *Lyropupa* within *Nesopupa* PILSBRY, 1900, to accommodate species described by the above authors. ANCEY (1904) elevated *Lyropupa* to the generic rank. Few more species were described by ANCEY (1904, 1904-1905) and COOKE (1908), and placed in the same genus. The only revision of the taxon was that by PILSBRY & COOKE (1918-1920), where *Lyropupa* comprised 22 species; 16 of those were new and many included subspecies and forms. The authors regarded *Vertigo costata* PEASE, 1871 and *Vertigo striatula* PEASE, 1871 as "lost species", and included DALL's (1890) mysterious *Vertigo cubana* as a distinct taxon, albeit with some reservations. The genus comprised three subgroups corresponding to subgenera: group of *Lyropupa lyrata*, section *Lyropupilla* PILSBRY et COOKE and section *Mirapupa* COOKE et PILSBRY.

Most of PILSBRY's materials of *Lyropupa* are deposited at the Bishop Museum, Honolulu. Additional, unrevised material that has accumulated in that collection since PILSBRY & COOKE's (1918-1920) revision, comprises several hundred times as many specimens. The Bishop Museum material constitutes over 90% world's material of *Lyropupa*. Most of the remaining fraction is kept at the Philadelphia Academy of Natural Sciences, and single lots, including paratypes of some taxa described in this paper - at the Museum of Natural History, Wrocław University; a minor fraction is scattered over other institutions.

III. MATERIAL AND ABBREVIATIONS

The Bishop Museum collection contains several thousand pupilloid samples from nearly as many localities on the six main islands: Oahu, Kauai, Molokai, Lanai, Maui and Hawaii - an evidence that the pupilloids of the area, if not thoroughly studied, have been very well collected. About 1000 samples of recent and subfossil material from ca. 250 localities contained *Lyropupa*; it is reasonable to assume that what I had at my disposal represented a complete or nearly complete set of species. It appears that in the future only very few taxa may be added to the list. Including them in the analysis would only slightly change the resulting picture of evolutionary and biogeographic events. Considering both the rapid destruction of subfossil localities and extermination of extant fauna as a result of human activities in the Hawaiian Islands, the chance of adding the few probably not yet discovered species is decreasing rather than increasing.

A total of over 68,000 specimens were examined from ca. 250 localities, including type material of nearly all the nominal taxa. A great majority (over 95%) of lots lack dates and collector names, hence only localities and sample numbers are given in the lists of the studied material. In those lists "r", "f" and "a" denote recent, subfossil and alcohol specimens, respectively.

Many samples in the collection are labelled "fossil", with not a single reference to the depth or age of the deposit from which they were obtained, but obviously of very different age. Below they are tentatively called "subfossil". Despite the abundant material, it is impossible to study any sequences of changes within species or to estimate when a species became extinct on an island.

Alcohol-preserved specimens of only three species were available, firstly, because some species are known as subfossil only, secondly, because many recent species are at present rare or have already been exterminated. Their state of preservation was rather poor, and all the specimens examined (19) proved aphyllid. Luckily, shells of *Lyropupa* offer a wide variety of taxonomically useful characters.

SEM photos of gold-coated shells were taken at the laboratory of the Field Museum of Natural History, Chicago.

The following abbreviations are used in the text:

* Collection names: BM - Bishop Museum, Honolulu; ANSP - Academy of Natural Sciences, Philadelphia; MCZ - Museum of Comparative Zoology, Harvard University, Cambridge; MNHW - Museum of Natural History, Wrocław University; RBI - Royal Belgian Institute, Brussels; USNM - United States National Museum of Natural History, Smithsonian Institution, Washington, D.C.

* Shell parameters: H - shell height, B - shell breadth, h - aperture height, b - aperture breadth, bw - body whorl height, H/B - height/breadth ratio, bw/H - relative height of body whorl.

IV. SYSTEMATIC REVIEW

Genus *Lyropupa* PILSBRY, 1900

Lyropupa PILSBRY 1900: 432 [as a subgenus of *Nesopupa*]. Type species: *Pupa lyrata* GOULD, 1843, by original designation.

Lyropupilla PILSBRY & COOKE 1918-1920: 247. Type species: *Lyropupa spaldingi* PILSBRY et COOKE, 1920, by original designation.

Mirapupa COOKE et PILSBRY, in PILSBRY & COOKE 1918-1920: 255. Type species: *Vertigo perlonga* PEASE, 1871 [= *Lyropupa costata* (PEASE, 1871)], by original designation.

SYSTEMATIC REMARKS

PILSBRY & COOKE's (1918-1920) subdivision of the genus *Lyropupa* into three taxa, corresponding to subgenera, only partly agrees with the results of my phylogenetic analysis. Since all the members of PILSBRY's (1900) *Lyropupa* are evidently very closely related, and the low number of species (30) does not require any subgeneric classification, I synonymise the two section names proposed by those authors with *Lyropupa* PILSBRY, 1900 and simply ignore the "group of *Lyropupa lyrata*". Species groups referred to below are of purely phylogenetic significance.

DIAGNOSE

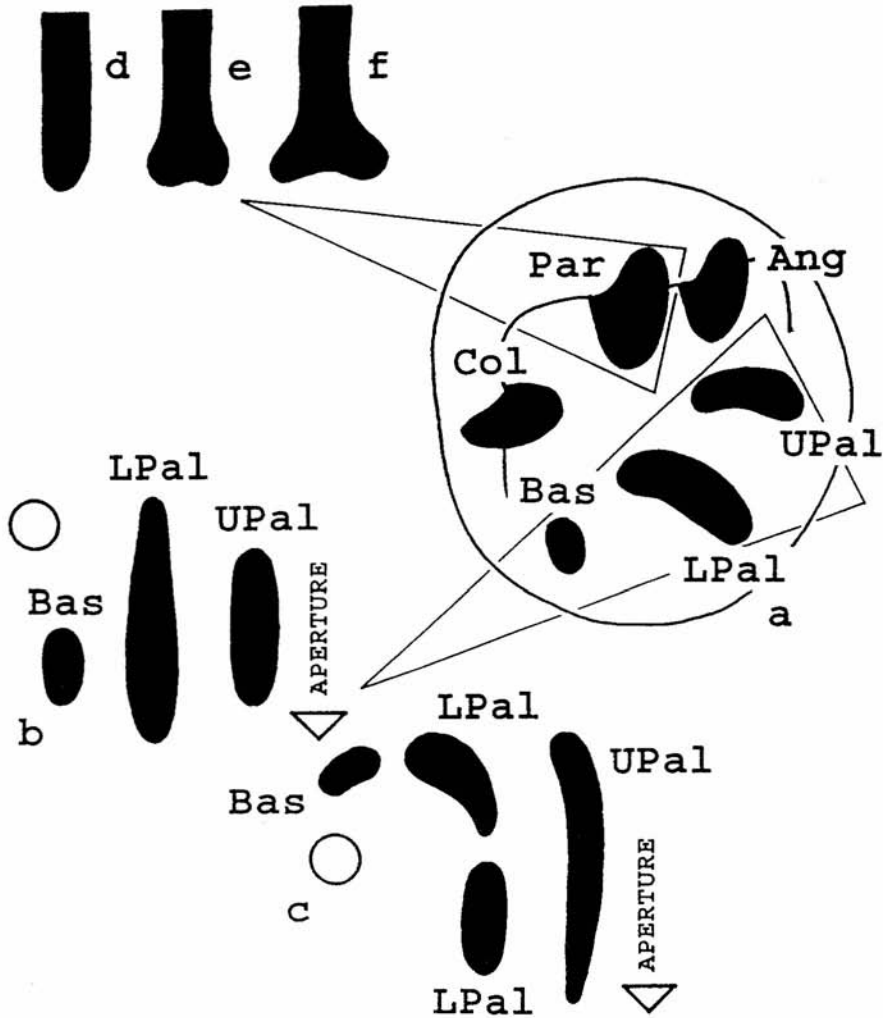
Shell ovate, ovate-conical or ovate-cylindrical, dextrous or sinistrous, costate, apertural barriers present. Gonad reduced to two lobes of a few acini each. Aphallism seems to be common. Apomorphies: angular tooth originally long and reaching to the very margin of lip; upper palatal tooth long, more or less distinctly bipartite, with a tendency to prolong to the very margin of lip, thus closing sinulus; basal tooth recessed; embryonic whorls originally coarsely wrinkled-granulose; parietal callus as thick as the rest of the lip, which is more or less detached.

DESCRIPTION

Shell dextrous or sinistrous, of slightly more than 4 to nearly 7 whorls; short to elongate oval, ovate-cylindrical, cylindrical, ovate-conical; spire straight or convex, apex usually gently rounded but in some species tapered or truncate; whorls from flat to strongly convex, in many species "shouldered"; suture from very shallow to deep. Shell height from ca. 1.5 to ca. 2.7 mm; height/breadth ratio from ca. 1.4 to ca. 2.3.

Aperture from almost regularly semi-oval or oval, through pear-shaped with a pronounced sinulus, to subquadrate or subtriangular. Lip in most species forms a "full circle" i.e. parietal callus is as thick as the rest of lip, and detached from the whorl above, sometimes forming a short trumpet; rarely parietal callus distinctly thinner than the rest of the lip; usually lip well thickened and well reflexed, rarely thin and not reflexed; its width varies between species.

Apertural barriers. For terminology and transformations of apertural barriers see fig. 1. Columellar tooth from well visible to invisible in front view; of varied shape: oblique-tubercular with lower end shifted towards lip and upper end ascending on columella; lamellate, in top view crescentic (with both ends produced towards lip to



1. Pupilloid apertural barriers and some of their transformations in *Lyropupa*. Diagrammatic. a - front view of basic pupilloid apertural barriers, b, c - top view of barriers of basal-palatal wall of a generalized pupilloid (b) and an advanced *Lyropupa* (c) after removing the rest of the shell; position of columella indicated as a circle, d-f - cross section of parietal tooth in a generalized pupilloid (d) and some advanced members of *Lyropupa* (e, f). Col - columellar tooth, Par - parietal tooth, Ang - angular tooth, UPal - upper palatal tooth, LPal - lower palatal tooth, Bas - basal tooth.

the same or different degree) or almost straight and occupying most of or entire columellar wall; its free margin usually thickened. Parietal tooth high lamellate, its free margin usually thicker, arcuate or straight; the tooth highest in middle or in its deeper-situated half; straight or its outer part deflected towards palatal wall; in top view almost straight, regularly crescentic or its inner end bent towards columella, sometimes very strongly; its free margin simple or flattened and dilated, sometimes to the point of becoming almost bifid; in some species the tooth displaced towards and behind the angular, so as to stand almost in line with it. Angular tooth either long, thin, lamellate, or reduced in height and/or length: ridge-like or elongate tubercular, reaching lip margin; or simple tubercular, situated very close to lip margin. Upper palatal tooth simple, straight lamellate of varied length; bi-partite: external part, closer to lip and facing angular somewhat lower; internal part somewhat higher; often between the parts an incision; the tooth tends to get prolonged to the very lip margin by a ridge, callus or very low lamella, thus closing sinus together with the angular tooth; in some species somewhat recessed from lip and/or simple. Lower palatal tooth always situated deeper than the upper, parallel to or divergent from it; from simple straight lamellate of arcuate free margin, through displaced very deep inside the shell or displaced both deep and high, so as to stand almost in line with the upper palatal tooth; its outer end may be callus-like diffuse; the tooth may split in two: external tubercular or lamellate part and internal part, situated transversely as a lamella or a long tubercle, sometimes accreted to the inner end of upper palatal. Basal tooth displaced fairly deep in the aperture: to the level of columellar tooth or behind it, rarely situated in front of it; elongated, transverse ridge-like or simple, tubercular; in some species displaced far beyond and above columellar, and forming a continuation of the split off, inner part of the lower palatal tooth. A partly or wholly "false" basal tooth, tubercular or elongatedly tubercular, often present; it corresponds to the latero-basal groove on the exterior of the body whorl.

Body whorl profile. Body whorl suture mostly straight, very rarely slightly descending. On body whorl in most species various combinations of grooves and impressions: two slightly convergent impressions of varied depth: from deep to almost imperceptible, corresponding in position to the palatal teeth; both impressions parallel and accompanied by a third, shorter, latero-basal impression; a single narrow groove in the middle of the body whorl, sometimes prolonged as far as above the aperture and gradually decreasing in depth; a flat-bottomed gutter in the middle of body whorl, often accompanied by a short latero-basal impression; the gutter often prolonged onto the higher whorls where it gradually decreases in depth; in some species body whorl smooth with no trace of grooves. Besides grooves or impressions, the following structures may appear on the body whorl: latero-basal hump, basal or latero-basal crest, basal "bump" or lateral "bumps". Exterior of body whorl wholly ribbed; ribs less distinct or completely reduced latero-basally; absent at the bottom of the gutter, or else altogether absent.

Ribbing. The number of ribs of penultimate whorl from ca. 10 to 45. Ribs from slightly oblique and almost straight to strongly flexuous or bent at an obtuse angle in

the middle; blunt or sharp; devoid of or provided with sharp periostracal crests; regular or irregular; continuous or incomplete and then grouped in pairs or triplets; irregularities of ribbing usually do not involve the first 2-3 definitive whorls.

Microsculpture of interspaces. Periostracal or mostly periostracal wrinkles short, straight, arranged randomly or mostly radially; on their background fine or rather coarse spiral ridges of varied spacing may occur; the ridges are mostly periostracal but partly calcareous, visible under stereomicroscope or only in SEM; on subfossil shells preserved only as incomplete faint traces.

Microsculpture of embryonic whorls. Coarsely to finely wrinkled-granulose, almost completely smooth or consisting of fine to rather coarse spiral ridges of varied spacing; the latter may be visible under stereomicroscope or, in most species, only in SEM.

Umbilicus. Circular to somewhat ovate, wide open, with whorls visible inside; narrow, oval, open; slit-like or completely sealed.

Colour. Fresh shells of recent species display all shades of brown and yellowish: from rich, deep chestnut to very light yellowish beige. Fossil shells vary from completely white and often semitransparent to dirty greyish and yellowish white. Some banded in middle of whorls (both recent and subfossil), the band being lighter than the rest of the shell. Apertural barriers and lip white or at least much lighter than the rest of the shell.

Reproductive system. All the specimens examined (19) representing three species (*L. spaldingi*, *lyrata* and *costata*) were aphyllid; the only peculiarity of the reproductive system is the reduction of the number of gonad lobes to two, each comprising 2-3 relatively big acini. Nothing indicates ovoviviparity; no specimen had embryos in female efferent ducts.

ECOLOGY

The ecology is known very fragmentarily. Most members of the groups *spaldingi* and *microthauma* inhabit the humid forest zone where they are found in leaf litter and on mossy stones; members of the group *ovatula* live under stones and logs in drier, more open habitats.

DISTRIBUTION

Hawaiian endemic, known from Oahu, Kauai, Maui, Molokai, Lanai, Hawaii, Kahoolawe and Niihau.

KEY FOR SPECIES GROUP IDENTIFICATION

1. Angular reduced in height and/or length, set very close to parietal
..... group of *L. spaldingi*, p. 384.
- Angular not reduced, set apart from parietal
..... 2.

2. Embryonic whorls seemingly smooth, lower palatal simple
 group of *L. microthauma*, p. 408
- Embryonic whorls wrinkled-granulose, lower palatal split partly or wholly
 group of *L. ovatula*, p. 431.

The group of *Lyropupa spaldingi*

DIAGNOSE

Sinistrous. Angular reduced in height and/or length, not deflected. Parietal simple, displaced towards or almost behind angular, most often its external part deflected palatalwards. Inner end of upper palatal visible without shell destruction or simply in front view. Lower palatal often recessed and/or displaced towards the upper palatal. Basal only slightly shifted behind columellar. Ribs regular; microsculpture of interspaces composed of fine, randomly arranged wrinkles. Embryonic whorls wrinkled-granulose or smooth. Apomorphies: reduced angular, displaced parietal. The most plesiomorphic group of *Lyropupa*; found on all the main islands except Kauai; 9 species endemic to particular islands.

IDENTIFICATION KEY

1. External part of parietal not deflected; angular reduced only in height, considerably (over 1/4 own length) overlaps parietal (figs 2-4)
 *scabra*, p. 385.
- External part of parietal deflected palatalwards; angular reduced in height and length, not or very slightly overlaps parietal
 2.
2. On body whorl a single narrow groove; lower palatal recessed and displaced upwards; parietal only slightly deflected;
 3.
- On body whorl a flat-bottomed gutter, impressions absent or vestigial; lower palatal not or slightly recessed, not displaced upwards
 4.
3. On body whorl a distinct basal bump; embryonic shell wrinkled-granulose
 5.
- On body whorl no or an indistinct basal bump; embryonic shell smooth
 6.
4. Lower palatal simple (figs 5-11)
 *spaldingi*, p. 387.
- Lower palatal split
 7.

5. Lower palatal divergent from the upper, ribs very coarse (figs 26-29)
 *anceyana*, p. 397.
- Lower palatal parallel to the upper, ribs fine (figs 30-33)
 *antiqua*, p. 399.
6. Columellar crescentic-tubercular (figs 34-37)
 *hawaiiensis*, p. 401.
- Columellar oblique-tubercular
 8.
7. Impressions on body whorl distinct (figs 21-25)
 *societatis* n. sp., p. 394.
- Impressions on body whorl vestigial or absent (figs 12-20)
 *mirabilis*, p. 390.
8. Columellar takes at most mid 1/3 columellar wall, whorls shouldered (figs 42-45)
 *ingrata* n. sp., p. 405.
- Columellar takes at least mid 1/2 columellar wall, whorl not shouldered (figs 38-42)
 *sparna*, p. 403.

***Lyropupa scabra* PILSBRY et COOKE, 1920**

Figures 2-4.

Lyropupa scabra PILSBRY & COOKE 1918-1920: 254-255, pl.26, figs 1, 2. Type locality: Ukulele, E Maui. Holotype: BM 11049; Paratypes: BM 12639 & ANSP 119465. See also note.

MATERIAL EXAMINED

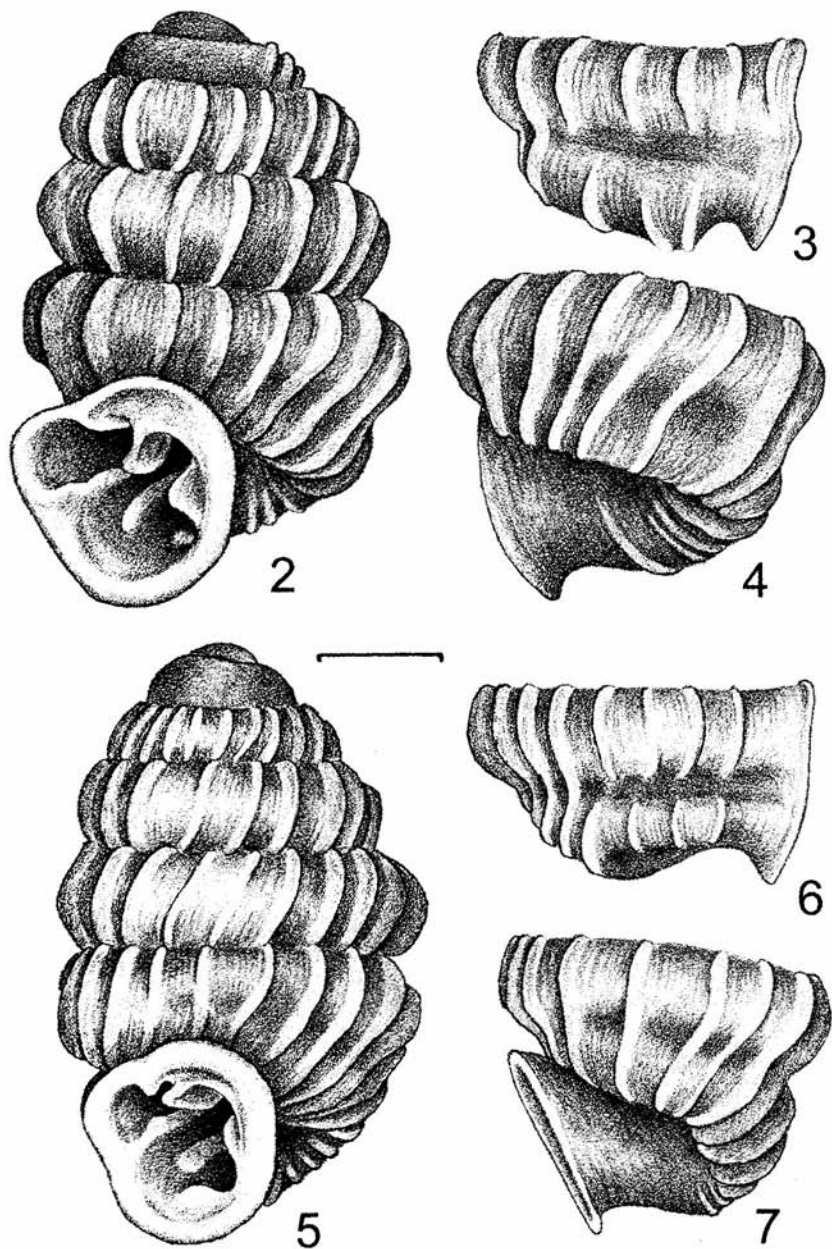
Maui E: Ukulele, BM: 11049, holotype; 12639, 3; ANSP: 119465, paratype.

Maui W: Lahaina, BM: 33921, 1; Maunahoama, BM: 12640, 1; no exact locality, BM: 21231, 1.

See also note.

DESCRIPTION

Shell ovate-conical; spire tapered, almost straight with shouldered whorls; apex bluntly rounded. Whorls 5.3-5.8, convex; suture deep. H: 2.28-2.76 mm; B: 1.44-1.59 mm; h: 0.89-1.09 mm; b: 0.86-0.98 mm; bw: 1.19-1.52 mm. H/B: 1.59-1.74; bw/H: 0.52-0.57. Aperture rounded triangular; sinulus fairly well marked. Lip slightly detached, reflexed, fairly narrow, thick. In aperture 5 or 6 teeth. Columellar visible in front view, robust; takes mid 1/3 columellar wall; in top view transversely, elongatedly tubercular; very thick. Parietal ca. 1/5 whorl long; set close to angular; high and fairly thick, with somewhat thicker edges; highest in middle; not deflected. Angular reduced in height to a very low thick lamella or a high ridge; 2x shorter than parietal and overlapping it considerably. Upper palatal 1/5 whorl long; division into parts distinct: part facing angular prominent, ridge-like; part facing parietal low and fairly thick lamellate. Lower palatal slightly recessed; not displaced upwards; starts at ca. 1/2 length of the lamellate part of the upper; is parallel to it, of equal length but much



2-4. *L. scabra* PILSBRY et COOKE, BM 12639, E Maui: 2 - front view, 3 - side view of body whorl, 4 - oblique umbilical view of body whorl. Figs 5-7. *L. spaldingi* PILSBRY, BM 16973, Maunakapu, Oahu: 5 - front view, 6 - side view of body whorl, 7 - oblique umbilical view of body whorl. Scale bar 0.5 mm.

higher and thicker; simple; outer end not diffuse. Basal robust, recessed somewhat behind columellar; visible in front view; elongatedly tubercular; convergent to palatals or transverse; in some specimens absent. Body whorl profile entirely ribbed, except ribs interrupted at the bottom of the gutter; half height of body whorl a straight, deep, flat-bottomed gutter of gradually decreasing depth; terminating on penultimate whorl above the aperture; an indistinct basal bump present. Body whorl suture straight. Umbilicus circular or somewhat oval, deep, open, with whorls visible inside. Sculpture sparse, regular, coarse, of 14-19 ribs on penultimate whorl. Ribs high and sharp with thick bases, flexuous; 1/4-1/3 interspace thick. Embryonic whorls wrinkled granulose. Colour light goldish brown.

DISTRIBUTION

E and W Maui; recent.

NOTE

The holotype is an aberrant shell. It differs from the remaining specimens in larger size, more numerous ribs on the penultimate whorl, shorter angular, both palatals ca. twice shorter and giving an impression of vestigial structures, columellar less robust; all the teeth appear to be corroded or not completely formed.

None of the localities mentioned by PILSBRY & COOKE (1918-1920), i.e. Ukulele and Maunahooma (on label BM 12640 spelled: Maunahoama) could be located on a map or found in the Hawaiian Gazetteer.

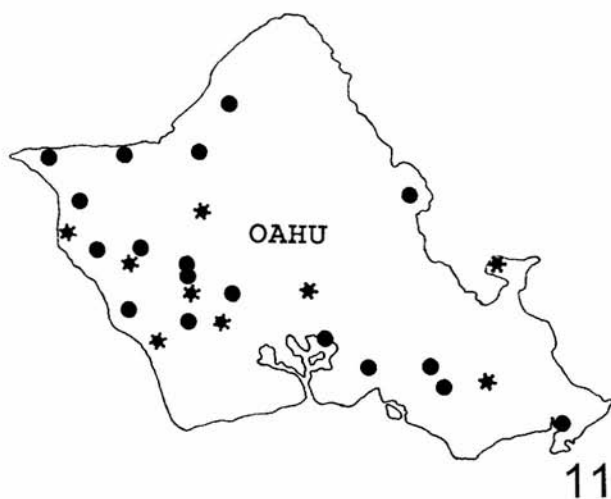
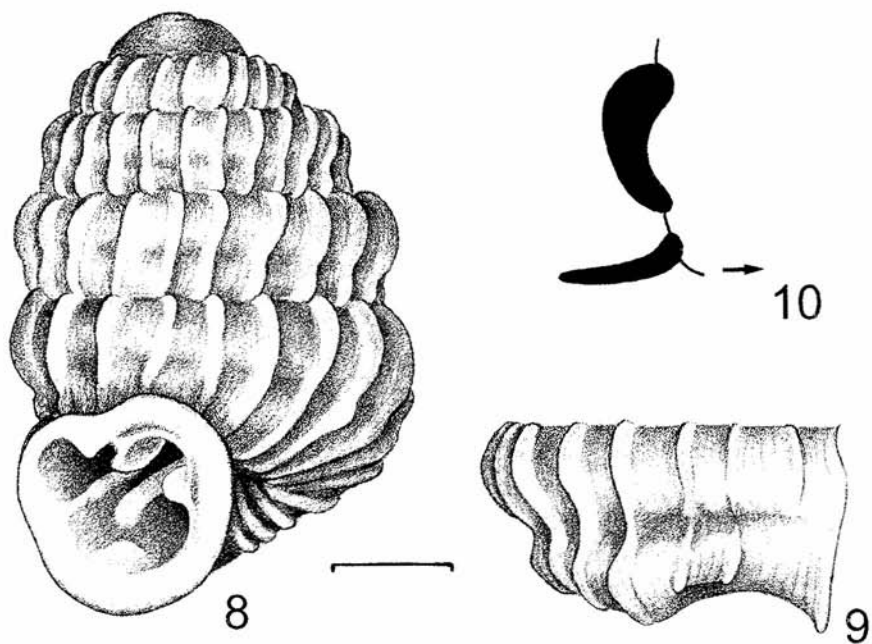
Lyropupa spaldingi PILSBRY, 1920

Figures 5-11.

Lyropupa spaldingi PILSBRY, in PILSBRY & COOKE 1918-1920: 248- 249, pl.21, figs 10, 12, 13. Type locality: Puu Kaua, Waianae Mts, Oahu. Holotype: BM 11048; Paratypes: BM 11048, ANSP 37192 & 119470.

MATERIAL EXAMINED

Oahu: Ekahanui, BM: 9368 ex 125630, 1 r; 125590, 1 r; 125873, 1 r; 177304, 1 f; 177325, 2 f; 177345, 11 f; 182917, 26 r; 211530, 1 f; ex 9369, 1 r; Glen Ada, BM: 44362, 8 r; Green Pk., BM: 16647, 17 r; 16648, 1 r; 16877, 6 r; 16878, 1 r; 16920, 5 r; 21862, 7 r; 59496, 17 r; 59546, 78 r; 59605, 2 r; 105844, 4 r; 105845, 1 f; 105863, 6 f; 105864, 11 r; 105906, 14 r; 105998, 2 r; 106103, 4 r; Haleauau, BM: 93360, 1 f; Halona, BM: 9385 ex 173215, 18 r; 113175, 2 r; 113194, 4 r; 113208, 7 r; 114249, 1 r; 173180, ca. 20 r; 173243, 1 r; 173264, 5 r; 173282, 14 r; Huliwai, BM: 114767, 2 r; 114768, 1 r; Kaaikukai, BM: 165248, 1 r; 176242, ca. 30 f; 176283, 27 f; 176352, 12 f; 176888, ca. 30 f; 176890, ca. 50 f; 176944, ca. 20 f; 177436, 2 f; 177437, 5 f; 182975, 6 r; 210677, 1 f; 210697, 5 f; 210751, 1 f; ex 176282, 1 r; ex 176243, 9 f; ex 176284, 42 rf; ex 210698, 7 f; Kalauao, BM: 121091, 1 r; Kamanaiiki, BM: 41160, 11 r; 41161, 1 r; Kamananui, BM: 112663, 4 r; Kanehoa, BM: 37085, 1 r; 37110, 1 r; Kanewai, BM: 117733, 2 r; 128592, 2 r; Kaumokuiki, BM: 129213, 1 r; 174451, ca. 40 f; 174452, ca. 10 r; Keaau, BM: 107944, 4 r; 174315, ca. 20 f; 174351, ca. 30 f; 175863, 6 f; 175878, 18 r; ex 174316, 2 f; Keawaawa, BM: 47320, 3 r; Kewapilau, BM: 166536, 11 r; 174382, 2 f; Kualoa Mts, BM: 92121, 1 r; Kupchou, BM: 9379 ex 128632, 1 r; 9380 ex 128633, 5 r; 59447, 42 r; ex 128633, 1 r; Leilehua, BM: 12414, 4 r; 12594 (=12414), 1 r; 16032, 1 r; 17038, 2 r; 17039, 55 r; 37264, 37 r;



8-11 - *L. spaldingi* PILSBRY, BM 189054, Pauoa, Nuuanu, Oahu: 8 - front view, 9 - side view of body whorl; scale bar 0.5 mm; 10 - top view of columellar and infracolumellar, palatal wall removed, diagrammatic; arrow indicates aperture; 11 - Distribution: asterisks - recent and subfossil, circles - recent.

Lualualei, BM: 9356 ex 113137, 1 r; 9357 ex 113552, 9 r; 9359 ex 116218-19, 6 r; 37135, 20 r; 37152, 19 r; 91757, 1 r; 91928, 1 r; 91935, 1 r; 112833, 1 r; 112903, 14 r; 112923, 2 r; 112946, 2 r; 113413, 4 r; 113438, 1 r; 113463, 9 r; 113619, 5 r; 113654, 12 r; 113699, 3 r; 113793, 1 r; 113840, 7 r; 116104, 20 r; 116105, 6 r; 116153, 1 r; 116171, ca. 20 r; 116267, ca. 50 r; 116268, ca. 20 r; 116374, 3 r; 116514, 8 r; 163233, 1 r; 183807, 16 r; 183827, 25 r; Makaha, BM: 17856, 14 r; 107717, 2 r; 118044, ca. 150 r; ex 17857, 4 r; Makua, BM: 34843, 1 r; 108061, 1 r; 108094, 2 r; 117950, 1 r; 117951, 1 r; 117987, 1 r; 118017, 19 r; 118045, ca. 20 r; 119504, 3 r; 119533, 2 r; 119576, 3 r; 119662, 4 r; 119697, 1 r; 119698, 1 r; Manimi Gulch, BM: 129166, 2 r; Mauna Kapu, BM: 16973, ca. 150 r; 16975, ca. 20 r; 18974, 34 r; 33168, 9 r; Moanalua, BM: 134781, 1 r; Mokuleia, BM: 17220, 3 r; 17274, 215 r; 17332, 31 r; 17350, 1 r; Nanakuli, BM: 9374 ex 128007, 1 r; 9376 ex 128109, 1 r; 54036, 1 r; 54093, 2 r; 54112, 4 r; 105627, 1 r; 105771, 1 f; 112734, 12 r; 127770, 2 r; 128153, 4 r; 182933, 21 r; 183515, 2 r; 186813, 6 r; Napepeiauoelolo, BM: 126900, 2 r; 127253, 1 r; 176827, 11 f; Nuuanu, BM: 35217, 4 r; 12379, 1 r; ex 12396, 2 r; ex 12398, 1 r; Opacula, BM: 93269, 2 r; 98091, 3 r; 98091, 5 r; 98092, 2 r; 122432, 7 r; 127690, 1 r; 167773, 1 r; Palawai, BM: 174020, 12 r; 174057, ca. 30 r; 174111, ca. 30 r; 174113, 1 r; 174171, 8 f; 174204, ca. 20 r; 174205, 1 f; 174206, ca. 40 f; 174207, ca. 100 r; 176870, 2 f; 177077, 6 f; 177107, 10 f; 177108, ca. 20 f; 177159, 5 f; 177191, 8 f; 177250, 11 f; 177492, 6 f; 177702, 206 f; ex 177109, 26 f; Palchua, BM: 10218 ex 33144, 1 r; 10219 ex 16975, 10 r; 10220 ex 40606, 1 r; 12415, 1 r; 16595, 1 r; 16802, 18 r; 16803, 1 r; 21920, 2 r; 33081, 106 r; 33127, 1 r; 33137, 37 r; 35836, 6 r; 35837, 4 r; 35863, 21 r; 35864, 5 r; 59352, 3 r; 59645, 5 r; 59646, 9 r; Palikea, BM: ex 93301, 1 r; 93303, 17 f; Papaia Valley, BM: ex 114135, 1 r; Pauoa, BM: 15816, 1 r; 189054, 2 r; 189055, 1 r; Pohakea, BM: 183662, 5 f; 183756, ca. 30 r; 183776, 7 r; Popouwela, BM: 17021, 1 r; 17911, 2 r; 33746, 5 r; 33771, 1 r; 35273, 2 r; 35440, 2 r; 114683, 1 r; 114685, 2 r; 119103, 2 r; 131722, 1 r; Pualii, BM: 9386 ex 176621, 1 r; 126075, 1 r; 174401, ca. 20 f; 175787, 1 f; 175822, 5 f; 177705, ca. 20 f; 180857, ca. 30 f; 180858, ca. 40 f; 184862, ca. 20 f; ex 176732, 1 f; Pukaulua, BM: 12416, 2 r; 42172, 2 r; 174401, 1 r; 174401, ca. 20 f; Puu Hapapa, BM: 211017, 1 r; 211031, 1 r; Puu Kaua, BM: 11048, holotype & 2 paratypes; 76915, 1 r; Puumialau, BM: 176499, ca. 20 f; ex 176500, 8 f; Tantalus, BM: 17410, 2 r; Waianae Valley, BM: 9366 ex 117389, 1 r; 22858, 5 r; 96470, 1 f; 117436, 3 r; no exact locality, BM: 17332, 5 r; 105653, 1 r; 185034, 4 a.

DESCRIPTION

Shell tumid to moderately tumid oval or ovate-conical; spire tapered, poorly convex or almost straight; apex tapered. Whorls 5.6-6.6, most often 5.8-6.3, convex or moderately so; suture deep or moderately so. H: 2.28-2.84 mm; B: 1.24-1.63 mm; h: 0.72-1.01 mm; b: 0.70-0.96 mm; bw: 1.14-1.41. H/B: 1.46-1.93; bw/H: 0.49-0.54. Aperture roughly semi-oval; sinulus poorly marked. Lip slightly detached, reflexed, fairly narrow, thick. In aperture 6-9 teeth. Columellar visible in front view; takes upper 1/2 or mid 1/4-1/3 columellar wall; in top view crescentic, with both ends produced towards lip. Parietal 1/4 whorl long, set almost exactly in line with angular; high and rather thick lamellate with thicker edges, highest within; outer part strongly deflected palatalwards. Angular reduced in height and length, low, thick lamellate or ridge-like; ca. 1/4 parietal long, not overlapping parietal. Upper palatal 1/5 whorl long and rather thick; division into parts distinct: part facing angular low lamellate or ridge-like; part facing parietal high lamellate. Lower palatal somewhat recessed, but not displaced upwards; starts at ca. 2/3 length of the lamellate part of the upper; 2/3 upper palatal long and parallel to it, but higher and thicker; simple; outer end not diffuse. Basal common in some populations; thick ridge-like, oblique or almost parallel to the palatals, in front view hidden behind the columellar. Infraparietal very rarely present, tubercular, set rather deep and very close to columellar wall. Infracolumellar present in most shells, small tubercular in front view; when palatal

wall is removed it turns out to continue as a fairly long, thick ridge, roughly parallel to the palatals. False basal present in most specimens. Body whorl profile has a deep, flat-bottomed but rather narrow gutter at half its height, corresponding to both palatals; in most shells the gutter prolonged above aperture at least as an incision in the middle of ribs; on the body whorl the ribs terminate above or in the gutter, or cross it as low ridges; 1/4 height from the bottom a shorter, deep, narrow impression terminating in an angular hump and delimiting a sharp ridge on the basal wall. Body whorl suture straight. Umbilicus nearly circular, deep, open, with whorls visible inside. Sculpture coarse and rather sparse, regular, of 15-22, in most shells 17-19 ribs on penultimate whorl. Ribs flexuous, especially on body whorl, sharp, thicker at base; often ribs on body and penultimate whorls bear incisions; ca. 1/3 interspace thick. Embryonic whorls wrinkled-granulose. Colour whitish-grey, whitish-yellowish, dirty creamy or very light beige.

DISTRIBUTION

Oahu; recent and subfossil. Fig. 11.

NOTE

Specimens from Kamaikai, Pauoa and Nuuanu (BM: 41160, 189054 and ex 12398) differ from typical shells in being very broad and almost conical, of very light yellowish-brown colour; they have very much thickened lip and the basal is visible even in front view.

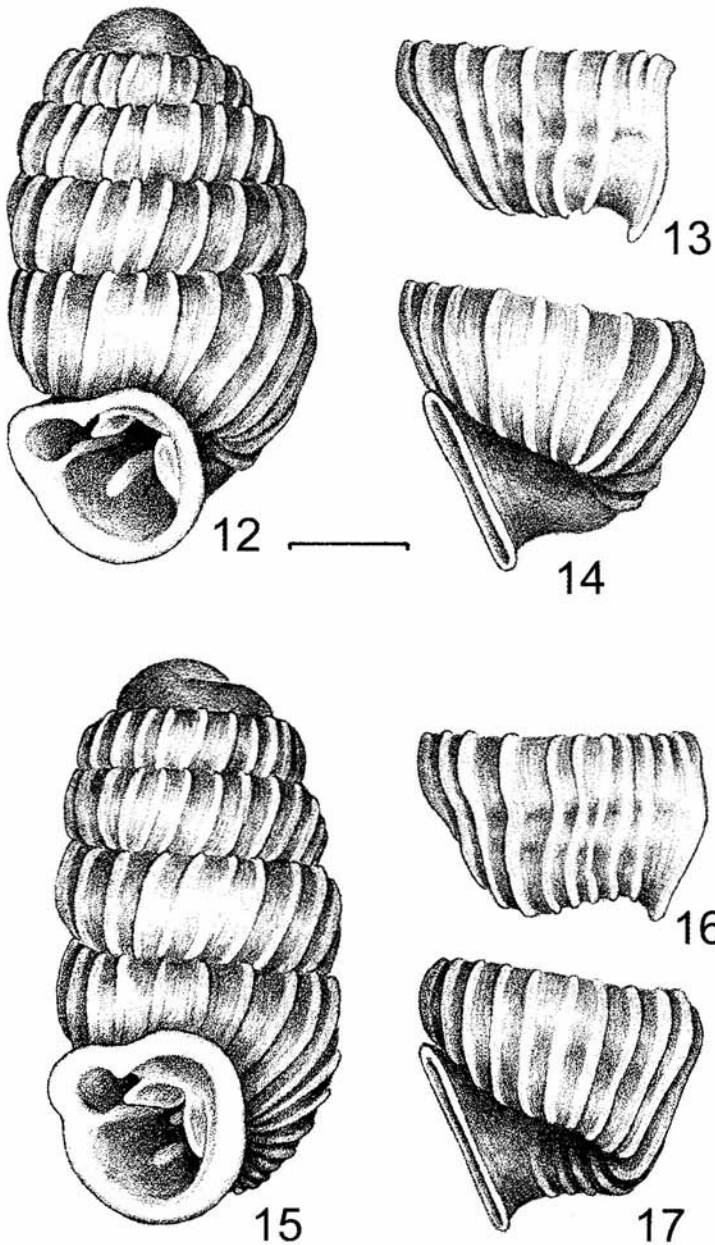
Lyropupa mirabilis (ANCEY, 1890)

Figures 12-20.

Pupa mirabilis ANCEY 1890: 339. Type locality: Oahu, no exact data. Lectotype: BM 18747, designated by PILSBRY & COOKE (1918-1920). See note.

MATERIAL EXAMINED

Oahu: Ekahanui, BM: 9434 ex 125731, 2 r; 125136, ca. 30 r; 125209, 3 r; 125315, 2 r; 125450, ca. 30 r; 125521, ca. 30 r; 125629, 13 r; 125686, 1 r; 125687, ca. 50 r; 125780, ca. 20 r; 125874, ca. 30 r; 177326, 19 r; 177567, 2 r; 177578, 6 r; 177595, ca. 20 r; 177619, 30 r; 183918, 26 r; 211449, ca. 1000 r; 211450, ca. 100 r; 211532, 6 r; 211533, 7 r; 211534, ca. 50 r; 211535, ca. 50 r; 211656, 1 r; 211697, ca. 30 r; 211744, 2 r; Green Pk., BM: 16649, 1 r; 21875, 2 r; 105600, ca. 20 r; 105907, 11 r; 105934, 2 r; 105999, 880 r; 106054, 4 r; 106104, ca. 40 r; Haleanau, BM: 93359, 3 r; 93422, 2 r; 123111, 1 r; Halona, BM: 113172, 9 r; 113248, 31 r; 113252, 1 r; 173179, ca. 40 r; 173216, 16 r; ex 173183, 12 r; Hiu, BM: 117640, ca. 20 r; 117641, 1 r; Huliwai, BM: 125044, 2 r; 126122, 18 r; 126206, ca. 50 r; 126326, 2 r; 126327, 1 r; 126445, ca. 20 r; 126645, 9 r; 132642, ca. 40 r; 133640, 32 r; 163301, 1 r; 177659, 2 f; 177660, 7 f; Kaaawa, BM: 114525, 1 r; Kaaikukai, BM: 126778, ca. 30 r; 127894, 12 r; 176243, 64 f; 176284, 61 rf; 176353, 21 f; 176889, ca. 20 f; 176945, 92 f; 177005, 1 f; 177006, 3 f; 177363, 2 r; 177384, 2 r; 177385, 20 r; 177438, 42 r; 182976, 64 r; 182977, 1 r; 210698, 39 f; 210748, 2 f; ex 176354, ca. 30 f; Kahuku, BM: 10217 ex 33449, 1 f; Kalena E, BM: 113302, 18 r; Kamananui, BM: 112525, 4 r; 112544, 22 r; 112576, 1 r; 112622, 24 r; 112664, 1 r; 112696, 8 r; 112702, 19 r; Kanehoa, BM: 37086, 4 r; Kanewai, BM: 117714, 2 r; 117734, 6 r; 117797, ca. 20 r; 117823, 10 r; Keaau, BM: 107945, 16 r; 174316, 61 rf; 175864, 1 f; 175865, 1 f; Keekee Gulch, BM: 129128, ca. 20 r; 129168, 16 r; 129178, 30 r; 129777, 14 r; Kole Kole Pass, BM: ex 98984, 1 r; Kupchau, BM: 59397,

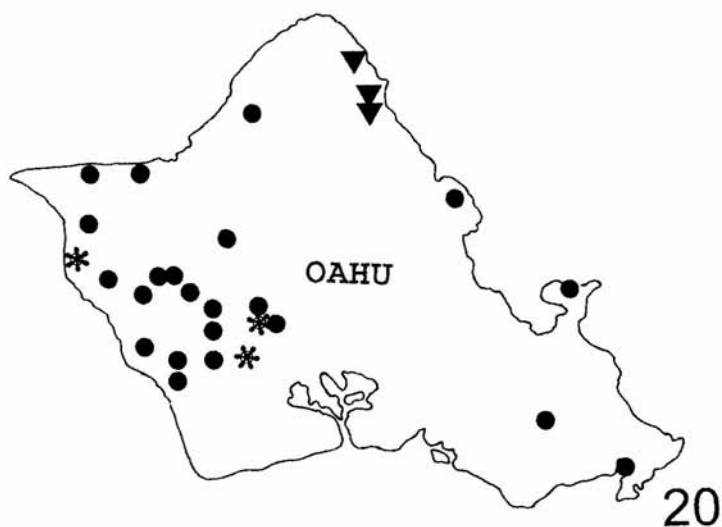
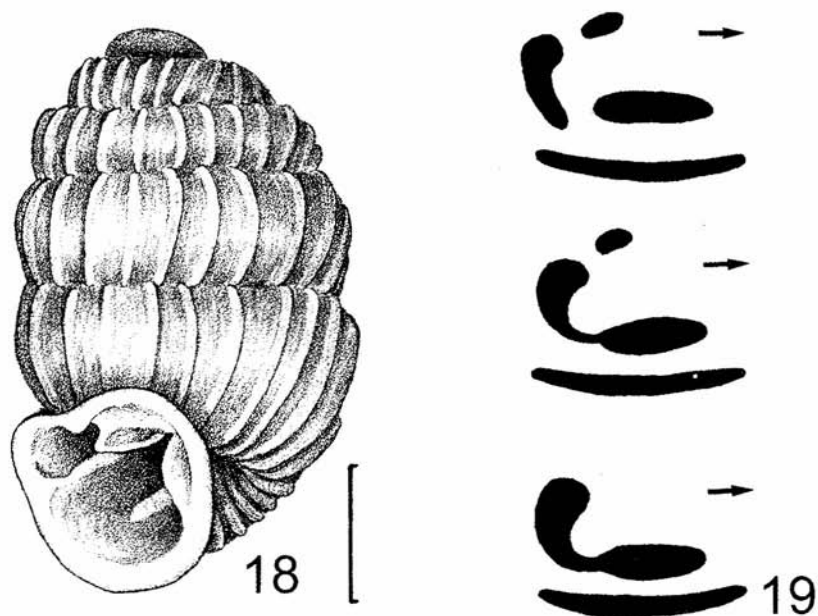


12-17. *L. mirabilis* (ANCEY): 12-14 - BM ex 172960, Waialele, Oahu: 12 - front view, 13 - side view of body whorl, 14 - oblique umbilical view of body whorl; 15-17 - BM 182936, Nanakuli, Oahu: 15 - front view, 16 - side view of body whorl, 17 - oblique umbilical view of body whorl. Scale bar 0.5 mm.

