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Hawaiian Lymnaeidae*

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INTRODUCTION

During the last three years I have been studying the family Lymnaeidae in order to produce a thorough systematic account of the group. For that purpose I have borrowed collections from various museums. Those from Bernice P. Bishop Museum, a comparatively rich material of shells and animals in alcohol, have proved the Hawaiian lymnaeid fauna to be the richest in the world in relation to its restricted geographical range. For that reason and because all Hawaiian species are endemic forms, this separate paper on the Hawaiian lymnaeid fauna has been prepared.

The systematic method used is based upon some general conclusions as to principles of variation and evolution within the group. I must confine this report to an account of the Hawaiian fauna, leaving general treatment of the group for my monographic survey of the family.

I wish to express my appreciation of the assistance received from the late Dr. C. Montague Cooke, Jr., of the helpfulness of Mr. Yoshio Kondo in connection with my studies of the Hawaiian material, and of the interest of Mr. W. J. Clench, who read the paper critically.

KEY TO SPECIES

A. Shell features.
Shell sinistral ..... **L. reticulata**
Shell dextral
Well-developed spire.
Whorls generally somewhat truncate. Suture very moderately sloping ..... **L. volutata**
Whorls not truncate. Suture ordinarily sloping ..... **L. rubella**

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Spire extremely short or entirely reduced.
Spire short. Aperture about three-fourths of shell length. Inner lip without a callus.....**L. aulacospira**
Spire entirely reduced. Aperture nearly as long as shell. Inner lip with a callus .....**L. newcombi**

B. Anatomical features.

Spermathecal duct short. Radula with the first laterals tricuspid.....**L. volutata**
Spermathecal duct long. Radula with the first laterals bicuspid.
Genital and mantle pores on the left side.....**L. reticulata**
Genital and mantle pores on the right side.
A well-developed fold occurs in the prostate.....**L. rubella**
No fold occurs in the prostate.
Penis sheath short and distinctly delimited from the praeputium.....
.....**L. aulacospira**
Penis sheath extremely short and not distinctly delimited from the praeputium .....**L. newcombi**

Lymnaea volutata Gould, Boston Soc. Nat. Hist., Proc. 2 : 211, 1848.

Shell (fig. 1). The outline of the shell shows a tendency to rhomboidal form. The spire is comparatively small with either more or less pointed apex. Its whorls are generally slightly truncate but sometimes not at all. The body whorl may be truncate. This whorl is dominant but hardly bulging. The suture is very gradually sloping, nearly perpendicular to the longitudinal axis of the shell. The aperture is not considerably expanded. The columella is twisted or

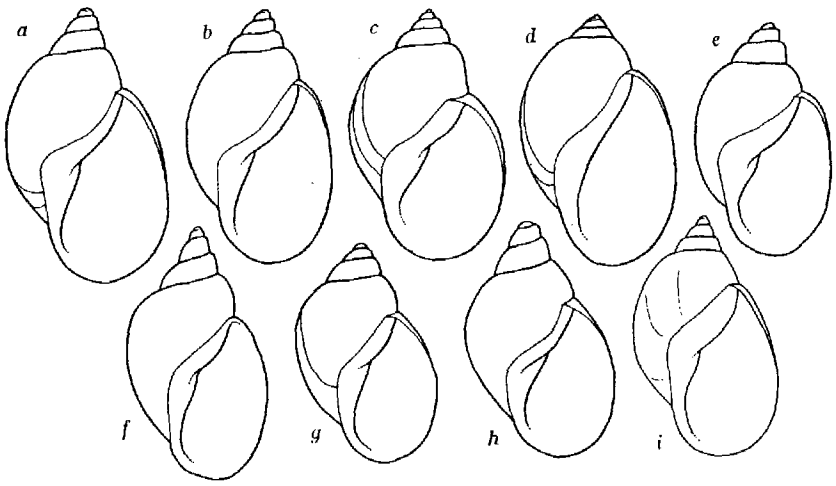

FIGURE 1.—Shells of *Lymnaea volutata:* **a, b,** from Kalalau Valley, Kauai (BBM 15633 and BBM 15645), shell heights 10 and 8.5 mm.; **c.** from Kailua, Oahu (BBM 168179), height 12 mm.; **d,** from Kewalo, Oahu (BBM 14765), 12 mm.; **e, f,** from Manoa, Oahu (BBM 14768), heights 8 and 9 mm.; **g, h,** from Nuuanu, Oahu (BBM 14764), heights 7 and 7.5 mm.; **i,** from Kalalau Valley, Kauai (BBM 15633), height 9 mm.

not. A columellar fold, as well as an umbilicus, usually occurs. This generally pale-colored shell has a fine sculpture parallel to the peristome.

Anatomy. The penis sheath and the penis are of about the same length (fig. 2, *a-c*). Well-developed muscular pillars occur in the distal portion of the praeputium (figure 2, *a*). Velum and sarcobelum are of about the same relative size as those in most Lymnaeae. The wall of the penis sheath is extremely thin. There are narrow proximal chambers separated by thin walls. A large split occurs in the longitudinal muscular layer of the penis. The prostate (fig. 2, *d, e*) has one large, inward-directed fold, but a rather large lumen is usually left. The spermathecal duct is either short or almost entirely absent (fig. 2, *f-h*). In the latter case the spermatheca is elongated or pyriform. The radula has tricuspid first laterals (fig. 2, *i*).