1 r, 59446, ca. 225 r, 128631, 7 r, 128632, ca. 30 r; ex 59449, 1 r; Laie, BM: 189556, 16 f; Leilehua, BM: 17037, 4 r, 90524, 2 r, 90533, 1 r; Lualualei, BM: 91612, 3 r, 91996, 2 r, 113138, 2 r, 113173, 1 r, 113377, 7 r, 113414, 1 r, 113461, 19 r, 113462, 1 r, 113524, 3 r, 113551, 11 r, 113590, 10 r, 113617, 14 r, 113652, 19 r, 113702, 11 r, 113739, 5 r, 113768, 1 r, 113780, 6 r, 113861, ca. 20 r, 113880, 3 r, BM 113903, 10 r, 113921, 3 r, 113935, 3 r, 113945, 3 r, 113946, 1 r, 113948, 2 r, 115980, 1 r, 115992, 1 r, 116028, 20 r, 116069, ca. 30 r, 116106, ca. 30 r, 116107, 7 r, 116110, ca. 50 r, 116111, ca. 20 r, 116152, 2 r, 116174, ca. 30 r, 116219, ca. 20 r, 116243, 10 r, 116266, ca. 30 r, 116344, 3 r, 116372, 20 r, 116476, 1 r, 116515, 7 r, 116516, 8 r, 116521, ca. 20 r, 116522, ca. 20 r, 116551, 8 r, 116552, 6 r, 116579, ca. 20 r, 116580, 2 r, 116582, ca. 50 r, 116584, 2 r, 116586, ca. 100 r, 163223, 1 r, 163232, 1 r, 177796, 10 r, 194478, 1 r; Makaha, BM: 17858, 13 r, 117866, 1 r, 117867, 1 r, 117881, 5 r, 118018, 7 r, 118046, 17 r, 118090, 5 r, 119503, 2 r, 119577, 3 r, 119606, 1 r, 119628, 1 r, 185166, 2 r, 185221, 37 r; ex 118044, ca. 50 r; Makua, BM: 112998, 1 r, 113037, 1 r, 119699, 1 r; Manuwaiahu Gulch, BM: 114252, 1 r; Manuwaikaalāi, BM: 176409, 5 f, 176436, 15 f; Mokuleia, BM: 17156, 1 r, 17275, 2 r, 128553, 1 r; Nanakuli, BM: 53907, 1 r, 54053, 1 r, 54094, 4 r, 54113, 4 r, 90043, 1 r, 105652, 2 r, 105687, ca. 30 r, 105712, 2 r, 105713, ca. 40 r, 105772, 1 r, 105804, 25 r, 112740, 13 r, 127969, 1 r, 128006, 6 r, 128007, 19 r, 128109, 3 r, 128152, ca. 50 r, 182695, 1 r, 182696, 11 r, 182836, 6 r, 182934, ca. 20 r, 182935, 7 r, 182936, ca. 625 r, 183352, 5 r, 183429, 1 r, 183453, ca. 30 r, 183487, ca. 50 r, 183853, 1 r; ex 183452, 2 r; Nanakuli Valley, BM: 172526, 1 r; Napepeiauolelo, BM: 126899, 12 r, 126960, ca. 20 r, 127015, 8 r, 127016, ca. 20 r, 127104, 22 r, 127105, 22 r, 127190, ca. 100 r, 127252, 1 r, 127531, ca. 20 r, 127584, 16 r, 127620, ca. 20 r, 127621, 3 r, 173895, 2 r, 173954, ca. 50 r, 173955, ca. 50 r; Pahole, BM: 166208, 15 r, 166240, 4 r, 183565, 2 r; Palawai, BM: 9372 ex 127466, 20 r, 9457 ex 127501, 6 r, 126835, 18 r, 127300, 1 r, 127418, ca. 20 r, 127420, 17 r, 127466, ca. 1000 r, 127691, 28 r, 163304, ca. 40 r, 174058, ca. 40 r, 174059, ca. 20 r, 174112, ca. 30 r, 177076, 2 f, 177109, 22 f, 177110, ca. 20 r, 177160, 4 f, 177192, 62 f, 177251, 127 f, 177703, 321 f, 180908, ca. 30 r, 180909, ca. 20 r, 183881, ca. 50 f; Palehua, BM: 33080, 12 r, 59353, 1 r, 59644, 3 r; Palikea, BM: 93302, 120 r, 93304, ca. 50 r; ex 93301, 1 r; Papaia Valley, BM: 9361 ex 112524, 1 r, 114047, 2 r, 114068, 1 r, 114114, 1 r, 114135, 5 r; Pohakea, BM: 183775, 6 r; Popouwela, BM: 9391 ex 31795, 2 r, 11046, 2 r, 33747, 1 r, 33792, 3 r, 33792, 4 r, 35272, 4 r, 114668, 8 r, 131677, ca. 20 r, 131704, 3 r, 131746, ca. 40 r, 131793, ca. 100 r, 131849, ca. 50 r, 131850, ca. 20 r, 131924, 309 r, 131925, ca. 20 r, 163264, 1 r, 163270, 1 r, 163274, ca. 20 r, 172709, 227 r, 172746, ca. 30 r; Pualii, BM: 126020, 1 r, 126048, 1 r, 126076, 13 r, 176622, ca. 50 f, 176622, 221 f, 176732, 45 rf, 176733, ca. 525 f, 176816, 1 f, 184861, ca. 20 r, 184863, ca. 20 r; Pukaulua, BM: 9365 ex 111067, 1 r, 93380, ca. 20 r, 93381, ca. 20 r, 93382, 2 r, 93383, 1 r, 117128, 3 r, 174402, 4 r; Puumialau, BM: 176477, 4 f, 176500, 80 f, 176540, 151 f; Waianae Valley, BM: 9381 ex 128601, 2 r, 22859, 1 r, 117437, 1 r, 117527, 2 r; Waialele, BM: 172899, 44 f, 172956, 61 f, 172957, 72 f, 172958, ca. 30 f, 173012, 38 f, 173046, 49 f, 173071, 1 f, 181001, 26 f; no exact locality, BM: 18747, lectotype r.

DESCRIPTION

Shell ovate-conical, from rather short to much elongate; rarely short oval; spire straight or very slightly convex; apex bluntly rounded. Whorls 5.4-6.7, most often 5.7-6.4, flat or moderately convex; suture shallow or moderately deep. H: 1.85-2.53 mm; B: 1.15-1.28 mm; h: 0.66-0.81 mm; b: 0.69-0.86 mm; bw: 1.06-1.28 mm. H/B: 1.59-2.15; bw/H: 0.49-0.56. Aperture rather broadly semi-oval or pear-shaped; sinulus poorly marked, but deeper inside almost closed. Lip not or very slightly detached, reflexed, narrow, well thickened. In aperture 6-7 teeth. Columellar from well to poorly visible in front view; takes upper 3/4-2/3 columellar wall; in top view almost straight or crescentic, with the upper or both ends slightly produced towards lip; rather thin lamellate with thicker edges. Parietal ca. 1/5 whorl long; set almost in line with angular, only their very ends overlapping; high and fairly thin lamellate with thicker edges; highest within; its outer part strongly deflected palatalwards. Angular reduced in length and height, very low thick lamellate or ridge-like; ca. 1/4 parietal



18-20. *L. mirabilis* (ANCEY): 18 - BM 129178, Keekee Gulch, Oahu, front view. Scale bar 0.5 mm. 19 - top view of palatals in two specimens, columellar wall removed, diagrammatic, arrow indicates aperture; 20 - Distribution: circles - recent, triangles - subfossil, asterisks - recent and subfossil.

long. Upper palatal 1/4 whorl long; division into parts distinct: part facing angular ridge-like; part facing parietal fairly thin, high lamellate, nearly touching the parietal. Lower palatal not recessed, nor displaced upwards; split: outer part close to the outer end of lamellate part of the upper; outer end not diffuse; robust tubercular or elongatedly so; inner part short and high lamellate; in top view transversely comma-shaped; almost perpendicular to the upper palatal and situated well before its inner end; free; partly or wholly invisible in front view. In populations from Keekee Gulch and Waialele (BM: 129178, 172960) the lower palatal ranges from incompletely (parts united by a callus bridge or separated only by a slight constriction) to completely split. Some shells have a small basal set at the level of columellar or slightly recessed; elongatedly tubercular, oblique; free. Body whorl profile entirely ribbed, only rarely ribs on its lower half somewhat less distinct; impressions corresponding to palatals absent or very shallow; the upper is longer; in shells with impressions a faint trace of basal crest is present. Umbilicus open, deep, oval or narrow, slit-like; rarely sealed. Body whorl suture straight or very slightly descending. Sculpture regular or somewhat irregular; of 16-26, most often 19-23 ribs on penultimate whorl. Ribs fine, flexuous on body whorl, from bluntish to rather sharp, 1/6-1/5 interspace thick. Embryonic whorls wrinkled-granulose. Colour from tawny to mat brown, goldish honey-brown or dark chestnut.

DISTRIBUTION

Oahu; recent and subfossil. Fig. 20.

NOTE

PILSBRY & COOKE (1918-1920) often referred to type specimens of earlier authors (ANCEY, PEASE) as "type" and "paratypes", and provided them with corresponding labels, though no types and paratypes had been designated originally. In such cases I term them "lectotype and paralectotypes, designated by PILSBRY & COOKE (1918-1920)".

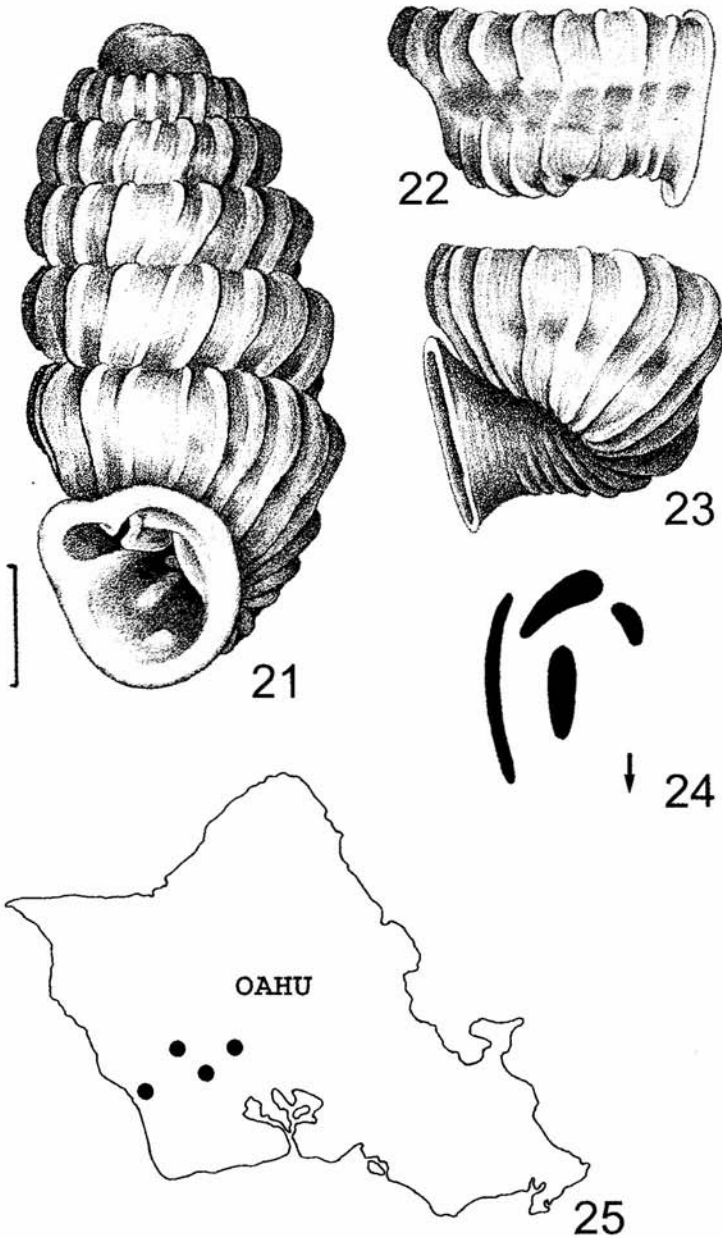
Populations from two localities are morphologically fairly distinct. Recent shells from Keekee Gulch (BM: 129178, 129777) differ from typical specimens in being very broadly oval, with very fine thin ribs, fewer (5.3-5.9 whorls) and higher (20-26) rib count on penultimate whorl. Subfossil shells from Waialele (BM ex 172960) differ from typical specimens in a more tapered spire, thinner lip and more distinct sinulus; parts of the split lower palatal still united by a callus and somewhat coarser ribs.

Lyropupa societatis n. sp.

Figures 21-25.

TYPE LOCALITY

Kupehau, Oahu.



21-25. *L. societatis* n. sp.: 21-23 - holotype, BM 59448, Kupehau, Oahu: 21 - front view, 22 - side view of body whorl, 23 - oblique umbilical view of body whorl. Scale bar 0.5 mm. 24 - top view of palatals and basal, columellar wall removed, diagrammatic, arrow indicates aperture; 25 - Distribution.

TYPE MATERIAL

Kupehau, Oahu: Holotype & 700 paratypes, BM 59448; 65 paratypes, MNHW ex BM 59448; Ekahanui, Oahu: 2 paratypes, BM 125566; 2 paratypes, BM 211531; Nanakuli, Oahu: 55 paratypes, BM 183452; 125 paratypes, BM ex 182936; 23 paratypes, BM ex 183487; Palawai, Oahu: 225 paratypes, BM ex 127466.

OTHER MATERIAL EXAMINED

Oahu: Kaaikukai, BM: 176889, 26, ex 176243, 7; Kupehau, BM: ex 59397, 3; ex 59446, 2; 59448, 765 juv.; 59449, 1; Mauna Kapu, BM: 33169, 1; ex 16973, 1; Nanakuli, BM: ex 183352, 1; Napepeiauolelo, BM: ex 127105, 13; Palawai, BM: ex 127691, 23; Palchua, BM: ex 59352, 1; Pualii, BM: ex 126020, 1.

DIAGNOSE

The new species is most similar to *mirabilis* (its sister species) and *spaldingi*. It differs from *mirabilis* in: 1. much more convex whorls, often shouldered; 2. deeper suture; 3. higher, coarser ribs, often incised like in *spaldingi*; 4. presence of false basal in nearly all shells; 5. distinct impressions on body whorl; 6. more pear-shaped aperture; 7. basal hidden behind columellar and nearly always present. It differs from *spaldingi* in: 1. more slender and more cylindrical shell; 2. split lower palatal (synapomorphy with *mirabilis*); 3. tubercular basal; 4. columellar much larger in front view; 5. darker colour; 6. shallower gutter on body whorl.

DESCRIPTION

Shell oval to very elongatedly so; often approaching cylindrical; spire poorly convex, feebly tapered; apex bluntly rounded. Whorls 5.7-6.9, most often 6.0-6.4 (holotype 6.7), convex or moderately so, often shouldered; suture deep or moderately so. H: 2.23-2.72 mm (holotype 2.65); B: 1.17-1.36 mm (holotype 1.28); h: 0.73-0.91 mm (holotype 0.80); b: 0.75-0.91 mm (holotype 0.83); bw: 1.16-1.39 mm (holotype 1.29); H/B: 1.76-2.21 (holotype 2.08); bw/H: 0.46-0.53 (holotype 0.49). Aperture pear-shaped; sinulus fairly well defined, deeper inside almost closed. Lip slightly detached, reflexed, fairly narrow, thick. In aperture 6-8 teeth. Columellar in front view from partly visible to almost invisible, takes upper 3/4 to whole columellar wall; in top view almost straight; sometimes its lower end very slightly displaced towards lip; rather thin lamellate. Parietal ca. 1/5 whorl long; set almost in line with angular; only their ends overlapping; high and rather thin with thicker edges; highest within; outer part strongly deflected palatalwards. Angular reduced in height and length; very low thick lamellate or ridge-like; 1/3 parietal long. Upper palatal 1/4 whorl long; no division into parts; all tooth moderately high and thin lamellate except the outer end, which gets gradually lower. Lower palatal not recessed, nor displaced upwards; split: outer part starts at ca. 1/3 length of the upper palatal and equals 1/3 its length; low thick lamellate or elongatedly tubercular; parallel to the upper palatal; outer end may be somewhat diffuse; inner part high lamellate, set obliquely relative to the inner end of upper palatal; overlaps it somewhat; partly visible or invisible in front view; in top view obliquely comma-shaped; free. Basal most often present; recessed behind columellar and invisible in front view; oblique, elongatedly tubercular; convergent to

the inner part of lower palatal. False basal strongly developed in most shells; in some weak or absent. Body whorl profile wholly ribbed; half its height a flat-bottomed gutter corresponding to palatals; in most shells the gutter rather shallow and gradually decreasing in depth, terminates above the aperture; ca. 1/6 height from the base a deep, short impression terminating in an angular hump and delimiting a basal crest; sometimes the impression displaced to basal position or, rarely, absent. Body whorl suture straight. Umbilicus from almost circular to oval, deep, open, with whorls visible inside. Sculpture regular, of 16-25 (holotype 17), most often 18-21 ribs on penultimate whorl. Ribs moderately coarse, sharp, thicker at base, somewhat flexuous, especially on body whorl; ca. 1/5-1/3 interspace thick. Embryonic whorls wrinkled-granulose. Colour from lightish beige to dark chestnut.

NAME DERIVATION

The name means "of a society"; the new species is dedicated to the Hawaiian Malacological Society.

DISTRIBUTION

Oahu; recent. Fig. 25.

Lyropupa anceyana COOKE et PILSBRY, 1920

Figures 26-29.

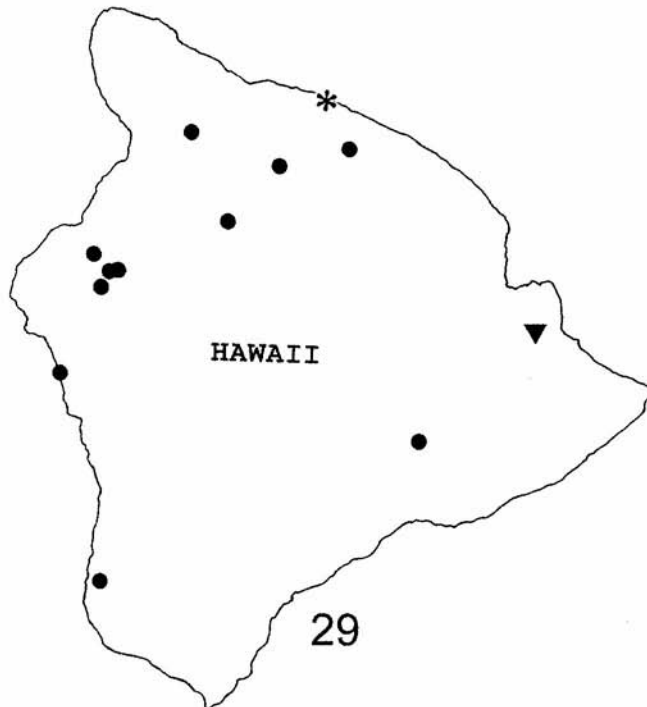
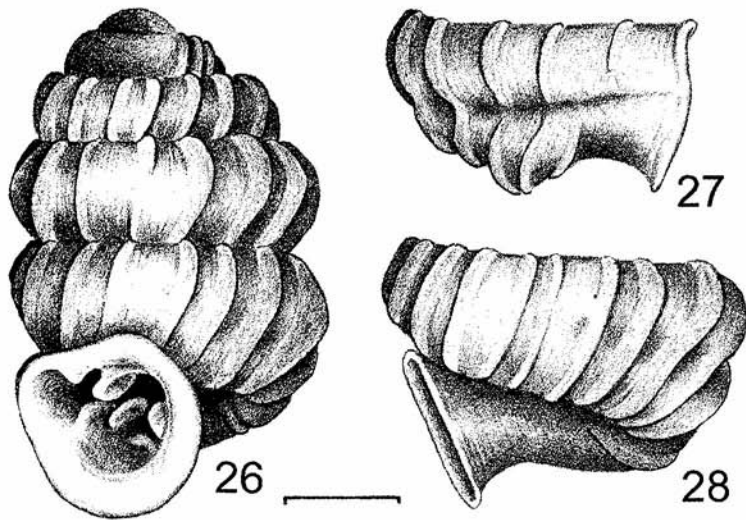
Lyropupa anceyana COOKE et PILSBRY, in PILSBRY & COOKE 1918-1920: 253-254, pl. 26, figs 3, 6. Type locality: Oloa, Hawaii. Holotype: BM 11050; Paratypes: BM 18743 & 18769, ANSP 119469.

MATERIAL EXAMINED

Hawaii: Oloa, ANSP: 119469, 2 paratypes; BM: 11050, holotype; 12434, 7; 12597 (=12434), 1; 18743, 2 paratypes; 18767, 1; 18769, 19 paratypes; 59132, 1.

DESCRIPTION

Shell broadly ovate-conical; spire tapered, straight or very poorly convex; apex tapered. Whorls 5.1-5.6, convex; suture deep. H; 2.19-2.28 mm; B: 1.29-1.46 mm; h: 0.75-0.84 mm; b: 0.76-0.84 mm; bw: 1.19-1.30 mm; H/B: 1.55-1.75; bw/H: 0.52-0.57. Aperture semi-oval; sinulus poorly marked. Lip slightly detached, reflexed, wide, very thick. In aperture 6 teeth. Columellar visible in front view; takes mid 1/3 columellar wall; in top view crescentic-tubercular; with both ends produced towards lip; very thick with thicker edges. Parietal 1/5 whorl long; set almost in line with angular and not overlapping; high and fairly thick lamellate with somewhat thicker edges; highest within; its outermost part somewhat deflected palatalwards. Angular reduced in length and height; ridge-like or elongatedly tubercular; ca. 1/4 parietal long; not overlapping. Upper palatal 1/6 whorl long; division into parts distinct; part facing angular vestigial, ridge-like or absent; part facing parietal low lamellate. Lower palatal recessed and displaced upwards; only the ends of both palatals overlap;



26-28. *L. anceyana* COOKE et PILSBRY, BM 12434, no locality data [probably Olaa, Hawaii]: 26 - front view, 27 - side view of body whorl, 28 - oblique umbilical view of body whorl. Scale bar 0.5 mm. 29. Distribution of *L. anceyana* COOKE et PILSBRY (triangle) and *L. hawaiiensis* ANCEY (circles - recent, asterisks - recent and subfossil).

slightly longer, but much higher and thicker than the upper; simple; oblique i.e. divergent from the upper; outer end not diffuse. Basal recessed behind columellar; visible in front view; robust, ridge-like or low, thick lamellate, oblique or transverse. Body whorl profile entirely ribbed; half its height a narrow, deep straight groove, ca. 1/3 whorl long; in the groove ribs interrupted; on the base a distinct bump, between the bump and the lip, base flattened or slightly concave. Body whorl suture straight. Umbilicus almost circular, deep, open, with whorls visible inside. Sculpture regular, sparse, very coarse, of 14-15 ribs on penultimate whorl. Ribs sharp with thick bases, not flexuous; 1/4-1/3 interspace thick. Embryonic whorls wrinkled-granulose. Colour light goldish-brown.

DISTRIBUTION

Hawaii, known from type locality only; recent. Fig. 29.

Lyropupa antiqua COOKE et PILSBRY, 1920

Figures 30-33.

Lyropupa antiqua COOKE et PILSBRY, in PILSBRY & COOKE 1918-1920: 250-251, pl.21, figs 8, 9, 11.

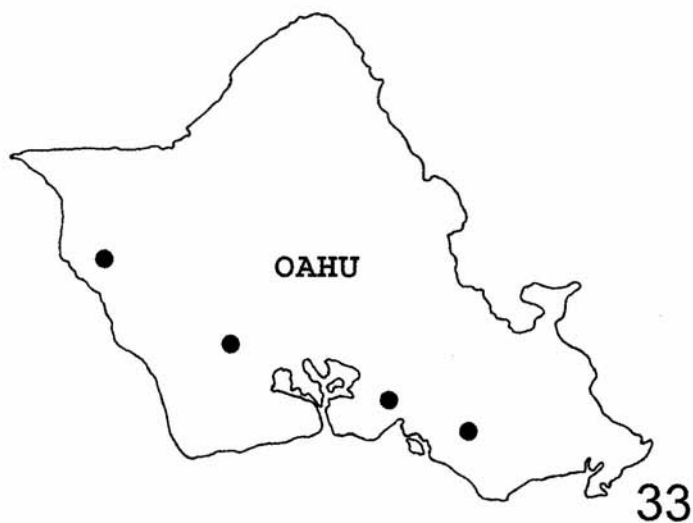
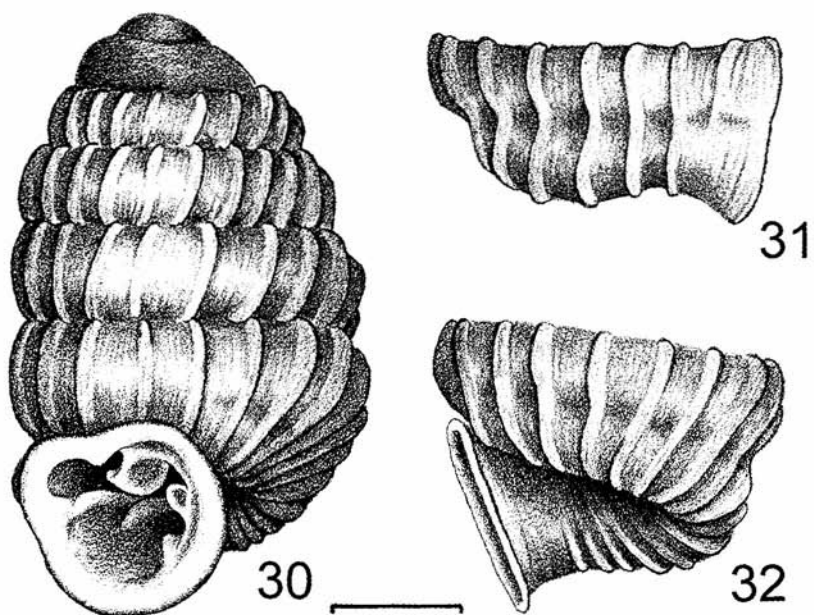
Type locality: Pleistocene deposits along the Upper Manoa Road, Manoa, Oahu. Holotype: BM 11047; Paratypes: BM 11047 & 45280, ANSP 119472.

MATERIAL EXAMINED

Oahu: Kaaikukai, BM: 176354, ca. 80; Kaumokuiki, BM: 174451, 155; Makaha, BM: ex 118044, 15; Manoa, BM: 11047, holotype & paratype; 43305, 3; 43361, 1; 43441, 2; 45280, ca. 100 paratypes; Moanalua, BM: 183090, 2; Palawai, BM: ex 177702, 14; ex 183881, ca. 50; Pualii, BM: ex 176733, ca. 500; Round Top, BM: 10216 ex 39901, 2; no exact locality, BM: 45280, 3.

DESCRIPTION

Shell ovate; spire slightly convex or straight; apex bluntly rounded. Whorls 5.9-6.4, most often 6.0-6.3, flat; suture shallow. H: 2.14-2.69 mm; B: 1.22-1.41 mm; h: 0.66-0.84 mm; b: 0.68-0.85 mm; bw: 1.08-1.31 mm; H/B: 1.67-1.94; bw/H: 0.49-0.53. Aperture pear-shaped; sinulus poorly marked. Lip detached, in some shells forming a short trumpet; reflexed and fairly narrow, rather thick. In aperture 5-7 teeth. Columellar visible in front view, takes mid or upper 1/3-1/2 columellar wall; in top view tubercular-crescentic; with both ends strongly produced towards lip; very thick with thicker edges. Parietal ca. 1/5 whorl long; set almost in line with angular so that their ends nearly or very slightly overlap; high and rather thin lamellate with thickened edges; its outer part deflected palatalwards; only outer end slightly bent palatalwards. Angular reduced in length and height, as a low elongate tubercle or ridge; 1/3 parietal long. Upper palatal 1/6 whorl long; division into parts distinct: part facing angular in shape of a low, callus-like ridge; part facing parietal rather high and thick lamellate. Lower palatal recessed and displaced upwards; parallel to the upper, thicker and higher; simple; only the ends of both palatals overlap; outer end not diffuse. In most shells a robust elongatedly tubercular basal at the level of columellar,



30-33. *L. antiqua* COOKE et PILSBRY, BM ex 176733, Pualii, Oahu: 30 - front view, 31 - side view of body whorl, 32 - oblique umbilical view of body whorl. Scale bar 0.5 mm; 33 - Distribution.

visible in front view; oblique. Some shells have a vestigial and very deeply set infraparietal. Body whorl profile entirely ribbed; half its height a deep, straight, narrow groove corresponding to the upper palatal, 1/2-2/3 whorl long (in shells from Manoa, BM 45280 there is a trace of a very shallow flat-bottomed gutter instead of a single groove); on basal wall a distinct bump; between it and lip a concavity or a flattening. Body whorl suture straight. Umbilicus circular, deep, open, with whorls visible inside. Sculpture regular and rather fine; of 14-21, most often 17-19 ribs on penultimate whorl. Ribs sharp with fairly thick bases; somewhat flexuous on body whorl; 1/5-1/4 interspace thick. Embryonic whorls wrinkled-granulose. Colour dirty creamy, whitish beige or dirty yellowish-white.

DISTRIBUTION

Oahu; subfossil. Fig. 33.

Lyropupa hawaiiensis ANCEY, 1904

Figures 29, 34-37.

Lyropupa mirabilis var. *hawaiiensis* ANCEY 1904: 68, pl.5, fig.19. Type locality: Hawaii, no exact data.

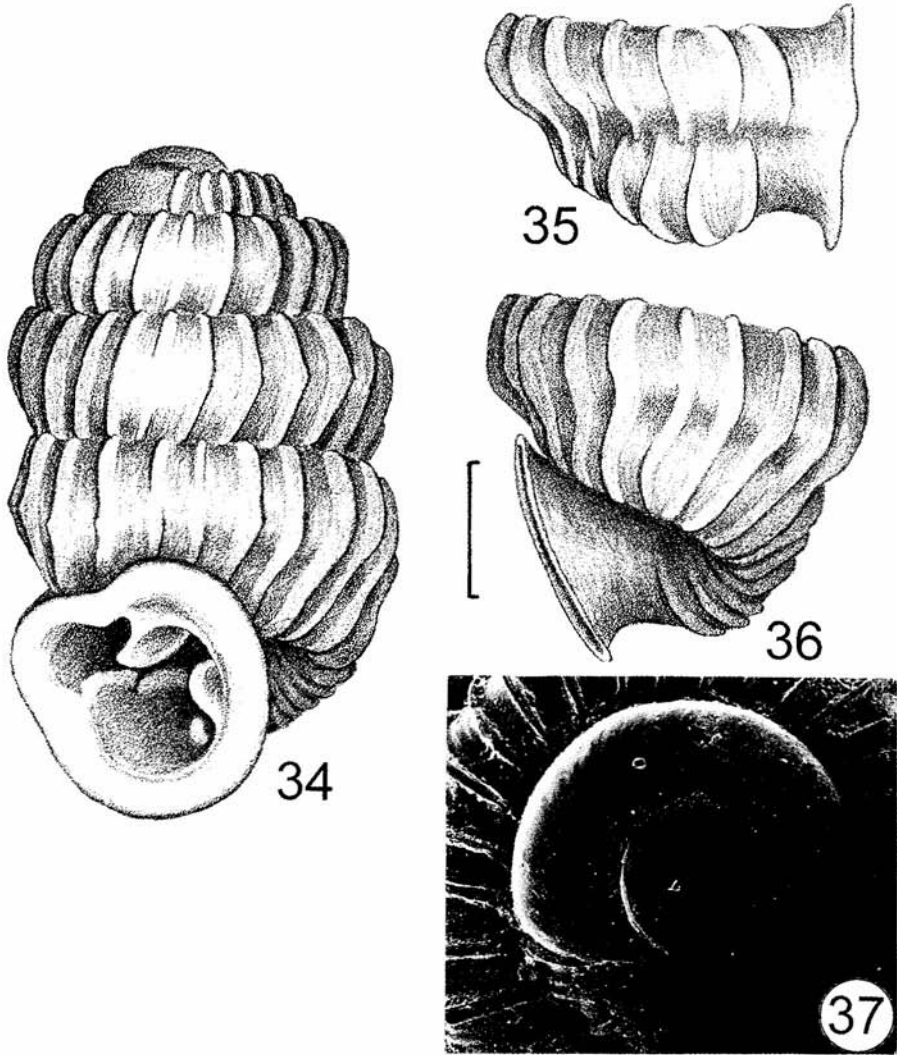
Lectotype: BM 18748; paralectotypes: BM 36656 & ANSP 119468, designated by PILSBRY & COOKE (1918-1920). See also note on *mirabilis*.

MATERIAL EXAMINED

Hawaii: Bird Forest, Hawaii National Park, BM: 184796, 3 r; Hamakua, BM: 19105, 160 r; Honomalino, BM: 47278, 12 r; Keauhou, BM: 39379, 1 r; Mana, BM: 10222 ex 36710, 4 r; 10223 ex 36709, ca. 20 r; 10234 ex 12432, ca. 40 r; 12431, ca. 20 r; 12432, ca. 100 r; 12432, ca. 100 r; 12433, ca. 20 r; 36709, 928 r; 36710, ca. 20 r; 36710, 6 r; 210554, ca. 20 r; Paauhau, BM: 210585, ca. 50 f; 210585, ca. 20 r; Palihooukapapa, BM: 11051, 2 r; 18753, 2 r; 18755, ca. 20 r; 36656, 565 r; 36656, ca. 30 r; 168257, ca. 50 r; 210637, ca. 100 r; Poohohoo, BM: 192068, 22 r; Puu Iki, BM: 172372, 2 r; Puuwaawaa, BM: 10235, 36 r; 10236 ex 50088, 9 r; 47911, 2 r; 49632, 9 r; 49663, 32 r; 49727, 30 r; 49870, 242 r; 49870, 3 r; 49910, 44 r; 49989, 2 r; 50050, 3 r; 50088, 14 r; 50118, 1 r; 53638, 3 r; 192254, 19 r; 192398, 8 r; Puu Waawau, BM: 172317, 10 r; Waikii, BM: 53028, ca. 50 r; 58932, 796 r; Waimea, BM: 10221 ex 36656, 29 r; 12595 ex 12432, 1 r; 18761, 1 r; no exact locality, BM: 18748, lectotype; 18749, 1 r; 18758, 9 r; 18760, 4 r; 18770, 1 r; 36656, 3 paralectotypes r; 49663, 19 r.

DESCRIPTION

Shell ovate; spire convex; apex bluntly rounded. Whorls 5.0-6.0, most often 5.2-5.8, flat to moderately convex, in some shells slightly shouldered; suture shallow to moderately deep. H: 2.31-2.70 mm; B: 1.22-1.46 mm; h: 0.76-0.96 mm; b: 0.76-0.99 mm; bw: 1.26-1.46 mm. H/B: 1.66-1.92; bw/H: 0.51-0.59. Aperture semi-oval; sinulus from poorly marked to distinct. Lip slightly detached, reflexed, wide, well thickened. In aperture 6-7 teeth. Columellar visible in front view; takes mid 1/3-2/3 columellar wall; in top view crescentic or obliquely crescentic, tubercular i.e. both its ends equally, or lower end more, produced towards lip; very thick with thicker edges. Parietal ca. 1/6-1/5 whorl long; set almost in line with angular, their ends nearly overlapping; high and fairly thick with poorly thickened edges; highest within; its



34-37. *L. hawaiiensis* ANCEY, BM 58932, Waikii, Hawaii: 34 - front view, 35 - side view of body whorl, 36 - oblique umbilical view of body whorl. Scale bar 0.5 mm. 37 - protoconch surface, SEM, 112x, BM 36656, Palihoukapapa, Hawaii.

outer part deflected palatalwards. Angular reduced in height and length; as a somewhat elongate tubercle; 1/4-1/3 parietal long. Upper palatal 1/6 whorl long; division into parts distinct: part facing angular very weak, callus-like or absent; part facing parietal low, thick lamellate. Lower palatal recessed deep and displaced upwards;

equal in length to the lamellate part of the upper, but higher and thicker; not or only very slightly overlapping it and divergent; outer end not diffuse. Basal big, callus-like, transversely or somewhat obliquely tubercular, at the level of or somewhat recessed behind columellar. Few shells have a vestigial, deep-set infraparietal. Body whorl profile entirely ribbed; half its height or somewhat higher a straight, narrow groove of gradually decreasing depth, reaching almost above the aperture or only 1/2-2/3 whorl long; on basal wall an indistinct bump. Body whorl suture straight. Umbilicus narrow, open, circular or oval; or almost sealed. Sculpture regular, of 17-26, most often 19-23 ribs on penultimate whorl. Ribs rather fine and high, sharp, on body and penultimate whorls flexuous; 1/6-1/4 interspace thick. Embryonic whorls smooth. Colour light greyish-brown.

DISTRIBUTION

Hawaii; recent and subfossil. Fig. 29.

Lyropupa sparna COOKE et PILSBRY, 1920

Figures 38-42.

Lyropupa sparna COOKE et PILSBRY, in PILSBRY & COOKE 1918-1920: 252-253, pl.22, figs 6, 7, 10, 11.

Type locality: Kalihi, Molokai. Holotype: BM 33627; Paratype: ANSP 108919.

Lyropupa sparna simulifera PILSBRY & COOKE 1918-1920: 253, pl.22, fig.13. Type locality: western ravine of Kamalo, Molokai. Holotype & Paratypes: ANSP 119429.

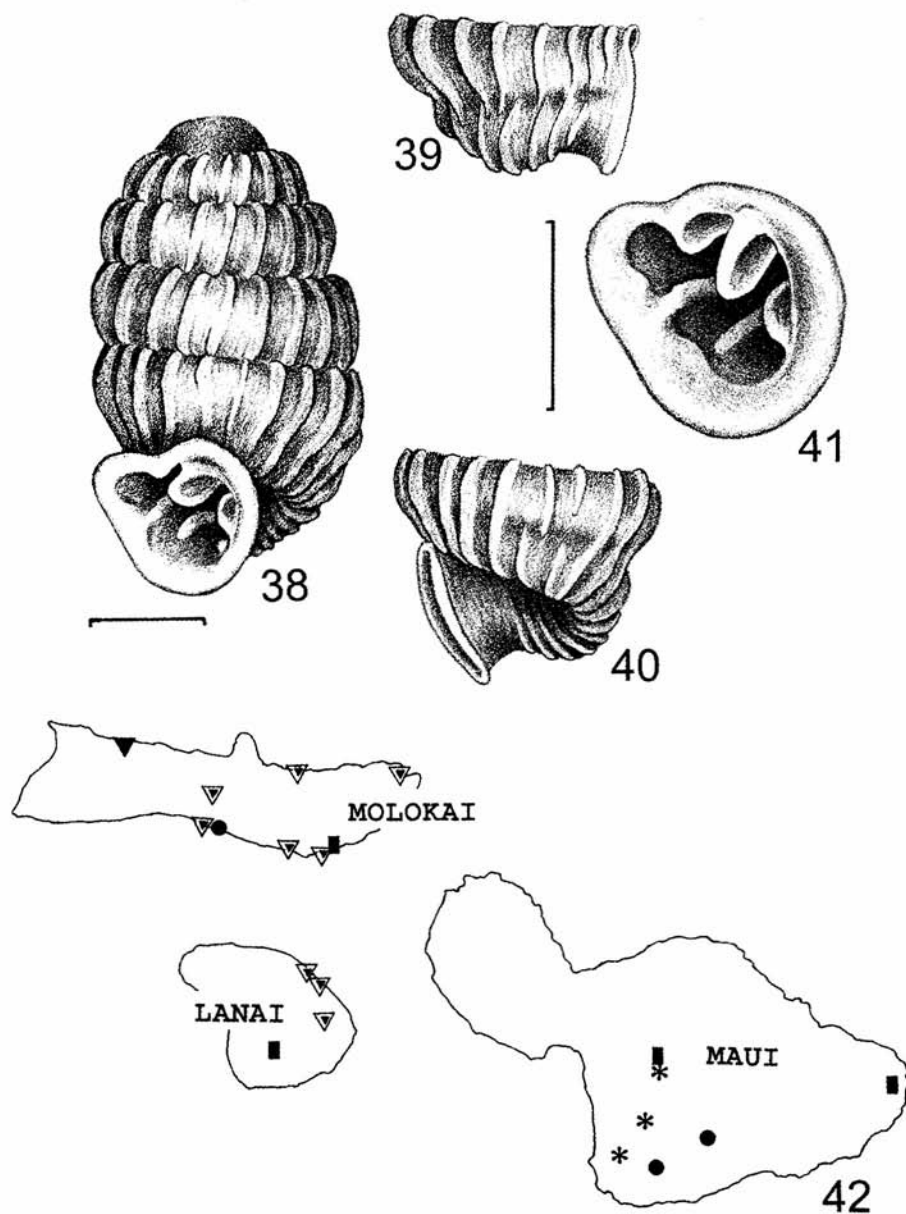
MATERIAL EXAMINED

Lanai: Kaiholena, BM: 34434, 1 r; Mahana, BM: 20084, 1 r; Maunalei, BM: 59897, 45 r; ex 59896, 1 r; no exact locality, BM: 34341, 2 r.

Molokai: Halawa, BM: 76102, 1 r; Kaiehu, BM: 45575, 1 f; Kalamaula, BM: 12410, 2 r; Kalihi, BM: 33627, holotype r of *sparna*; 33627, 1 r; Kamalo, ANSP: 119429, holotype & 6 paratypes r of *sparna simulifera*; Kaunakakai, BM 23864, 1 r; 23881, 1 r; Kawela, BM: 24392, 1 r; Waikolu, BM: 189489, 1 r.

DESCRIPTION

Shell elongatedly oval; spire slightly convex; apex bluntly rounded. Whorls 5.2-5.8, fairly convex; suture rather deep. H: 1.95-2.25 mm; B: 1.09-1.28 mm; h: 0.63-0.77 mm; b: 0.66-0.78 mm; bw: 1.01-1.23 mm; H/B: 1.63-2.00; bw/H: 0.49-0.54. Aperture irregularly pear-shaped; sinulus poorly marked but "pulled out". Lip only slightly detached or forming a short trumpet, reflexed, rather narrow, very thick. In aperture 5-6 teeth. Columellar visible in front view; takes mid 1/2-2/3 columellar wall; in top view obliquely tubercular, with upper end ascending on columella and lower produced towards lip; very thick. Parietal 1/5 whorl long; set almost in line with angular; only their ends overlap; high and fairly thick with thicker edges; highest within; its outer part deflected palatalwards. Angular reduced in length and height: elongatedly tubercular, low thick lamellate, ridge-like or nil; 1/4 parietal long. Upper palatal 1/6 whorl long; division into parts distinct: part facing angular vestigial ridge-



38-41. *L. sparna* COOKE et PILSBRY: 38-40 - BM 59897, Huola, Maunalei, Lanai: 38- front view, 39 - side view of body whorl, 40 - oblique umbilical view of body whorl; scale bar 0.5 mm. 41 - *L. sparna sinulifera* PILSBRY et COOKE, paratype, ANSP 119429, Kamalo, Molokai, oblique view of aperture. Scale bar 0.5 mm. Fig. 42. Distribution of *L. sparna* COOKE et PILSBRY: double triangles - recent, solid triangles - subfossil; and *L. ingrata* n. sp.: solid circles - recent, rectangles - subfossil, asterisks - recent and subfossil.

like; part facing parietal low lamellate. Lower palatal recessed and displaced upwards; starts at 1/2 length of the lamellate part of the upper; equals it in length but is thicker and higher; parallel to the upper; simple; outer end not diffuse. Basal recessed behind columellar; only partly visible or invisible in front view; transversely or obliquely elongatedly tubercular; in some shells absent. Body whorl profile entirely ribbed; at half its height a narrow, deep, straight groove of gradually decreasing depth; 1/2-2/3 whorl long; on basal wall a very weak bump and a flattening between it and lip. Body whorl suture straight. Umbilicus open, narrow, circular or oval. Sculpture regular, of 19-22 ribs on penultimate whorl. Ribs fine, rather sharp, on body whorl somewhat flexuous; 1/5-1/3 interspace thick. Embryonic whorls smooth. Colour light greyish brown.

DISTRIBUTION

Molokai, Lanai; recent and subfossil. Fig. 42.

NOTE

The form described as *sparna sinulifera* differs from typical shells in the following characters: aperture more detached to form a short straight trumpet; angular tooth somewhat more pronounced and upper palatal coming closer to the aperture; basal in most shells absent; angular low lamellate instead of elongatedly tubercular. It is known from Kamalo and Waikolu on Molokai, as recent only.

Lyropupa ingrata n. sp.

Figures 42-45.

TYPE LOCALITY

Keokea, E Maui.

TYPE MATERIAL

Keokea, E Maui: Holotype & ca. 200 paratypes f, BM 52824; 22 paratypes r, BM 59256; Pulehu, E Maui: 123 paratypes f, BM 190936; 22 paratypes f, BM 190982; 10 paratypes f, MNHW ex BM 190936.

OTHER MATERIAL EXAMINED

Lanai: Kaohai, BM: 104043, 1 f.
Maui E: Auwahi, BM: 52481, 2 r; Hana, BM: ex 210270, 1 f; Kula, BM: 47352, 4 r; 76719, 37 r; Ulupalakua, BM: 52761, 1 f; 116741, 2 r; Waiakoa, BM: 104150, 55 r; 164408, 12 f.
Maui W: Mahinahina, BM: 167923, 1 f.
Molokai: Kaluaaha, BM: 33340, 1 f; Kaunakakai, BM: 23881, 1 r.

DIAGNOSE

A sister species to *sparna* from which it differs in the following characters: 1. more cylindrical shape; 2. blunter spire; 3. shouldered whorls each of which is higher; 4. more semi-oval aperture; 5. distinctly flexuous ribs; 6. shallower and shorter

groove on body whorl; 7. smaller columellar taking at most mid 1/3 columellar wall; 8. lower palatal less recessed and less displaced upwards; 9. basal, when present, well visible in front view; 10. wider lip.

DESCRIPTION

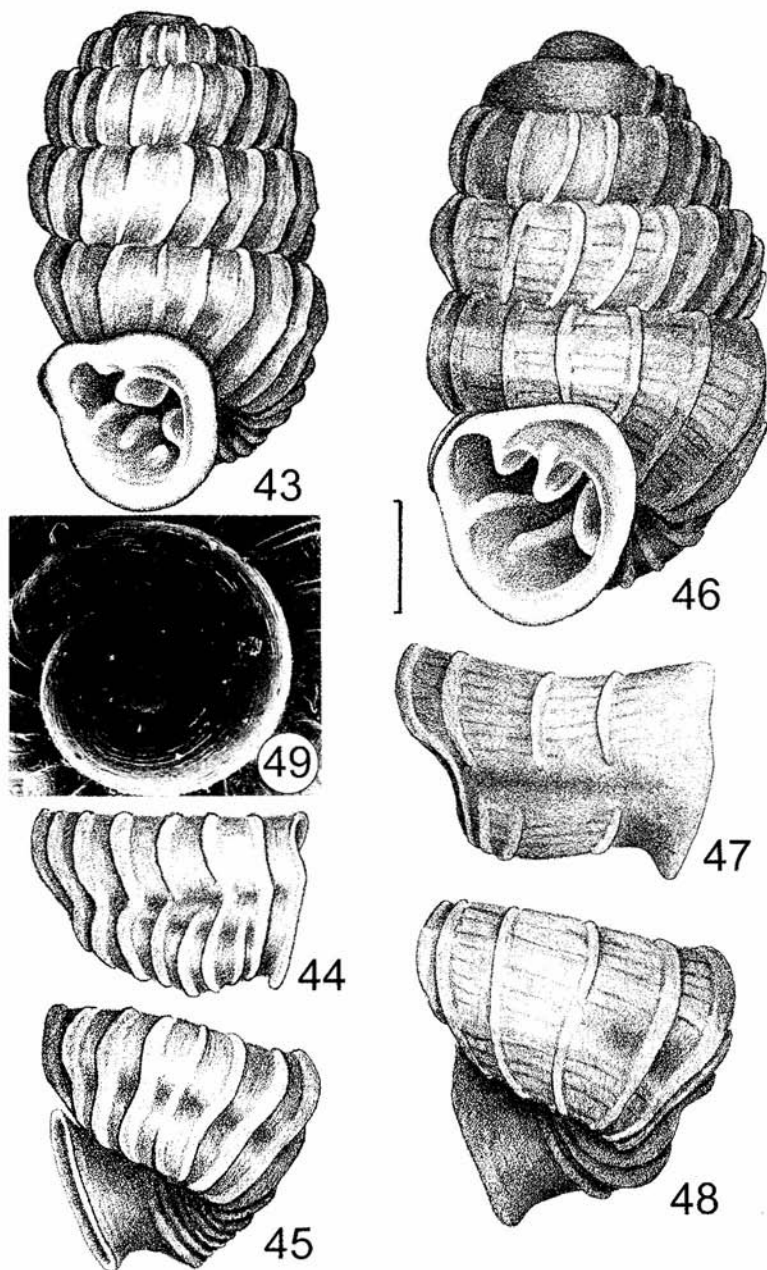
Shell cylindrical to somewhat ovate-cylindrical; spire convex, dome-like, apex broadly rounded. Whorls 4.9-5.9, most often 5.1-5.5 (holotype 5.5), moderately to fairly convex, somewhat shouldered; suture moderately deep to shallow. H: 1.96-2.36 mm (holotype 2.16); B: 1.11-1.25 mm (holotype 1.21); h: 0.68-0.85 mm (holotype 0.76); b: 0.73-0.90 mm (holotype 0.76); bw: 1.11-1.34 mm (holotype 1.18); H/B: 1.65-2.13 (holotype 1.78); bw/H: 0.51-0.62 (holotype 0.55). Aperture semi-oval or rounded triangular; sinus from distinct to poorly marked, but always "pulled out". Lip detached, in most shells forming a short trumpet, reflexed, rather wide and thick. In aperture 6 teeth. Columellar visible in front view; takes mid 1/4-1/3 columellar wall; in top view obliquely elongatedly tubercular, with upper end ascending on columella and lower displaced towards lip; very thick. Parietal 1/5 whorl long; set almost in line with angular, so that only their very ends overlap; high and fairly thick with thicker edges, highest within; outer part deflected palatalwards. Angular reduced in length and height; elongatedly tubercular; 1/4 parietal long. Upper palatal 1/6 whorl long; division into parts distinct: part facing angular vestigial ridge-like; part facing parietal low lamellate. Lower palatal somewhat recessed and displaced upwards; starts at 1/2 length of the lamellate part of the upper; equals it in length, but higher and thicker; parallel to it; outer end not diffuse. Basal not or only slightly recessed behind columellar; visible in front view; simple or obliquely to almost transversely elongatedly tubercular; only rarely vestigial. Very rarely a vestigial infraparietal present. Body whorl profile entirely ribbed, half its height a long, straight, distinct groove of gradually decreasing depth, in most shells reaching above aperture or somewhat further. Below it a much shorter, shallower impression. On base an indistinct bump. Body whorl suture straight or very slightly ascending. Umbilicus oval, narrow, open to almost sealed. Sculpture regular, of 16-23 (holotype 16), most often 18-22 ribs on penultimate whorl. Ribs fine, sharp, distinctly flexuous on the last two whorls, high, 1/6-1/4 interspace thick. Embryonic whorls smooth. Colour dirty light brown or dirty beige, or else just brown.

NAME DERIVATION

Ingratus means "unwelcome". When, being already convinced that I had finished the revision, I discovered the new species, it was anything but welcome.

DISTRIBUTION

Molokai, Lanai, Maui; recent and subfossil. Fig. 42.



43-45. *L. ingrata* n. sp., holotype, BM 58824, Keokca, E Maui: 43 - front view, 44 - side view of body whorl, 45 - oblique umbilical view of body whorl. Figs 46-49. *L. rhabdota* COOKE et PILSBRY, holotype, BM 11040, Pelekunu, Molokai: 46 - front view, 47 - side view of body whorl, 48 - oblique umbilical view of body whorl. Scale bar 0.5 mm; 49 - protoconch surface, SEM, 101x, BM 24871, Pelekunu, Molokai.

The group of *Lyropupa microthauma*

DIAGNOSE

Sinistrous, exceptionally dextrous. Angular not reduced, often slightly deflected palatalwards. Parietal simple, not displaced, at most very slightly deflected palatalwards. Inner end of upper palatal visible without shell destruction or simply in front view. Lower palatal simple, not displaced, in some species divergent from the upper; its outer end often callus-like diffuse. Basal only slightly shifted behind columellar. Microsculpture of interspaces composed of spiral ridges on the background of fine, radial/unordered wrinkles. Embryonic whorls spirally sculptured. Apomorphy: spiral sculpture of embryonic whorls. Sister taxon to the *ovatula* group (synapomorphies: spiral ridges on definitive whorls, periostracal wrinkles in interspaces radially oriented); found on all the main islands except Kauai; 11 species, 9 of them endemic to particular islands.

IDENTIFICATION KEY

1. Lower palatal with outer end callus-like, inner end invisible in oblique view and divergent 2.
- Lower palatal with outer end distinct, inner end visible in oblique view and not divergent 3.
2. Sinulus almost closed 4.
- Sinulus different 5.
3. Columellar not drooping (figs 46-49) *rhabdota*, p. 409.
- Columellar drooping 6.
4. Columellar visible in front view, spire straight or poorly convex (figs 76-80) *microthauma*, p. 426.
- Columellar quite or nearly invisible in front view, spire convex (figs 81-84) *dissimulator* n. sp., p. 428.
5. Sinulus distinct, on body whorl a flattening (figs 73, 74) *thaanumi*, p. 425.
- Sinulus poorly defined, on body whorl 2 convergent impressions (figs 70-72) *striatula*, p. 421.
6. No sinulus, on ribs periostracal crests 7.
- Sinulus present, no crests on ribs 8.

7. Apex truncate (figs 68, 69)
 *truncata*, p. 420.
- Apex bluntly rounded (figs 65, 67)
 *clathratula*, p. 418.
8. Dextrous (figs 56-58)
 *cyrta*, p. 414.
- Sinistrous
 9.
9. Upper palatal with no division into parts (figs 50-53)
 *pluris*, p. 410.
- Upper palatal divided into parts (figs 50-53)
 10.
10. Ribs coarse and sparse (figs 59-65)
 *lanaiensis*, p. 415.
- Ribs fine and densely arranged (figs 53-55)
 *adepts* n. sp., p. 412.

***Lyropupa rhabdota* COOKE et PILSBRY, 1920**

Figures 46-49, 53.

Lyropupa rhabdota COOKE et PILSBRY, in PILSBRY & COOKE 1918-1920: 239-240, pl.20, fig.2. Type locality: Pelekunu, Molokai. Holotype: BM 11040; Paratypes: BM 24871 & ANSP 119456.

MATERIAL EXAMINED

Molokai: Pelekunu, BM: 11040, holotype; 2 lots 24871, 3 paratypes.

DESCRIPTION

Shell sinistrous, regularly ovate; spire convex; apex bluntly rounded. Whorls 5.6-5.8, moderately convex, not shouldered; suture moderately deep. H: 2.46-2.58 mm; B: 1.40-1.48 mm; h: 0.94-1.01 mm; b: 0.87-0.97 mm; bw: 1.40-1.46 mm; H/B: 1.69-1.84; bw/H: 0.56-0.57. Aperture rather elongatedly semi-oval; sinulus poorly defined. Lip not or very slightly detached, reflexed, fairly narrow, thick. In aperture 5 teeth. Columellar visible in front view; takes upper 1/2-2/3 columellar wall; in top view oblique tubercular, with upper end ascending on columella, lower produced towards lip; very thick. Parietal ca. 1/5 whorl long; high and thin with somewhat thicker edges, highest in middle; its outer part not or very slightly deflected palatalwards. Angular; ca. 2/3 parietal in length; high and thin; not or only slightly bent palatalwards. Upper palatal starts 1/4 whorl from lip; no division into parts; lamellate, highest at 1/3 length and somewhat recessed from lip; lip somewhat thickened at this level. Lower palatal starts at ca. 1/3 length of the upper, equal to it in height but somewhat shorter and thicker; parallel; outer end distinct; inner end visible in oblique view. None of the shells has accessory teeth. Body whorl entirely ribbed, save ribs somewhat blurred between the impressions or at the bottom of the impression; a single broad and

shallow or 2 slightly convergent impressions barely indicated and ca. 1/3 whorl long. Body whorl suture straight or very slightly ascending. Umbilicus broad oval to narrow oval, deep, open. Sculpture regular, of 14-16 ribs on penultimate whorl. Ribs coarse, blunt, low, not or very slightly flexuous on body whorl; 1/4 interspace thick. Spiral ridges in interspaces fine, moderately dense, visible under stereomicroscope; on embryonic whorls moderately dense, fine, visible under stereomicroscope. Colour goldish brown, with an indistinct lighter band in the middle of body and penultimate whorls.

DISTRIBUTION

Molokai, known from type locality only: recent. Fig. 53.

Lyropupa pluris PILSBRY et COOKE, 1920

Figures 50-53.

Lyropupa rhabdota pluris PILSBRY & COOKE 1918-1920: 240-241, pl.20, figs 3, 4, 5. Type locality: Kaunakakai, Molokai. Paratype: Kalihi, Molokai, BM 34898.

MATERIAL EXAMINED

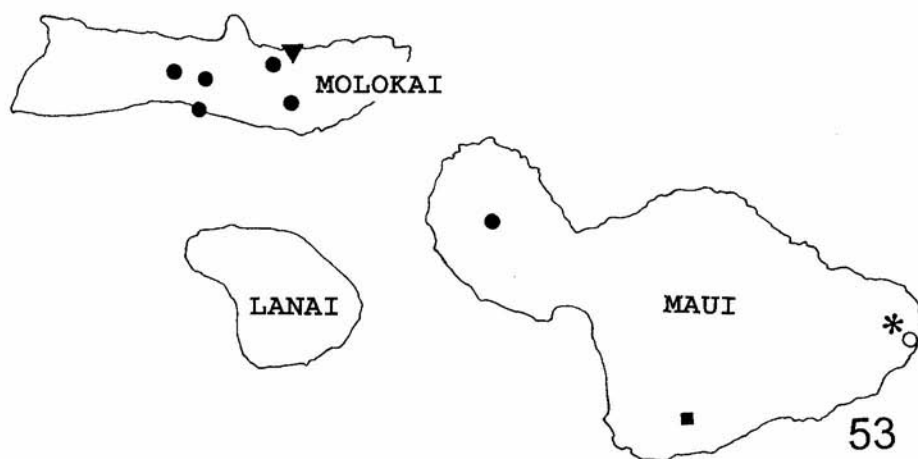
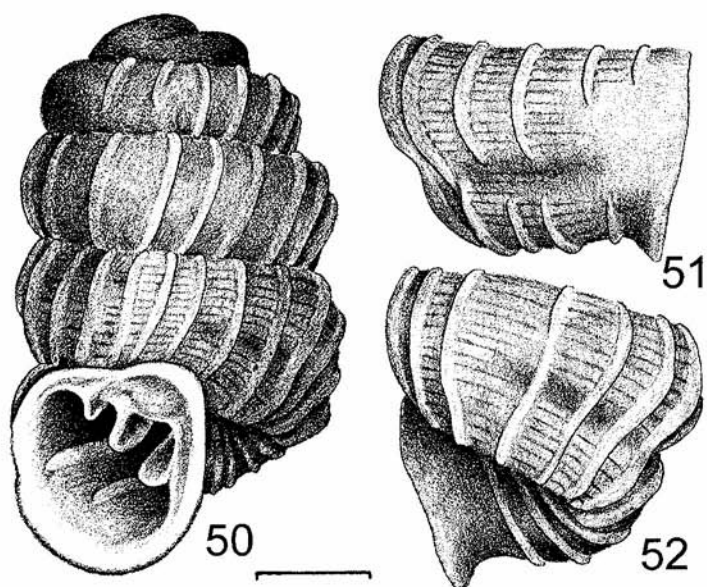
Maui E: Hana, BM: 210104, 3 f; 210269, 14 f.

Maui W: Maunahooma, BM: 21003, 1 r, 21049, 3 r, 21100, 3 r, 168849, 3 r.

Molokai: Kalamaulu, BM: 15922, 3 r; 36564, 5 r; 59127, 5 r; Kalihi, BM: 34898; Kamalo, BM: 34950, 1 r; Poholua, BM: 35182, 4 r; Wailau Pali, BM: 24151, 1 r.

DESCRIPTION

Shell sinistrous; short ovate or short ovate-cylindrical; spire convex; apex broadly rounded: more so in specimens from Molokai, slightly less so in those from Maui. Whorls 4.9-5.7; most often 5.1-5.3, moderately convex; upper shouldered; suture moderately deep. H: 2.25-2.53 mm; B: 1.40-1.51 mm; h: 0.89-1.01 mm; b: 0.84-0.95 mm; bw: 1.30-1.46 mm; H/B: 1.53-1.80; bw/H: 0.53-0.64. Aperture broadly semi-oval; sinulus poorly distinct. Lip not detached, well reflexed, wide, poorly thickened. In aperture 5 teeth. Columellar visible in front view; takes upper 1/2 columellar wall; strongly drooping; in top view oblique tubercular, with upper end ascending on columella, lower produced towards lip; fairly thick. Parietal ca. 1/5 whorl long; high and thin with somewhat thicker edges; highest in middle; straight or almost imperceptibly deflected palatalwards. Angular; ca. 2/3 parietal long; thin and high; not or only slightly deflected palatalwards. Upper palatal terminates 1/4 whorl from lip; no division into parts; lamellate, highest at 1/3 length; somewhat recessed from lip which at that place bears a slight incision. Lower palatal starts at 1/3 length of the upper; parallel to it, somewhat shorter but of equal height and thickness or somewhat thicker; inner end visible in oblique view; outer end distinct. No shell has accessory teeth. Body whorl regularly ribbed, but ribs absent in mid 1/3; with one long impression corresponding to upper palatal and terminating above the aperture, or 2 impressions:



50-52. *L. pluris* PILSBRY et COOKE, BM 36564, Kalamaulu, Molokai: 50 - front view, 51 - side view of body whorl, 52 - oblique umbilical view of body whorl. Scale bar 0.5 mm. 53. Distribution of *L. rhabdota* COOKE et PILSBRY (solid triangle), *L. pluris* PILSBRY et COOKE (solid circles - recent, hollow circles - subfossil), *L. adeps* n. sp. (asterisk) and *L. thaunumi* COOKE et PILSBRY (solid square).

the upper corresponds to the upper palatal, 1/3 height from suture, straight, distinct; lower corresponding to the lower palatal, convergent to the upper impression; after 1/4 whorl they fuse to form a single narrow groove prolonged almost to the point above aperture. Body whorl suture straight. Umbilicus narrow slit-like, sealed or oval, open, deep. Sculpture regular, of 15-17 ribs on penultimate whorl. Ribs rather coarse, blunt, not flexuous, save some on the back of body whorl (flexuous in the groove); ca. 1/6 interspace thick. Spiral ridges in interspaces fairly distinct and densely arranged, visible under stereomicroscope; on embryonic whorls rather densely arranged, fine, visible under stereomicroscope. Colour from light goldish or yellowish brown to chestnut.

DISTRIBUTION

Molokai, W Maui: recent; E Maui: fossil. Fig. 53.

NOTE

The species was originally described as a subspecies of *L. rhabdota*. Phylogenetically, it is closer to *adepts* n. sp., *cyrta* and *lanaiensis* (cf. fig. 147). It differs from the superficially similar *rhabdota* in an array of very constant characters: 1. much blunter spire; 2. shouldered whorls; 3. wider aperture; 4. less thickened but wider and more reflexed lip; 5. thinner and more fragile shell; 6. finer ribs; 7. longer impression on body whorl; 8. lack of even a faintest banding; 9. thinner and strongly drooping columellar; 10. thinner lower palatal; 11. umbilicus often almost sealed or sealed.

Lyropupa adepts n. sp.

Figures 53-55.

TYPE LOCALITY

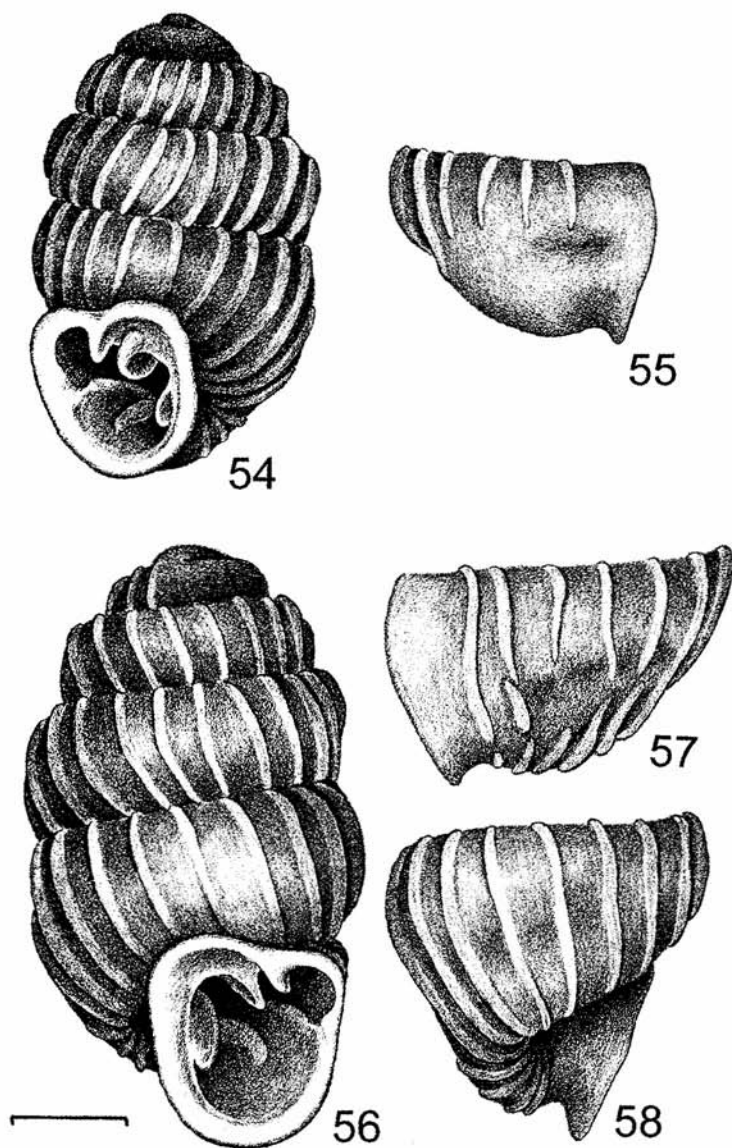
Hana, E Maui.

TYPE MATERIAL

Hana, E Maui: Holotype & 40 paratypes, BM 210270; 15 paratypes, BM 198436; 56 paratypes, BM 190437; 2 paratypes, BM ex 210104; 3 paratypes, MNHW ex BM 210270.

DIAGNOSE

Phylogenetically, it stands closest to *pluris*, *cyrta* and *lanaiensis*, but in appearance is unlike any of them: much smaller and covered with much finer, denser arranged ribs. In its size and ribbing in may resemble *microthauma* from which it differs in the following characters: 1. more tumid shell with much more convex spire (even compared with the tumid form of *microthauma*), 2. much less distinct sinulus, 3. small, tubercular, drooping columellar, 4. outer end of lower palatal not diffuse, 5. inner end of lower palatal not divergent, visible in oblique view, 6. narrower, less reflexed lip, 7. upper palatal reaching lip as a ridge.



54-55. *L. adeps* n. sp., holotype, BM 210270, Hana, E Maui: 54 - front view, 55 - side view of body whorl. Figs 56-58. *L. cyrta* COOKE et PILSBRY, paratype, BM 36707, Mana, Hawaii: 56 - front view, 57 - side view of body whorl, 58 - oblique umbilical view of body whorl. Scale bar 0.5 mm.

DESCRIPTION

Shell sinistrous, tumid oval; spire convex; apex bluntly rounded or somewhat flattened. Whorls 4.6-5.0 (holotype 5.0), moderately convex or convex; suture deep or moderately so. H: 1.96-2.25 mm (holotype 2.01); B: 1.23-1.31 mm (holotype 1.24); h: 0.71-0.86 mm (holotype 0.79); b: 0.73-0.83 mm (holotype 0.75); bw: 1.18-1.36 mm (holotype 1.19). H/B: 1.56-1.76 (holotype 1.63); bw/H: 0.59-0.61 (holotype 0.59). Aperture rather broadly semi-oval; sinulus fairly well marked. Lip not or only slightly detached, somewhat reflexed, narrow, thick. In aperture 5-6 teeth. Columellar visible in front view; takes upper 1/2-2/3 columellar wall; in some shells slightly drooping; in top view oblique tubercular; with upper end ascending on columella and lower produced towards lip; thick. Parietal ca. 1/5 whorl long; high and thin with thicker edges; highest in middle; not deflected. Angular ca. 1/2 parietal long; high and thin; not or very slightly deflected palatalwards. Upper palatal terminates 1/5 whorl from lip; division into parts distinct: part facing angular vestigial, ridge-like; part facing parietal lamellate. Lower palatal starts at ca. 1/3 length of lamellate part of the upper; equals it in height and length, but thicker; parallel to the upper; outer end distinct; inner end visible in oblique view. Some shells have a small tubercular basal situated at the level of columellar. Body whorl profile irregularly ribbed, with no or a blurred and shallow impression at half its height. Body whorl suture straight. Umbilicus narrow oval, slit-like open or nearly sealed. Sculpture somewhat irregular, of densely packed ribs, 21-26 (holotype 22) on penultimate whorl. Ribs rather fine, blunt, not flexuous; 1/3-1/2 interspace thick. Traces of spiral ridges in interspaces rather densely arranged, fine, visible in SEM; on embryonic whorls rather densely arranged, visible in SEM. Colour pale yellowish brown.

NAME DERIVATION

The word means "fat" or "one who is fat". The shell of the new species has a body whorl resembling a pot belly.

DISTRIBUTION

E Maui, type locality only; subfossil. Fig. 53.

***Lyropupa cyrta* COOKE et PILSBRY, 1920**

Figures 56-58, 62.

Lyropupa cyrta COOKE et PILSBRY, in PILSBRY & COOKE 1918-1920: 268, pl.23, figs 9, 10. Type locality: Mana, Hawaii. Holotype: BM 11060; Paratypes: BM 36707.

MATERIAL EXAMINED

Hawaii: Mana, BM: 11060, holotype; 11110, ca. 20; 12439, 19; 36707, 60 paratypes; 210555, 6; Palihooukapapa, BM: 18754, 9; Waimea, BM: 12602 (=12437), 1; 18763, 1; no exact locality, BM: 18757, 16; 18766, 1.

DESCRIPTION

Shell dextrous, oval or elongatedly so; spire poorly convex; apex gently rounded. Whorls 5.1-5.4, poorly convex to flattish; suture shallow. H: 2.50-2.70 mm; B: 1.39-1.46 mm; h: 0.88-0.96 mm; b: 0.82-0.88 mm; bw: 1.51-1.62; H/B: 1.74-1.91; bw/H: 0.56-0.61. Aperture elongatedly semi-oval; sinulus very poorly defined. Lip slightly detached, reflexed, narrow, moderately thick. In aperture 5 teeth. Columellar visible in front view, takes upper 1/2 columellar wall; in most shells drooping; in top view oblique lamellate-tubercular; with upper end ascending on columella and lower produced towards lip; thick. Parietal ca. 1/5 whorl long; high and thin with thicker edges; highest in middle; in some shells its outer part almost imperceptibly deflected palatalwards. Angular ca. 2/3 parietal long; high and thin; not or slightly deflected palatalwards. Upper palatal terminates 1/5 whorl from lip; division into parts distinct: part facing angular absent or nearly so; part facing parietal low lamellate. Lower palatal starts at ca. 1/3 length of the upper; equals it in length and height but is thicker; parallel to the upper; outer end distinct; inner end visible in oblique view. No accessory teeth. Body whorl profile entirely regularly ribbed or ribs broken in the middle; impressions absent or a short, shallow impression corresponding to the upper palatal. Body whorl suture straight. Umbilicus oval, very narrow slit-like open, or sealed. Sculpture regular, of 16-18 ribs on penultimate whorl. Ribs fairly coarse and sharp, not flexuous; 1/5-1/4 interspace thick. Traces of spiral ridges in interspaces fine, rather densely arranged, visible in SEM; on embryonic whorls fine, rather densely arranged, visible in SEM. Colour white or brownish white.

DISTRIBUTION

Hawaii; subfossil. Fig. 62.

***Lyropupa lanaiensis* COOKE, 1920**

Figures 59-65.

Lyropupa rhabdota lanaiensis COOKE, in PILSBRY & COOKE 1918-1920: 241, pl.20, fig.6. Type locality: Lanai, no exact data. Holotype & Paratype: BM 11041; Paratypes: BM 34182 & ANSP 119451.

MATERIAL EXAMINED

Lanai: Mahana, BM: 34216, 1 r; Waiapaa, BM: 20038, 1 r; no exact locality, BM: 11041, holotype & paratype r; 34182, 3 paratypes r; 34138, 7 r; 34165, 2 r; 34208, 1 r; 34250, 1 r; 34268, 1 r; 34286, 6 r; 34523, 2 r; ANSP: 119451, paratype r.

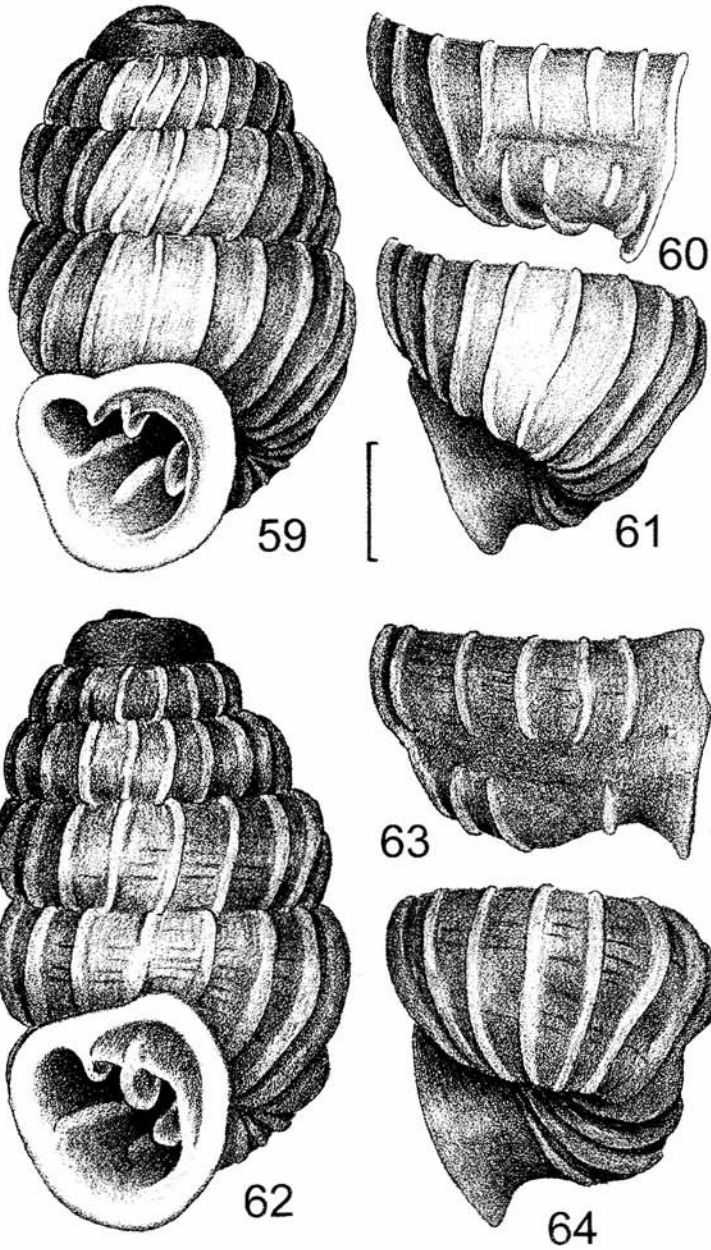
Maui E: Hana, BM: 190435, 9 f.

Maui W: Honokowai, BM: 36775, 4 r.

Hawaii: Honomalino, BM: 47277, 30 f.

DESCRIPTION

Shell sinistrous, ovate with broad base; spire poorly convex, tapered; apex narrowly rounded. Whorls 4.6-5.8, moderately convex, upper somewhat "shoul-



59-64. *L. lanaiensis* COOKE: 59-61: subfossil form, BM 47277, Honomalino, Hawaii: 59 - front view, 60 - side view of body whorl, 61 - oblique umbilical view of body whorl. 62-64: recent form, BM 34165, Lanai, no exact data: 62 - front view, 63 - side view of body whorl; 64 - oblique umbilical view. Scale bar 0.5 mm.

dered"; suture moderately deep. H: 2.23-2.66 mm; B: 1.39-1.54 mm; h: 0.83-1.05 mm; b: 0.78-0.96 mm; bw: 1.24-1.56 mm; H/B: 1.53-1.77; bw/H: 0.53-0.61. Aperture semi-oval; sinulus poorly marked. Lip not or slightly detached, reflexed, rather wide, not much thickened. In aperture 5-6 teeth. Columellar visible to almost invisible in front view; takes upper 1/2-2/3 columellar wall; in most shells drooping; in top view oblique tubercular; with upper end ascending on columella and lower end produced towards lip; moderately thick. Parietal ca. 1/4 whorl long; high and thin with thicker edges; highest in middle; its external part not or almost imperceptibly deflected palatalwards. Angular; ca. 1/2 parietal long; high and thin; not or only slightly deflected palatalwards. Upper palatal terminates 1/5 whorl from lip; division into parts distinct: part facing angular vestigial, ridge-like; part facing parietal low lamellate. Lower palatal starts at ca. 1/2 length of the upper; as long and high as its lamellate part and parallel to it; thicker; outer end distinct; inner end visible in oblique view. Few shells have a vestigial or small tubercular basal parallel to the palatals; recessed behind columellar, but partly visible in front view. Body whorl profile entirely ribbed or ribs interrupted in middle; with 2 convergent impressions of varied length and depth, corresponding to palatals; when long, they may fuse ca. 1/3 whorl from aperture to form a single shallow groove. Body whorl suture straight. Umbilicus narrow, oval, open, deep, or slit-like. Sculpture regular, of 16-20 ribs on penultimate whorl; ribs coarse, rather sharp, not flexuous; 1/6-1/4 interspace thick. Subfossil shells have somewhat finer and denser arranged ribs. Spiral ridges in interspaces fine, rather densely arranged; on embryonic whorls rather densely arranged, fine, both visible in SEM and in some shells under stereomicroscope. Colour goldish brown to light dirty beige, in some shells with a narrow lighter band just above middle of definitive whorls.

DISTRIBUTION

Lanai, W Maui, recent, E Maui, Hawaii, subfossil. Fig. 65.

NOTE

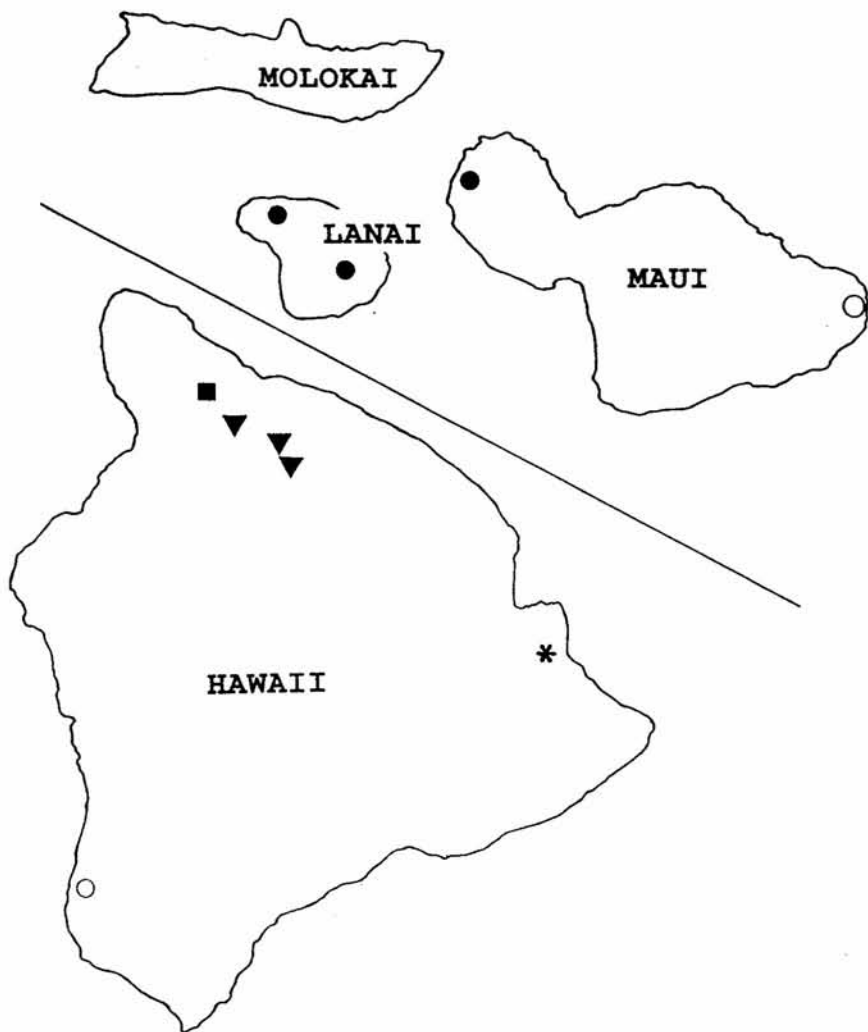
L. lanaiensis was originally described as a subspecies of *L. rhabdota*. Actually, it is closer related to *cyrta*, *pluris* and *adepts* (cf. fig.147), and differs from *cyrta*, which it externally resembles, in the following characters: 1. being sinistrous, 2. usually deeper and longer grooves on body whorl, 3. columellar usually smaller in front view, 4. wider lip, especially parietal callus, 5. upper whorls shouldered, 6. more distinct outer part of upper palatal.

The subfossil form differs from recent shells in a lower number of whorls (4.6-5.2), somewhat finer and denser arranged ribs (17-20) and less pronounced impressions on the body whorl.

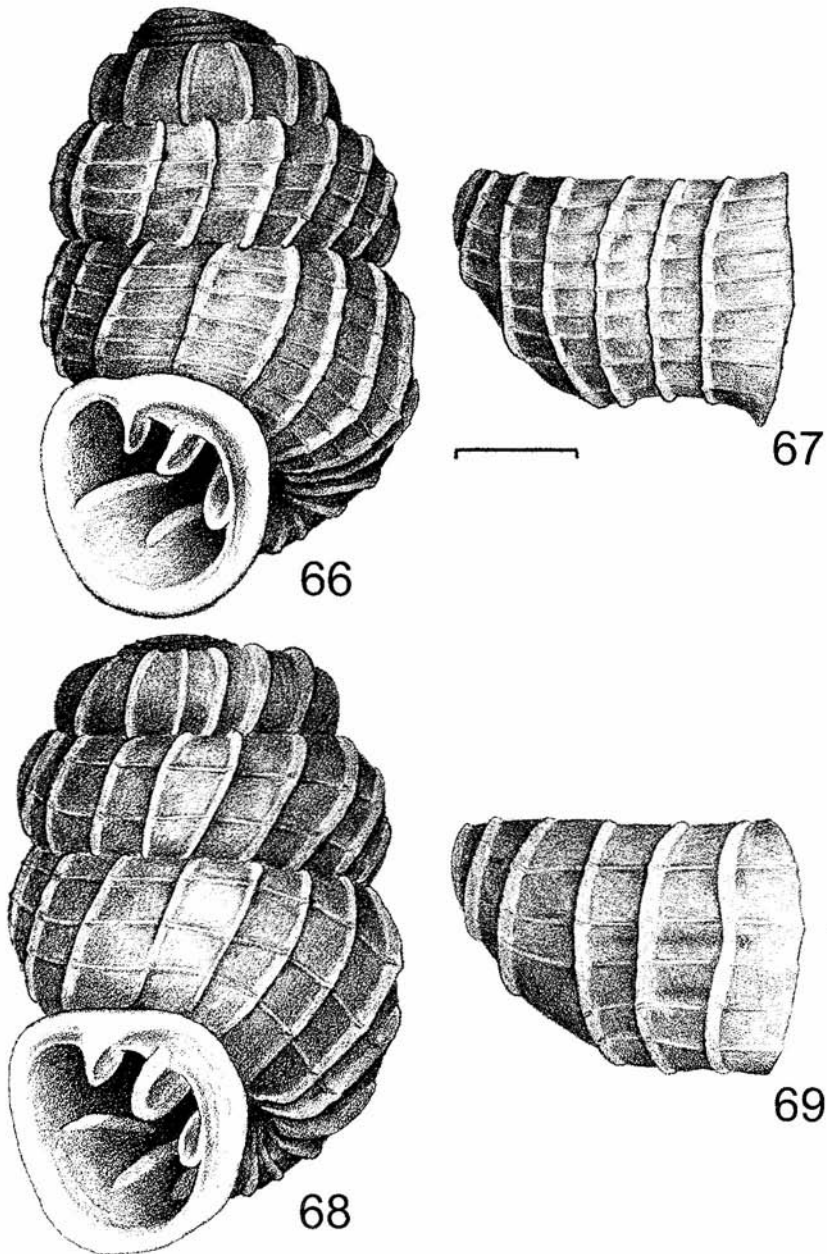
Lyropupa clathratula ANCEY, 1905

Figures 65-67.

Lyropupa clathratula ANCEY 1904-1905: 125, pl. VII, fig. 19. Type locality: Oloa, Hawaii. Lectotype: BM 18742; Paralectotypes: BM 12435 & ANSP 119436, designated by PILSBRY & COOKE (1918-1920). See also note on *mirabilis*.



65. Distribution of *L. cyrta* COOKE et PILSBRY (triangles), *L. lanaiensis* COOKE (solid circles - recent, hollow circles - subfossil), *L. clathratula* ANCEY (asterisk) and *L. truncata* COOKE (square).



66-67. *L. clathratula* ANCEY, paratype, BM 12435, Olaa, Hawaii: 66 - front view, 67 - side view of body whorl. 68-69. *L. truncata* COOKE, holotype, BM 15411, Kohala Mts, Hawaii: 68 - front view, 69 - side view of body whorl. Scale bar 0.5 mm.

MATERIAL EXAMINED

Hawaii: Oloa, BM: 12435, 2 paralectotypes, 12598 (=12435), 1; 18742, lectotype; 18768, 1; 18768, 3.

DESCRIPTION

Shell sinistrous, broad oval with broad base; spire tapered, slightly convex; apex bluntly rounded. Whorls 4.9-5.0, moderately convex; suture moderately deep. H: 2.41-2.43 mm; B: 1.49-1.51 mm; h: 0.99-1.01 mm; b: 0.95 mm; bw: 1.48-1.53 mm; H/B: 1.61-1.62; bw/H: 0.61-0.63. Aperture broadly semi-oval; sinulus virtually none. Lip not detached, almost not reflexed, narrow, thin. In aperture 5-6 teeth. Columellar visible in front view; drooping; takes mid-upper 1/2 columellar wall; in top view oblique tubercular with upper end ascending on columella and lower produced towards lip; very thick. Parietal ca. 1/5 whorl long; high and thin with thicker edges; highest in middle; its outer part very slightly deflected palatalwards. Angular ca. 1/2 parietal long; high and thin; very slightly deflected palatalwards. Upper palatal terminates 1/4 whorl from lip; no division into parts; somewhat recessed from lip; thin and low lamellate, of even height or highest in middle. Lower palatal starts at ca. 1/3 length of the upper; equals it in height and length, but thicker; parallel to the upper; inner end visible in oblique view; outer end distinct. Some shells have basal, elongated, parallel to the palatals; recessed somewhat behind columellar but visible in front view. Body whorl profile entirely ribbed, with no or only traces of impressions corresponding to palatals. Body whorl almost imperceptibly ascending. Umbilicus narrow, oval, open. Sculpture regular but "roguish"; of 16-17 ribs on penultimate whorl; ribs rather fine, not flexuous, with periostracal crests on top, fairly low, somewhat distorted where crossed by periostracal spiral ridges; 1/8-1/6 interspace thick. Spiral ridges in interspaces fairly sparsely arranged, coarse; visible under stereomicroscope; on embryonic whorls dense and rather coarse, visible under stereomicroscope. Colour uniformly darkish brown.

DISTRIBUTION

Hawaii, type locality only: recent. Fig. 65.

***Lyropupa truncata* COOKE, 1908**

Figures 65, 68-69.

Lyropupa truncata COOKE 1908: 211, text figure. Type locality: Kohala Mts., Hawaii. Holotype: BM 15411.

MATERIAL EXAMINED

Hawaii: Kohala Mts, BM: 15411, holotype; 36996, 1.

DESCRIPTION

Shell sinistrous, ovate cylindrical; spire somewhat convex; apex flatly truncate. Whorls 4.8, rather poorly convex but markedly shouldered; suture deep. H: 2.36-2.55

mm; B: 1.55-1.60 mm; h: 0.96-1.10 mm; b: 0.93-0.97 mm; bw: 1.53-1.66 mm; H/B: 1.52-1.59; bw/H: 0.65. Aperture broadly semi-oval; sinulus almost none. Lip not detached, poorly reflexed, narrow, thin. In aperture 6 teeth. Columellar visible in front view; drooping; takes mid/upper 1/2 columellar wall; in top view oblique tubercular; with upper end ascending on columella and lower produced towards lip; very thick. Parietal ca. 1/5 whorl long; high and thin with thicker edges; highest in middle; not deflected. Angular ca. 1/2 parietal long; high and thin; very slightly deflected palatalwards. Upper palatal terminates 1/4 whorl from lip; no division into parts; thin and low lamellate; highest in middle; somewhat recessed from lip. Lower palatal starts at ca. 1/3 length of the upper; equals it in height and length, but thicker; parallel to the upper; inner end visible in oblique view; outer end distinct. Basal elongatedly tubercular; parallel to the palatals; somewhat recessed behind columellar but visible in front view. Body whorl profile entirely ribbed; with traces of impressions corresponding to the palatals (holotype) or no impressions. Body whorl suture straight. Umbilicus very narrow, open or nearly sealed (holotype). Sculpture regular but "roguish"; of 15-16 ribs on penultimate whorl; ribs rather fine, low, with periostracal crests, not flexuous but somewhat distorted where crossed by spiral ridges. Spiral ridges in interspaces sparse and coarse, visible under stereomicroscope; on embryonic whorls dense and rather coarse, visible under stereomicroscope. Colour uniformly darkish chestnut.

DISTRIBUTION

Hawaii, type locality only; recent. Fig. 65.

Lyropupa striatula (PEASE, 1871)

Figures 70-72, 75.

Vertigo striatula PEASE 1871: 461. Type locality: Kalapana, Hawaii. Lectotype: BM 59022, present designation. See note.

Lyropupa magdalenae var. *prisca* ANCEY 1904: 68, pl.5, fig.19. Type locality: Hawaii, no exact data. Lectotype: BM 18746; Paralectotypes: BM 2 lots 18756 & ANSP 119453, designated by PILSBRY & COOKE (1918-1920). See also note on *mirabilis*. **Syn. n.**

Lyropupa rhabdota baldwiniana COOKE, in PILSBRY & COOKE 1918-1920: 241-242, pl.20, figs 7, 8. Type locality: Iao, W Maui. Holotype: BM 11042; Paratypes: BM 38949 & ANSP 119457. **Syn. n.**

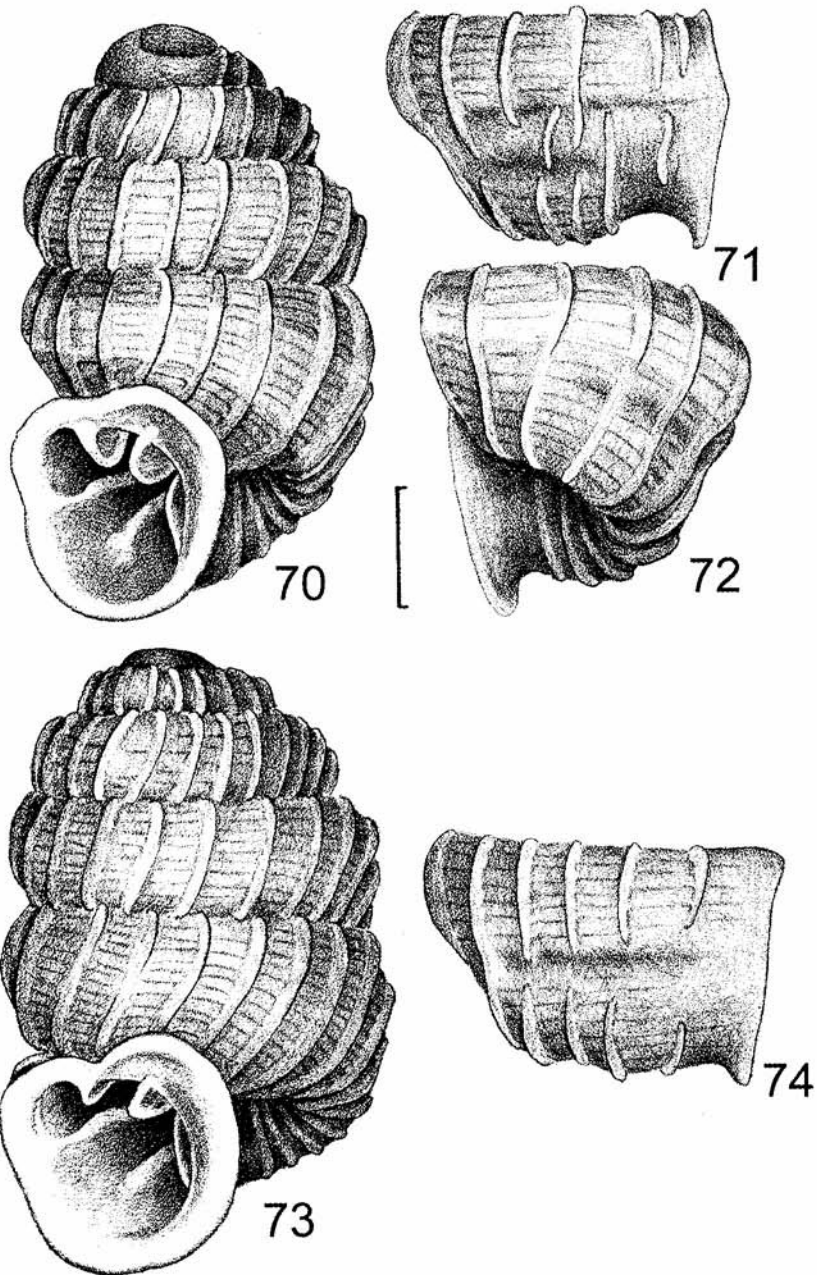
MATERIAL EXAMINED

Lanai: Maunalei, BM: 59896, ca. 1000 f; no exact locality, BM: 36961, 1 r; 45529, 3 f.

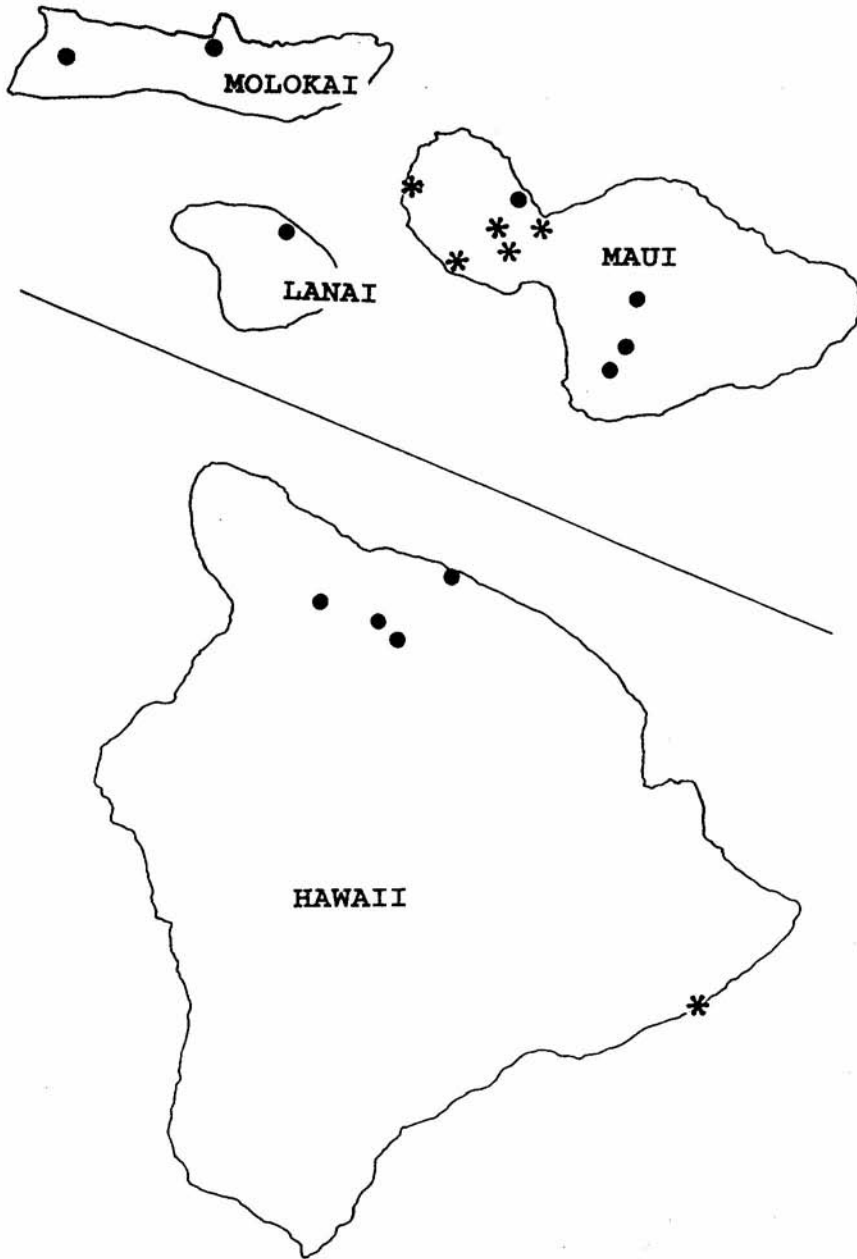
Maui E: Kaunauhane, Ulupalakua, BM: 116740, 49 f; Keokea, BM: 52822: ca. 120 f; Nahiku, BM: 21626, 1 r; Waiakoa, BM: 104149, ca. 50 f.

Maui W: Honokowai, BM: 12429, 23 r; 12596=12429, 2 r; Iao, BM: 11042, holotype r of *rhabdota baldwiniana*; 38949, ca. 65 paratypes r of *rhabdota baldwiniana*; 38950, 4 r; ANSP: 119457, paratype r of *rhabdota baldwiniana*; Olowalu, BM: 59130, 2 r; Waiehu, BM: 115914, 14 f; Waikapu, BM: 38799, 13 r; 76680, 12 r; no exact locality, BM: 59129, 8 r; 59131, 4 r.

Molokai: Kalaupapa, BM: 33394, 5 f; Mauna Loa, BM: 37413, 6 f.



70-72. *L. striatula* (PEASE), BM 12429, Honokowai, W Maui: 70 - front view, 71 - side view of body whorl, 72 - oblique umbilical view of body whorl. Figs 73-74. *L. thaunumi* COOKE et PILSBRY, paratype, BM 36896, Auwahi, E Maui: 73 - front view, 74 - side view of body whorl. Scale bar 0.5 mm.



75. Distribution of *L. striatula* (Pease): asterisks - recent, circles - subfossil.

Hawaii: Kalapana, BM: 59022, lectotype r of *striatula*; Mana, BM: 10214 ex 12430, 6 f; 11044, 2 f; 12430, ca. 1000 f; 12436, ca. 30 f; 36708, ca. 1000 f; 36708, 3 f; 36708, 32 f; 210553, 38 f; Paauihau, BM: 210584, ca. 40 f; Palihooukapapa, BM: 18756, 22 paralectotypes f of *magdalenae prisca*; 18756, 4 paralectotypes f of *magdalenae prisca*; 36655, 3 f; 168256, ca. 20 f; 210636, ca. 40 f; Waimea, BM: 12593 (=12430), 1 f; 18746, lectotype f of *magdalenae prisca*; 18762, 3 f; no exact locality, BM: 18759, 24 f.

DESCRIPTION

Shell sinistrous, oval to broad oval; spire convex, tapered; apex narrowly rounded. Whorls 4.6-5.4, convex and somewhat "shouldered"; suture fairly deep. H: 2.26-2.92 mm; B: 1.43-1.71 mm; h: 0.93-1.15 mm; b: 0.89-1.10 mm; bw: 1.35-1.75 mm; H/B: 1.55-1.82; bw/H: 0.58-0.64. Aperture elongatedly semi-oval; sinus poorly defined. Lip not detached, reflexed, fairly narrow, thin. In aperture 5-6 teeth. Columellar in front view only partly visible or invisible; takes upper 2/3-3/4 columellar wall; in top view almost vertical, somewhat oblique; with upper end ascending on columella and lower produced towards lip; thick lamellate. Parietal 1/5 whorl long; high and thin with thicker edges; highest in middle; its outer part not or almost imperceptibly deflected palatalwards. Angular; ca. 2/3 parietal long; high and thin; not or only slightly deflected palatalwards. Upper palatal ca. 1/4 whorl long; division into parts distinct: part facing angular ridge-like; part facing parietal lamellate. Lower palatal starts at ca. 1/2 length of the upper; is somewhat shorter than its lamellate part, higher and thicker; outer end callus-like; inner end invisible in oblique view and divergent; sometimes not only front end diffuse but the whole outer section callus-like. Most shells have a small but distinct elongatedly tubercular basal, situated somewhat behind columellar; in others basal vestigial or none. Body whorl profile entirely ribbed, but ribs broken in middle; two impressions correspond to the palatals; both impressions convergent, at the back of body whorl they fuse to form a single, poorly marked groove. Body whorl suture straight. Umbilicus nearly circular, deep, open but rather narrow. Sculpture regular; of 16-21, most often 17-19 ribs on penultimate whorl. Ribs coarse, sharp, not flexuous; 1/5-1/4 interspace thick. Spiral ridges in interspaces rather densely arranged, fine, usually visible under stereomicroscope, but in some shells only in SEM; on embryonic whorls densely arranged, fine, visible in SEM. Colour brownish white, with a lighter band ca. 1/4 whorl broad in mid of the last three whorls; some shells unbanded.

DISTRIBUTION

Hawaii; subfossil; Lanai; subfossil; Maui; subfossil and recent. Fig. 75.

NOTE

PILSBRY & COOKE (1918-1920) could not locate PEASE's original specimens. As his description was by no means clear, they suspected *striatula* Pease to be a synonym of *clathratula* Ancey and suspended their judgement "ignoring *V. striatula* as a lost species unless new evidence is found" (PILSBRY & COOKE 1918-1920: 246). In the collection of the Bishop Museum I found a specimen corresponding with a somewhat

misformulated description by PEASE (1871), bearing a red label, with an inscription "*Lyropupa striatula* PSE, Paratype, Kalapana, Hawaii 59022". The label could have been written by [?] C. M. COOKE, the then mollusc curator at the Bishop Museum, after 1920. In the absence of any previous formal designation, I hereby designate the specimen no. 59022, Bishop Museum as lectotype of *Vertigo striatula* PEASE. The above description should be regarded as a re-description of the "lost species".

***Lyropupa thaanumi* COOKE et PILSBRY, 1920**

Figures 53, 73, 74.

Lyropupa thaanumi COOKE & PILSBRY, in PILSBRY & COOKE 1918-1920: 242-243, pl. 20, figs 12, 13.

Type locality: Auwahi, E Maui. Holotype: BM 11043; Paratypes: BM 36896 & ANSP 119452.

MATERIAL EXAMINED

E Maui: Auwahi, BM: 11043, holotype & paratype; 36896, 5 paratypes; 36896, 3.

DESCRIPTION

Shell sinistrous, from very short to fairly long ovate-cylindrical; spire convex, apex bluntly rounded. Whorls 5.0-5.8, rather convex, shouldered; suture moderately deep. H: 2.43-2.76 mm; B: 1.57-1.66 mm; h: 0.93-1.05 mm; b: 0.91-1.01 mm; bw: 1.51-1.59 mm; H/B: 1.48-1.76; bw/H: 0.56-0.68. Aperture rather broadly oval; sinulus distinct. Lip not detached or slightly so, reflexed, rather narrow, thin. In aperture 5-6 teeth. Columellar invisible in front view or nearly so; takes upper 2/3-3/4 columellar wall; in top view vertical, straight, with both ends produced towards lip; moderately thick lamellate; its outer surface flat or nearly so. Parietal 1/5 whorl long; set rather deep; thin and high with somewhat thicker edges; highest in middle; its outer part not or only imperceptibly deflected palatalwards. Angular ca. 2/3 parietal long; high and thin; not or very slightly deflected palatalwards. Upper palatal over 1/4 whorl long; division into parts distinct: part facing angular very low lamellate or ridge-like; part facing parietal rather high lamellate. Lower palatal; starts at ca. 1/3 length of the upper; equal to 2/3 its length; outer end callus-like; inner end invisible in oblique view and divergent, sometimes nodule-like broadened. Some shells have a small, somewhat elongatedly tubercular basal, recessed behind columellar and invisible in front view. Body whorl profile somewhat irregularly ribbed; half its height a shallow, narrow impression ca. 1/2 whorl long. Body whorl suture straight. Umbilicus from round to oval, deep, open. Sculpture regular, of 17-20 ribs on penultimate whorl. Ribs fairly coarse but sharp, on body whorl somewhat flexuous. Spiral ridges in interspaces rather densely arranged, fine, visible under stereomicroscope; on embryonic whorls fine, densely arranged, visible in SEM. Colour: rather dark chestnut brown.

DISTRIBUTION

E Maui, known from type locality only; recent. Fig. 53.

NOTE

L. thaanumi is most similar to *striatula* and may be mistaken for it. It differs in the following characters: 1. broader rounded apex (in *striatula* more tapered); 2. blunter ribs; 3. columellar invisible or only partly visible in front view (in *striatula* often at least partly visible); 4. parietal recessed deeper inside the shell; 5. outer part of upper palatal much more pronounced; 6. lower whorls (i.e. each whorl is lower); 7. on body whorl a flattening instead of 2 convergent impressions (as if a remnant of grooves; in *striatula* 2 impressions present); 8. mid 1/3 of body whorl bare or very weakly ribbed (in *striatula* body whorl entirely ribbed); 9. more distinct sinulus.

***Lyropupa microthauma* ANCEY, 1905**

Figures 76-80.

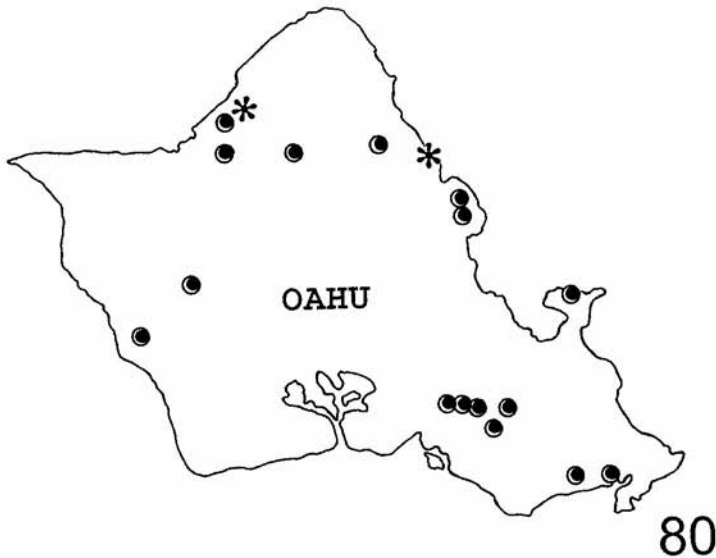
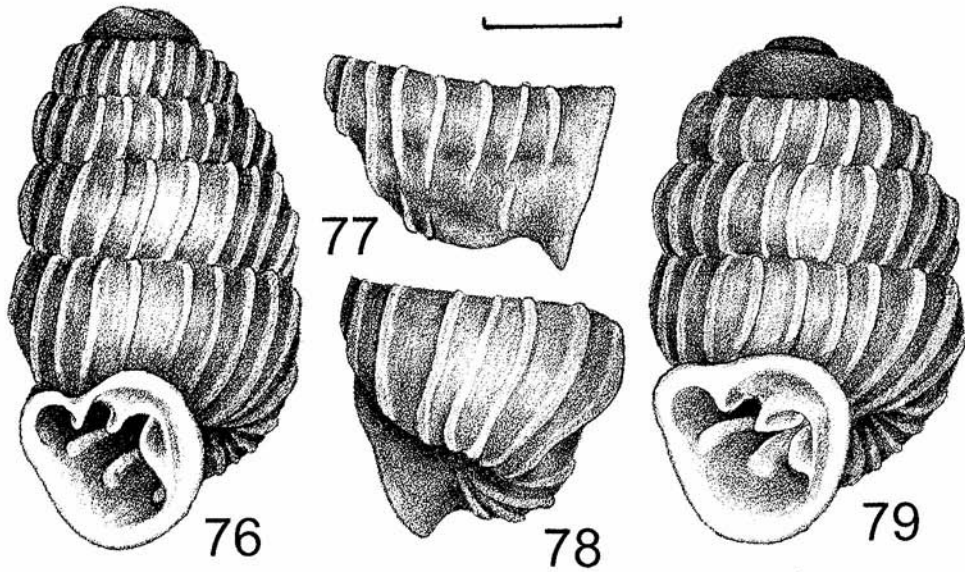
Lyropupa microthauma ANCEY 1904-1905: 126, pl. VII, fig. 20. Type locality: Nuuanu, Oahu. Lectotype: BM 18750; Paralectotype: BM 18751. Present designation.

MATERIAL EXAMINED

Oahu: Glen Ada, BM: 17689, 15 r; Kaaawa, BM: 19422, 1 r; 92175, 1 r; Kaipapau, BM: 11123 ex 21562, 3 r; 19249, 1 r; 21496, 49 r; 21501, 1 r; 21509, 5 r; 21562, 25 r; Kamanaiki, BM: 41162, 1 r; 41896, 1 r; Kapalama, BM: 108680, 1 r; 109294, 1 r; 162288, 2 r; Kawaiiki, BM: 132053, 13 r; 176004, 22 r; 176033, 5 r; Kawailoa, BM: 132127, 1 r; 175972, 28 r; 176170, ca. 20 r; 176186, 3 r; 176214, 2 r; Kawaiui, BM: 176060, 1 r; 176072, 3 r; Keawaawa, BM: 16276, 3 r; 47319, 2 r; 47319, 2 r; Kole Kole Pass, BM: 98984, 6 r; Kualoa Mts., BM: 92697, 1 r; Kuliouou, BM: 54025, 3 r; Lualualei, BM: 9358 ex 113903, 2 r; 9359 ex 116028, 3 r; 9363 ex 116521, 7 r; 9364 ex 116551, 1 r; 113824, 9 r; 113841, 4 r; 116517, 8 r; 116518, 2 r; Moanalua, BM: 20800, 3 r; 168848, 2 r; Nuuanu, BM: 10210 ex 17689, 13 r; 11045, 1 "topotype for *illus.*"; 12405, 1 r; 12406, 1 r; 12407, 1 r; 15344, 1 r; 16377, 1 r; 18750, lectotype r; 18751, paralectotype r; 21732, 2 r; 23653, 1 r; 23822, 1 r; 35514, 6 r; Nuuanu Pali, BM: 168847, 6 r; Opaepala, BM: 59125, 2 r; 134691, 1 r; 165976, 1 r; Pali, BM: 20455, 6 r; Pukaulua, BM: 2408, 3 r; 12605 (=12408), 1 r; 42245, 2 r; 117067, 7 r; 117085, 3 r; 174400, 14 r; ex 93382, 1 r; Punaluu, BM: 45121, 1 f; Tantalus, BM: 12404, 11 r; 12409, 1 r; 12604 (=12404), 1 r; 16137, 2 r; 17409, 1 r; 59126, 2 r; 109263, 1 r; Waialele, BM: 172960, ca. 200 f; no exact locality, BM: 35514, 3 r.

DESCRIPTION

Shell sinistrous, from rather short oval to elongatedly ovate-conical; spire straight to poorly convex; apex broadly rounded or bluntly flattened. Whorls 5.1-6.1, most often 5.3-5.8, flat to moderately convex; suture shallow to moderately deep. H: 1.72-2.14 mm; B: 1.00-1.16 mm; h: 0.59-0.71 mm; b: 0.64-0.73 mm; bw: 0.96-1.16 mm; H/B: 1.55-1.94; bw/H: 0.49-0.59. Aperture rounded triangular; sinulus almost closed. Lip not or only slightly detached, reflexed, narrow, slightly thickened. In aperture 5-6 teeth. Columellar well visible in front view; takes from upper 3/4 to entire columellar wall; in top view thick lamellate or tubercular; crescentic; its long axis almost vertical, with both ends equally, or upper more, produced towards lip. Parietal ca. 1/5 whorl long; high and rather thick with thicker edges; highest in middle; somewhat deflected palatalwards. Angular ca. 1/4 parietal long; rather thick and moderately high; not or slightly deflected palatalwards. Upper palatal terminates 1/4 whorl from



76-80. *L. microthauma* ANCEY: 73-75 - BM 21496, Kaipapau, Oahu: 76 - front view, 77 - side view of body whorl, 78 - oblique umbilical view of body whorl; 79 - BM 17689, Glen Ada, Oahu, front view. Scale bar 0.5 mm. 80 - Distribution: circles - recent, asterisks - subfossil.

lip; no division into parts; lamellate, somewhat recessed from lip and highest at its outer end or reaching lip and of even height. Lower palatal starts at ca. 1/2 length of the upper; somewhat shorter but higher and thicker; inner end invisible in oblique view, divergent; anterior end callus-like or only slightly so. Basal set level with columellar or somewhat recessed; invisible or partly visible in front view; elongatedly tubercular; parallel or convergent to palatals; sometimes absent. Body whorl profile entirely ribbed or ribs blurred on its lower half; no or two shallow impressions corresponding to the palatals. Body whorl suture straight. Umbilicus from narrow circular to oval, deep, open or nearly completely sealed. Sculpture fine, from regular to somewhat irregular; of 19-27, most often 21-26 ribs on penultimate whorl. Ribs fine, low, blunt, not flexuous; 1/4-1/2 interspace thick. Spiral ridges in interspaces rather densely arranged, indistinct, fine, visible in SEM; on embryonic shell moderately densely arranged and fairly coarse, visible in SEM. Colour goldish brown.

DISTRIBUTION

Oahu; recent and subfossil. Fig. 80.

NOTE

A somewhat different population lives in Glen Ada (BM 17689). It differs from typical specimens in more tumid shell; wider lip; shorter columellar occupying only mid 1/3-2/3 columellar wall and having its upper end produced towards lip; more distinct impressions on body whorl.

Lyropupa dissimulator n. sp.

Figures 81-84.

TYPE LOCALITY

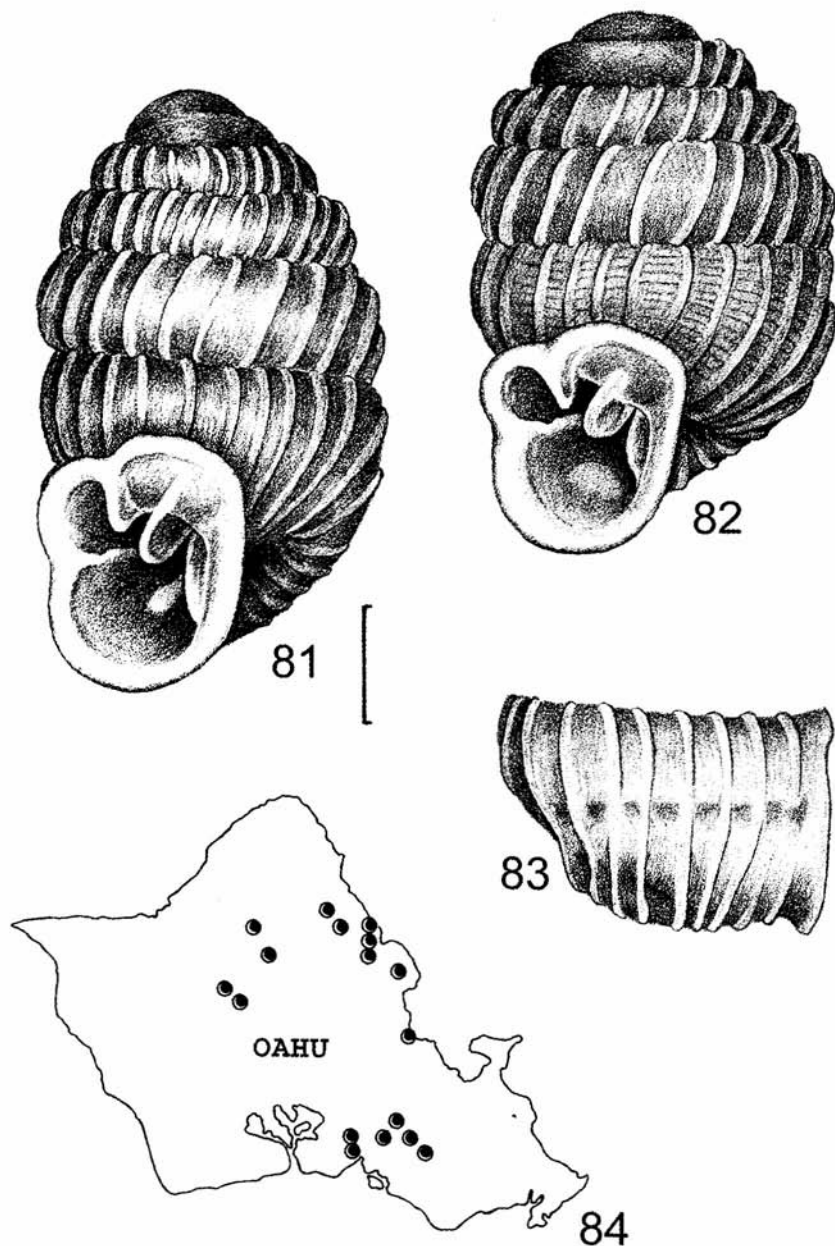
Nuuanu, Oahu.

TYPE MATERIAL

Nuuanu, Oahu: Holotype & 10 paratypes, BM ex 16376; 25 paratypes, BM 12391; 6 paratypes, MNHW ex BM 12391; 3 paratypes, BM 12392; 13 paratypes, BM 12395; 4 paratypes, BM 12397; 3 paratypes, BM 16483; 1 paratype, BM 34827; 8 paratypes, BM ex 12396; Kaipapau, Oahu: 39 paratypes, BM 21494; 34 paratypes, BM 21510; 58 paratypes, BM 21563; Kamaikai, Oahu: 1 paratype, BM ex 41849, Kawaiiki, Oahu: 3 paratypes, BM ex 176003.

OTHER MATERIAL EXAMINED

Oahu: Kahaluu, BM: 41297, 1; Kahana, BM: 99060, 1; Kahauiki, BM: 46193, 1; Kaipapau, BM: 19248, 2; 19888, 6; 21495, 9; 21502, 1; Kalihi, BM: 19973, 1; Kaliuwaa, BM: 19232, 3; 19329, 3; 19358, 12; Kamaikai, BM: 162363, 1; ex 44033, 1; Kawaiiki, BM: 132052, 3; Kualoa Mts, BM: 92253, 1; 92272, 1; Moanalua, BM: 42141, 1; 49168, 2; 101117, 2; 134782, 1; Ohuimano, BM: 41073, 1; Peahinaia, BM: 100735, 1; Poamoho, BM: 165908, 3; Punaluu, BM: 10233, 6; Puu Piei, BM: 93541, 1; Tantalus, BM: 15907, 2; 109262, 1; Wahiawa, BM: 59123, 1.



81-84. *L. dissimulata* n. sp.: 81-82 - holotype, BM ex 16376, Nuuanu, Oahu: 81 - front view, 82 - side view of body whorl; 83 - paratype, BM ex 41849, Kamaikai, Oahu, front view. Scale bar 0.5 mm.
84 - Distribution.

DIAGNOSE

Though not closely related, at first glance it may resemble *lyrata*. It differs in the following characters: 1. embryonic whorls under stereomicroscope smooth instead of wrinkled granulose (in SEM spirally striated); 2. finer and denser packed ribs; 3. more tumid shell with less convex whorls; 4. more elongated aperture with broader reflexed lip, especially parietal callus more expanded; 5. parietal much less recessed; 6. lower palatal simple, diffuse only at its outer end, but neither split nor constricted. Actually sister species to *microthauma* from which, however, it differs at first glance in a much bigger size, convex spire and much more tumid shape.

DESCRIPTION

Shell sinistrous, ideally oval to almost spherical; spire broadly convex, apex bluntly rounded. Whorls 5.0-6.1, most often 5.3-5.7 (holotype 6.0), rather flat; suture fairly shallow. H: 2.23-2.59 mm (holotype 2.51); B: 1.33-1.55 mm (holotype 1.45); h: 0.88-1.08 mm (holotype 1.03); b: 0.78-0.99 mm (holotype 0.85); bw: 1.28-1.44 mm (holotype 1.34). H/B: 1.53-1.73 (holotype 1.71); bw/H: 0.55-0.60 (holotype 0.53). Aperture elongatedly semi-oval; sinulus almost closed. Lip not detached, reflexed, wide but not visibly thickened. In aperture 5-6 teeth. Columellar in front view quite invisible or nearly so; takes upper 3/4 to entire columellar wall; in oblique view like a fairly thick lamellate concave "ear", set on columella; crescentic, both ends equally, or lower end more, produced towards lip. Parietal well over 1/5 whorl long; high and rather thick with thicker edges; highest in middle; not deflected. Angular high and rather thick; over 1/2 parietal long; somewhat deflected palatalwards. Upper palatal terminates 1/4 whorl from lip; division into parts none or very indistinct i.e. tooth evenly lamellate or its part facing angular slightly lower; somewhat recessed from lip which at that place is incised. Lower palatal starts at ca. 1/2 length of the upper; outer end callus-like; inner end invisible in oblique view and divergent. Usually no accessory teeth; sometimes a very small, tubercular basal, invisible in front view, recessed behind columellar, elongate, parallel or convergent to the palatals. Body whorl profile with its lower part devoid of ribs or irregularly ribbed; at half its height a very shallow longer impression corresponding to the upper palatal, a somewhat deeper and shorter impression corresponds to the lower palatal and delimits a slight blunt basal crest. Body whorl suture straight or very slightly ascending. Umbilicus almost circular, open, deep, with whorls visible inside. Sculpture regular, of 19-29, most often 21-26 (holotype 27) ribs on penultimate whorl. Ribs blunt and fairly coarse; not flexuous; roughly 1/2 interspace thick. Spiral ridges in interspaces indistinct, fine, rather densely arranged, visible in SEM or under stereomicroscope; on embryonic whorls densely arranged, fine, indistinct, visible in SEM. Colour from light honey brown to deep chestnut, tinged with red.

NAME DERIVATION

The word means dissembler, one who puts on the appearance of someone else. The species has succeeded in pretending to be *lyrata* for quite a long time.

DISTRIBUTION

Oahu; recent. Fig. 84.

NOTE

A slightly different form occurs in Kaipapau, Kamañaki and Kawaiiki. In those specimens the impressions on body whorl are almost absent, the columellar is less oblique i.e. well visible in front view, the shell is lighter and very short oval; the umbilicus is narrower and in some shells completely sealed; the spiral sculpture is more pronounced and most shells have basal.

The group of *Lyropupa ovatula*

DIAGNOSE

Dextrous, exceptionally sinistrous. Angular and upper palatal long or very long. Parietal not displaced, simple or with broadened and flattened free margin. Inner part of upper palatal often invisible without shell destruction. Lower palatal split partly or wholly. Basal in most species shifted very deep behind columellar. Ribs often irregular, incomplete, grouped in pairs or triplets. Microsculpture of interspaces composed of spiral ridges on the background of irregularly/radial fine wrinkles. Embryonic whorls wrinkled-granulose. Apomorphy: split lower palatal. A sister taxon to the *microthauma* group (synapomorphies: radially ordered wrinkles in interspaces, spiral ridges on definitive whorls); 10 species, half of which are found on more than one main island.

IDENTIFICATION KEY

1. Lower palatal entire or incompletely but distinctly united; if split, shell ovate and basal absent 2.
- Lower palatal completely split or its parts connected by a vestigial callus bridge 3.
2. Basal absent, shell ovate (figs 85-90) *lyrata*, p. 432.
- Basal present, shell ovate-cylindrical or cylindrical (figs 91-97) *kahoolavensis*, p. 437.
3. Upper palatal short, its inner end with inner part of lower palatal and basal visible in front view, on body whorl a very long deep groove terminating above aperture (figs 98-101) *hybrida* n. sp., p. 441.
- Upper palatal so long, that its inner end with inner part of lower palatal and basal invisible in front view; no groove on body whorl exceeds 1/3 whorl 4.

4. Parietal simple (figs 103-109) *costata*, p. 444.
- Parietal free margin broadened and flattened 5.
5. Upper palatal-inner part of lower palatal-basal form an arc, impressions on body whorl shallow or absent 6.
- Upper palatal-inner part of lower palatal-basal not arcuate, impressions on body whorl distinct 7.
6. Inner part of lower palatal partly or wholly accreted to upper palatal (figs 110-113) *cubana*, p. 449.
- Inner part of lower palatal free (figs 114-117) *captiosa* n. sp., p. 452.
7. On body whorl a distinct crescentic basidorsal hump 8.
- On body whorl no such hump 9.
8. Shell ovate, narrowed equally on both ends, ribs very fine and irregular (figs 134-139) *micra*, p. 459.
- Shell tumid ovate with broader base, ribs rather coarse and regular (figs 140-145) *lualualeiensis* n. sp., p. 464.
9. Inner part of lower palatal visible without shell destruction (figs 125-133) *ovatula*, p. 456.
- Inner part of lower palatal invisible without shell destruction (figs 120-124) *plagiptyx*, p. 454.

Lyropupa lyrata (GOULD, 1843)

Figures 85-90.

Pupa lyrata GOULD 1843: 139. Type locality: Oahu [originally stated as "Hawaiian Islands", the exact island later established by JOHNSON 1964]. Lectotype: MCZ 169233; Paralectotype: MCZ 169234, designated by PILSBRY & COOKE (1918-1920). See also note on *mirabilis*.

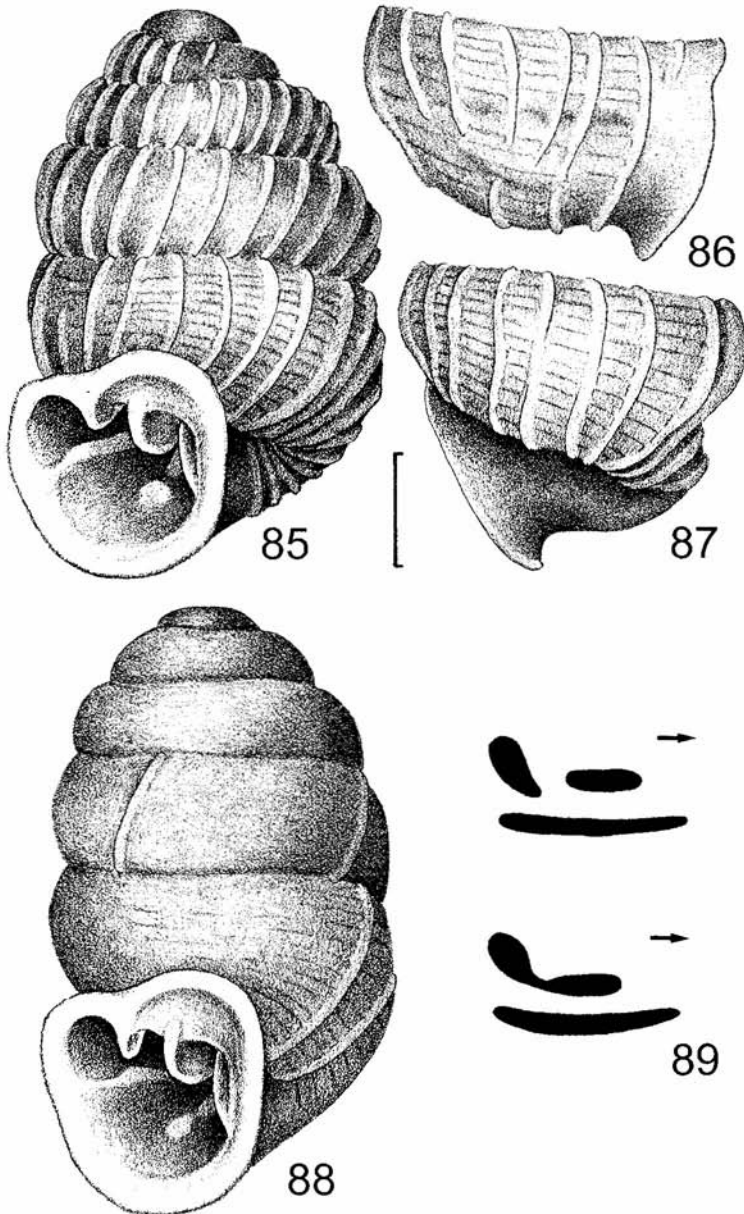
Pupa magdalenae ANCEY 1890: 716. Type locality [stated later in ANCEY 1904-1905]: Palama, Oahu. Lectotype: BM 18744; Paralectotypes: BM 18745 & ANSP 119455, designated by PILSBRY & COOKE (1918-1920). See also note on *mirabilis*.

Lyropupa carbonaria ANCEY 1904-1905: 125, pl.7, fig.21. Type locality: Nuuanu, Oahu. Lectotype & Paralectotypes: BM 18752, designated by PILSBRY & COOKE (1918-1920). See also note on *mirabilis*.

Lyropupa lyrata gouldi PILSBRY & COOKE 1918-1920: 235, pl.19, figs 8, 9. Type locality: Kamaikai, Oahu. Paratypes: BM 1118.

Lyropupa lyrata uncifera COOKE et PILSBRY, in PILSBRY & COOKE 1918-1920: 236-237, pl.19, figs 12, 13. Type locality: 1.5 miles W of Kahuku, Oahu. Paratypes: BM 33449.

Lyropupa lyrata fossilis COOKE et PILSBRY, in PILSBRY & COOKE 1918-1920: 237-238, pl.19, figs 7, 11. Type locality: Manoa, Oahu. Holotype: BM 11039; Paratypes BM 45279 & ANSP 119462.



85-89. *L. lyrata* (GOULD): 85-87 - BM 43934, Pali Road, Oahu: 85 - front view, 86 - side view of body whorl, 87 - oblique umbilical view of body whorl; 88 - BM 46282, Palolo, Oahu, front view. Scale bar 0.5 mm. 89 - top view of palatals of two specimens, columellar wall removed, diagrammatic, arrow indicates aperture.

MATERIAL EXAMINED

Kauai: Haena, BM: 37535, 9 f; 52066, 16 f; 77956, 7 f; 77970, 1 f; 78011, 8 f; 93811, ca. 50 f; 118914, 1 f; 118928, 15 f; 167632, 2 f; 168345, 13 f; 168346, 1 f; 184346, 1 f; 184350, ca. 50 f; 190229, 3 f; 190755, ca. 30 f; 190756, ca. 30 f; 190757, ca. 200 f; 212080, 1 f; Hanalei, BM: 180554, 1 f; Kalalau, BM: 79945, 1 f; Kalihikai, BM: 77888, 1 f; 77902, 4 f; 77924, 3 f; 77934, ca. 30 f; 100240, 1 f; 118651, 1 f; 190489, ca. 50 f; 190590, 8 f; 210149, 2 f; Kalihiwai, BM: 77864, ca. 50 f; Kapaa, BM: 59020, 8 r; Limahuli, BM: 11038, 1 f; 15680, 2 f; 17069, 5 f; 17069, 1 f; 17069, ca. 30 f; 77823, 8 f; 93747, ca. 30 f; 118828, 4 f; 118863, 1 f; 124173, 2 f; 124201, ca. 20 f; 124300, 1 f; 124347, ca. 30 f; 167977, 1 f; 168369, 3 f; 184301, ca. 50 f; 184324, 27 f; Waipa, BM: 86287, 25 f; 86287, 5 f; 86288, 6 f; 88433, 8 f; 124403, ca. 50 f; 124539, 11 f; Waipaa, BM: 100282, 5 f; 100298, 19 f; 100298, ca. 30 f;

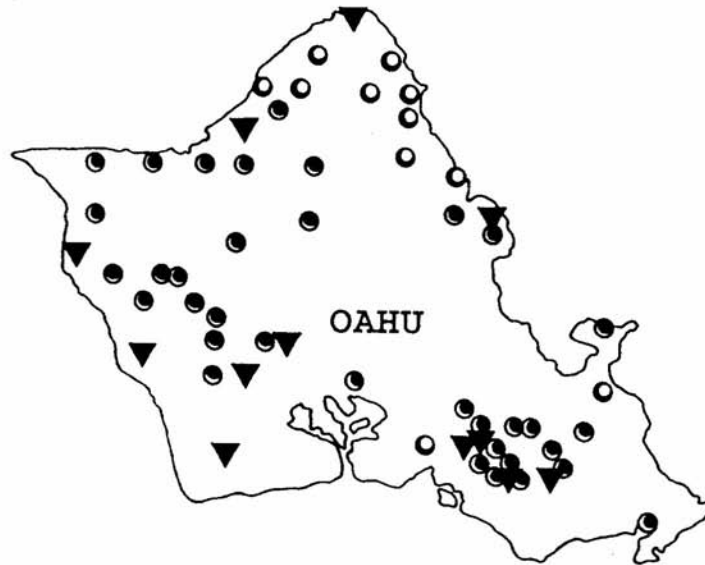
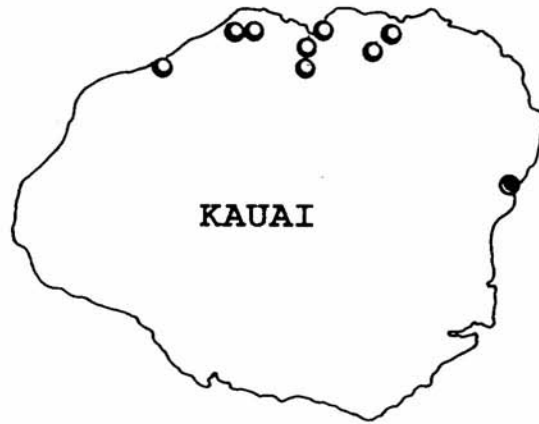
Oahu: Ekahanui, BM: 9369 ex 125873, 2 r; 125688, 2 r; 177324, 14 r; 177344, 13 f; 177577, 1 r; 177594, 2 r; 177618, 6 r; 183916, 37 r; 211451, 6 r; 211529, ca. 60 r; 211696, 4 r; Glen Ada, BM: 15310, 3 r; 15317, 3 r; 16588, ca. 50 r; 17688, 29 r; 41931, 32 r; Green Pk., BM: 59495, ca. 20 r; 59497, 3 r; 59545, 22 r; 105843, 1 r; 106053, 1 r; 106102, 13 r; Haleanau, BM: 163176, 1 r; Halona, BM: 113155, 2 r; 113174, 2 r; 113234, 1 r; 113252, 3 r; 173178, ca. 50 r; 173215, 5 r; Helemano, BM: 22135, 1 r; 22687, 8 r; Hiu, BM: 117630, 1 r; 117630, 1 r; 117639, 4 r; Huliwai, BM: 9384 ex 133642, 2 r; 133643, 3 r; ex 133642, 1 r; Kaaawa, BM: 90399, 4 r; 90429, 16 r; 90952, 23 f; 91025, 5 f; 91039, 2 r; 91065, 1 r; 91413, 2 r; 91511, 1 r; 91581, 7 r; 92174, 15 r; Kaaikukai, BM: 126743, ca. 30 r; 127895, 1 r; 165247, 4 f; 176241, ca. 30 f; 176244, ca. 30 f; 176282, 15 f; 176351, ca. 20 f; 176887, ca. 50 f; 176943, 1 f; 177004, 24 f; 177362, 23 r; 177383, 15 r; 177435, 19 r; 182974, 21 r; 210696, 1 f; Kahana, BM: 92091, 2 r; Kahuku, BM: 33449, 5 paratypes f of *lyrata uncifera*; 33449, 13 paratypes f of *lyrata uncifera*; 60061, ca. 300 f; 60061, ca. 100 f; 60062, 4 f; 77317, 5 f; Kahuku Pt., BM: 210203, ca. 30 r; 210329, 3 f; 210363, 8 f; Kailua, 52597, 1 f; 77639, 2 f; Kaipapau, BM: 33522, 25 f; 44540, 3 f; 172873, ca. 30 f; 172874, 1 f; Kalena E, BM: 113303, 41 r; Kalihi, BM: 22118, 4 r; 45758, 3 r; 45766, 20 r; 45791, ca. 50 r; 45808, 4 r; 45815, ca. 50 r; 45815, 1 r; 45816, 2 r; 45964, 4 r; 45973, 5 r; 90592, 16 r; 90612, 7 r; 101116, 88 r; Kaliouou, BM: 54026, 11 r; Kamaikai, BM: 1188, 2 paratypes r of *lyrata gouldi*; 41849, 22 r; 41895, ca. 40 r; 41895, 5 r; 42152, 5 r; 43678, ca. 60 r; 43678, 38 r; 43678, 97 r; 43678, 2 r; 43678, 2 r; 43687, 1 r; 43754, ca. 30 r; 43755, 6 r; 44033, 19 r; 101115, 1 r; 162362, 11 f; 215555, ca. 20 r; Kamananui, BM: 9355 ex 112702, 1 r; 112524, 9 r; 112543, 1 r; 112623, 7 r; Kanehoa, BM: 17750, 3 r; 37084, 1 r; 37109, 2 r; Kanewai, BM: 117808, 1 r; 117824, 3 r; 117825, 8 r; Kapalama, BM: 12377, 2 r; 12403, 9 r; 12607 (=12403), 1 r; 108679, 12 f; 109290, 1 r; 109292, ca. 50 r; 109293, 1 r; 162286, 15 r; 162287, 8 r; 170107, 60 r; 170186, ca. 100 r; Kaumokuiki, BM: 174450, ca. 30 f; Kawaiiki, BM: 176003, ca. 50 r; 176005, 24 r; Kawaiiloa, BM: 44578, 10 f; 52638, 3 f; 132110, 1 r; 173113, ca. 20 f; 173142, 2 f; 175971, 1 f; 176169, 10 r; 176185, 5 r; 176213, 2 f; Keaau, BM: 9389 ex 174351, 2 r; 107943, 32 r; 175877; 4 f; Keawaawa, BM: 47318, 3 r; 54252, 1 r; Keekee Gulch, BM: 129130, 1 r; Kole Kole Pass, BM: 98983, 11 r; Konahuanui, BM: 12376, 1 r; Kualoa Mts, BM: 92260, 1 r; 92696, 1 r; 97870, 3 r; Kupehau, BM: 59396, 4 r; 59445, ca. 30 r; 128633, 5 r; ex 59447, 3 r; Laie, BM: 44670, ca. 50 f; 180978, 6 f; 189554, ca. 50 f; 189555, 2 f; Leilehua, BM: 16031, 1 r; 90523, 1 r; Luakaha, BM: 12384, ca. 100 r; 12591 (=12354), 3 r; 16403, 7 r; Lualualei, BM: 9360 ex 116267, 6 r; 9362 ex 116521, 2 r; 37153, 30 r; 54145, 1 r; 91612, 21 r; 91635, 1 r; 91756, 1 r; 91784, 1 r; 91812, 4 r; 104304, 1 r; 112831, 3 r; 112832, ca. 125 r; 112868, 3 r; 112885, 2 r; 112902, 25 r; 113041, 2 f; 113093, 16 r; 113137, 18 r; 113465, 12 r; 113497, 3 r; 113525, 3 r; 113525, 19 r; 113588, ca. 30 r; 113655, 6 r; 113700, 1 r; 113766, 11 r; 113781, 4 r; 113794, 4 r; 113809, 9 r; 113825, ca. 30 r; 113839, 12 r; 113901, 10 r; 115979, 6 r; 115991, 1 r; 116002, ca. 50 r; 116027, 30 r; 116068, 11 r; 116172, 11 r; 116218, 20 r; 116220, 7 r; 116221, 4 r; 116244, 7 r; 116422, 1 r; 116455, 5 r; 116456, 5 r; 116457, 4 r; 116479, 1 r; 116494, 2 r; 116512, 2 r; 116513, 3 r; 116549, 9 f; 116550, 3 r; 116578, ca. 50 f; 116581, 14 r; 163220, 1 f; 183826, 4 r; 194477, 3 r; Makaha, BM: 9367 ex 119577, 1 r; 17857, 3 r; 184164, 19 r; 184165, 19 r; 185220, 10 r; 185246, 1 r; 185269, 1 r; 117864, 2 r; 117880, 1 r; 117902, 2 r; 119505, 1 r; ex 118044, 3 r; Makaleha, 185034, 18 r; 185036, 10 r; Makiki, BM: 16507, 20 r; Makua, BM: 108126, 1 r; Malaekahana, BM: 11037, paratypes f of *lyrata uncifera*; 41001, 3 f; 41001, ca. 30 f; 41001, 20 f; 44750, ca. 30 f; 44799, 1 f; Manoa, BM: 10208 ex 43305, 1 f; 10209 ex 43361, 3 f; 11039 ex 45279, holotype f of *lyrata fossilis*; 12411, 1 f; 12412, 7 f; 12413, 2 f; 12592 (=12412), 1 f; 37881, ca. 30 f; 39937, ca. 30 f; 40644, 4 f; 43016, ca. 20 r; 43070, 1 f; 43105, 15 f;

43233, ca. 50 f; 43304, 15 f; 43389, 35 f; 43440, ca. 50 f; 43485, 4 f; 43531, 4 f; 44032, 3 f; 45232, 1 f; 45279, ca. 100 f; 45279, 1 f; 45334, ca. 50 f; 89001, 1 r; 109227, 1 f; 163989, 1 r; Mauna Kapu, BM: 16976, 17 r; Moanalua, BM: 52251, 2 f; Nanakuli, BM: 9375 ex 128007, 2 r; 9377 ex 128109, 2 r; 89962, 1 r; 90000, 1 r; 90014, 1 r; 105686, 2 r; 112738, 7 r; 127871, 1 r; 127872, 1 r; 177518, 1 r; 182694, 1 r; 182932, 4 r; 183307, 1 r; 186812, 2 r; ex 183452, 1 r; Nanakuli Valley, BM: 172642, 1 r; Napepeiaulelo, BM: 9370 ex 126900, 1 r; 127191, 2 r; 127532, 5 r; 173894, 2 r; 173953, 16 r; 176826, 13 f; ex 127105, 1 r; Niniko, BM: 21787, 19 r; Nuuanu, BM: 10212, 1 r; 11122 ex 18752, paralectotype r of *lyrata carbonaria*; 12378, 1 r; 12385, ca. 40 r; 12386, 1 r; 12387, 16 r; 12388, 31 r; 12389, 10 r; 12390, 24 r; 12393, 1 r; 12396, 1 r; 12394, 4 r; 12398, 33 r; 12399, ca. 50 r; 12400, 25 r; 12401, 6 paralectotypes r of *lyrata carbonaria*; 12402, 6 r; 15343, 18 r; 15343, ca. 50 r; 15362, 4 r; 15370, 24 r; 15386, 5 r; 15750, 22 r; 15760, 1 r; 16376, 60 r; 18741, lectotype r of *lyrata carbonaria*; 18752, 11 paralectotypes r of *lyrata carbonaria*; 19630, 31 r; 19647, 53 r; 20447, 4 r; 20454, 1 r; 20461, ca. 50 r; 20875, 14 r; 21694, 3 r; 23652, 2 r; 23667, ca. 125 r; 23820, 1 r; 35502, 7 r; 35515, 5 r; 37847, 1 r; 39055, 1 r; 43612, 15 r; 51334, 2 r; 76775, 1 r; 101114, 1 r; 168845, 3 r; ex 12391, 6 r; ex 35217, 1 r; Nuuanu Pali, BM: 168846, 2 r; Olomana, BM: 100852, 1 r; 100865, 1 r; Opauala, BM: 59124, 2 r; 165950, 1 r; Pahole, BM: 166241, 2 f; Palama, BM: 185485, 5 r; 18744, lectotype of *magdalenae*; 18745, 2 paralectotypes of *magdalenae*; 18745, 12 paralectotypes of *magdalenae*; Palawai, BM: 9388 ex 174204, 1 r; 123880, 2 f; 126836, 7 r; 127465, 25 r; 127499, 2 r; 174019, 5 f; 174056, 20 f; 174110, ca. 20 f; 174170, 2 f; 174203, ca. 40 f; 177106, 21 f; 177190, 1 f; 177249, 19 f; 177491, 21 r; 177701, ca. 125 f; 180906, ca. 50 r; 180907, ca. 20 r; 182611, 2 r; ex 127466, 9 r; ex 174207, 7 f; Palehua, BM: 33144, 15 r; 33157, 23 r; 35894, 4 r; 40606, 3 r; 59351, 5 r; Pali BM: 43934, 55 r; 43934, 2 r; Palikea, BM: 93301, ca. 125 r; Palolo, BM: 17545, 4 f; 23993, 1 r; 40514, 7 r; 46282, 31 r; 47190, 5 r; 54000, 1 r; 59120, 3 r; 185647, 5 r; 185648, 14 r; Papaia Valley, BM: 114136, 3 r; Pauoa, BM: 17903, 2 r; 43598, 4 r; 162318, 11 r; 189033, 9 r; 189034, 10 r; Pohakea, BM: 183755, 1 r; 183774, 1 r; Popouwela, BM: 10211 ex 17911, 1 r; 33745, 4 r; 35245, 1 r; 114682, 3 r; 114684, 2 r; 114686, 4 r; 119102, 16 r; 131660, 1 r; 131721, 1 r; 131747, 13 f; 131794, 5 f; 131848, 3 f; 131923, 1 f; 172708, 20 f; 172745, 2 f; Pualii, BM: 9387 ex 173730, 1 r; 175786, 5 f; 175821, ca. 30 f; 176621, 1 f; 176730, ca. 30 f; 180855, ca. 30 f; 183849, 1 r; 184860, 22 r; ex 176733, 70 f; Pukaulua, BM: 93379, 5 r; 117069, 1 r; 117129, ca. 30 r; 174399, ca. 20 r; Punaluu, BM: 45120, ca. 225 f; Pupukeya, BM: 175614, 1 f; 175636, 19 f; 175677, 3 f; 175713, 3 f; 175729, 15 f; 175766, 10 f; Puumialua, BM: 176476, 1 r; 176498, 3 f; 176539, ca. 30 f; Round Top, BM: 21980, 1 r; 21996, ca. 30 r; 39901, 2 f; 130051, 4 r; 130067, 3 r; Tantalus, BM: 12380, ca. 100 r; 12381, 11 r; 12382, ca. 30 r; 12382, ca. 225 r; 12383, 4 r; 12589 (=12382), 1 r; 12590 (=12382), 1 r; 16136, 3 r; 17388, 3 r; 59121, 3 r; Waialeale, BM: 176111, ca. 50 f; Waianae Valley, BM: 117389, 6 r; 117460, 1 r; 117460, 1 r; 128601, 2 r; 128602, 1 r; Waiu, BM: 36921, 2 r; 59122, 6 r; Waieli, BM: 9406 ex 131752, 1 r; Waialele, BM: 172898, ca. 225 f; 172900, ca. 40 f; 172932, ca. 30 f; 172955, 18 f; 173011, ca. 50 f; 173013, ca. 30 f; 173045, ca. 50 f; 173070, ca. 50 f; 181000, ca. 50 f; Waimanalo, BM: 40903, 1 f; 172776, 1 r; Waimea, 176086, 3 f; Waimuno, BM: 40678, 1 r; 40678, 1 f; no exact locality, BM: 74884, 5 r; 162318, 5 a; 170444, 1 r; 184246, 1 a. no locality data: BM: 9378 ex 128632, 2 f; 15343, 2 r; 18645, 1 r; 18762, 1 r.

DESCRIPTION

Shell sinistrous, ovate; spire convex, rather tapered; apex bluntly rounded. Whorls 5.1-5.6, most often 5.2-5.5, moderately convex, rarely flat; suture moderately deep, rarely shallow. H: 2.06-2.75 mm; B: 1.25-1.60 mm; h: 0.79-1.12 mm; b: 0.75-1.05 mm; bw: 1.25-1.72 mm. H/B: 1.52-1.94; bw/H: 0.58-0.65. Aperture semi-oval; sinus rather distinct. Lip not or only slightly detached, well reflexed, fairly broad and somewhat thickened; its parietal part expanded. In aperture 5 teeth. Columellar in front view almost invisible, takes most of or entire columellar wall; in top view crescentic, with both ends equally, or lower end more, produced towards lip; rather thin lamellate with thicker edges. Parietal ca. 1/5 whorl long; high and fairly thick lamellate with slightly or much thickened edges; highest within; its outer part straight

or slightly deflected palatalwards; simple. Angular high and fairly thick; equals parietal in length and overlaps it for 1/2 length; outer part somewhat deflected palatalwards. Upper palatal ca. 1/4 whorl long; its inner end visible in oblique view; division into parts distinct; part facing angular low lamellate or prominent ridge-like; part facing parietal high and thin lamellate. Lower palatal partly or completely split:



90. Distribution of *L. lyrata* (GOULD): white-margined circles - recent, black-margined circles - subfossil, triangles - recent and subfossil.

outer part callus-like, elongatedly tubercular or thick lamellate, of varied length, starts at ca. 1/2 length upper palatal; inner part united with it by a callus or various thickness or not at all; high short lamellate or comma-shaped tubercular, situated well before the inner end of upper palatal, and parallel or slightly divergent from it; very rarely the tooth is almost entire. No accessory teeth. Body whorl may be regularly ribbed save the base, sometimes space between the impressions or whole lower half of the whorl ribbed less distinctly or bare; 2 short and shallow, somewhat convergent impressions correspond to palatals; the lower delimits an indistinct blunt basal crest. Body whorl suture straight. Umbilicus almost circular, open, deep, narrow. Sculpture usually regular, of 17-21, most often 18-20 ribs on penultimate whorl; ribs coarse, blunt, not flexuous; 1/3-1/2 interspace thick. A part of specimens from some populations differ in having irregular, often incomplete and/or randomly arranged ribs, which sometimes may be very few or even absent (the form described as *lyrata gouldi*). Spiral ridges in interspaces rather densely arranged, in most shells visible under stereomicroscope, rarely only in SEM. Colour variable: from somewhat reddish chestnut brown to light goldish brown; body and penultimate whorl unbanded or narrowly lighter banded in middle, varying even within populations.

DISTRIBUTION

Kauai, Oahu; recent and subfossil. Fig. 90.

NOTE

Subspecies described within *lyrata*: *uncifera* and *fossilis* (PILSBRY & COOKE 1918-1920) are, when more material is examined, well within the variability range of typical populations, and thus are not justified. The form with sparse and/or irregular ribs, referred to as *lyrata gouldi* (PILSBRY & COOKE 1918-1920: 235) is found along with typical shells. Kauaian specimens, termed by PILSBRY & COOKE (1918-1920: 237) "Kauaian race", differ from shells from Oahu in being generally more elongate and having on an average somewhat fewer ribs.

Lyropupa kahoalavensis PILSBRY et COOKE, 1920

Figures 91-97.

Lyropupa kahoalavensis PILSBRY & COOKE 1918-1920: 256-258, pl.22, figs 1-4, 8, 9. Type locality: Hakioawa Bay, Kahoolawe. Paratypes: BM 36009.

Lyropupa kahoalavensis puukolekolensis PILSBRY & COOKE 1918-1920: 258, pl.26, figs 9, 12. Type locality: Puukolekole, Molokai. Paratypes: BM 15923.

MATERIAL EXAMINED

Oahu: Ewa, BM: 35607, 600 f; Koko Head, BM: 21939, 67 r; Waimanalo, BM: 172805, 71 f.

Kahoolawe: Ahapuiki, BM: 11611 ex 36059, 8 r; 36059, ca. 20 r; Hakioawa, BM: 36009, 13 paratypes r of *kahoalavensis*; 36009, 69 paratypes of r *kahoalavensis*; 36039, 9 r; 36046, 1 r; 81685, ca. 20 r; 81694, 1 r; Hanakea, BM: 36026, ca. 20 r; Kanapou, BM: 11108, 32 r; 11610 ex 36175, ca. 125 r; 11612 ex 36133, 3 r; 11613 ex 36150, 6 r; 11614 ex 36114, 5 r; 11615 ex 36133, 25 r; 11616 ex 36150, ca. 20 r; 11617 ex 36175, 10 r; 36082, ca. 20 r; 36097, 6 r; 36114, ca. 30 r; 36115, 1 r; 36133,

ca. 20 r; 36150, ca. 40 r; 36175, 1 r; 36175, 18 r; 81676, ca. 20 r; 104278, 4 r; 104279, 7 r; 104280, 10 r; Schooner Bay, BM: 11089, 1 r; no exact locality, BM: 94030, 8 r; 108636, ca. 20 f; 208613, 13 f; 208626, ca. 20 f; 208647, ca. 20 f; 208662, ca. 20 f; 208680, 7 f; 208690, 7 f.

Lanai: Kaa, BM: 52618, 1 r; Kaena Pt., BM: 94007, 24 r; 94008, 8 r; Kaohai, BM: 104045, 3 f; 104046, ca. 20 f; 104047, 1 r; Keanapapa Pt., BM: 11608 ex 45531, 4 f; 11609 ex 34715, 1 f; Maunalei, BM: 45560, ca. 20 f; 59871, 2 r; 59898, ca. 50 r; 59898, ca. 100 r; 59899, 1 r; no exact locality, BM: 34715, 16 f; 45531, ca. 20 f.

Maui E: Auwahi, 45073, ca. 20 f; 52452, 3 r; 52483, 5 r; 59133, 2 r; Hana, BM: 190438, 4 r; 210271, 29 f; Kanaio, BM: 40059, 1 r; Kaunauhana, BM: 116742, ca. 200 f; 116743, 1 r; 116744, 2 r; Keokeya, BM: 52825, ca. 20 r; 52826, 1 f; 59214, 15 r; 59257, 1 r; Ulupalakua, BM: 52762, ca. 20 r; 76611, 8 r.

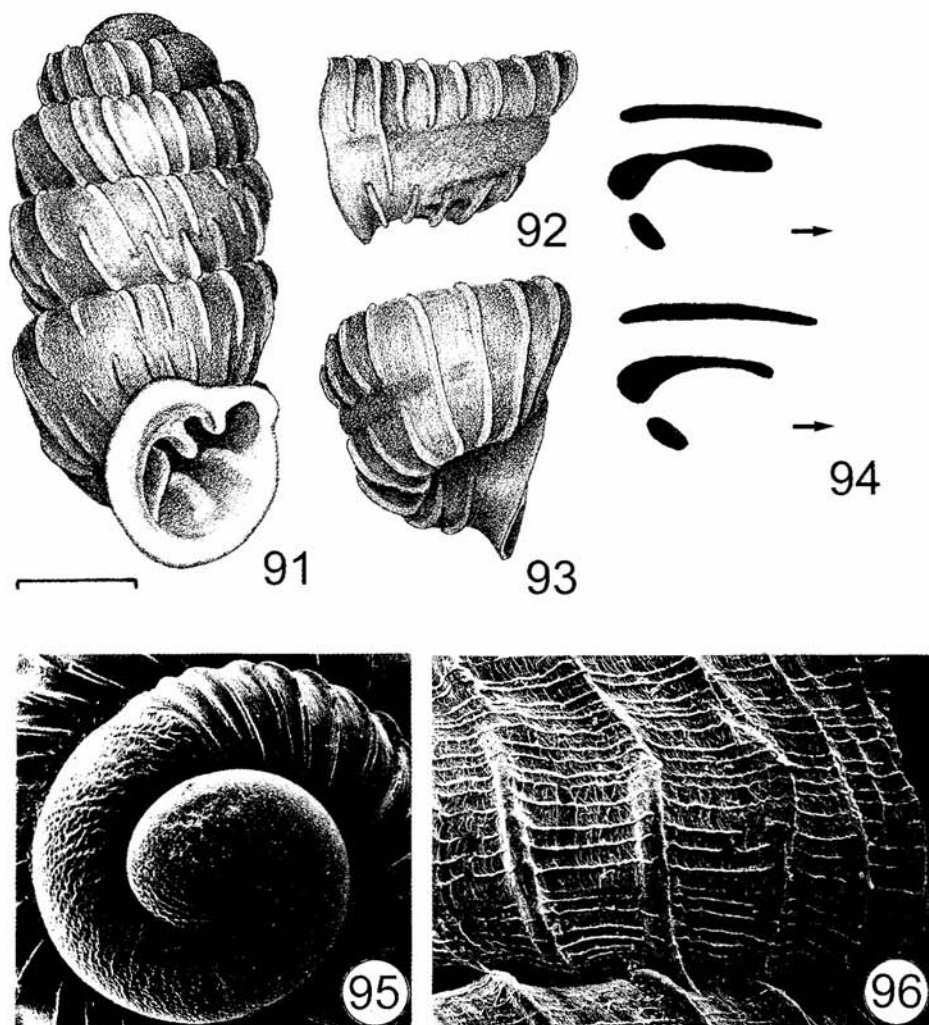
Maui W: Alaeloa, BM: 167862, 15 f; 167864, 15 f; 167896, 17 f; Lahaina, BM: 192538, 2 r; Mahinahina, BM: 49207, 1 r; 59994, 2 r; 59995, 2 f; 167924, 3 f; Waiehu, BM: 115890, ca. 20 f; 115915, ca. 30 f; 116699, 5 f; Wailuku, BM: 59786, 11 r.

Molokai: Kaiehu, BM: 11095, 6 r; 45576, 541 f; 45576, 1 r; 45577, 1 r; 47391, ca. 40 r; 47391, ca. 100 r; 47391, 13 r; 184477, 235 f; 184526, 484 f; Kailio Pt., BM: 37432, 10 r; Kalainawawaa, BM: 40110, 8 r; 40138, 2 r; 40158, 5 r; 47420, 1 r; 52369, 6 r; Mauna Loa, BM: 33335, 1 r; 37412, 2 r; 37462, 17 r; 37488, 188 f; 37488, ca. 20 r; 52341, 6 r; Mokolaelau, BM: 33369, 8 r; Moomomi, BM: 33378, 2 r; 33415, 1 r; 33416, 1 r; Puu Kolekole, BM: 15923, 8 paratypes r of *kahoolavensis puukolekolensis*; 15923, 11 paratypes r of *kahoolavensis puukolekolensis*; 15923, 5 r.

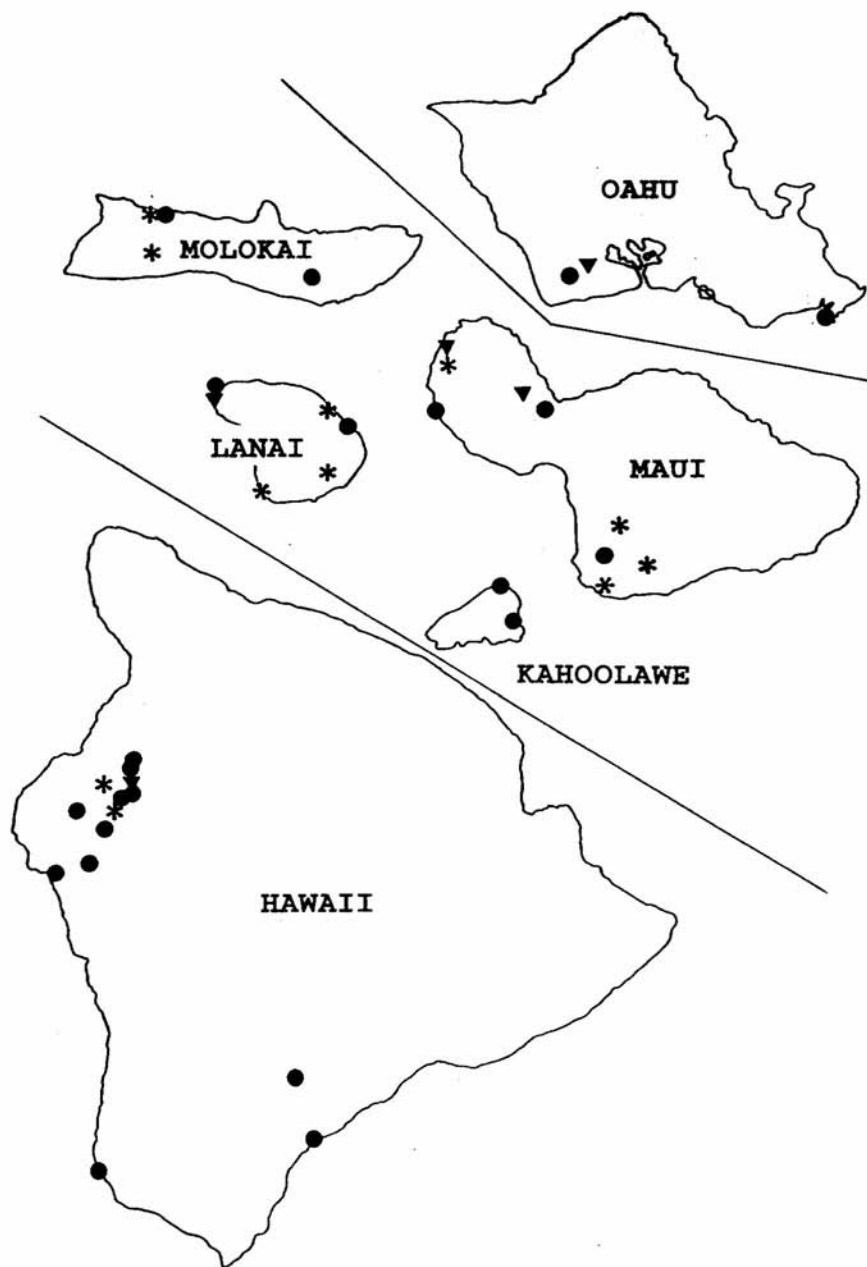
Hawaii: Huehue, BM: 42598, 25 r; 42600, ca. 50 r; 42600, 9 r; Kapua, BM: 39444, 1 r; Kapulehu, BM: 42644, ca. 50 r; Kau, BM: 39631, 1 r; 77363, ca. 30 r; 77384, ca. 20 r; 77422, 16 r; 77423, 27 r; 77424, 5 r; 77428, 12 r; 77464, ca. 50 r; 77465, 1 r; Kaupulehu, BM: 39515, 7 r; Kona, BM: 11619 ex 18765, 2 r; 11620 ex 12438, ca. 20 r; 11622 ex 42675, 9 r; 12438, 8 r; 12603 ex 12438, 1 r; 18965, 11 r; 42641, ca. 20 r; 58942, 3 r; 58943, ca. 20 r; 58944, 3 r; Okoe, BM: 46067, 5 r; Poohohoo, BM: 192069, 2 f; 192070, 2 r; Punaluu, BM: 23081, 1 r; Pupunui, BM: 39357, 1 r; Puuanahulu, BM: 50064, ca. 20 r; Puuhuluhulu, BM: 172393, 13 f; Puu Iki, BM: 11624 ex 49990, 1 r; 172062, 1 r; 172095, 11 r; 172096, 3 r; 172097, 13 r; 172370, ca. 20 r; Puuwaawaa, BM: 11621 ex 39787, 3 r; 11623 ex 49664, ca. 20 r; 11625 ex 50020, ca. 20 r; 39472, 1 r; 39496, 7 r; 39734, 28 r; 39759, 3 r; 39787, ca. 20 r; 39787, 19 r; 47892, 1 r; 47950, 1 r; 48008, 2 r; 49633, 4 r; 49664, ca. 20 r; 49694, ca. 20 r; 49728, ca. 40 r; 49769, ca. 20 r; 49797, ca. 20 r; 49833, ca. 40 r; 49871, ca. 30 r; 49911, 12 r; 49938, ca. 20 r; 49967, 15 r; 49990, ca. 20 r; 50020, ca. 30 r; 50089, 7 r; 50119, 5 r; 53673, 2 r; 94079, ca. 20 r; 171889, 3 r; 172169, 4 r; 192128, 1 r; 192156, ca. 20 r; 192170, 1 r; 192255, 2 f; 192278, ca. 30 f; 192298, 2 r; 192307, ca. 30 f; 192328, ca. 20 r; 192350, ca. 20 f; 192369, 1 r; 192380, 12 f; 192399, 6 f; 194589, 18 r; 194601, 3 r; Waiaha, BM: 42675, 27 r; 42677, 18 r; 42677, 6 r.

DESCRIPTION

Shell dextrous, from short to elongate cylindrical or ovate-cylindrical; spire straight or somewhat convex; apex broadly rounded. Whorls 4.4-6.1; flat, feebly convex or flat and shouldered; suture shallow or moderately deep. H: 1.98-2.56 mm; B: 1.00-1.17 mm; h: 0.68-0.85 mm; b: 0.65-0.81 mm; bw: 1.11-1.36 mm. H/B: 1.75-2.20; bw/H: 0.52-0.58. Aperture rather broadly semi-oval; sinulus fairly distinct. Lip detached, rarely forms a short trumpet; reflexed, rather narrow, its thickness varies between populations. In aperture 5-7 teeth. Columellar may be well visible, partly or nearly invisible in front view; takes at least mid 2/3, but usually upper 3/4 or entire columellar wall; thin lamellate with thicker edges; in top view crescentic with both ends somewhat produced towards lip. Parietal ca. 1/5 whorl long, high and thin with somewhat thickened or not thickened edges; highest in middle; not or slightly deflected palatalwards; simple. Angular high and thin; ca. 2/3 parietal length and overlapping it for 1/2 length; not or only slightly deflected palatalwards. Upper



91-96. *L. kahoolavensis* PILSBRY et COOKE: 91-93 - paratype, BM 36009, Hakioawa Bay, Kahoolawe: 91 - front view, 92 - side view of body whorl, 93 - oblique umbilical view of body whorl. Scale bar 0.5 mm. 94 - top view of palatals in two specimens, columellar wall removed, diagrammatic, arrow indicates aperture. 95 - protoconch surface, SEM, 127x, BM 36009, Hakioawa Bay, Kahoolawe; 96 - definitive whorl surface, SEM, 140x, BM 47912, Puuwaawaa, Hawaii.



97. Distribution of *L. kahoolavensis* PILSBRY et COOKE: circles - recent, triangles - subfossil, asterisks - recent and subfossil.

palatal less than 1/4 whorl long; inner end visible in front view; undivided or divided: entirely low lamellate or part facing angular somewhat lower, slightly recessed from lip. Lower palatal entire or incompletely split; its inner part always comma-shaped and set not quite in line with the outer part; when incompletely divided, both parts united by a robust callus bridge or (*kahoolavensis puukolekolekolensis*) by a thin but distinct bridge; outer part diffuse at its outer end. Basal elongate tubercular, set at acute angle to the wide end of the inner part of lower palatal; free; sometimes vestigial or absent. False basal small, vestigial or nil. Body whorl profile ribbed entirely or only in its upper half; 2 narrow distinct impressions correspond to palatals; upper up to 2/3 whorl long, lower up to 1/3 whorl long; parallel or convergent; in some shells also a third, basal impression; some shells have a moderate or weak basidorsal hump; rarely on body whorl there are bumps resembling those in *ovatula kona*, but weaker. Body whorl suture straight. Umbilicus oval, narrow, open or slit-like. Sculpture variable: from rather coarse and regular to fine and unordered, on penultimate whorl 13-28 ribs. Rib quality very variable: from coarse and blunt or fine, sharp and regular, through slightly irregular to incomplete and unordered; often halves of ribs on upper and lower parts of penultimate or two mid whorls shifted relative to each other; ribs may be grouped in pairs or triplets; on body whorl there are nearly always some irregularities - when unbroken, ribs are at least flexuous; on upper two definitive whorls ribs always regular; 1/7-1/3 interspace thick. Spiral ridges in interspaces rather densely arranged, from coarse and visible under stereomicroscope to fine and visible only in SEM. Colour golden-yellowish or chestnut brown; subfossil shells white or dirty white, semitransparent or opaque.

DISTRIBUTION

Oahu, Lanai, Molokai, Maui, Hawaii, Kahoolawe; subfossil and recent. Fig. 97.

NOTE

In most specimens from Puukolekole (*kahoolavensis puukolekolensis*) the lower palatal is almost completely split (only a callus bridge) and whorls are usually fewer (4.4-4.9 compared to 4.8-6.1 in typical shells). In my opinion these are within the range of usual interpopulation differences and the population does not merit subspecific status.

Lyropupa hybrida n. sp.

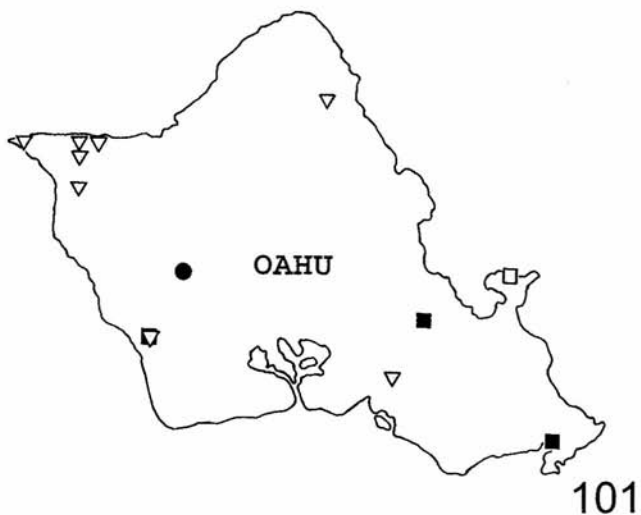
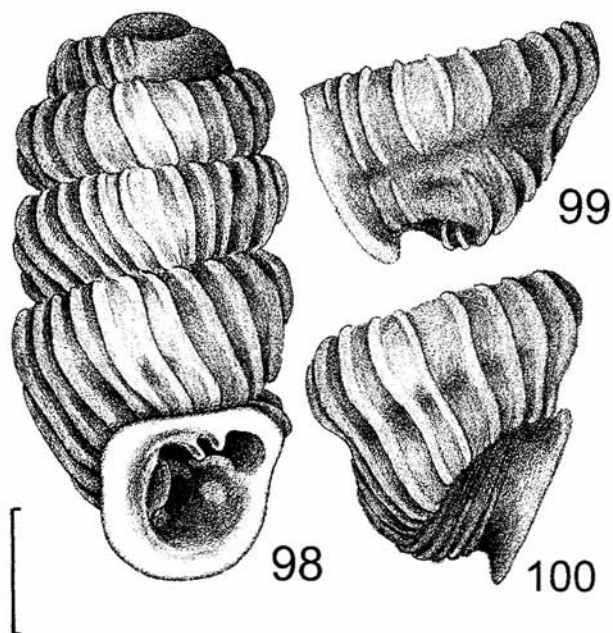
Figures 98-101.

TYPE LOCALITY

Kanehoa, Oahu.

TYPE MATERIAL

Kanehoa, Oahu: Holotype & 8 paratypes: BM 40934; 1 paratype: MNHW ex BM 40934.



98-100. *L. hybrida* n. sp., holotype, BM 40934, Kanchoa, Oahu: 98 - front view, 99 - side view of body whorl, 100 - oblique umbilical view of body whorl. Scale bar 0.5 mm. Fig. 101. Distribution of *L. hybrida* n. sp. (solid circles), *L. plagiopyx* PILSBRY et COOKE (hollow triangles) and *L. lualaleiensis* n. sp. (solid squares - recent, hollow squares - subfossil).

DIAGNOSE

In its general appearance the new species resembles cylindrical forms of *kahoolavensis*, though it differs markedly in the following characters: 1. completely split lower palatal; 2. smaller and almost straight columellar; 3. outer part of lower palatal in most shells almost completely reduced; 4. very deep impressions on body whorl, the uppermost being prolonged above aperture; 5. basal visible in front view; 6. presence of a callus bridge between basal and the base of columella. It differs from *costata*, which it may also resemble, in the following characters: 1. elongated cylindrical shape with shouldered whorls; 2. aperture much smaller relative to entire shell; 3. outer part of lower palatal absent or small; 4. much smaller and straight columellar; 5. the uppermost groove on body whorl deep and very long; 6. distinct basal hump instead of weak basidorsal hump; 7. inner part of lower palatal set at the very end of upper palatal; 8. basal visible in front view; 9. false basal small, vestigial or absent; 10. presence of callus bridge between basal and base of columella.

DESCRIPTION

Shell dextrous, cylindrical; apex broadly rounded. Whorls 5.2-5.4 (holotype 5.3), flat, strongly shouldered; suture very deep. H: 2.10-2.28 mm (holotype 2.28); B: 1.10-1.15 mm (holotype 1.14); h: 0.69-0.70 mm (holotype 0.70); b: 0.74-0.76 mm (holotype 0.74); bw: 1.09-1.25 mm (holotype 1.25); H/B: 1.83-2.00 (holotype 2.00); bw/H: 0.55-0.57 (holotype 0.55). Aperture obliquely pear-shaped; sinulus distinct. Lip detached or even forming a very short trumpet; reflexed, narrow, thick. In aperture 6-7 teeth. Columellar well visible in front view; takes mid 2/3 columellar wall; thin lamellate with poorly thickened edges; in top view almost straight, with both ends only slightly produced towards lip. Parietal ca. 1/6 whorl long; high and thin with not or only poorly thickened edges; highest in middle; simple; not or only slightly deflected palatalwards. Angular high and thin; ca. 2/3 parietal long, overlaps it for 1/2 length; not or very slightly inclined palatalwards. Upper palatal less than 1/4 whorl long; its inner end and inner part of lower palatal visible in front view; division into parts distinct: part facing angular very low lamellate, almost ridge-like; part facing parietal low lamellate; the tooth not recessed from lip. Lower palatal split: outer part from absent, through vestigial to a small, diffuse, elongated tubercle; inner part short, thick lamellate, set before the inner end of the upper palatal and overlapping it, somewhat divergent from it; free. Basal elongate tubercular, set at an obtuse angle to the inner part of lower palatal; partly accreted or free; visible in front view and united with the base of columella by a low callus "bridge". False basal absent or vestigial. Body whorl profile wholly ribbed or some ribs interrupted between impressions; the topmost impression corresponds to the upper palatal, deep and long, terminating above aperture; mid impression short and shallow or absent; bottom impression deep and very short; below and behind it a strong basal hump. Body whorl suture straight. Umbilicus oval, narrow, open deep. Sculpture regular, of 19-22 (holotype 20) ribs on penultimate whorl. Ribs coarse, fairly sharp; some ribs on penultimate whorl slightly flexuous or broken; 1/6-1/4 interspace thick. Traces of

rather densely arranged spiral ridges visible only in SEM. Colour light goldish brown.

NAME DERIVATION

Hybrida means a hybrid. The species looks like a mysterious hybrid of *costata*, *kahoolavensis* and some third species.

DISTRIBUTION

Oahu, subfossil; type locality only. Fig. 101.

Lyropupa costata (PEASE, 1871)

Figures 102-109.

Vertigo costata PEASE 1871: 461. Type locality: Hawaii, no exact data. Lectotype: BM 59021, present designation. See note.

Vertigo perlonga PEASE 1871: 462. Type locality: Oahu, no exact data. Lectotype: MCZ 48063, designated by PILSBRY & COOKE 1918-1920. **Syn. n.** See also note on *mirabilis*.

Lyropupa perlonga interrupta PILSBRY & COOKE 1918-1920: 261-262, pl.22, fig.5; pl.25, figs 1-4, 10. Type locality: Kahuku, Oahu. Paratypes: BM 11091.

Lyropupa perlonga filocostata COOKE et PILSBRY, in PILSBRY & COOKE 1918-1920: 262-263, pl.23, fig.12. Type locality: Limahuli, Kauai. Holotype: BM 11057, Paratypes: BM 15677.

MATERIAL EXAMINED

Kauai: Haena, BM: 37534, 11 f; 52067, 11 r; 52068, 1 r; 77971, 3 r; 77989, 7 r; 78012, 4 r; 93815, ca. 20 r; 118929, 7 r; 167633, 1 f; 167634, 2 f; 168348, 15 f; 184351, 25 f; 190758, ca. 20 f; 212081, 4 f; Hanamaulu, BM: 116627, 3 r; 116660, 3 r; 118572, 4 r; 119005, 12 r; 119063, 2 r; 167986, 3 f; ex 119007, ca. 30 r; Honopu, BM: 49231, 5 f; Kaakaaniu, BM: 190548, 1 f; Kalalau, BM: 15662, 1 r; 15663, 2 r; Kalihikai, BM: 77903, 4 r; 77935, 15 r; 77937, 12 r; 88465, 1 r; 100241, 2 r; 100242, 4 r; 190491, 2 f; 190591, ca. 20 f; Kalihiwai, BM: 77865, 18 r; 92618, 2 r; Kapaa, BM: 19439, 5 r; 19439, 10 r; 19549, 10 r; 212214, 9 f; Kipu Kai, BM: 37685, 1 r; 37708, 1 f; Koloa, BM: 35807, 7 f; 52053, 2 r; 100423, 1 r; 100424, 1 r; 168321, 1 f; Limahuli, BM: 11057, holotype r of *perlonga filocostata*; 15677, 124 paratypes r of *perlonga filocostata*; 17067, ca. 20 r; 77821, ca. 20 r; 93750, 18 f; 93785, 25 f; 118829, 25 r; 118864, 21 r; 118866, 1 r; 124175, ca. 20 f; 124202, ca. 20 r; 124301, ca. 20 r; 124329, 16 f; 124350, 19 f; 167978, 1 f; 168365, 4 f; 184302, 7 f; 184325, ca. 20 f; Mahaulepu, BM: 7874, 1 r; 17831, ca. 20 r; 52093, 7 r; 78033, 10 r; 78094, 8 r; 78095, ca. 20 r; 78130, 1 r; 78166, 1 r; 100365, 1 r; 100366, 5 r; 100433, 16 f; 100434, 1 f; 100533, 1 r; 100547, 2 f; 118764, 1 r; 118797, 2 r; 190464, 4 f; ex 52092, 1 r; Moloaa, BM: 190518, 5 f; 210119, 2 f; Papaa, BM: 118638, 2 r; Papalinaloa, BM: 100335, 1 r; Polihale, BM: 212307, 3 f; Wailua, BM: 16056, ca. 20 r; 19473, ca. 20 r; 19519, 7 r; 20909, ca. 20 r; 100118, 26 r; 210169, ca. 30 f; ex 20909, ca. 30 r; Waipa, BM: 86290, 1 f; 86291, ca. 20 f; 88434, 7 r; Waipaa, BM: 100283, 3 r; 100299, 12 r; 124404, 19 f; 124540, 7 f; Waipouli, BM: 78195, 18 r; 100166, 19 r; 118968, 9 r; ex 78196, 1 r.

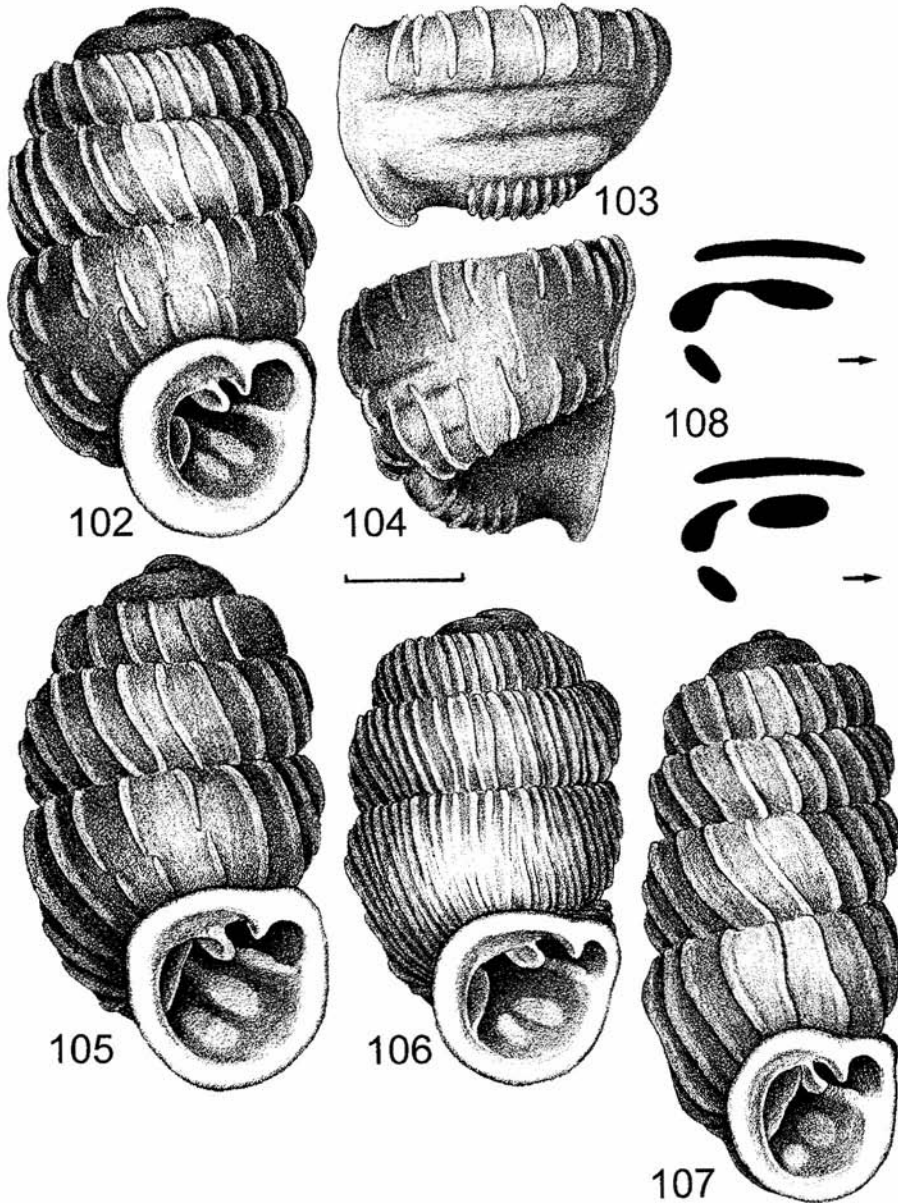
Lanai: no exact locality, BM: 34741, 5 f.

Maui W: Waiehu, BM: 115915, ca. 450 r.

Molokai: Kaiehu, BM: 184477, ca. 50 f; 184501, 15 f; 184522, ca. 20 f; 184524, 21 f; 184525, 3 f; 184526, ca. 100 f; 184582, 2 f; 184583, 8 f; Kailio Pt., BM: 11605 ex 37432, 8 r; 40085, 1 r; Kalainawawaa, BM: 52357, 19 f; Kaluaaha, BM: 33339, 1 f; Mauna Loa, BM: 37461, 19 f; 52342, ca. 30 f; Moomomi, BM: 11604 ex 37378, 2 r.

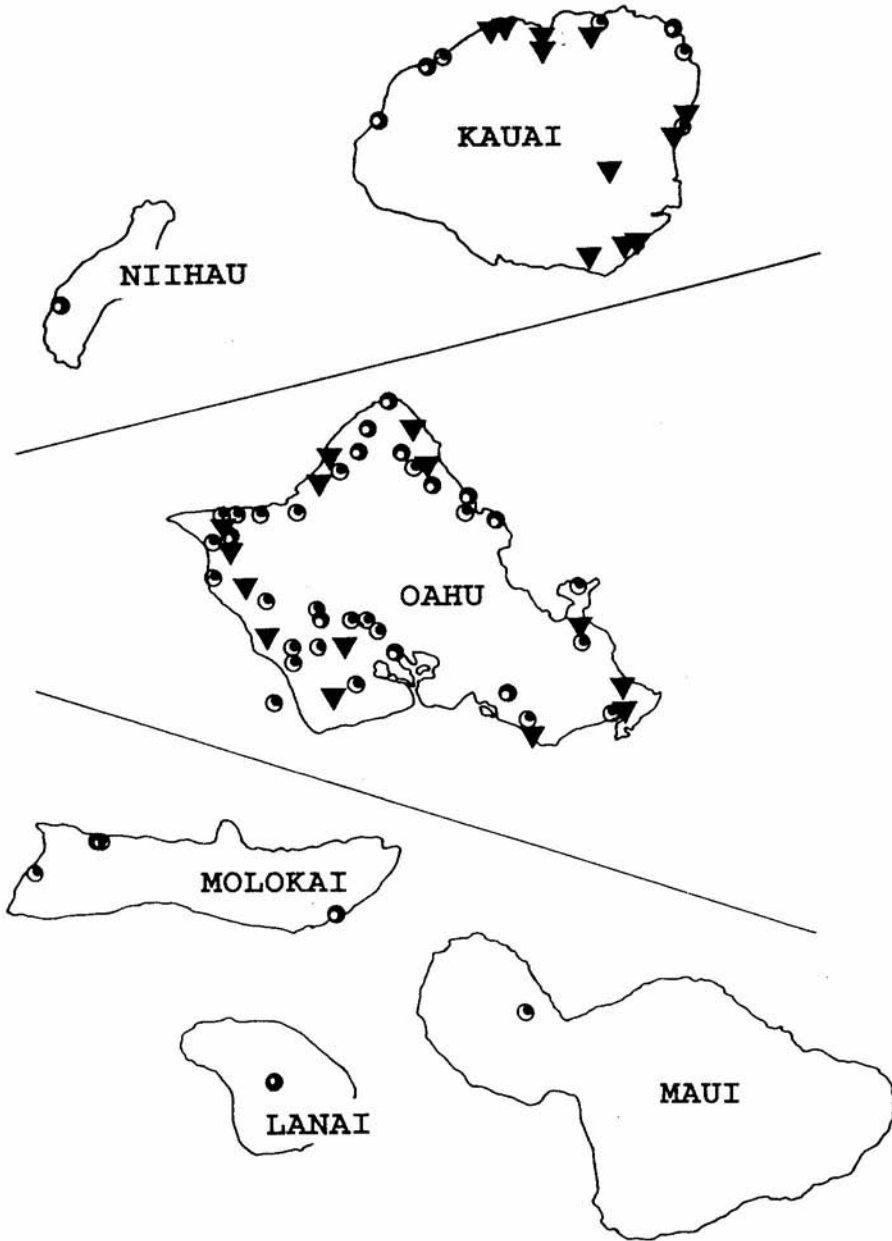
Niihau: Kiekie, BM: 37748, 1 f; no exact locality, BM: 11058, 1 r; 16313, 1 f.

Oahu: Diamond Head, BM: 10243 ex 12425, 1 r; 10244 ex 15216, 1 r; 11052, 1 r; 11055, 1 r; 12425, 7 f; 12599 ex 12425, 1 r; 15201, 32 f; 15216, 4 f; Ekahanui, BM: 125451, 4 r; 177327, 4 r; 177579, ca. 20 r; 177580, ca. 20 r; 177596, 3 r; 177649, 22 r; 183919, 11 r; 211452, 1 r; 211536, 19 r; Ewa, BM: 35607, ca. 20 r; 35630, ca. 20 r; Ewa Plain, BM: 77687, ca. 50 r; 77688, ca. 20 r; 77689, 3



102-108. *L. costata* (PEASE): 102-104 - BM 112856, Lualualei, Oahu: 102 - front view, 103 - side view of body whorl, 104 - oblique umbilical view; 105-107 - front views of: 105 - BM 45281, no locality data, 106 - paratype of *L. perlonga filocostata* COOKE et PILSBRY, BM 15677, Limahuli, Kauai, 107 - BM ex 172805, Waimanalo, Oahu. Scale bar 0.5 mm. 108 - top view of palatals and basal of two specimens, columellar wall removed, diagrammatic, arrow indicates aperture.

r; 77691, ca. 20 r; Haili, BM: 175912, 21 r; Halona, BM: 113153, 2 r; 113154, 8 r; 113250, 4 r; 172182, ca. 20 r; 173181, ca. 20 r; 173181, 42 r; 173183, ca. 200 r; 173217, 19 r; 173244, 5 r; 173245, ca. 20 r; 173265, 6 r; 173283, 2 r; 173284, ca. 20 r; Huliwai, BM: 126446, 18 r; Kaaawa, BM: 90953, 1 f; Kaaikukai, BM: 126744, 1 r; 176245, 18 f; 176285, 26 f; 176892, 3 f; 176946, ca. 30 f; 177007, 2 f; 177364, 1 r; 182978, 5 r; 210699, 4 f; Kaelepulu, BM: 11090, 20 r; Kahanahaiki, BM: 172677, ca. 20 f; 172693, 7 f; Kahuku, BM: 10254 ex 33447, ca. 20 r; 10256 ex 33447, ca. 20 r; 11091, 31 paratypes f of *perlonga interrupta*; 11106, ca. 20 r; 33447, 840 f; 33448, 4 f; 45002, 3 f; 45239, 1 r; 52459, ca. 30 f; 52459, 8 f; 60063, 1342 r; 60065, 7 r; 60066, ca. 75 r; 60067, ca. 50 r; 77318, 1 f; 181072, ca. 20 r; Kahuku Pt., BM: 210204, 7 f; 210330, 1 f; 210364, 8 f; Kailua, BM: 10242 ex 35736, 2 r; 10248 ex 35713, 2 f; 10249 ex 35736, ca. 20 f; 10250 ex 35762, 1 f; 10251 ex 40963, 8 r; 35713, 7 f; 35736, ca. 20 f; 35762, ca. 40 f; 40963, ca. 40 f; 52599, 1 f; 77571, 20 f; 77606, 2 r; 77607, ca. 75 f; 77610, ca. 20 r; 77640, 2 f; 77641, 15 f; Kaipapau, BM: 33525, 2 f; 33525, 2 f; 44541, 4 f; 172875, 8 f; 172876, 7 f; 172877, ca. 40 f; Kaluakaula, BM: 211920, 13 f; 211921, 11 f; Kamanani, BM: 112526, 19 r; 112545, 17 r; 112577, 1 r; 112697, 7 r; Kanchoa, BM: 37061, 1 r; 37087, 1 r; Kapapa, BM: 52519, 7 f; Kaumokuiki, BM: 174453, ca. 30 r; Kawaihapai, BM: 40810, 1 r; 174531, 4 r; Kawailoa, BM: 10257 ex 44579, 4 r; 40339, 14 f; 44579, 21 f; 44615, ca. 50 f; 44908, 5 f; 44926, 6 f; 44952, 1 f; 44954, 110 f; 45205, 4 f; 52639, 9 f; 173114, ca. 20 f; 173116, 1 f; 173117, 5 f; 173143, ca. 20 f; Keauau, BM: 107925, 7 r; 107937, 12 r; 107946, 10 r; 174273, ca. 20 r; 174317, 1 r; 174352, 26 r; 175879, 2 r; ex 174316, 1 r; Kealia, BM: 17312, ca. 50 f; 17313, 1 r; Keawaawa, BM: 54253, 1 r; Keawaula, BM: 42985, 2 r; Kewapilau, BM: 134872, 1 r; 134873, 2 r; 174383, ca. 20 r; Koko Crater, BM: 164013, 1 f; 164024, ca. 30 f; Koko Head, BM: 11053, 3 r; 20538, 2 f; 168843, 1 f; Kupehau, BM: 128634, 1 r; Laie, BM: 10255 ex 44671, 23 f; 10258 ex 44671, ca. 20 r; 33563, 2 f; 44658, 1 f; 44671, ca. 100 f; 44672, 2 f; 44892, 2 f; 180979, ca. 30 r; 189557, ca. 30 f; Leilehua, BM: 90525, 3 r; Lualualei, BM: 37134, 1 r; 37151, 3 r; 40865, 23 f; 91614, 3 r; 112829, 14 r; 112830, 10 r; 112834, 1 r; 112856, 82 r; 112857, ca. 20 r; 112867, 2 r; 112886, 1 r; 112904, 1 r; 112905, 9 r; 112931, 1 r; 113040, 4 r; 113073, 9 r; 113078, 26 r; 113084, 10 r; 113085, 13 r; 113094, 4 r; 113100, 19 r; 113101, 11 r; 113102, 6 r; 113113, 18 r; 113136, 4 r; 113336, 8 r; 113340, ca. 30 r; 113354, 3 r; 113355, 21 r; 113378, 3 r; 113379, 3 r; 113412, 4 r; 113550, 23 r; 113589, 2 r; 113618, 8 r; 113653, 2 r; 113701, 1 r; 113740, 2 r; 113767, 1 r; 113779, 7 r; 113795, 7 r; 113810, 8 r; 113827, 2 r; 113862, 5 r; 113881, 1 r; 113902, 1 r; 115993, 1 r; 116003, 3 r; 116029, 5 r; 116030, 1 r; 116051, 23 r; 116052, 3 r; 116070, 11 r; 116109, 28 r; 116154, 3 r; 116173, 33 r; 116222, 7 r; 116245, 8 r; 116269, 20 r; 116345, 3 r; 116373, ca. 20 r; 116583, 1 r; 116585, ca. 20 r; 116604, 1 r; 116423, 10 r; 116424, ca. 30 r; 116426, 10 r; 116436, 2 r; 116458, 1 r; 116459, 1 r; 116477, 1 r; 116497, 18 r; 116520, 17 r; 116553, 3 r; 163214, 9 r; 163219, 4 r; 163239, ca. 30 r; 163244, 2 r; 163247, 9 r; 163258, 5 r; 163291, 1 r; 163292, 1 r; 163289, 3 r; 177797, 1 r; 183808, 13 r; 183828, 6 r; 183829, 11 r; 194479, 17 r; Makaha, BM: 117882, 1 r; 185222, ca. 30 r; Makua, BM: 11054, 1 r; 42924, 3 r; 42944, 121 r; 107677, ca. 20 r; 108127, 3 r; 211892, ca. 20 f; 211893, 8 f; Malaekahana, BM: 10259 ex 44751, ca. 20 f; 10260 ex 44800, 9 f; 10261 ex 44750, 1 f; 40998, ca. 30 r; 40998, ca. 100 f; 40999, 15 f; 41000, 1 f; 44709, 9 f; 44725, ca. 30 f; 44725, ca. 50 f; 44726, 12 f; 44751, ca. 30 f; 44751, 10 f; 44751, ca. 1000 f; 44752, 12 f; 44800, ca. 100 f; 44801, 6 f; 44841, 16 f; 44842, 4 f; 52944, 2 f; 52968, 30 f; 52969, 2 f; Manana Islet, BM: 175942, 1 r; 175948, ca. 20 r; Manoa, BM: 10245 ex 45281, 1 r; 10246 ex 12417, 1 r; 10247 ex 39836, 1 r; 12420, 16 f; 12421, 1 f; 12423, 16 f; 12600 ex 12423, 1 f; 38317, ca. 20 f; 43232, 67 f; 45281, 14 f; 45335, 70 f; 109228, 1 f; 163212, 1 f; 170182, 6 f; Maunaloa, BM: 98959, 2 r; Mokapu, BM: 36786, 5 r; 42253, 3 r; 177784, ca. 20 r; Mokuleia, BM: 11601 ex 43626, 1 r; 128554, 1 r; Nanakuli, BM: 54035, 2 r; 177522, 4 r; 183354, 3 r; Nanakuli Valley, BM: 172479, 1 r; 172527, 2 r; 172655, 2 r; Napepeiauoalelo, BM: 163260, 1 r; 176828, 5 r; Palama, BM: 174021, 4 r; Palawai, BM: 9373 ex 127466, 1 r; 174060, ca. 20 r; 174114, 12 r; 174172, 1 r; 174208, ca. 20 f; 177111, 17 f; 177193, 1 f; 177252, 5 f; 177704, ca. 30 f; 183882, 5 f; Palehua, BM: 33156, 1 r; 38076, 1 r; Papaia Valley, BM: 107606, 1 r; 114116, 1 r; 163238, 1 r; Pohakea, BM: 176578, 3 f; 183663, 1 f; Popouwela, BM: 131678, 17 r; 131705, 1 r; 131723, 7 r; 131748, ca. 20 r; 131749, ca. 30 r; 131795, ca. 50 r; 131851, ca. 30 r; 131926, 3 r; 163262, 6 r; 163273, 1 r; 172747, 2 r; Pualii, BM: 175823, 31 r; 176623, 8 f; 176675, 1 f; 176734, ca. 30 f; 180856, 6 r; 183850, 2 r; 184864, 10 r; Pukaulua, BM: 93384, 7 r; 117068, 3 r; 174403, 5 r; Punaluu, BM: 45122, ca. 20 f; Punch Bowl, BM: 40773, 1 f; Pupukea, BM: 175637, ca. 50 f; 175638, 11 f; 175714, 6 f; 175730, ca. 20 f; 175767, 3 f; Puumialau, BM: 176478, 2 f; 176501, 3 f; Puu Pici, BM: 93542, 1 r;



109. Distribution of *L. costata* (PEASE): white-margined circles - recent, black-margined circles - subfossil, triangles - recent and subfossil.

Waialeale, BM: 176112, ca. 40 f; Waianae Valley, BM: 117390, 1 r; Waieai, BM: 9405, 4 r, 172710, 51 r; Waialeale, BM: 172901, ca. 20 f; 172933, ca. 20 f; 173014, 15 f; 173047, 14 f; 173074, ca. 50 f; 181002, ca. 20 r; 181003, 4 r; ex 172899, 1 f; ex 173046, 1 f; Waimanalo, BM: 10252 ex 40900, ca. 20 r; 10253 ex 40900, 2 r; 40900, ca. 20 f; 40901, 1 r; 172777, 5 f; 172778, ca. 20 f; 172806, 1 f; 172807, 23 f; 172808, ca. 30 f; 172827, 7 f; 172828, ca. 30 f; 172850, 8 f; 172851, 7 f; 183216, 7 f; ex 172805, 4 f; Waipio, BM: 40946, 2 f;

Hawaii: Kona, BM: 18764, 5 r; no exact locality, BM: 59021, lectotype of *costata*.
no locality data, BM: 44751, 1 r; 1980-12A, 10 a.

DESCRIPTION

Shell dextrous; shape variable: from cylindrical to tumid ovate or ovate-cylindrical; spire almost straight to convex; apex broadly rounded. Whorls 4.6-6.0, most often 4.8-5.2, flat, in cylindrical shells upper whorls shouldered; suture moderately deep or (when whorls shouldered) deep. H: 1.55-2.41 mm; B: 0.88-1.36 mm; h: 0.59-0.93 mm; b: 0.56-0.93 mm; bw: 0.94-1.39 mm; H/B: 1.50-2.26; bw/H: 0.53-0.61. Aperture broadly semi-oval; sinulus distinct. Lip detached, rarely forming a short trumpet; reflexed, narrow, moderately thick. In aperture 6-7 teeth. Columellar from well visible to almost invisible in front view, takes entire columellar wall; thin lamellate with thicker edges; in top view crescentic, with both ends somewhat produced towards lip. Parietal ca. 1/5 whorl long; high and thin lamellate with thicker edges; highest behind middle; somewhat deflected palatalwards; simple. Angular high and thin; equals parietal in length and overlaps it for 1/2 length; somewhat deflected palatalwards. Upper palatal ca. 1/4 whorl long; its inner end and inner part of lower palatal at least partly visible without shell destruction; division into parts indistinct or nil: part facing angular low lamellate; part facing parietal as high or somewhat higher; the tooth slightly recessed from lip. Lower palatal split: outer part in front view like a broad, blunt tubercle, prominent but somewhat callus-like diffuse; inner part comma-shaped, starting well before the end of the upper palatal; free; rarely both parts united by a very low and thin callus bridge. Basal elongatedly tubercular, set in line with the wide end of the inner part of lower palatal; free. False basal present; elongatedly tubercular, parallel to outer part of lower palatal. Body whorl profile wholly ribbed or ribs interrupted in middle; on body whorl 3 narrow parallel impressions corresponding to the upper palatal (the longest), lower palatal (medium) and false basal (the shortest); behind and below them a basidorsal hump pronounced to various degree but never very prominent. Body whorl suture straight. Umbilicus slit-like open or sealed. Sculpture mostly regular, of 13-23, rarely up to 35 ribs on penultimate whorl; ribs rather sharp, often flexuous, not very coarse; or decidedly sharp; some few may be broken; rarely ribs irregular, broken and tending to occur in pairs and triplets; 1/6-1/4 interspaces thick. Spiral ridges in interspaces rather densely arranged; in some shells visible under stereomicroscope; in others only in SEM. Colour golden brown, yellowish or greyish white, or pure semitransparent white.

DISTRIBUTION

Niihau, Kauai, Oahu, Maui, Molokai, Lanai, Hawaii; recent and subfossil. Fig. 109.

NOTE

Vertigo costata was described by PEASE (1871) and then referred to by ANCEY (1892) who knew it only from PEASE's (1871) description. PILSBRY & COOKE (1918-1920) could neither identify the species described, nor locate PEASE's original specimens, and those sent by PEASE to the Philadelphia Academy of Natural Sciences were actually *Lyropupa thaumasia* [= *cubana*], but "this species is far broader than PEASE's measurements indicate" (PILSBRY & COOKE 1918-1920: 272). In the collection of the Bishop Museum (no. 59021) there is a specimen bearing a red label "*Lyropupa (Mir) costata* PSE, Paratype, Kona, Hawaii". The specimen is partly damaged, with most of the lip broken off, but apparently adult. It is conspecific with *Lyropupa perlonga* and probably was not in the collection at the time of PILSBRY & COOKE's (1918-1920) revision, or else was overlooked by them. In spite of this, since the measurements and incomplete description given by PEASE (1871) agree with it, I synonymise the two names and designate the above specimen as lectotype of *Vertigo costata* PEASE, 1871.

***Lyropupa cubana* (DALL, 1890)**

Figures 110-113, 118.

Vertigo cubana DALL 1890: 1-2, pl. 1: figs 1, 2. Terra typica: Cuba [error]. Type: USNM 87645. See note.

Lyropupa thaumasia COOKE et PILSBRY, in PILSBRY & COOKE 1918-1920: 270-272, pl. 24, figs 13-15; pl. 25, fig. 14. Type locality: Hanakapiai, Kauai. Holotype: BM 11061; Paratypes: BM 15575 & ANSP 119449. **Syn. n.**

MATERIAL EXAMINED

Kauai: Haena, BM: 10241 ex 37534, 9 f; 19760, 11 f; 36370, 2 r; 52069 (=17066), 19 f; 77972, 4 f; 77988, 17 f; 78013, 8 f; 93812, 17 f; 93813, ca. 20 f; 93814, 5 f; 93816, ca. 20 f; 118930, 20 f; 118931, 1 f; 118932, 6 f; 167636, 1 f; 190759, 10 f; Hanakapiai, BM: 11061, holotype & paratype r; 15556, 1 r; 15570, 2 r; 15575, 11 r; 15575, 55 r; 17107, 12 r; 35593, 1 r; 79924, 4 r; 79932, 1 r; 124260, 4 r; 124523, 6 r; Hanakoa, BM: 86424, 2 r; 86498, 1 r; 88304, 5 r; 88349, 6 r; 88406, 6 r; 88417, 1 r; 104086, 4 r; 124529, 1 r; 124480, 5 r; 124496, 6 r; Kalalau, BM: 79946, 1 r; 86453, 4 r; 124455, 3 r; Kalihikai, BM: 88466, 3 f; Kipu, BM: 17802, 1 r; Koaie, BM: 107257, 2 r; Koloa, BM: 100576, 1 f; Limahuli, BM: 10240 ex 17066, 1 f; 11062, 2 r; 15678, 11 f; 15678, ca. 20 f; 15679, 2 f; 17066, ca. 20 f; 17066, 1 f; 77822, 17 f; 93748, ca. 20 f; 93749, 4 f; 93751, 7 f; 93752, 15 f; 93786, 3 f; 93787, ca. 20 f; 93788, ca. 20 f; 118830, 4 f; 118831, 7 f; 118865, 13 f; 118867, 19 f; 124203, 15 f; 124204, 58 f; 124328, 26 f; 124348, 16 f; 124349, 46 f; 184304, 8 f; Lumahai, BM: 86382, 1 r; Nounou, BM: 42325, 3 r; 81048, 1 r; Olokele, BM: 12428, 1 r; 79851, 2 r; Waiahuakua, BM: 88398, 1 r; 124516, 2 r; Waipa, BM: 86292, 12 f; 86326, 2 r; 86332, 4 r; 88435, 2 f; 124392, 2 r; 124405, 2 f; 124541, 1 r; Waipaa, BM: 100284, 2 f; no exact locality, BM: 19439, 1 f.

DESCRIPTION

Shell dextrous, short oval with broad base to almost spherical; spire convex; apex gently rounded; rarely the whole shell tapered. Whorls 4.9-5.4, delicately but distinctly convex; suture shallow. H: 1.76-2.06 mm; B: 1.14-1.30 mm; h: 0.66-0.79 mm; b: 0.62-0.76 mm; bw: 0.99-1.14 mm; H/B: 1.48-1.71; bw/H: 0.54-0.62. Aperture elongatedly semi-oval; sinulus distinct. Lip not detached, reflexed, fairly wide,

moderately thick. In aperture 6 teeth. Columellar well visible in front view; takes entire columellar wall; thin lamellate with thicker edges; in top view crescentic, with both upper and lower end produced towards lip. Parietal ca. 1/5 whorl long; high and thin with thicker edges; highest in its inner half; its mid 2/3 with free margin strongly flattened and broadened; somewhat deflected palatalwards. Angular high and thin, ca. 2/3 parietal long and overlapping it for 1/2 length; somewhat deflected palatalwards. Upper palatal ca. 1/3 whorl long; inner end invisible in front view; division into parts distinct; part facing angular low lamellate; then the tooth highest and gradually decreasing in height; not recessed from lip; inner end partly accreted to the inner part of lower palatal. Lower palatal split; its outer part elongate tubercular, from small to robust; inner part rather high short lamellate, forming a continuation of upper palatal and partly accreted to it; its lower end united with basal by a callus. Basal elongate tubercular or low short lamellate, set in line with the inner part of lower palatal. In some shells the three teeth nearly continuous i.e. wholly accreted. Body whorl profile entirely ribbed, with only a flattening or rarely a slight impression corresponding to external part of lower palatal; behind the flattening a barely perceptible hump; sometimes hump stronger, giving an angular appearance to the base; in some shells the depression and hump are nearly completely devoid of ribs. Body whorl suture straight. Umbilicus circular, open, deep, with whorls visible inside; only slightly distorted by body whorl. Sculpture regular, of 24-32, most often 25-29 ribs on penultimate whorl; ribs not flexuous, fairly coarse and blunt; 1/3-1/2 interspace thick. Spiral ridges in interspaces very faint and rather densely arranged, visible only in SEM. Colour light goldish or yellowish brown.

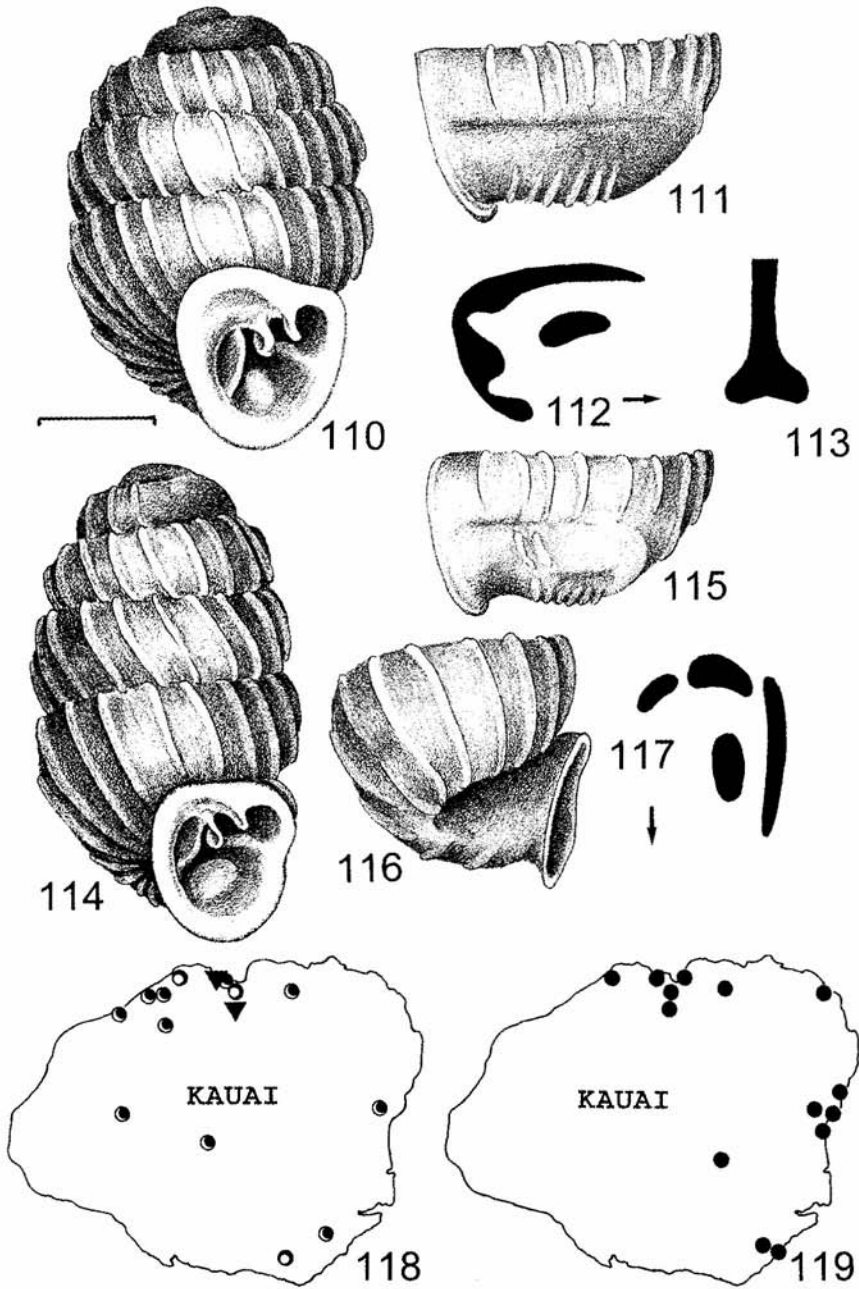
DISTRIBUTION

Kauai; recent and subfossil. Fig. 118.

NOTE

PILSBRY & COOKE (1918-1920) suggested that DALL's (1890) *cubana* and their own *thausasia* might be very closely related, nonetheless they described the latter species as new. DALL's (1890) and PILSBRY & COOKE's (1918-1920) descriptions of *cubana* agree very closely with specimens of *thausasia*, and DALL's only specimen is within the variability range. DALL's (1890) name, even if inadequate, is older. BOSS et al. (1968) erroneously state Cuba as the type locality of *cubana*, repeating it after

110-113. *L. cubana* (DALL): 110-111 - paratype of *L. thausasia* COOKE et PILSBRY, BM 15575, Hanakapiai, Kauai: 110 - front view, 111 - side view of body whorl, 112 - top view of palatals and basal, columellar wall removed, diagrammatic, arrow indicates aperture; 113 - cross-section through the mid part of parietal in *L. cubana* (DALL) and *L. captiosa* n. sp., diagrammatic. 114-117. *L. captiosa* n. sp.: 114-116 - holotype, BM 19521, Wailua, Kauai: 114 - front view, 115 - side view of body whorl, 116 - oblique umbilical view of body whorl. Scale bar 0.5 mm. 117 - top view of palatals and basal, columellar wall removed, diagrammatic, arrow indicates aperture. 118. Distribution of *L. cubana* (DALL): white-margined circles - recent, black-margined circles - subfossil, triangles - recent and subfossil. 119. Distribution of *L. captiosa* n. sp.



DALL (1890: 2) who commented on his specimen as follows: "It was received from the collection of the late Dr. SHURTLEFF, now belonging to Wesleyan University, Middletown, Conn., and was obtained by him from the late Prof. C. B. ADAMS, or at least still occupies the tiny glass tube, stopped with sealing wax [...] and a tiny label on which is written 'Pupa... Cuba' in Professor ADAMS' well-known chirography". According to PILSBRY & COOKE (1918-1920: 269) "There can be little doubt that the locality Cuba was an error. Professor ADAMS received and described land shells from the Hawaiian Islands [...]".

Lyropupa captiosa n. sp.

Figures 114-117, 119.

TYPE LOCALITY

Wailua, Kauai.

TYPE MATERIAL

Wailua, Kauai: Holotype & ca. 5000 paratypes, BM 19521; ca. 1000 paratypes, BM 16057; 73 paratypes, BM 16057; 13 paratypes, BM 19456; ca. 100 paratypes, BM 19474; ca. 1000 paratypes, BM 19475; 67 paratypes, BM 19515; 10 paratypes, BM 19517; 22 paratypes, BM 19520; 19 paratypes, BM 19520; ca. 1000 paratypes, BM 19521; 18 paratypes, BM 20895; 23 paratypes, BM 20909; ca. 200 paratypes, BM 20909; ca. 200 paratypes, BM 20909; ca. 100 paratypes, BM 37613; ca. 100 paratypes, BM 37640; 17 paratypes, BM 100119; 138 paratypes, BM 100120; 381 paratypes, BM 210170; 9 paratypes, BM 210171; 50 paratypes, MNHW ex BM 19521; Nounou, Kauai: 12 paratypes, BM 81047.

OTHER MATERIAL EXAMINED

Kauai: Aweoweonui, BM: 100548, 3; Haena, BM: 167635, 5; 168347, 5; 184352, 91; 190761, 2; 212082, 1; Hanalei, BM: 180555, 1; Hanamaulu, BM: 116628, 74; 116661, 748; 116662, 1; 118571, 82; 118606, 220; 118608, 1; 118609, 4; 118633, 1; 119006, ca. 300; 119007, ca. 3000; 119064, ca. 300; 167987, 10; 167988, ca. 200; Kalihikai, BM: 77904, 2; 77936, 12; 100242, 4; 118652, 3; 190490, 26; 190592, 42; Kapaa, BM: 19238 ex 19550, 1; 19438, 56; 19550, 27; 49283, 4; 49300, 1; 212213, 2; Limahuli, BM: 124174, 9; 124302, 28; 124303, 1; 124330, 1; 168364, 1; 184303, 8; ex 184304, f; Mahaulepu, BM: 52094, 14; 78032, 52; 78131, 1; 78167, 5; 100364, 15; 100435, 4; 100435, 28; 100486, 11; 116793, 3; 118734, 3; 118765, 5; 190463, 8; Moloaa, BM: 190517, 10; 190563, 2; 210120, 6; Wailua, 19237 ex 19473, 5; 19472, 5; 19516, 1; 49253, 1; 49262, 3; Waipa, BM: 86293, 4; ex 26293, 1; Waipaa, BM: 100304, 7; Waipouli, BM: 78196, 42; 100167, 91; 118969, 41; no exact locality, BM: 190373, 8.

DIAGNOSE

A sister species to *cubana*. It differs from the latter in the following characters: 1. much narrower shell with less convex spire; 2. less expanded and detached or trumpet-like parietal callus; 3. fewer ribs on penultimate whorl; 4. coarser and wider spaced ribs; 5. less flattened and less thickened edge of parietal; 6. more bent and thicker angular, resulting in a smaller and more closed sinulus; 7. thicker lip; 8. outer part of lower palatal broader and generally bigger; 9. upper palatal of much more even height; 10. inner part of lower palatal not united with upper palatal; 11. basal not united with the inner part of lower palatal; 12. narrower umbilicus; 13. columellar in

front view smaller as a result of somewhat more oblique position; 14. more subquadrate aperture; 15. lower impression on body whorl deeper, upper present (in *cubana* absent).

DESCRIPTION

Shell dextrous, oval to elongatedly so; spire almost straight, tapered; apex bluntly rounded. Whorls 4.9-5.4 (holotype 5.3), moderately convex; suture moderately deep. H: 1.83-2.21 mm (holotype 2.04); B: 1.03-1.17 mm (holotype 1.13); h: 0.63-0.75 mm (holotype 0.70); b: 0.63-0.74 mm (holotype 0.67); bw: 1.05-1.17 mm (holotype 1.09). H/B: 1.63-2.08 (holotype 1.81); bw/H: 0.49-0.60 (holotype 0.53). Aperture semi-oval or subquadrate; sinulus almost closed. Lip detached, sometimes forming a short trumpet; reflexed, rather broad and fairly thick. In aperture 6 teeth. Columellar from well to partly visible, or almost invisible in front view; takes entire columellar wall; thin lamellate with thicker edges; in top view crescentic, with both ends produced towards lip. Parietal ca. 1/5 whorl long; high and thin with thicker edges; highest in its inner half; its mid 2/3 free margin widened and flattened; somewhat deflected palatalwards. Angular high and thin; ca. 2/3 parietal long; overlaps it for 1/2 length; somewhat deflected palatalwards; reaches lip. Upper palatal ca. 1/3 whorl long; inner end invisible in front view; division into parts distinct: part facing angular low lamellate; part facing parietal high lamellate; not recessed from lip. Lower palatal split: outer part as a big, robust, simple tubercle; inner part like a high, blunt tooth set just before the end of upper palatal; free. Basal elongate tubercular; set in line with the inner part of lower palatal; free. Body whorl profile with lower half devoid of ribs or nearly so; a flattening or a shallow impression corresponds to lower palatal; behind and below the impression a very weak hump; a narrow, shallow impression corresponds to the part of upper palatal closer to lip; both impressions convergent. Body whorl suture straight. Umbilicus narrow, deep, circular, only slightly distorted by body whorl. Sculpture regular, of 14-21, most often 16-19 (holotype 17) ribs on penultimate whorl; ribs coarse, blunt, not flexuous, 1/5-1/4 interspace thick. Faint and incomplete traces of spiral ridges in interspaces visible in SEM. Colour white, yellowish or greyish.

NAME DERIVATION

The name means deceptive; the new species did its utmost to be mistaken for *cubana*.

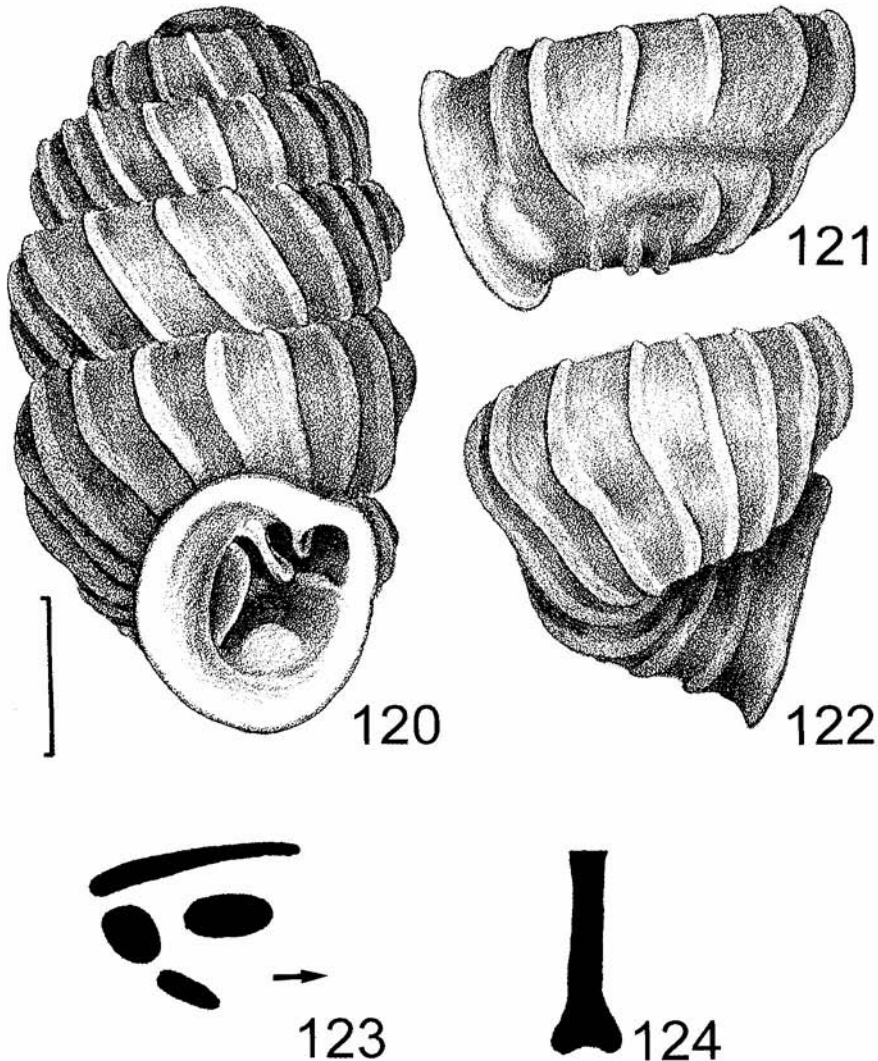
DISTRIBUTION

Kauai; subfossil. Fig. 119.

Lyropupa plagiptyx PILSBRY et COOKE, 1920

Figures 101, 120-124.

Lyropupa plagiptyx PILSBRY & COOKE 1918-1920: 267-268, pl.24, figs 8, 11, 12. Type locality: Kawaihapai, Oahu. Paratype: BM 35648.



120-124. *L. plagiptyx* PILSBRY et COOKE: 120-122 - BM 173314, Kealia, Oahu: 120 - front view, 121 - side view of body whorl, 122 - oblique umbilical view of body whorl. Scale bar 0.5 mm. 123 - top view of palatals and basal, columellar wall removed, diagrammatic, arrow indicates aperture; 124 - cross-section through the mid part of parietal, diagrammatic.

MATERIAL EXAMINED

Oahu: Haili, BM: 175914, ca. 20; Kaena Pt., BM: 11602 ex 42985, 1; Kaluakauila, BM: 211919, ca. 20; Kamanai, BM: 172678, ca. 50; 172694, ca. 20; Kawaihapai, BM: 35648, paratype; 35648, 1; 174532, 1; Kealia, BM: 173314, ca. 300; Makua, BM: 42923, 10; 211891, ca. 20; Nanakuli, BM: 177519, 4; 177520, 15.

DESCRIPTION

Shell dextrous, ovate to elongatedly so, as a result of ribbing somewhat angular; spire straight (disregarding shouldered whorls); apex gently rounded. Whorls 4.9-5.5, shouldered; suture deep. H: 1.97-2.31 mm; B: 1.08-1.30 mm; h: 0.67-0.82 mm; b: 0.65-0.78 mm; bw: 1.11-1.28 mm; H/B: 1.58-1.90; bw/H: 0.54-0.59. Aperture semi-oval; sinus distinct. Lip detached, rarely forming a short trumpet; moderately reflexed, moderately broad, thick. In aperture 6 teeth. Columellar partly or wholly invisible in front view; takes entire columellar wall; thin lamellate with thicker edges; in top view crescentic, with upper end much more produced towards lip than the lower. Parietal ca. 1/4 whorl; high and thin with somewhat thicker edges; highest behind middle; in top view crescentic, with inner end bent towards columella; its outer half slightly deflected palatalwards, with very slightly or slightly broadened and flattened free margin. Angular high and thin; equals parietal in length and overlaps it for 1/2 length; somewhat deflected palatalwards; reaches lip. Upper palatal ca. 1/3 whorl long; inner end invisible in front view; division into parts distinct: part facing angular low lamellate; part facing parietal fairly high lamellate; not recessed from lip. Lower palatal split: its outer part elongate tubercular, in front view often tooth-like; inner part like a high, blunt tooth, set well before the end of upper palatal; free. Basal elongate tubercular, set in line with the inner part of lower palatal; free. Body whorl profile ribbed only in its upper part and at very base; its middle bare; two shallow but distinct impressions correspond to palatals; convergent; just between the lower impression and lip a small hump resembling an enlarged rib; in some shells hump absent. Body whorl suture straight. Umbilicus oval, open, deep. Sculpture regular and very coarse, of 13-18, most often 15-17 ribs on penultimate whorl; ribs coarse, very prominent, blunt, slightly flexuous, on upper halves of whorls higher than on lower; 1/5-1/4 interspace thick. Faint and incomplete traces of spiral ridges in interspaces visible only in SEM. Colour light brown or dirty white.

DISTRIBUTION

Oahu; subfossil. Fig. 101.

NOTE

Apart from the inner part of lower palatal, *plagiopyx* differs from typical shells of *ovatula* in more convex and more shouldered whorls, coarser and blunter ribs, lower outer part of upper palatal, shallower impressions on body whorl, posterior bump on body whorl absent or nearly so, anterior bump always present and poorly marked basal crest. In shape and ribbing it may resemble specimens of *ovatula* described as ssp. *kona*, but differs from them, besides the inner part of lower palatal,

in shallower impressions on body whorl and in posterior bump on body whorl much weaker, even if present.

***Lycopupa ovatula* COOKE et PILSBRY, 1920**

Figures 125-133.

Lycopupa ovatula COOKE et PILSBRY, in PILSBRY & COOKE 1918-1920: 265-266, pl.23, fig.11; pl.24, figs 1-5. Type locality: Kaelepulu, Oahu. Paratypes: BM 35648.

Lycopupa ovatula kona PILSBRY & COOKE 1918-1920: 266-267, pl.26, figs 5, 10, 11, 14. Type locality: North Kona at Huehue, Hawaii. Paratypes: BM 42599.

MATERIAL EXAMINED

Oahu: Diamond Head, BM: 10265 ex 15216, 1 f; Ewa Plain, BM: 77690, 9 f; Kaelepulu, BM: 40962, 1 f; Kahala, BM: 45373, 14 f; Kailua, BM: 10262 ex 35713, 1 f; 10263 ex 35736, 1 f; 35763, ca. 20 f; 40961, 25 paratypes f of *ovatula*; 53598, 5 f; 77573, ca. 30 f; 77609, 137 f; 77643, 9 f; 77644, ca. 20 f; 189620, 2 f; Kawailoa, BM: 10264 ex 38317, 1 f; Koko Head, BM: 20549, 1 f; 168842, 1 f; Manoa, BM: 10266 ex 39836, 2 f; 11059, 2 f; 12417, 8 f; 12418, 5 f; 12422, 13 f; 16667, 1 f; 38319, ca. 20 f; 39836, ca. 20 f; 39938, ca. 20 f; 43388, ca. 20 f; 43530, 3 f; 45281, ca. 30 f; ex 43232, 2 f; Round Top, BM: 39902, 2 f; Wailupe, BM: 93676, ca. 20 f; Waimanalo, BM: 40902, 3 f; 172780, 12 f; 172806, 1 f.

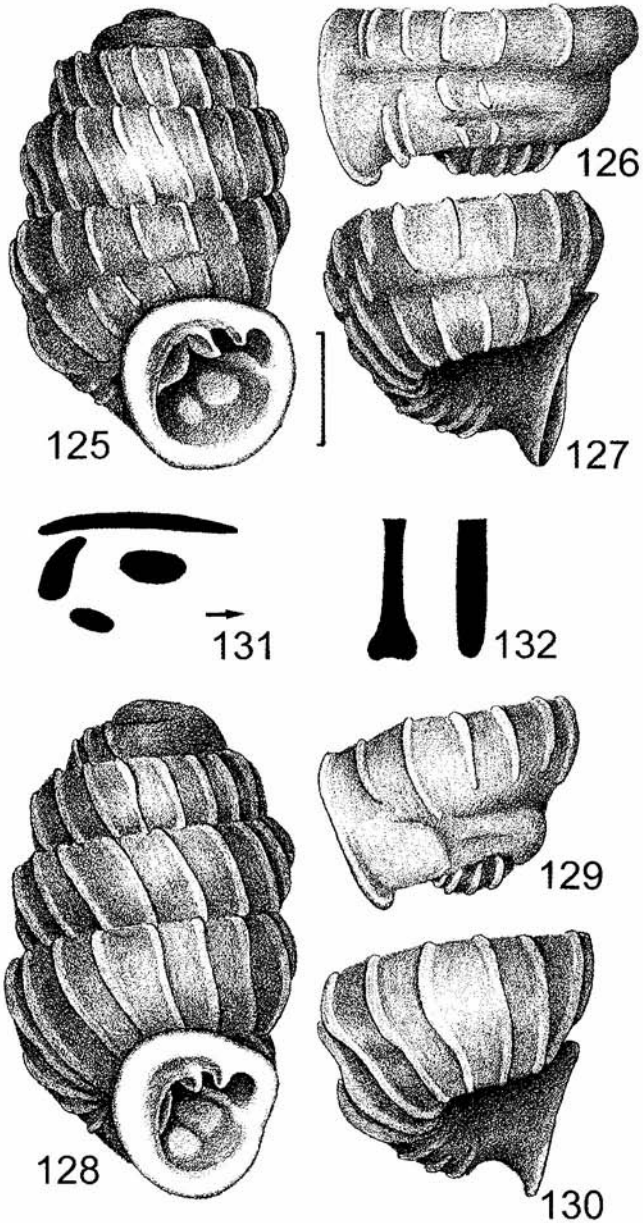
Lanai: Maunalei, BM: 59898, ca. 4000 f; 59900, 12 f; ex 59896, 1 f; no exact locality, BM: 45530, 1 f.

Molokai: Kaiehu, BM: 11094 ex 45577, 1 f; 184499, 15 f; 184500, 12 f; Kailio Pt., BM: 37433, 1 f; Kalainawawaa, BM: 40157, 1 f; 47441, 3 f; 52358, 9 f; 52371, 4 f; Moomomi, BM: 33434, 1 f.

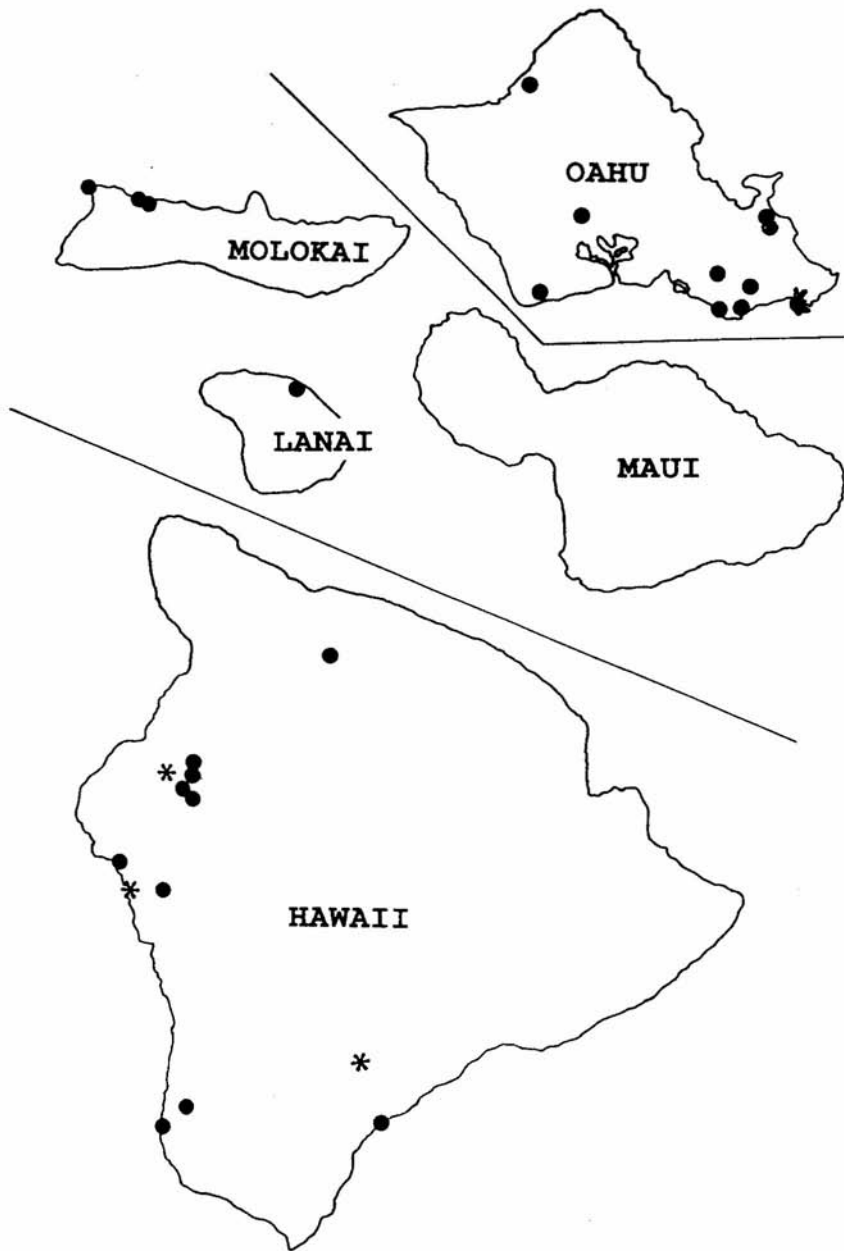
Hawaii: Honomalino, BM: 47279, 16 f; Huehue, BM: 42599, 36 paratypes f of *ovatula kona*; 42600, 264 f; Kapua, BM: 46211, 4 f; Kau, BM: 77364, 1 f; 77425, ca. 400 r; ex 77425, 1 f; Kaupulehu, BM: 11626 ex 39515, 2 f; 42642, ca. 20 f; 42643, 3 f; Kona S, BM: 47279, 17 f; ex 47279, 1 f; ex 47279, 11 f; Mana, BM: 12437, ca. 100 f; Punaluu, BM: 47253, 17 f; Puuanahulu, BM: 11631 ex 49833, 8 f; 11633 ex 50064, 5 f; Puuhuluhulu, BM: 11628 ex 49694, 6 f; Puu Iki, BM: 11632 ex 50020, 3 f; Puuwaawaa, BM: 11109, 25 f; 11627 ex 38787, 11 f; 47912, 1 r; 50020, ca. 300 r; 192209, 426 f; ex 50020, 4 f; Waiaha, BM: 42676, ca. 20 f; ex 42625, 5 r; Waihou, BM: 11629 ex 49769, 3 f; 11630 ex 49797, 8 f; no exact locality, BM: 39810, 1 f.

DESCRIPTION

Shell dextrous, oval to somewhat elongatedly oval; spire poorly convex or straight, tapered; apex gently rounded. Whorls 4.7-5.1, rather flat, upper shouldered; suture shallow. H: 1.96-2.66 mm; B: 1.10-1.40 mm; h: 0.71-0.99 mm; b: 0.68-0.96 mm; bw: 1.15-1.51 mm. H/B: 1.66-2.05; bw/H: 0.49-0.58. Aperture semi-oval; sinulus distinct. Lip detached, sometimes forming a short trumpet; well reflexed, fairly broad, thick. In aperture 7 teeth. Columellar visible or partly invisible in front view, takes entire columellar wall; thin lamellate with thicker edges; in top view somewhat crescentic, with lower end more produced towards lip than the upper. Parietal ca. 1/6 whorl long; thin lamellate with somewhat thicker edges; high; highest behind middle; outer part somewhat deflected palatalwards; in top view slightly crescentic, inner end bent towards columella; simple or its free margin very slightly broadened in its outer 1/3. Angular high and thin, somewhat deflected palatalwards; equals parietal in length and overlaps it 1/2 length. Upper palatal ca. 1/3 whorl long;



125-132. *L. ovatula* COOKE et PILSBRY: 125-127 - BM 42600, Huehue, Hawaii: 125 - front view, 126 - side view of body whorl, 127 - oblique umbilical view of body whorl; 128-130 - paratype of *L. ovatula kona* PILSBRY et COOKE, BM 42599, Huehue, Hawaii: 128 - front view, 129 - side view of body whorl, 130 - oblique umbilical view of body whorl. Scale bar 0.5 mm. 131 - top view of palatals and basal columellar wall removed, diagrammatic, arrow indicates aperture; 132 - cross-section through the mid part of parietal, diagrammatic.



133 - Distribution of *L. ovatula* COOKE et PILSBRY: circles - subfossil, asterisks - recent and subfossil.

its inner end invisible without destroying the shell; division into parts distinct: part facing angular low lamellate; part facing parietal higher; somewhat recessed from lip. Lower palatal split: its outer part broad, robust, elongatedly tubercular; inner part comma-shaped; starting well before the end of upper palatal; free. Basal elongate tubercular; forms an approximately right angle with the inner part of lower palatal. False basal robust, parallel to the outer part of lower palatal. Body whorl profile wholly ribbed, with 3 parallel impressions of nearly equal length, and a basidorsal hump and basal crest. In some shells on the side of body whorl two bumps, pronounced to various degree, often very strongly. Body whorl suture straight. Umbilicus oval, narrow, deep, open. Sculpture regular, of 14-21 ribs on penultimate whorl; ribs coarse, blunt to rather sharp, slightly flexuous; on umbilical side of body whorl some few may be split in halves, with halves shifted relative to each other; 1/5-1/4 interspace thick. Spiral ridges in interspaces rather closely spaced, fine, indistinct, visible only in SEM. Colour light yellowish-greyish brown or chestnut brown.

DISTRIBUTION

Lanai, most probably subfossil only; Molokai, subfossil; Hawaii, recent and subfossil; Oahu, subfossil. Fig. 133.

NOTE

The form with prominent bumps on body whorl was described as a subspecies *ovatula kona* (PILSBRY & COOKE 1918-1920). The tendency to form such bumps is expressed in nearly all populations, and whenever material is sufficiently abundant, such specimens are found, and are especially frequent on Oahu and Hawaii, but present also on Lanai and Molokai. They seem to represent a morphological form rather than a subspecies. Some Hawaiian shells, both subfossil and recent, differ from those from Oahu in more shouldered whorls, somewhat sharper ribs and longer impressions on body whorl; fresh shells are greyish brown; false basal is more robust, often elongatedly oval; in some shells lip forms a short trumpet; in some populations shells are chestnut brown and apertures are smaller relative to the entire shell; some shells are very elongatedly oval to almost cylindrical; some have incipient bumps on the side of body whorl. Subfossil shells from Mana, Hawaii, are bigger, their apertures are broad relative to the entire shell, they are oval and have no bumps whatsoever. Lanaian shells are much like specimens from Hawaii, but the aperture is bigger and ribs somewhat blunter.

Lyropupa micra COOKE et PILSBRY, 1920

Figures 134-139, 146.

Lyropupa micra COOKE et PILSBRY, in PILSBRY & COOKE 1918-1920: 263-264, pl.23, fig.7; pl.25, figs 5-7. Type locality: Kaelepu, Kailua, Oahu. Paratypes: BM 11092.

Lyropupa micra percostata PILSBRY & COOKE 1918-1920: 264, pl.25, figs 11, 12. Type locality: Kaelepu, Kailua, Oahu. Paratypes: BM 11093, 2 lots 11104.

Lyropupa micra maunaloae PILSBRY & COOKE 1918-1920: 264, pl.25, figs 8, 9. Type locality: Mauna Loa, Molokai. Paratypes: BM 37411.

MATERIAL EXAMINED

micra micra

Oahu: Diamond Head, BM: 10273 ex 12425, 2 r; 10274 ex 15216, 1 r; Ewa, BM: 35608, 3 f; Haili, BM: 175913, 52 f; Kaelepulu, BM: 11056, 1 r; 11092, 25 paratypes r of *micra*; 11093, 20 paratypes r of *micra percostata*; Kahala, BM: 45374, 13 f; Kahuku, BM: 11597 ex 45002, 1 r; 11598 ex 45002, 1 r; 181073, 1 r; Kahuku Pt., BM: 210205, 1 f; 210365, 1 f; Kailua, BM: 10269 ex 35761, 6 r; 10270 ex 38317, 2 r; 10271 ex 35713, 1 r; 10272 ex 35736, 13 r; 10276 ex 35713, 4 r; 10277 ex 35736, 25 f; 10278 ex 35762, ca. 20 r; 11104, 8 paratypes r of *micra percostata*; 11104, 30 paratypes r of *micra percostata*; 11590 ex 35762, 21 r; 35761, ca. 20 f; 40964, 9 r; 40965, ca. 50 f; 52600, 2 f; 77572, 18 r; 77608, 10 r; 77642, 23 r; 189618, 3 f; 189619, 4 f; ex 77607, ca. 75 r; Kawaihapai, BM: 40819, 2 f; Kawailoa, BM: 11107, 22 f; 11593 ex 44615, 6 f; 11595 ex 44908, 3 f; 11596 ex 44926, 2 f; 11599 ex 44954, 9 r; 11600 ex 40839, 2 r; Keekee Gulch, BM: 129169, 1 r; Koko Head, BM: 20537, 3 f; 168844, 2 f; Lanikai, BM: 119370, 1 r; Makua, BM: 35365, 3 f; 42945, 1 f; 42972, 4 r; 107676, ca. 20 r; Malakahana, BM: 11594 ex 44751, 1 r; Manoa, BM: 12424, 4 f; 16666, 1 f; 38318, 15 f; 39837, 11 f; 39839, 75 f; 170183, 5 f; 170184, 1 f; Manuwaikaalāi, BM: 176410, 2 f; Maunaloa, BM: 98955, 1 r; Mokapu, BM: 10275 ex 42253, 1 r; Mokuleia, BM: 43626, 1 r; Nanakuli, BM: 89957, 1 r; 89963, 1 r; 177521, ca. 30 r; 177523, ca. 20 r; Pupukea, BM: 175678, 2 f; 175698, 1 f; 175715, ca. 20 f; Waialeale, BM: 176113, 6 f; Waialele, BM: 173115, 66 f; Wailupe, BM: 93677, ca. 20 f; Waimanalo, BM: 11592 ex 40899, 4 r; 40881, 4 f; 40898, ca. 20 f; 40899, 17 f; 171781, 13 f; 172779, ca. 80 f; 172809, ca. 30 f; 172829, ca. 30 f; 172852, ca. 20 r; 172853, 6 f; 183217, 14 f; 183218, 7 f; Waipio, BM: 11591 ex 40964, 5 r.

Molokai: Kaiehu, BM: 11603 ex 45577, 1 r; 11606 ex 47391, 2 r; 184523, 8 f; Kailio Pt., BM: 11605 ex 37432, 8 r; Kalainawawaa, BM: 11607 ex 47420, 4 r; 47440, 7 r; 52370, ca. 20 r; Moomomi, BM: 167946, 2 f; 167947, 1 f; 184433, 1 f; 184434, 1 f; Mauna Loa, BM: 37411, 2 paratypes of *micra maunaloae*, f; 37487, 13 r; 37487, 9 r; 37487, 1 r; 37487, ca. 20 f.

Lanai: Kaohai, BM: 104044, 156 f.

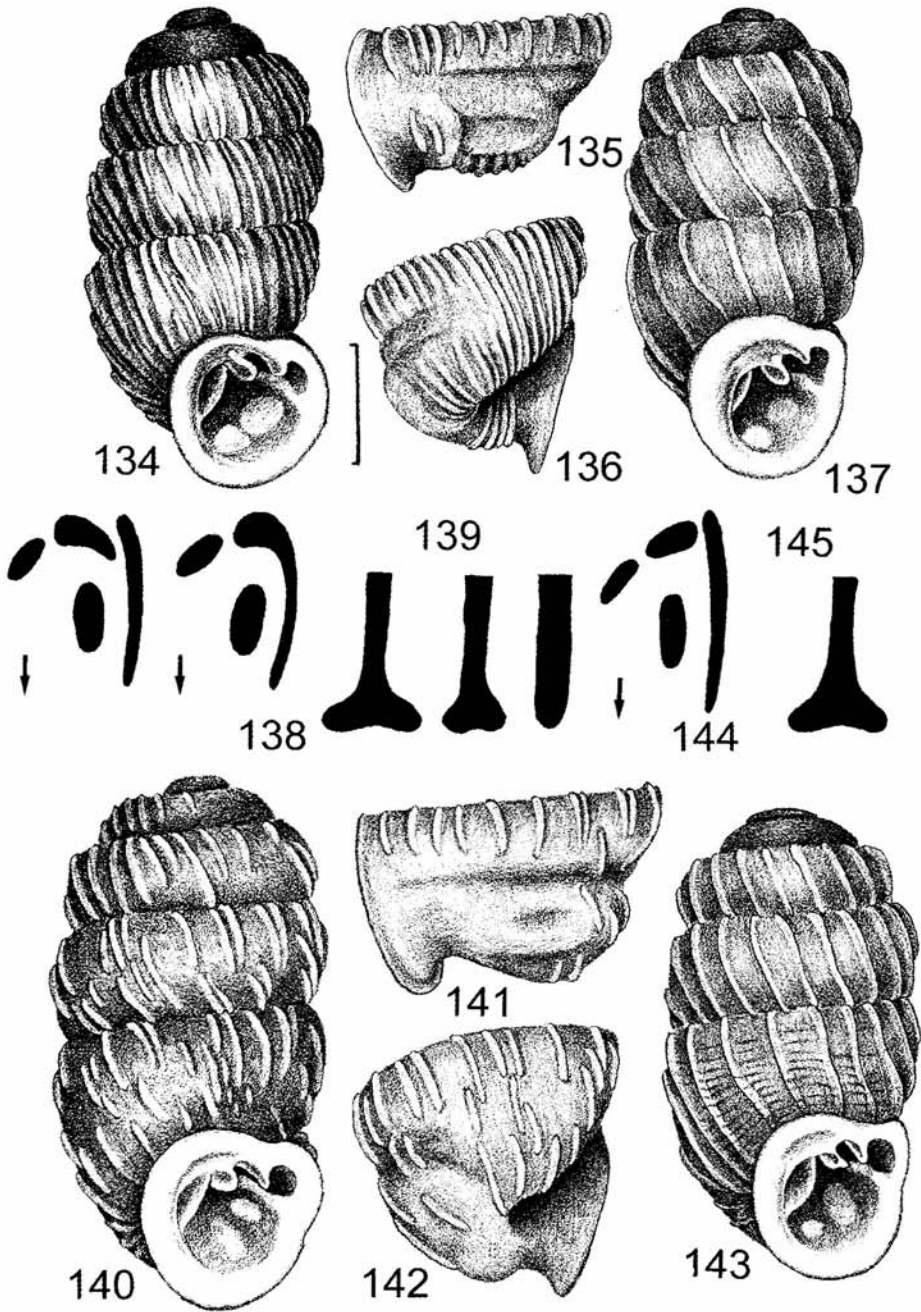
Maui W: Alaeloa, BM: 167863, 7 f; 167897, 1 f; Mahinahina, BM: 59996, 9 r; 167925, 3 f; Waihee, BM: 77718, 3 r.

See also *micra continua* ssp. n.

DESCRIPTION

Shell dextrous, ovate with both ends equally narrow or nearly so, from short to elongate; spire convex; apex gently rounded. Whorls 4.6-5.4, flat; suture shallow. H: 1.65-2.18 mm; B: 85-1.06 mm; h: 0.56-0.78 mm; b: 0.56-0.80 mm; bw: 0.96-1.29

134-139. *L. micra* COOKE et PILSBRY: 134-136 - *L. micra micra* COOKE et PILSBRY, BM 39837, Rocky Hill, Oahu: 134 - front view, 135 - side view of body whorl, 136 - oblique umbilical view of body whorl; 137 - *L. micra continua* n. ssp., holotype, BM 52319, Koloa, Kauai, front view; 138 - top view of palatals and basal in *micra micra* (left) and *micra continua* n. ssp. (right), columellar wall removed, diagrammatic, arrow indicates aperture; 139 - cross-section through the mid part of parietal in 3 shells, diagrammatic. Figs 140-145. *L. lualualei* n. sp.: 140-142 - paratype, BM ex 173183, Halona, Lualualei, Oahu: 140 - front view, 141 - side view of body whorl, 142 - oblique umbilical view of body whorl; 143 - holotype, BM 173182, Halona, Lualualei, Oahu, front view. Scale bar 0.5 mm. 144 - top view of palatals and basal, columellar wall removed, diagrammatic, arrow indicates aperture; 145 - cross-section through the mid part of parietal.



mm; H/B: 1.76-2.05; bw/H: 0.59-0.61. Aperture obliquely pear-shaped; sinus "pulled out" and almost closed. Lip slightly to distinctly detached; not much reflexed, narrow but thick. In aperture 7 teeth. Columellar in front view partly or wholly invisible; takes entire columellar wall; thin lamellate with thicker edges; in top view almost straight, with both ends very slightly produced towards lip. Parietal ca. 1/5 whorl long; high and thin lamellate with thicker edges; highest in its inner half; in top view crescentic, with inner end bent towards columella; outer 2/3 free margin broadened and flattened, in some shells rather strongly; rarely simple; slightly deflected palatalwards. Angular high and thin; as long as parietal, overlaps it for 1/2 length; slightly deflected palatalwards. Upper palatal ca. 1/4 whorl long; its inner end invisible in front view; division into parts indistinct: part facing angular lower, part facing parietal somewhat higher lamellate; not recessed from lip. Lower palatal split: outer part elongatedly tubercular, in front view robust, transverse tubercular or (Kauaian shells) callus-like diffuse; inner part free, comma-shaped, starting well before the inner end of upper palatal or (Kauaian shells) accreted to the inner end of upper palatal. Basal elongated tubercular, free; set in line with broad end of the inner part of lower palatal (when the latter accreted) or at an obtuse angle to it (when not). False basal present, nearly as big as the outer part of lower palatal, parallel to it. Body whorl profile rarely wholly ribbed, most often only its upper and basalmost parts ribbed, middle bare; on body whorl 3 parallel narrow impressions corresponding to the upper palatal (the longest), lower palatal (medium) and false basal (the shortest); behind and below them a pronounced, crescentic basidorsal hump terminating below the upper palatal. Body whorl suture straight. Umbilicus from narrow, slit-like open to nearly sealed. Sculpture irregular to almost random; of 19-45 ribs on penultimate whorl; ribs from fine blunt and somewhat flexuous to sharp, irregular, incomplete and grouped in pairs or triplets; 1/3-1/2 interspaces thick; some subfossil shells nearly devoid of ribs probably as a result of corrosion in the deposit. Spiral ridges in interspaces faint, vestigial, visible only in SEM. Colour brownish or greyish white, or very light creamy yellow, semitransparent; most shells orange-coloured by soil.

DISTRIBUTION

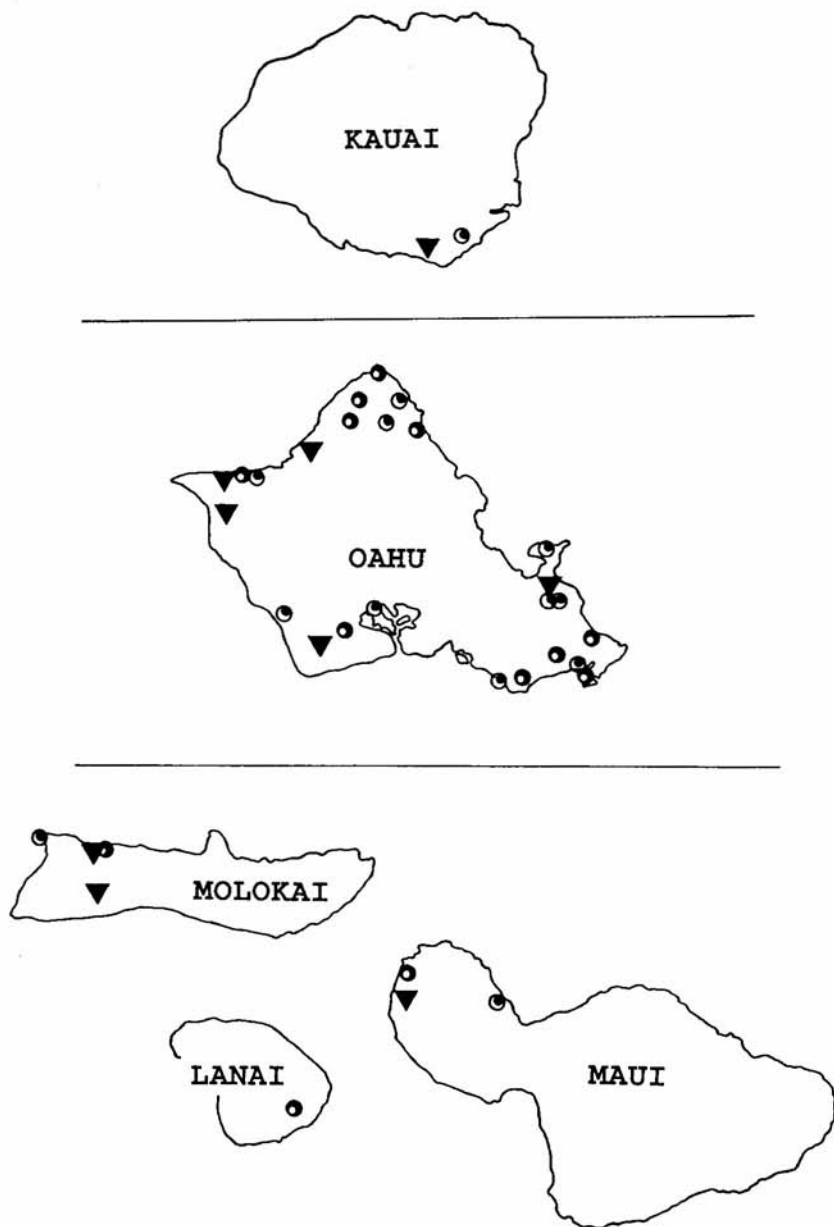
Oahu, Maui, Molokai, Lanai; subfossil and recent. Fig. 146.

- *Lyropupa micra continua* ssp. n.**TYPE LOCALITY**

Koloa, Kauai.

TYPE MATERIAL

Koloa, Kauai: Holotype & 60 paratypes f, BM 52319; 230 paratypes r, BM 52052; 26 paratypes r, MNHW ex BM 52052; Mahaulepu, Kauai: ca. 50 paratypes r, BM 52092.



146. Distribution of *L. micra* COOKE et PILSBRY: white margined circles - recent, black-margined circles - subfossil, triangles - recent and subfossil.

DIAGNOSE

The new subspecies differs from *micra* s.s. in 1. much smaller, diffuse outer part of the lower palatal; 2. accreted inner part of lower palatal; 3. more prominent and wider spaced ribs. Shell of 4.7-5.3 whorls (holotype 5.1), 19-33 (holotype 19) ribs on penultimate whorl. H: 1.78-2.05 mm (holotype 1.96); B: 0.91-1.00 mm (holotype 0.97); h: 0.60-0.70 mm (holotype 0.69); b: 0.60-0.70 mm (holotype 0.66); bw: 1.03-1.16 mm (holotype 1.10); H/B: 1.87-2.13 (holotype 2.02); bw/H: 0.55-0.60 (holotype 0.56). Except these characters all the above description of *micra* s.s. is valid also for the new subspecies.

NAME DERIVATION

The name (*continua*=continuous) refers to the inner part of lower palatal which is continuous with the inner end of upper palatal.

DISTRIBUTION

Kauai; subfossil and recent. Fig. 146.

***Lyropupa lualualeiensis* n. sp.**

Figures 101, 140-145.

TYPE LOCALITY

Halona, Lualualei, Oahu.

TYPE MATERIAL

Halona, Lualualei, Oahu: Holotype & ca. 500 paratypes r, BM ex 173183; 77 paratypes r, BM 173182; 20 paratypes r, MNHW ex BM ex 173183; Lualualei, Oahu: 4 paratypes, BM ex 112856.

OTHER MATERIAL EXAMINED

Oahu: Nanakuli, BM: 54035, 2 r, Popouwela, BM: ex 172710, 18 r, Pualii, BM: ex 176733, 4 f, Pukaloa, BM: ex 174401, 1 f.

DIAGNOSE

The new species may at first glance resemble *costata* or *micra* (its sister species). It differs from the former in 1. much smaller aperture compared to the entire shell; 2. broadened and flattened free margin of parietal; 3. inner end of upper palatal and inner part of lower palatal wholly invisible in front view; 4. more thickened lip; 5. pronounced basidorsal hump like in *micra*; 6. more closed sinulus. It differs from the latter in 1. being much broader; 2. having more prominent and more regular, wider spaced ribs; 3. much more broadened and flattened free margin of parietal.

DESCRIPTION

Shell dextrous; tumid ovate-cylindrical; spire convex; apex broadly rounded. Whorls 4.8-5.4 (holotype 5.0), flat; suture moderately deep. H: 1.76-2.16 mm (holotype

1.94); B: 1.00-1.16 mm (holotype 1.05); h: 0.63-0.76 mm (holotype 0.70); b: 0.64-0.78 mm (holotype 0.69); bw: 1.03-1.21 mm (holotype 1.14); H/B: 1.67-1.90 (holotype 1.85); bw/H: 0.55-0.62 (holotype 0.59). Aperture almost circular, except "pulled out" sinus. Lip slightly detached, narrow, somewhat reflexed, well thickened. In aperture 7 teeth. Columellar in front view invisible or nearly so; takes whole columellar wall; thin lamellate with thicker edges; in top view rather strongly crescentic, with both ends equally produced towards lip. Parietal ca. 1/5 whorl long; high and thin with thicker edges; highest in its inner 1/3; in top view crescentic, with inner end bent towards columella; external 2/3 of free margin very strongly broadened and flattened; slightly deflected palatalwards. Angular high and thin; as long as parietal and overlapping it for 1/2 length; reaches lip; somewhat deflected palatalwards. Upper palatal over 1/4 whorl long; inner end invisible in front view; division into parts very indistinct: part facing angular somewhat lower lamellate than that facing parietal; not recessed from lip. Lower palatal split: outer part in front view flat, broad tubercular, in top view elongated; inner part like a short, blunt tooth set perpendicular to the inner end of upper palatal; free. Basal elongatedly tubercular; set in line with the inner part of lower palatal; free. False basal present, prominent, parallel to the outer part of lower palatal. Body whorl profile wholly ribbed; with 3 parallel impressions: the longest corresponds to the upper palatal, the shortest to the outer part of lower palatal, the medium to the false basal; crescentic basidorsal hump terminates below the upper palatal. Body whorl suture straight. Umbilicus deep, open, oval; narrow. Sculpture fairly regular, of 19-32 (holotype 20) ribs on penultimate whorl. Ribs moderately coarse, rather blunt, of even height, slightly flexuous; on body whorl some may break in halves and halves are displaced relative to each other; 1/8-1/6 interspace thick; in some shells ribs tend to be grouped in twos or triplets and incomplete. Ribbing varies within populations. Spiral ridges in interspaces rather densely arranged, visible only in SEM or under stereomicroscope. Colour light yellowish or goldish brown.

NAME DERIVATION

The name is derived from the name of the type locality - Lualualei.

DISTRIBUTION

Oahu; recent and subfossil. Fig. 101.

V. PHYLOGENETIC ANALYSIS

CHARACTER ANALYSIS

Homoplasy is common among the pupilloids (POKRYSZKO 1994) which results in serious difficulties when attempting phylogenetic inferences, and requires additional assumptions and especially careful character analysis. Essentially, the genus *Nesopupa* PILSBRY was assumed as out-group (synapomorphies: finely wrinkled sculpture of interspaces, calcareous-periostracal ribs, gonad reduced to two lobes of few acini each, albeit with the reservation that the latter character may be size-correlated; cf.

POKRYSZKO 1994). Because relationships within the pupilloids are still far from being understood, several other genera had to be referred to in obscure cases, despite some objections to such an approach (e.g. FOREY et al. 1995).

Together, 23 characters were used, with 49 character states. Most were binary; the few multistate characters which were evidently ordered as indicated by their individual variation (3, 4, 12, 16 in the matrix) were coded additively. The character matrix is presented in Table 1. Species autapomorphies and generic synapomorphies were excluded from the analysis in order not to overestimate the consistency index (BROOKS et al. 1986). The cladogram was constructed with Hennig86 programme.

The greatest significance was attributed to those characters that generally appear rarely or not at all in other pupilloid taxa: 1. spiral sculpture of embryonic whorls and 2. of definitive whorls, 3. radial arrangement of fine wrinkles in the interspaces, 4. special transformations of angular tooth (see below), 5. displacement of parietal tooth behind the angular, 6. shift of basal tooth far behind columellar, 7. lower palatal tooth recessed and displaced towards the upper, 8. free margin of parietal tooth flattened and dilated. For such characters homoplasy was "forbidden". The first five of them proved to be the most inclusive. Another important character, split of the palatal tooth, shows one homoplasy "enforced" by the distribution of six other characters.

The following character sets were used to construct the cladogram: microsculpture of interspaces, microsculpture of embryonic whorls, components of apertural barriers (columellar, parietal, angular, upper and lower palatal, basal); body whorl profile and rib quality. Though the components of apertural armature are sometimes viewed as one complex structure (e.g. SHILEYKO 1984), the wide range of combinations of characters of apertural barriers found in members of other pupilloid taxa (e.g. vertiginids, gastrocoptins, chondrinids, *Leiostyla* R. T. LOWE; for review see PILSBRY 1922-1926, GITTENBERGER 1973, SHILEYKO 1984, POKRYSZKO 1990, 1994, 1996) is a very strong indication that the evolution of their component-structures is uncorrelated. For this reason they are considered separately. The characters are analysed below, character states being specified for each.

Ribbing. The presence of ribs is shared by all the members of *Lyropupa* and *Nesopupa* PILSBRY. Moderately coarse, straight, regular, uninterrupted ribs appear to be plesiomorphic at the generic level (*Nesopupa* PILSBRY). In the course of their evolution such ribs may: become flexuous, increase or decrease their thickness and get slightly irregular in their height and arrangement; the height may vary along or between ribs. These characters too often vary between individuals, populations and species to be attributed any phylogenetic significance. Only two modifications of ribbing represent apomorphic character states. A tendency to form interrupted ribs grouped in pairs or triplets seems to support the monophyly of the *ovatula* group (cf. species descriptions), albeit with the reservation that such ribs appear in most species of the group, but not in all, and in some only in a very low proportion of specimens. For this reason the character was excluded from the analysis (SAETHER 1986). The presence of periostracal crests on top of ribs - synapomorphy of the pair *clathratula truncata* - shows no homoplasies.

Table 1. Genus *Lyropupa*. Character matrix. 1 - parietal tooth: not displaced (0), displaced (1); 2 - angular tooth: unreduced (0), reduced (1); 3 - parietal tooth: not deflected (0), moderately deflected (1), much deflected (2); 4 - lower palatal tooth, entire (0), split (1), split and inner part displaced (2); 5 - lower palatal tooth: not displaced (0), displaced (1); 6 - basal bump on body whorl: absent (0), present (1); 7 - embryonic whorls: granulose (0), smooth (1); 8 - columellar tooth: straight (0), obliquely tubercular (1); 9 - spiral ridges in interspaces: absent (0), present (1); 10 - wrinkles in interspaces: unordered (0), radial (1); 11 - embryonic whorls: granulose (0), spirally sculptured (1); 12 - columellar tooth: straight (0), moderately drooping (1), strongly drooping (2); 13 - periostracal crests on ribs: absent (0), present (1); 14 - sinus: present (0), absent (1); 15 - palatal teeth: parallel (0), divergent (1); 16 - sinus: open (0), partly closed (1), wholly closed; 17 - basal tooth: not recessed (0), recessed (1); 18 - upper palatal tooth: short (0), prolonged (1); 19 - margin of parietal tooth: narrow (0), flattened and dilated (1); 20 - palatal teeth: not arranged in arcuate position (0), arranged in arcuate position (1); 21 - angular tooth: short (0), prolonged (1); 22 - lateral bumps on body whorl: absent (0), present (1); 23 - basidorsal hump on body whorl: absent (0), present (1).

character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
outgroups	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>scabra</i>	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>spaldingi</i>	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>societatis</i>	1	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>mirabilis</i>	1	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>anceyana</i>	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>antiqua</i>	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>hawaiiensis</i>	1	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>ingrata</i>	1	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>sparna</i>	1	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>rhabdota</i>	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
<i>pluris</i>	0	0	0	0	0	0	0	0	1	1	1	2	0	0	0	0	0	0	0	0	0	0	0
<i>adeps</i>	0	0	0	0	0	0	0	1	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0
<i>cyrta</i>	0	0	0	0	0	0	0	1	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0
<i>lanaiensis</i>	0	0	0	0	0	0	0	1	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0
<i>clathratula</i>	0	0	0	0	0	0	1	1	1	2	1	1	0	0	0	0	0	0	0	0	0	0	0
<i>truncata</i>	0	0	0	0	0	0	0	1	1	1	2	1	1	0	0	0	0	0	0	0	0	0	0
<i>striatula</i>	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>thaanumi</i>	0	0	0	0	0	0	0	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0
<i>dissimulator</i>	0	0	0	0	0	0	0	1	1	1	0	0	0	1	2	0	0	0	0	0	0	0	0
<i>microthauma</i>	0	0	0	0	0	0	0	1	1	1	0	0	0	1	2	0	0	0	0	0	0	0	0
<i>lyrata</i>	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>kahoolavensis</i>	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>hybrida</i>	0	0	0	2	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>costata</i>	0	0	0	2	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0
<i>captiosa</i>	0	0	0	2	0	0	0	1	1	0	0	0	0	0	0	1	1	1	1	1	0	0	0
<i>cubana</i>	0	0	0	2	0	0	0	1	1	0	0	0	0	0	0	1	1	1	1	1	0	0	0
<i>plagiopyx</i>	0	0	0	2	0	0	0	1	1	0	0	0	0	0	0	1	1	1	1	0	1	1	0
<i>ovatula</i>	0	0	0	2	0	0	0	1	1	0	0	0	0	0	0	1	1	1	1	0	1	1	0
<i>luailualeiensis</i>	0	0	0	2	0	0	0	1	1	0	0	0	0	0	0	1	1	1	1	0	1	0	1
<i>micra</i>	0	0	0	2	0	0	0	1	1	0	0	0	0	0	0	1	1	1	1	0	1	0	1

Microsculpture of interspaces. In most *Nesopupa* PILSBRY the periostracum of definitive whorls bears randomly oriented, fine, short and straight wrinkles. Some members of *Lyropupa* preserved this character state; it is found in the *spaldingi* group and is plesiomorphic at the generic level. In the *microthauma* and *ovatula* groups the wrinkles become generally radially oriented; the character is a synapomorphy of these groups, with no homoplasies. In both of them, on the background of the wrinkles, spiral ridges appear, of partly periostracal but mostly calcareous nature; they are visible, though poorly, in SEM even on subfossil shells devoid of periostracum. The expression of this character varies between species and populations (*ovatula*, *costata*, *kahoolavensis*, *lualualeiensis*), and sometimes even within populations (*costata*, *kahoolavensis*) from spiral striation, well visible under stereomicroscope, to visible only in SEM under 100x or higher magnification. The character is a synapomorphy of the groups of *microthauma* and *ovatula*, with no homoplasies.

Microsculpture of embryonic whorls. In *Lyropupa* the protoconch surface is originally finely granulose. This condition has been generally preserved also in *Nesopupa* Pilsbry. Most species of the *spaldingi* group and all members of the *ovatula* group have their embryonic whorls coarsely wrinkled-granulose, though in some members of the *spaldingi* group (*hawaiiensis*, *ingrata*, *sparna*) the whorls have later become completely smooth (apomorphic at species group level; no homoplasies). In the *microthauma* group the embryonic whorls are spirally sculptured, in some the spiral ridges being coarse and very prominent. The character shows no homoplasies; it is regarded as a synapomorphy of all the members of the group.

Components of apertural barriers.

* Columellar tooth. In both *Nesopupa* PILSBRY and *Lyropupa* the tooth is much variable in shape. It is very difficult to use it for constructing phylogeny, since nearly all character states are found also in *Nesopupa* Pilsbry and other related taxa. Comparison with *Nesopupa* Pilsbry indicates that a lamellate columellar is plesiomorphic at the generic level. Transformation of the lamella into an obliquely tubercular structure happened independently in the *spaldingi* (pair *ingrata/sparna*) and *microthauma* (7 species) groups, with a different result: in the *microthauma* group the columellar has a tendency to be "drooping" to various degree, which is absent in *sparna* and *ingrata*. These two transformations are apomorphies: one of the pair *ingrata/sparna*, the other of most members of the *microthauma* group.

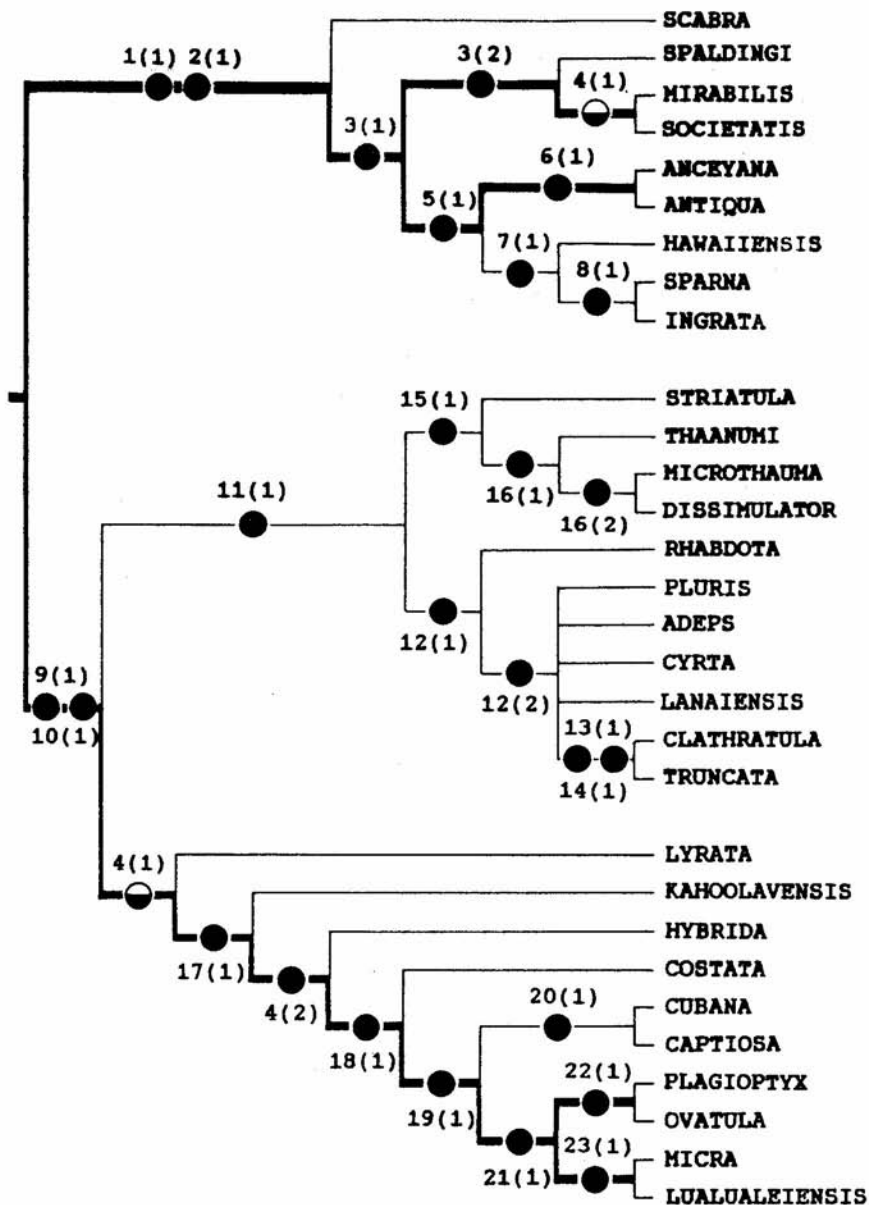
* Parietal tooth. In *Nesopupa* PILSBRY, as well as in such pupilloid genera as e.g. *Vertigo* O. F. MÜLLER, *Leiostyla* R. T. LOWE, *Chondrina* REICHENBACH, the tooth is simple lamellate, of nearly even height or with arcuate free margin, not bent or deflected in any plane and situated roughly in the middle of parietal wall. It preserves the plesiomorphic position and shape in some *Nesopupa* PILSBRY and *Lyropupa* (*microthauma* group). In the *spaldingi* group the parietal becomes displaced towards the palatal wall, so as to be finally situated almost or exactly in line with the angular. This condition is a synapomorphy of all the members of the group, with no homoplasies. In all such species, except *scabra*, it is accompanied by deflection of the outer part of the parietal towards the palatal wall in vertical plane, in some (*spaldingi*, *societatis*,

mirabilis) very strongly. The character constitutes their synapomorphy, with no homoplasies. In some members of the *ovatula* group the free margin of parietal gets flattened and dilated, sometimes almost "bifid" (synapomorphy of 6 members of the group; no homoplasies).

* Angular tooth. In its plesiomorphic condition the tooth is just a short, straight lamella, highest in middle or of even height, somewhat removed from the lip (*Nesopupa* PILSBRY, most *Vertigo* O. F. MÜLLER). In *Lyropupa* it originally reaches the very lip margin and is fairly long (autapomorphy of the genus). In the *spaldingi* group it gets reduced in height and/or length to a low ridge, an elongate tubercle or a simple tubercle located very close to the lip margin. In no case does it leave any doubt that an originally long and later reduced structure is concerned. In some species (e.g. *spaldingi*, *mirabilis*) individual variation of the tooth clearly indicates its gradual reduction. The character constitutes a synapomorphy of the group *spaldingi*, with no homoplasies. In some members of the *ovatula* group (*micra*, *lualualeiensis*, *ovatula*, *plagiopyx*), the angular gets further prolonged to become equal in length to the parietal. The condition is synapomorphic for those four species, with no homoplasies.

* Upper palatal tooth. The plesiomorphic state of this tooth is a simple, rather short lamella, recessed from the lip (*Nesopupa* PILSBRY, *Vertigo* O. F. MÜLLER, *Gastrocopta* WOLLASTON and various other pupilloids). The synapomorphy of all the members of *Lyropupa* is that the tooth is long, reaching the very lip margin and most often consists of two, more or less distinct, parts: external, facing the angular, somewhat lower (its section at the lip margin often the highest), and internal, somewhat higher and of even height. Its evolution within the genus involved a variety of transformations. A gradual closing of the sinulus by increasing the height of the upper palatal happened in the group *microthauma* (*thaanumi*, *microthauma*, *dissimulator*; no homoplasies). Prolonging the upper palatal up to 1/3 whorl inside the shell is shared by 7 species of the *ovatula* group (synapomorphy, no homoplasies). Considerable shortening of the tooth, combined with recessing it from the lip margin, so that the sinulus disappears completely, is a synapomorphy of the pair *clathratula/truncata*, displaying no homoplasies. Another transformation is accretion of the inner part of the split lower palatal (see below) to the inner end of the upper palatal. This is autapomorphy of *cubana*, independently acquired also by some Kauaian populations of *micra* and was excluded from the analysis. The upper palatal, inner part of lower palatal and basal may become situated in one, regularly arcuate line; synapomorphy of the pair *cubana/captiosa*; the character shows no homoplasies. Disappearance of the border between the inner and outer part of the upper palatal varies very much between populations and individuals and was omitted from the analysis.

* Lower palatal tooth. In its plesiomorphic condition (*Nesopupa* PILSBRY, many *Gastrocopta* WOLLASTON, *Vertigo* O. F. MÜLLER, numerous other pupilloids) it is a fairly long and high, straight lamella. This character state has been preserved by more plesiomorphic members of the *spaldingi* group and some members of the *microthauma* group. The tooth undergoes the following transformations. In five members of the *spaldingi* group it becomes shortened, recessed deep in the aperture, and displaced



147. Cladogram of the genus *Lyropupa*. Numbering of characters corresponds to that in the character matrix (tab. 1). Character states specified in parentheses. Shortest and longest speciation sequences indicated with thicker lines.

higher up on the palatal wall, so as to become situated very close to the inner end of the upper palatal (synapomorphy; no homoplasies). In members of two species groups (*spaldingi*, *ovatula*) the lower palatal becomes split in two parts. The outer part remains lamellate or gets reduced to an elongate tubercle, the inner part shifts deeper inside and assumes an oblique or transverse position and a shape of a short lamella, or elongated "comma", completely independent of the outer half. Some populations of *mirabilis* (Keekee Gulch, BM 129178, 129777) display a variation of this tooth testifying to its division. The character is a synapomorphy of the *ovatula* group, and, as a homoplasy (indicated by the distribution of 6 other characters), a synapomorphy of the pair *mirabilis/societatis* in the *spaldingi* group. Furthermore, the split off inner part of the lower palatal may fuse to the inner end of the upper palatal (see above) partly or wholly, and to the shifted basal (see below), again partly or wholly. Finally, a complete, straight lower palatal, whose outer end may become callus-like diffuse, becomes divergent from, instead of parallel to, the upper palatal. The character state is a synapomorphy of the quartet *striatula*, *thaanumi*, *dissimulator* and *microthauma*, with no homoplasies.

* Basal tooth. The basal in all members of *Lyropupa* that have it, is situated in basal position and recessed to the level of or behind the columellar. Its location (out-groups: *Nesopupa* PILSBRY, *Vertigo* O. F. MÜLLER, *Gastrocopta* WOLLASTON) is a synapomorphy of the genus *Lyropupa*. Furthermore, in all members of the group *ovatula*, except *lyrata*, the tooth is displaced very far beyond the columellar, so as to form a continuation of the split off, inner part of the lower palatal (see above), as an elongate tubercle situated in line with it or fused to it partly or wholly. This is a synapomorphy of all the species involved, with no homoplasies. In the *spaldingi* group the basal has a tendency to assume a shape of a tubercle situated transversely relative to the palatals, but is often individually variable and was excluded from the analysis, though it seems to support the monophyly of the group. In the *microthauma* group it either remains parallel to the palatals (plesiomorphy; out-group *Nesopupa* PILSBRY), gets reduced to a tubercle or disappears. Its reduction, being a common homoplasy among pupilloids (cf. POKRYSZKO 1994), was excluded from the analysis.

* Body whorl profile. The presence of two somewhat convergent impressions corresponding to the palatal teeth (*Vertigo* O. F. MÜLLER, some *Gastrocopta* WOLLASTON, some *Nesopupa* PILSBRY) is plesiomorphic. This condition is found in various members of all the species groups within *Lyropupa*. On the body whorl a wide, flat-bottomed gutter may appear (e.g. some members of the *spaldingi* group) or a single, long, narrow groove (other members of that group), or else the impressions may disappear completely (e.g. *truncata*, *clathratula*); all these character states display many homoplasies with scattered members of other taxa (e.g. *Nesopupa* PILSBRY, some *Vertigo* O. F. MÜLLER and various other pupilloid taxa), in most species they vary individually very much and at best are autapomorphies of some species (cf. species descriptions). For this reason they were excluded from the analysis. Besides, the following structures may appear on the exterior of the body whorl: a distinct bump at the base of body whorl (synapomorphy of the pair *antiqualanceyana*), a crescentic basidorsal hump (synapomorphy of *micrallualaleiensis*), and lateral bumps

(synapomorphy of *ovatula/plagioptyx*). None of the three characters displays homoplasies.

Lip. Most pupilloids including *Nesopupa* PILSBRY have a well developed and reflexed lip and a relatively thin parietal callus. These two character states are plesiomorphic. "Closing" lip to a full circle by thickening the parietal callus is a synapomorphy of the genus *Lyropupa*.

PHYLOGENY

The most parsimonious cladogram (fig.147) is 28 steps long, CI = 0.96, RI = 0.99, RC = 0.95. It is resolved except the quartet *adeps/cyrtallanaiensis/pluris*. The four species have a drooping columellar (synapomorphy with the pair *truncatal/clathratula*) but lack any apomorphy of their own, thus constituting a typical non-A group (ELDRIDGE & CRACRAFT 1980). The genus includes three fairly distinct phylogenetic lineages, here termed: *spaldingi* group, *microthauma* group and *ovatula* group.

VI. ORIGIN, SPECIATION AND DISPERSAL

BACKGROUND

The Hawaiian Archipelago consists of a series of atolls, reefs, islets and islands oriented along a 2500-km NW-SE axis and located between 154°41' and 171°75' W longitude, and 18°54' to 28°15' N latitude. It forms the SE end of a much larger line of low islands and seamounts, the Hawaiian Ridge, extending 3,493 km NW and then turning sharply northward; the S-N oriented part known as the Emperor Chain continues for another 2,327 km (CARSON & CLAGUE 1995).

All the erstwhile and existing islands of the Hawaiian-Emperor Chain were formed successively over a fixed volcanic "hot spot" beneath the northeastward-moving Pacific tectonic plate (MORGAN 1971). The magma perforates the plate at intervals to form discrete volcanoes as the plate moves over the hot spot. The highest points may rise above sea level as emergent oceanic islands.

The older, westernmost islands of the Hawaiian Archipelago are either no longer emergent (Kure, Midway, Pearl and Hermes Reef, Lisianski, Laysan), or consist of small pinnacles of volcanic rock (French Frigate Shoals), or else have been reduced to rocky islets (Necker, Nihoa, Kaula). The eight younger islands: Niihau, Kauai, Oahu, Molokai, Lanai, Kahoolawe, Maui and Hawaii, are scattered over ca. 600 km stretch of the ocean and separated from each other by channels of a width ranging from about a dozen km between Molokai and Maui to over 100 km between Kauai and Oahu (STEARNS 1966). The distance to the nearest continent - North America - is 3000 km.

Each island consists of one or more volcanic domes. The age of the main six (largest and highest) islands, is the following: Kauai 5.1 myr, Oahu 3.7 myr, Lanai 1.3 myr, Molokai 1.9 myr, Maui 1.3 myr, Hawaii 0.43 myr (potassium-argon ages and

paleomagnetic declination measurements; McDougall & Swanson 1972, Simon 1987).

The entire geological development of three of the islands: Lanai, Molokai and Maui took place in the Pleistocene. As a result of fluctuations of the ocean level, caused by intermittent removal and release of water by forming and melting glaciers, these islands became repeatedly connected and disconnected (Simon 1987). When connected, Lanai, Molokai and Maui formed one big island and are often collectively termed Maui Nui (James & Olson 1993).

Table 2. Distribution of *Lyropupa* in the Hawaiian Islands; R - recent, F - subfossil.

species/island	Kauai	Oahu	Lanai	Molokai	Maui	Hawaii	Niihau	Kahoolawe
<i>scabra</i>	-	-	-	-	R	-	-	-
<i>spaldingi</i>	-	RF	-	-	-	-	-	-
<i>mirabilis</i>	-	RF	-	-	-	-	-	-
<i>societatis</i>	-	R	-	-	-	-	-	-
<i>anceyana</i>	-	-	-	-	-	R	-	-
<i>antiqua</i>	-	F	-	-	-	-	-	-
<i>hawaiiensis</i>	-	-	-	-	-	RF	-	-
<i>sparna</i>	-	-	RF	RF	-	-	-	-
<i>ingrata</i>	-	-	RF	RF	RF	-	-	-
<i>rhabdota</i>	-	-	-	R	-	-	-	-
<i>pluris</i>	-	-	-	R	RF	-	-	-
<i>adepts</i>	-	-	-	-	F	-	-	-
<i>cyria</i>	-	-	-	-	-	F	-	-
<i>lanaiensis</i>	-	-	R	-	RF	F	-	-
<i>clathrotula</i>	-	-	-	-	-	R	-	-
<i>truncata</i>	-	-	-	-	-	R	-	-
<i>striatula</i>	-	-	F	-	RF	F	-	-
<i>thaanumi</i>	-	-	-	-	R	-	-	-
<i>microthauma</i>	-	RF	-	-	-	-	-	-
<i>dissimulator</i>	-	R	-	-	-	-	-	-
<i>lyrata</i>	RF	RF	-	-	-	-	-	-
<i>kahoolavensis</i>	-	RF	RF	RF	RF	RF	-	RF
<i>hybrida</i>	-	F	-	-	-	-	-	-
<i>costata</i>	RF	RF	RF	RF	RF	RF	RF	-
<i>cubana</i>	RF	-	-	-	-	-	-	-
<i>captiosa</i>	F	-	-	-	-	-	-	-
<i>plagiopyx</i>	-	F	-	-	-	-	-	-
<i>ovatula</i>	-	F	F	F	-	RF	-	-
<i>micra</i>	RF	RF	RF	RF	RF	-	-	-
<i>luualalei</i>	-	RF	-	-	-	-	-	-
total	5	14	8	8	10	10	1	1

The surface area of the six main islands ranges from ca. 365 (Lanai) to 10,424 km² (Hawaii), the elevation - from ca. 1000 (Lanai) to 4,205 m a.s.l. (Hawaii) (for particular islands see table 7).

The Hawaiian Islands lie in the path of northeasterly trade winds that persist throughout the year (STEARNS 1985). During the winter they are occasionally interrupted by southerly or "kona" winds that blow for a few days at a time (STEARNS 1985).

As a result of the trade-winds, the windward-facing slopes and crests of the islands receive much more rainfall than the leeward ones. For example, in one of the most humid spots on Kauai the annual rainfall may reach 12000 mm, while a locality at the coast of the same island receives less than 5% of that (TALIAFERRO 1959).

The native Hawaiian forests which originally covered the entire islands (ZIMMERMANN 1948) have been to a large extent replaced by communities of introduced plants. Only fragments have remained of the main forest and shrub ecosystems (FOSBERG 1963): *Metrosideros* forest of moderately moist and wet localities at fairly low to moderate elevations, cloud forest of higher altitudes, mixed mesophytic forest of low elevations and especially of dryland sclerophyll forest.

DISTRIBUTION

The distribution of members of *Lyropupa* is presented in table 2.

Only two (*kahoolavensis* and *costata*) of the 30 species inhabiting the Hawaiian Islands have dispersed to Kahoolawe and Niihau. Both are otherwise widely distributed in the archipelago.

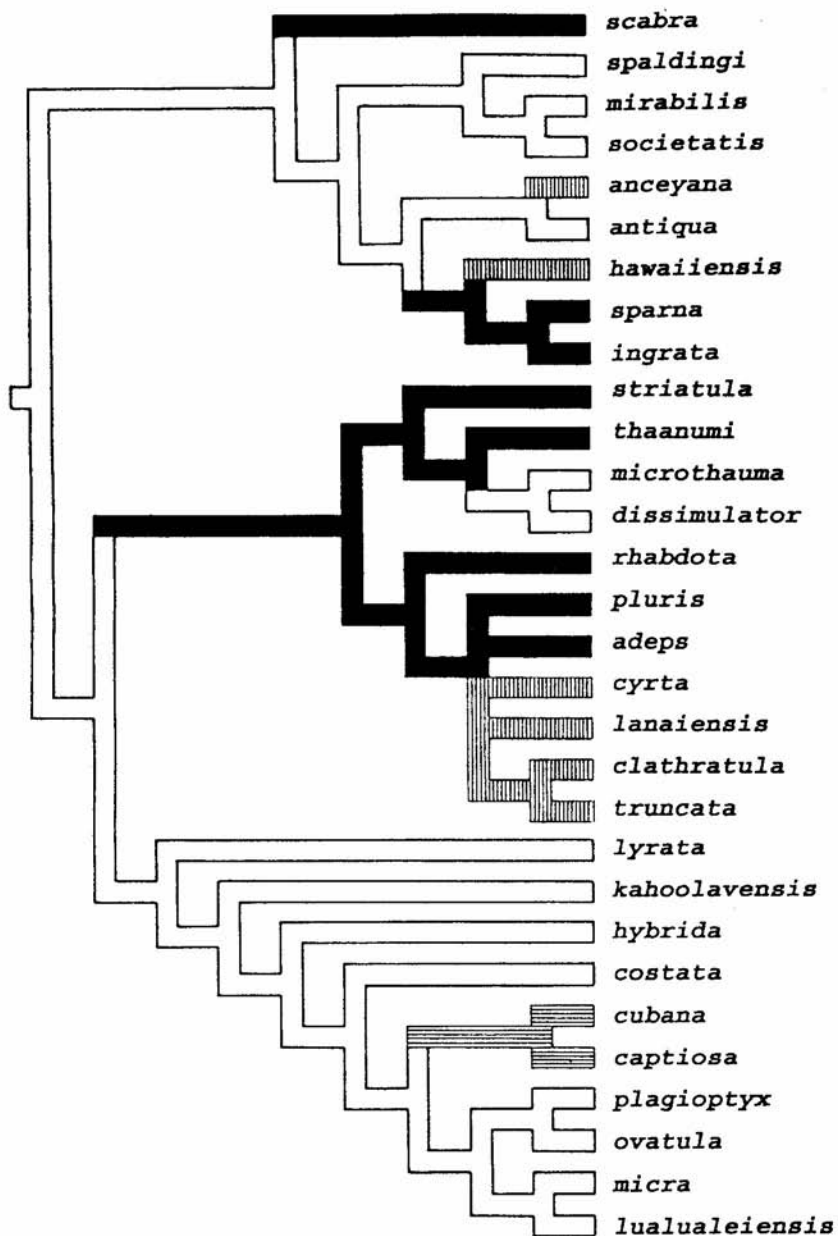
Twenty species are single-island endemics and, when Maui, Molokai and Lanai are considered jointly as Maui Nui, the number of endemic species increases to 23.

Species of two phylogenetic groups (*spaldingi* and *microthauma*) are mostly endemic, whereas most members of the third and apparently the most derived group - *ovatula* - are more widely distributed (tab. 2). No species of the *spaldingi* group is distributed wider than the three component islands of Maui Nui. Five of the seven widely distributed species are members of the *ovatula* group, and the remaining two (*striatula*, *lanaiensis*) belong to the *microthauma* group.

Oahu is the richest in species (14, 9 of them being endemic), closely followed by Maui Nui (13, 7 endemic) and Hawaii (10, 5 endemic). Kauai, with its 5 species (2 endemic), is the poorest.

ORIGIN OF THE GENUS

The origin of the first colonisers that later gave rise to both *Lyropupa* and *Nesopupa* PILSBRY, its most probable sister-group, is unclear; the Hawaiian Islands are evidently the headquarters of the two genera. Their links with other pupilloid taxa are equally obscure. The superfamily is distributed worldwide, and doubts exist as to its monophyly and phylogeny (POKRYSZKO 1994). It is easier to envisage dispersal from SE Asia for the following reasons.



148. Cladogram of the genus *Lyropupa*. Parts of phylogeny that took place on particular islands indicated as follows: Oahu - white, Maui Nui - black, Hawaii - horizontal hatching, Kauai - vertical hatching. Non-endemic species indicated only for their respective islands of origin.

1. That region harbours a rich, diverse, old and partly plesiomorphic pupilloid fauna (for review see PILSBRY 1916-1918, 1918-1920, 1922-1926), and was most probably one of its radiation centres.

2. Only few terrestrial taxa in Hawaii show New World affinities (GRESSITT 1978, SIMON 1987, OTTE 1989, COX & MOORE 1993, ASQUITH 1994, 1995). In most cases the affinities are either Asian or can be traced back only to the now submerged older islands of the Hawaiian-Emperor Chain (SOLEM 1981, COWIE 1992, DESALLE 1995, LOWREY 1995).

3. Data on the wide dispersibility of many components of the Hawaiian biota (FOSBERG 1963, GRESSITT & YOSHIMOTO 1963) indicate that propagules from the continents, including Asia, have continually played a role in colonisation of the Hawaiian Islands.

4. Numerous islands - potential stepping stones - exist between SE Asia and Hawaii (CARSON & CLAGUE 1995). America, with its fairly derived and not very diverse pupilloids, though situated closer to the Hawaiian Islands, is not connected with them by any possible stepping stones.

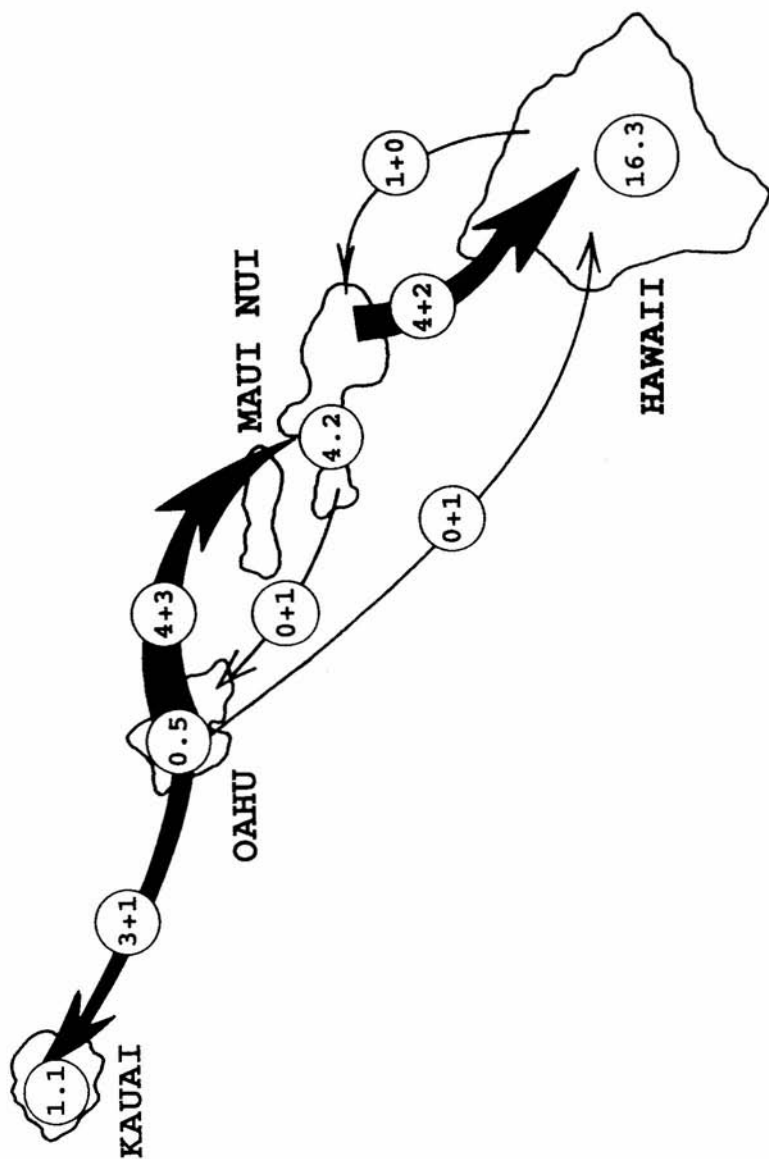
For these reasons SE Asia is a safer guess, but still a guess only.

The split *Lyropupa-Nesopupa* must have occurred already on one of the islands. It is unlikely that the genus originated on one of the older, now submerged, islands of the Hawaiian-Emperor Chain. Such an origin was postulated for some insect taxa (SIMON 1987, CARSON & CLAGUE 1995 and references contained therein), but there are also well-documented instances of origin of plant and animal genera on younger, now-emergent islands. A plant genus *Tetramolopium* (*Asteraceae*) most probably originated on Maui (LOWREY 1995), and a spider genus *Tetragnatha* appears to have originated on Kauai (GILLESPIE & CROOM 1995).

Members of all the phylogenetic groups of *Lyropupa* (*spaldingi*, *microthauma*, *ovatula*) are found on Oahu; each group has endemic species there. Rather plesiomorphic representatives of two groups (*spaldingi* and *ovatula*) live on that island. The degree of its endemism is the highest (cf. tab.7). Considering the evolution of the genus in terms of time available for endemic species to evolve, its radiation started most probably on Oahu. Compared to its neighbours, Oahu, with its lowest elevation and area only slightly exceeding that of Kauai, harbours the most numerous species; of 30 species Oahu has 14 (9 endemic), Kauai 5 (2 endemic), Maui Nui 13 (7 endemic) and Hawaii 10 (5 endemic). On Kauai only the *ovatula* group is present; two of the five species (*cubana* and *captiosa*) are apomorphic endemics, the other three are dispersalists. On Maui Nui all the three groups of *Lyropupa* are found, but the *ovatula* group is represented by dispersalists only. Likewise, Hawaii has members of all the groups of *Lyropupa*, but of the *ovatula* group only dispersalists are present. The evidence points to Oahu as the place of origin of *Lyropupa*.

SPECIATION RATE AND FREQUENCY

The reconstructed phylogeny and knowledge of the age of the islands combined make it possible to calculate the minimum speciation frequency and minimum



149. Dispersal routes and colonisation frequency. Number of dispersal events specified for each route: the first values in circles on arrows represent dispersal events necessary to account for distribution of non-endemic species, the second values - those necessary to account for phylogeny. Values in circles on islands denote colonisation frequency.

speciation rate, irrespective from the (unknown) mechanism of speciation. The values calculated are minimum values, since *Lyropupa* may be younger than Oahu.

Speciation frequency is expressed as the mean number of speciation events within the genus per 1 myr. Speciation rate is the mean number of consecutive speciation events within a phylogenetic sequence (lineage) within 1 myr.

Formation of a forest of *Metrosideros polymorpha*, the most common tree species in the Hawaiian rainforests, on a lava flow, takes ca. 400 years (ATKINSON 1970, STEMMERMANN 1983, MUELLER-DOMBOIS 1987, DRAKE & MUELLER-DOMBOIS 1993). Since the value is negligible compared with the age of the islands, the geological age of the islands was assumed as the time of their becoming snail-inhabitable: Kauai - 5.1 myr; Oahu - 3.7 myr; Lanai - 1.3 myr; Molokai - 1.9 myr; Maui - 1.3 myr; Hawaii - 0.43 myr.

Because of the Pleistocene connections between the islands of Lanai, Molokai and Maui, they are biogeographically treated as one unit, its age being assumed as 1.9 myr. They have more species in common than any of them has with any other island.

Speciation rate and frequency were calculated based on the cladogram, assuming each of its nodes as a speciation event, and considering the limitations imposed by the age of the islands.

The longest speciation sequence (fig.147) (Oahu: *ovatula* group: *ovatula* and *micra* sequences) comprises 9 consecutive events, the shortest (Oahu: *spaldingi* group: *mirabilis* sequence) involves 5 events. The number of consecutive events within the *spaldingi* group is 5-6, *microthauma* group 6, *ovatula* group 8-9, the respective speciation rates being: 1.35-1.62, 1.62 and 2.16-2.43 events/1 myr. The rates are fairly similar between the groups, the group *ovatula* being the only lineage with a somewhat higher speciation rate. One of the reasons may be its better dispersal ability, as evidenced by non-endemic distribution of the majority of its species.

Fragments of longer speciation sequences found on younger islands are also informative. Two such fragments on Maui Nui, in the groups *spaldingi* (*ingrata* sequence) and *microthauma* (*thaanumi* sequence) comprise 3 and 4 consecutive events, respectively, resulting in 1.58-2.10 event/1 myr. The only Hawaiian fragment corresponds to the unresolved part of the cladogram and comprises 1 or, possibly, 2 events, resulting in 2.37-4.68 event/1 myr. Except for the uncertain value 4.68, the rates correspond rather closely to those calculated for the entire sequences.

Speciation frequency within the genus is ca. 8.3 (30 speciations in 3.7 myr). Of the 30 speciation events, 22 took place within single islands (cf. dispersal chapter), and only 8 involved island-to-island dispersal. The intra-island speciation frequency is thus 5.95, the inter-island 2.16 events/1 myr.

Because of the distinct bias towards the intra-island speciation, the expected number of intra-island pairs of sister species should exceed that of inter-island pairs. The number of the former pairs is 7 (possibly 9; 2 pairs in the unresolved fragment of the cladogram may be inter- or intra-island pairs, cf. fig.147), of the latter - only 3 (possibly 1).

Most intra-island speciations (13) took place on Oahu, fewer on Maui Nui (5-6) and Hawaii (2-3), and only one on Kauai. The uncertainty as to Maui Nui and Hawaii

results from the unresolved quartet in the cladogram (cf. fig.147). The respective frequencies are 3.51, 2.63-3.17, 4.68-6.99 and 0.27 events/1 myr.

Even assuming the higher of the two values for Maui Nui and the lower of the two for Hawaii, the speciation frequency on that island is the highest, whereas on Kauai it is the lowest. The low-frequency speciation on Kauai may be an artefact resulting from the assumption that the actual time available equalled the age of Oahu (3.7 myr). Kauai is small and far from the source of colonisers. The only speciation that took place on the island was the most recent in a sequence of 9 events that started on Oahu. The differences between Oahu and Maui Nui on one hand, and Hawaii on the other, are more difficult to explain. Both Oahu and Maui Nui should favour speciation, the former by virtue of its topography (two parallel mountain ranges separated by a deep valley), the latter because of its history (connecting and disconnecting islands). The varied topography and comparatively very large size of Hawaii, though important factors, do not seem sufficient to account for its high-frequency speciation. On the other hand, the short time interval (0.43 myr), for which the mean frequency for Hawaii was calculated, may well reflect the actual speciation frequency during the initial stage of island colonisation. A lack of competition and the presence of "unfilled ecological niches" are often regarded as conducive to radiation (SIMON 1987, ELDRIDGE 1989 and literature contained therein). In this case the apparent differences in speciation frequency between the islands would only reflect the fact that an initial period of speciation on each was followed by a low-frequency period of various duration.

DISPERSAL AND COLONISATION

- island-to-island dispersal

Apart from dispersal events accounting for the distribution of non-endemic species (5 species of *ovatula* group, *striatula*, *lanaiensis*), minimum number of dispersal events was assumed, in accordance with parsimony criterion. Literature data (for review see SOLEM 1990) provide evidence that intra-island speciation is actually the most frequent case with land snails on islands. Such a speciation, when not excluded, was regarded as more parsimonious than speciation plus island-to-island dispersal. Dispersal of an ancestor of a species endemic to an island to that island was regarded as more parsimonious than a dispersal of the common ancestor of the whole group to the island and subsequent return of some members to the original island. The most parsimonious view on dispersal necessary to account for phylogeny is presented in fig. 148.

Kauai and Maui Nui are both older and closer to Oahu than is Hawaii; Kauai is older than Oahu. Maui Nui, though about twice younger than Oahu, is roughly twice closer to it than is Kauai. Those two islands could be the first to be colonised. Assuming accidental dispersal, they could well have been colonised at approximately the same time. Hawaii, the youngest and farthest from Oahu, could be the last to be invaded. However, in the cladogram, the first speciation event necessitating dispersal to Kauai is event 7 (*ovatula* group: *cubana* sequence), the first event necessitating dispersal to Maui Nui is event 2 (*spaldingi* and *microthauma* groups). The islands

were invaded at phylogenetically different time by members of the groups which evolved at approximately the same rate (cf. speciation chapter), which would indicate that Maui Nui could be the first to be colonised from Oahu. This is supported by the fact that apparently only 4 of the total of 20 island-to-island dispersals within *Lyropupa* took place from Oahu to Kauai, while the remaining 16 were between Oahu, Maui Nui and Hawaii (cf. figs 148, 149). Furthermore, considering the sequence of colonisations in terms of time available for evolving endemics, both Maui Nui and Hawaii are "older" i.e. have more numerous endemic species (7 and 5, respectively) than Kauai (2) and higher degree of endemism (tab.7) which would indicate a longer time available for colonisation and evolution. In terms of the length of speciation sequences observed on each island, Kauai is also the very last. It is quite possible that it was also the last to be colonised.

Table 3. Dispersal of non-endemic species

species	route(s)	no. of events
<i>lyrata</i>	Oahu-Kauai	1
<i>ovatula</i>	Oahu-Maui Nui-Hawaii	2
<i>micra</i>	Oahu-Kauai and Oahu-Maui Nui	2
<i>costata</i>	Oahu-Kauai and Oahu Maui Nui-Hawaii	3
<i>kahoolavensis</i>	Oahu-Maui Nui-Hawaii	2
<i>striatula</i>	Maui Nui-Hawaii	1
<i>lanaiensis</i>	Hawaii-Maui Nui	1

The colonisation sequence: Oahu-Maui Nui-Hawaii-Kauai is the most plausible.

Disregarding dispersal to Kahoolawe and Niihau, there were 12 dispersal events accounting for the distribution of non-endemic species (tab.3). Another 8 dispersal events are the minimum necessary to account for phylogeny (tab.4). The resulting dispersal frequency is 5.41 event/1 myr. Of the total of 20 dispersal events only 6 were from Oahu to Kauai (4), from Maui Nui to Oahu (1) or from Hawaii to Maui-Nui (1), the remaining 14 being along the route Oahu-Maui Nui-Hawaii.

The frequency of dispersal from NW to SE is ca. 7.37, from SE to NW ca. 1.5 event/1 myr. The NW-SE direction as the main direction of dispersal was also found in the Hawaiian drosophilids by CARSON (1987) and KANESHIRO et al. (1995), in crickets of the family *Gryllidae* by SHAW (1995) and in the *Collembola* by CHRISTIANSEN & BELLINGER (1994). The differences between the colonisation frequency of the islands do not have to be explained by a one-way dispersal factor (see below), but the apparently uni-directional dispersal calls for an explanation.

Wind is thought to be the most important factor in dispersal of small land snails to (and between) islands that were never connected with continents (VAGVOLGYI 1976). The northeasterly trade winds that persist throughout the year are probably not strong enough to account for dispersal and, additionally, their direction (NE-SW) is almost

exactly perpendicular to the main dispersal route (NW-SE). The sporadic southerly "kona" winds offer an equally poor explanation for the NW-SE dispersal route. None of the remaining conceivable dispersal agents (e.g. birds, ocean currents and, in historical times, humans) is uni-directional.

Table 4. Dispersal events necessary to account for phylogeny

ancestor	from	to
1. ancestor of <i>scabra</i>	Oahu	Maui Nui
2. ancestor of <i>anceyana</i>	Oahu	Hawaii
3. common ancestor of <i>hawaiiensis/lingratal/sparna</i>	Oahu	Maui Nui
4. ancestor of <i>hawaiiensis</i>	Maui Nui	Hawaii
5. common ancestor of <i>microthauma</i> group	Oahu	Maui Nui
6. comm. anc. of <i>cyrtallanaiensis/clathratula/truncata</i>	Maui Nui	Hawaii
7. common ancestor of <i>microthauma/dissimulator</i>	Maui Nui	Oahu
8. common ancestor of <i>captiosa/cubana</i>	Oahu	Kauai

Another possibility is that, though the probability of dispersal in all the directions is equal (random beginning of a journey), the chances of successful colonisation vary between islands. This is supported by the fact that Kauai was colonised only by members of the *ovatula* group, apparently much more euryoecious and thus better dispersalists.

Colonisation frequency expressed as the mean number of colonisation events per 1 million years varies between the islands. It is the lowest on Oahu, colonised from Maui Nui (0.5 event/1 myr) and Kauai (1.1 event/1 myr), colonised from Oahu. Maui Nui, also colonised mostly from Oahu and once from Hawaii, has a higher colonisation frequency of 4.2 event/1 myr. It is the highest in Hawaii, colonised from both Oahu and Maui Nui, and amounts to 16.3 event/1 myr; the colonisation frequency decreases distinctly with increasing age of the island (fig. 149).

Oahu, with its small size and lowest elevation, could start being invaded by dispersalists from Maui Nui only after the latter had acquired its snail fauna. Kauai, the smallest and most remote, could avoid being colonised for a long time. Hawaii, though young, is the largest and closest to Maui Nui, the main source of its colonisers. Furthermore, when Oahu emerged, let alone started sending scouts to other islands, Kauai was already 1.4 million years old, probably with fully developed biota. The same came true for Oahu when the first colonisers from Maui Nui could arrive. Successful colonisation is often regarded as more likely in unsaturated ecosystems, i.e. the immigration rate drops as the biota of the island approaches the equilibrium level (MACARTHUR & WILSON 1963). Hence a lower-frequency colonisation of such areas could be expected. Like with the mean speciation frequency, the values calculated might reflect the initial period of fairly intense immigration, followed by a

comparatively stagnant period whose duration depended on the age of the island. Thus the differences would at least partly reflect a bias introduced by the fact that while there was no such "initial period" for Kauai and Oahu, on Hawaii it still lasts or has lasted until recently. Maui Nui would represent an intermediate situation. The whole picture is blurred by intra-island speciation, and by the fact that the evolution apparently started on Oahu, not on Kauai, but if the rule applied, the colonisation frequency should actually decrease with increasing age of the island.

- dispersal within Maui-Nui

Since the age of the component islands of Maui Nui ranges from 0.8 (E Maui) to 1.9 myr (Molokai, W Maui) (SIMON 1987), during the Ice Age parts of it were still non-existent or their vegetation had not yet developed. The question is whether the land bridges appeared sufficiently early and lasted long enough to facilitate dispersal over the whole area of Maui Nui, or if they disappeared before the genus really radiated on the three islands. The whole island of Maui Nui harbours 13 species of *Lyropupa*, 7 of them being endemic. The non-endemic species are 4 members of the *ovatula* group, all dispersalists that evolved most probably on Oahu, and two species, *striatula* and *lanaiensis*, shared with Hawaii. If the connection lasted long enough to allow an even dispersal, the present day fauna should conform to PATTERSON & ATMAR's (1986) nested subset pattern. It conforms to it only partly (tab.5).

Table 5. Distribution of species endemic to Maui Nui

island	species			
Maui	<i>ingrata</i>	-----	<i>pluris</i>	plus 3 endemics
Molokai	<i>ingrata</i>	<i>sparna</i>	<i>pluris</i>	plus 1 endemic
Lanai	<i>ingrata</i>	<i>sparna</i>	-----	no endemics

Maui's and Lanai's sets are subsets to that of Molokai, but only disregarding endemics of the component islands. The absence of endemic species on Lanai is best explained by the fact that, being low and sheltered from the trade winds by other islands, it is relatively very dry (STEARNS 1985).

One explanation of the pattern is that the three islands, being closest to each other, acquired some common species as a result of island-to-island dispersal. Another is that species common to two or three islands could have used land bridges and become subsequently isolated. Hawaii, not very remote from Maui Nui, shares with it only *striatula*, *lanaiensis* and dispersalist species found also on other islands. This would speak in favour of the role of land bridges in dispersal.

The radiation on the component islands of Maui Nui is not monophyletic (cf. fig.147). *L. pluris* and *adeps* are related to the pair *cyrtallanaiensis* that originated probably on Hawaii; *thaanumi* is close to the pair *microthaumaldissimulator* from Oahu, *ingrata* and *sparna* are sister species, next related to *hawaiiensis* from Hawaii,

while *scabra* is the most plesiomorphic member of the *spaldingi* group. The only pair of sister species that evolved on Maui Nui is *ingratalsparna*, the former distributed on the three islands, the latter on Lanai and Molokai. This is an indication that their common ancestor could have arrived and speciated before the land bridges came into existence, and then dispersed. The fact that three species found on Maui and one found on Molokai are absent each from the remaining two islands may be partly explained by their origin on Maui Nui after the land connections have disappeared. At least some of those five species might have come into existence when Maui and Molokai were already separate islands. Except *scabra*, a plesiomorphic species with an essentially Oahuan sister taxon, all of them are fairly or very derived species with sister taxa on Oahu, Hawaii, or within Maui Nui.

The distribution of non-endemic species within Maui Nui (tab.6) conforms to the nested subset pattern. Strikingly, Lanai, the smallest, driest and ecologically the least diverse, with no endemics of its own, has all the six non-endemic species while Maui and Molokai have five and four, respectively. Possible explanations are: *micra*, *costata* and *kahoolavensis* arrived before or during the "land bridge period" and dispersed evenly while *ovatula* and *lanaiensis* arrived later and dispersed accidentally. Based on phylogeny, it can be assumed that *striatula* evolved on Maui Nui and from there dispersed to Hawaii, especially that it is rather plesiomorphic. *L. ovatula* and *lanaiensis* are rather derived. Could they have evolved before the "land bridge period", but disperse only later, accidentally? A simple but likely explanation would be that on the respective islands from which *striatula*, *ovatula* and *lanaiensis* are absent, they simply have not been found.

Table 6. Distribution of non-endemic species on Maui Nui

species/island	Maui	Molokai	Lanai
<i>micra</i>	X	X	X
<i>costata</i>	X	X	X
<i>kahoolavensis</i>	X	X	X
<i>striatula</i>	X	-	X
<i>ovatula</i>	-	X	X
<i>lanaiensis</i>	X	-	X

POSSIBLE CORRELATES OF DISTRIBUTION

General rules applying to radiation of land snails on islands were summarized by SOLEM (1990 and references contained therein). His conclusions are to the effect that for land snails in situ speciation is possible in any ecologically favourable area over 1 km², that island situations are not equilibria situations, since the proportion of immigration to in situ speciation is low, and for these reasons no species-area-age-elevation correlations apply to land snails.

Lyropupa, as a strictly endemic taxon, with a history limited to the Hawaiian Islands, offers a possibility to test these statements (tab.7).

Table 7. Number of species, endemism, island area, age and elevation

island	species	endemism	area [km ²]	age [myr]	elevation [m a.s.l.]
Kauai	5	2 (40%)	1,437	5.6-3.8	1,575
Oahu	14	9 (ca. 64%)	1,564	3.4-2.2	1,233
Maui Nui	13	7 (ca. 54%)	2,927	1.8-0.8	3,058
Molokai	8	1 (ca. 13%)	673	1.8-1.3	1,570
Lanai	8	0	365	ca. 1.3	ca. 1,000
Maui	10	3 (30%)	1,889	1.3-0.8	4,205

Irrespective from whether we consider Molokai, Lanai and Maui as separate islands or collectively as Maui Nui, there is no correlation with any factor.

Lyropupa is not the only snail taxon that does not conform to MACARTHUR & WILSON's (1963) model. The same was noted in the case of whole snail faunas of the Indo-Melanesian area, Reunion, Mauritius, Polynesia and Micronesia (SOLEM 1990 and references contained therein). Other "non-conformers" are Hawaiian insects: *Collembola* (CHRISTIANSEN & BELLINGER 1994) and the genus *Ptycta* (*Psocidae*) (THORNTON 1984).

Probably the main reason for non-applicability of MACARTHUR & WILSON's (1963) model to some radiations is an ability of certain taxa to speciate efficiently in situ i.e. without colonising new islands. Only 8 colonisation events and as many as 29 speciation events are necessary to account for the phylogeny and distribution of *Lyropupa*, which makes ca. 3.6 speciation events per 1 colonisation.

COWIE (1992) analysed snails of the genera *Partula* and *Samoana* from the Society Islands, and concluded that their diversity resulted mainly from intra-island speciation, with relatively few inter-island colonisation events. In many other snail taxa (*Endodontidae*, *Charopidae*, genus *Achatinella*) from various Pacific islands the ratio speciation:colonisation ranges from 2 to 30 (data from COOKE & KONDO 1960, SOLEM 1981). According to CHRISTIANSEN & BELLINGER (1994) the number of speciation events per colonisation for the Hawaiian *Collembola* is 2, for the beetles - 19, and for all the Hawaiian insects - 26. In the genus *Ptycta* that ratio exceeds 3 (THORNTON 1984) and in Hawaiian *Drosophila* it amounts to 11.5 (CARSON et al. 1970). A similar bias towards the intra-island speciation was found in a Hawaiian spider genus *Tetragnatha* (GILLESPIE & CROOM 1995) and two cricket genera: *Laupala* (30 speciation events per 6 colonisations) and *Prognathogryllus* (26 speciations per 8 colonisations) (OTTE 1989, 1994, SHAW 1995).

Reasons for and mechanisms of non-applicability of MACARTHUR & WILSON's (1963) model are discussed in detail elsewhere (POKRYSZKO in press).

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REFERENCES

- ANCEY, C. F., 1890. Mollusques nouveaux de l'archipel Hawai, de Madagascar et de l'Afrique Equatoriale. Bull. Soc. Mal. France, 7: 339-347.
- , 1892. Etudes sur la faune malacologique des îles Sandwich. Memoires de la Societe Zoologique de France, 5: 708-722.
- , 1904. Report on semi-fossil land shells found in the Hamakua district, Hawaii. Journal of Malacology, 11: 65-71.
- , 1904-1905. On some non-marine Hawaiian Mollusca. Proc. Malac. Soc. London, 6: 117-128, pl. VII.
- ASQUITH, A., 1994. An unparsimonious origin for the Hawaiian Metrargini (*Heteroptera: Lygaeidae*). Annals of the Entomological Society of America, 87: 207-213.
- , 1995. Evolution of *Sarona* (*Heteroptera, Miridae*). Speciation on geographic and ecological islands. 90-120 in: W. L. WAGNER, V. A. FUNK [eds.]. Hawaiian biogeography. Evolution on a hot spot archipelago. Smithsonian Institution Press, Washington and London.
- ATKINSON, I. A. E., 1970. Successional trends in the coastal and lowland forest of Mauna Loa and Kilauea volcanoes, Hawaii. Pacific Science 24: 387-400.
- BOSS, K. J., ROSEWATER, J., RUHOFF, F. A., 1968. The zoological taxa of William Healey DALL. Smithsonian Institution, United States National Museum, Washington, D. C., Bull. 287: 1-427.
- BROOKS, D. R., O'GRADY, R. T., WILEY, E. O., 1986. A measure of the information content of phylogenetic trees, and its use as an optimality criterion. Systematic Zoology 35: 571-581.
- CARSON, H. L., 1987. Tracing ancestry with chromosomal sequences. Trends in Ecology and Evolution 2, 7: 203-207.
- CARSON, H. L., CLAGUE, D. A., 1995. Geology and biogeography of the Hawaiian Islands. 14-29 in: W. L. WAGNER, V. A. FUNK [eds.]. Hawaiian biogeography. Evolution on a hot spot archipelago. Smithsonian Institution Press, Washington and London.
- CARSON, H. L., HARDY, D. E., SPIETH, H. T., STONE, W. S., 1970. The evolutionary biology of the Hawaiian *Drosophilidae*. 437-543 in: M. K. HECHT, W. C. STEERE [eds.]. Essays in evolution and genetics in honor of Theodosius DOBZHANSKY. A supplement to evolutionary biology. North Holland Publishing Company, Amsterdam.
- CHRISTIANSEN, K., BELLINGER, P., 1994. Biogeography of Hawaiian *Collembola*: the simple principles and complex reality. Oriental Insects 28: 309-351.
- COOKE, C. M., 1908. A new species of *Lyropupa* from Hawaii. Occasional Papers of the B. P. Bishop Museum, 3: 211-212.
- COOKE, C., M., KONDO, Y., 1960. Revision of *Tornatellinidae* and *Achatinellidae* (*Gastropoda, Pulmonata*). Bull. Bernice P. Bishop Mus. 221: 1-303.
- COWIE, R. H., 1992. Evolution and extinction of *Partulidae*, endemic Pacific land snails. Phil. Trans. R. Soc. Lond. B. 335: 167-191.
- COX, C. B., MOORE, P. D., 1993. Biogeography. An ecological and evolutionary approach. Blackwell Scientific Publications, Oxford.
- DALL, W. M., 1890. Description of a new species of land shell from Cuba - *Vertigo cubana*. Proceedings of the United States National Museum, 13: 1-2.

- DESALLE, R., 1995. Molecular approaches to biogeographic analysis of Hawaiian *Drosophilidae*. 72-89 in: W. L. WAGNER, V. A. FUNK [eds.]. Hawaiian biogeography. Evolution on a hot spot archipelago. Smithsonian Institution Press, Washington and London.
- DRAKE, D. R., MUELLER-DOMBOIS, D., 1993. Population development of rain forest trees on a chronosequence of Hawaiian lava flows. *Ecology* 74: 1012-1019.
- ELDRIDGE, N., 1989. Time frames. The evolution of punctuated equilibria. Princeton Science Library, Princeton.
- ELDRIDGE, N., CRACRAFT, J., 1980. Phylogenetic patterns and the evolutionary process. Method and theory in comparative biology. Columbia University Press, New York.
- FOREY, P., HUMPHRIES, C. J., KITCHING, I. L., SCOTLAND, R. W., SIEBERT, D. J., WILLIAMS, D. M., 1995. Cladistics. A practical course in systematics. Clarendon Press, Oxford.
- FOSBERG, F. R., 1963. Plant dispersal in the Pacific. 273-281 in: J. L. GRESSITT [ed.]. Pacific basin biogeography: a symposium. Bishop Museum Press, Honolulu.
- GILLESPIE, R. G., CROOM, H. B., 1995. Comparison of speciation mechanisms in web-building and non-web-building groups within a lineage of spiders. 121-146 in: W. L. WAGNER, V. A. FUNK [eds.]. Hawaiian biogeography. Evolution on a hot spot archipelago. Smithsonian Institution Press, Washington and London.
- GOULD, A. A., 1843. Conclusion of "Monograph of the *Pupadae* of the United States". *Proc. Bost. Soc. Nat. Hist.* 1: 138-139.
- GRESSITT, J. L., 1978. Evolution of the endemic Hawaiian cerambycid beetles. *Pacific Insects* 18: 137-167.
- GRESSITT, J. L., YOSHIMOTO, C. M., 1963. Dispersal of animals in the Pacific. 283-292 in: J. L. GRESSITT [ed.]. Pacific basin biogeography: a symposium. Bishop Museum Press, Honolulu.
- JAMES, H. F., OLSON, S. L., 1983. Flightless birds. *Natural History* 92: 30-40.
- JOHNSON, R. J., 1964. The recent *Mollusca* of Augustus Addison GOULD. Smithsonian Institution, United States National Museum, Washington, D. C., *Bull.* 239: 1-182, 45 pls.
- KANESHIRO, K. Y., GILLESPIE, R. G., CARSON, H. L., 1995. Chromosomes and male genitalia of Hawaiian *Drosophila*. 57-71 in: W. L. WAGNER, V. A. FUNK [eds.]. Hawaiian biogeography. Evolution on a hot spot archipelago. Smithsonian Institution Press, Washington and London.
- LOWREY, T. K., 1995. Phylogeny, adaptive radiation and biogeography of Hawaiian *Tetramolopium* (*Asteraceae, Astereae*). 195-220 in: W. L. WAGNER, V. A. FUNK [eds.]. Hawaiian biogeography. Evolution on a hot spot archipelago. Smithsonian Institution Press, Washington and London.
- MACARTHUR, R. H., WILSON, E. O., 1963. An equilibrium theory of insular zoogeography. *Evolution* 17: 373-387.
- MCDUGALL, I., SWANSON, D. A., 1972. Potassium-argon ages from the Hawaii and Pololu volcanic series, Kohala Volcano, Hawaii. *Bulletin of the Geological Society of America* 83: 3731-3738.
- MORGAN, J., 1971. Convection plumes in the lower mantle. *Nature* 230: 42-43.
- MUELLER-DOMBOIS, D., 1987. Forest dynamics in Hawaii. *Trends in Ecology and Evolution* 2, 7: 216-220.
- OTTE, D., 1989. Speciation in Hawaiian crickets. 482-526 in: D. OTTE, J. A. ENDLER [eds.]. Speciation and its consequences. Sinauer Associates, Sunderland, MA.
- OTTE, D., 1994. The crickets of Hawaii: origin, systematics and evolution. The Orthoptera Society/Academy of Natural Sciences of Philadelphia.
- PATTERSON, B. D., ATMAR, W., 1986. Nested subsets and the structure of insular mammalian faunas and archipelago. *Biol. Journ. Linn. Soc.* 28: 65-82.
- PEASE, H., 1871. Catalogue of the land shells inhabiting Polynesia, with remarks on their synonymy, distribution and variation, and descriptions of new genera and species. *Proc. Zool. Soc. London*, 29: 449-492.
- PILSBRY, H. A., 1900. The genesis of mid-Pacific faunas. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 1900: 568-581.
- PILSBRY, H. A., COOKE, C. M., 1918-1920. *Manual of Conchology*. 2, 25: *Pupillidae* (*Gastrocoptinae, Vertiginidae*). Philadelphia: 225-404, I-IX.
- POKRYSZKO, B. M., 1990. The *Vertiginidae* of Poland (*Gastropoda: Pulmonata: Pupilloidea*) - a systematic monograph. *Ann. Zool.*, 43: 133-257.

- POKRYSZKO, B. M., 1994. On the mono(?)phyly and classification of the *Pupilloidea/Orthurethra* (*Gastropoda: Pulmonata: Stylommatophora*). *Genus*, **5**: 371-390.
- POKRYSZKO, B. M., 1996. The *Gastrocoptinae* of Australia (*Gastropoda: Pulmonata: Pupilloidea*): systematics, distribution and origin. *Invertebrate Taxonomy*, **10**: 1085-1150.
- POKRYSZKO, B. M., in press. Dlaczego ślimaki nie stosują się do teorii MacArthura i Wilsona? (lub vice versa). [Why don't snails conform to MacArthur and Wilson's theory? (or vice versa)] [in Polish with an English summary]. *Zoologica Poloniae*.
- SAETHER, O. A., The myth of objectivity - post-Hennigian deviations. *Cladistics* **2**: 1-13.
- SHAW, K. L., 1995. Biogeographic patterns of two independent Hawaiian cricket radiations (*Laupala* and *Prognathogryllus*). 39-56 in: W. L. WAGNER, V. A. FUNK [eds.]. *Hawaiian biogeography. Evolution on a hot spot archipelago*. Smithsonian Institution Press, Washington and London.
- SIMON, Ch., 1987. Hawaiian evolutionary biology: an introduction. *Trends in Ecology and Evolution* **2**, **7**: 175-178.
- SOLEM, A., 1981. Land snail biogeography: A true snail's pace of change. 197-237 in: G. NELSON, D. E. ROSEN [eds.]. *Vicariance biogeography*. Columbia University Press, New York.
- SOLEM, A., 1990. Limitations of equilibrium theory in relation to land snails. *International Symposium on Biogeographical Aspects of Insularity, Rome 1987. Atti dei Convegni Linzei* **85**: 97-116.
- STEARNS, H. T., 1985. *Geology of the State of Hawaii*. Second Edition. Pacific Books, Palo Alto, California.
- STEMMERMANN, L., 1983. Ecological studies of Hawaiian *Metrosideros* in a successional context. *Pacific Science* **37**: 361-373.
- TALIAFERRO, W. J., 1959. *Rainfall of the Hawaiian Islands*. Honolulu, Hawaii Water Authority.
- THORNTON, I., W. B. 1984. *Psocoptera of the Hawaiian Islands*. Part III. The endemic *Ptycta* complex (*Psocidae*): systematics, distribution and evolution. *International Journal of Entomology* **26**: 1-128.
- VAGVOLGYI, J., 1976. Body size, aerial dispersal, and origin of the Pacific land snail fauna. *Systematic Zoology* **24**: 465-488.
- ZIMMERMANN, E. C., 1948. *Insects of Hawaii*. Vol. 1. Introduction. Honolulu, University of Hawaii Press.