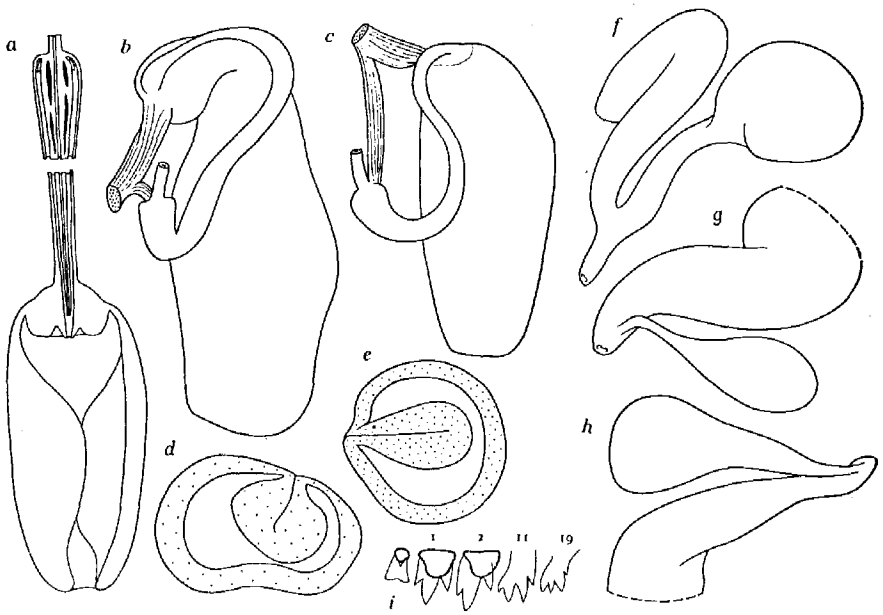

FIGURE 2.—Anatomy of *Lymnaea volutata:* **a,** longitudinally sectioned male copulatory organ, the black areas indicating lacunae or splits in muscular tissue, magnification about 22 ×; **b, c,** male copulatory organs, about 30 ×; **d, e,** schematic cross section through prostate, about 25 ×; **f-h,** spermathecal system and most distal part of female gonoduct, about 30 ×; **i,** central and some teeth from right side of a transverse row of radula, 300 ×. (For detailed explanation, see figure 8.)

Type: Oahu, U. S. Exploring Expedition, possibly in the United States National Museum.

Range: Niihau, Kauai, Oahu, Molokai, Maui, and Hawaii (fig. 3).

Niihau: Kapaka Spring, 750 ft., July 16, 1947, H. St. John and

L. D. Tuthill (210508); Kapaka Valley, 300 ft., July 16, 1947, St. John and Tuthill (210514).

Kaui: Hanamaula, at seashore, 100 yards north of dairy, south of stream, November 3, 1936, E. Y. Hosaka (168017); Hanalei, rice field, May 24, 1928, R. H. Van Zwaluwenburg (92512); Kalalau Valley, July 17, 1907, C. S. Davies (15633); entrance to Kalalau Valley, July 18, 1907, C. M. Cooke, Jr. (15645).

Oahu (Koolau): Manoa, Waihinui Valley, on wet rock wall, January 12, 1929, Marie C. Neal and E. H. Bryan, Jr. (93588); Manoa, taro patches, May 1905, C. M. Cooke, Jr. (14762); Manoa, spring opposite chalet, July 31, 1907, C. M. Cooke, Jr. (14768); Nuuanu, Luakaha Falls, July 4, 1905, C. M. Cooke, Jr. (14764); Kewalo, ditch from rice mill, July 12, 1905, C. M. Cooke, Jr. (14765); Kewalo, taro patches, July 12, 1905, C. M. Cooke, Jr. (14766); Kewalo, near coconut trees, July 17, 1905 (14767); Pacific Heights, November 20, 1907, H. E. Podmore (15830); valley west of Kuliouou Valley [east Niu], May 16, 1909, I. Spalding (19177); Punaluu, ditch near railroad track, May 12, 1907, C. N. Forbes (19411); Punaluu, above road, August 8, 9, 14, 22, 1917, C. M. Cooke, Jr., C. M. Cooke III, B. Oliveira, F. Girdler, Tomonari (45171); Kaipapau, August 11, 1909, C. M. Cooke, Jr., and Hazel Mesick (19867); Palolo Stream, under water, on rocks, March 24, 1919, C. F. Mant (47195); Kailua, Campos Dairy, small swamp, December 4, 1936, J. E. Alicata (168179); Moiliili, back of Kaimuki Pump, Andrade's Well, October 9, 1915, A. Gouveia (40436).

Oahu (Waianae): Kawaihapai, rice patch at foot of talus, February 1913, C. N. Forbes and C. M. Cooke, Jr. (35675); Mokuleia, Makaleha central valley, July 14, 1932, G. W. Russ and d. A. Welch (114036); Lualualei, Puhawai, 1932, Jane Winne and d. A. Welch (128678, 128680); Puu Hapapa, north slope, 1,750 ft., in stream, March 8, 1948, J. Tobin and Y. Kondo (211058-211060); same locality, March 19, 1948, Mr. and Mrs. W. Murnan, Y. Kondo (211005); Kukuiula, October 16, 1923, N. L. H. Krauss (164321).

Molokai: Mapulehu Valley, June 4, 1919, C. F. Mant (47750).

Maui: Lahaina, about 1905, D. D. Baldwin (14770); Waikamoi Gulch, on belt road, under wet stones, August 17, 1928, C. S. Judd (92491).

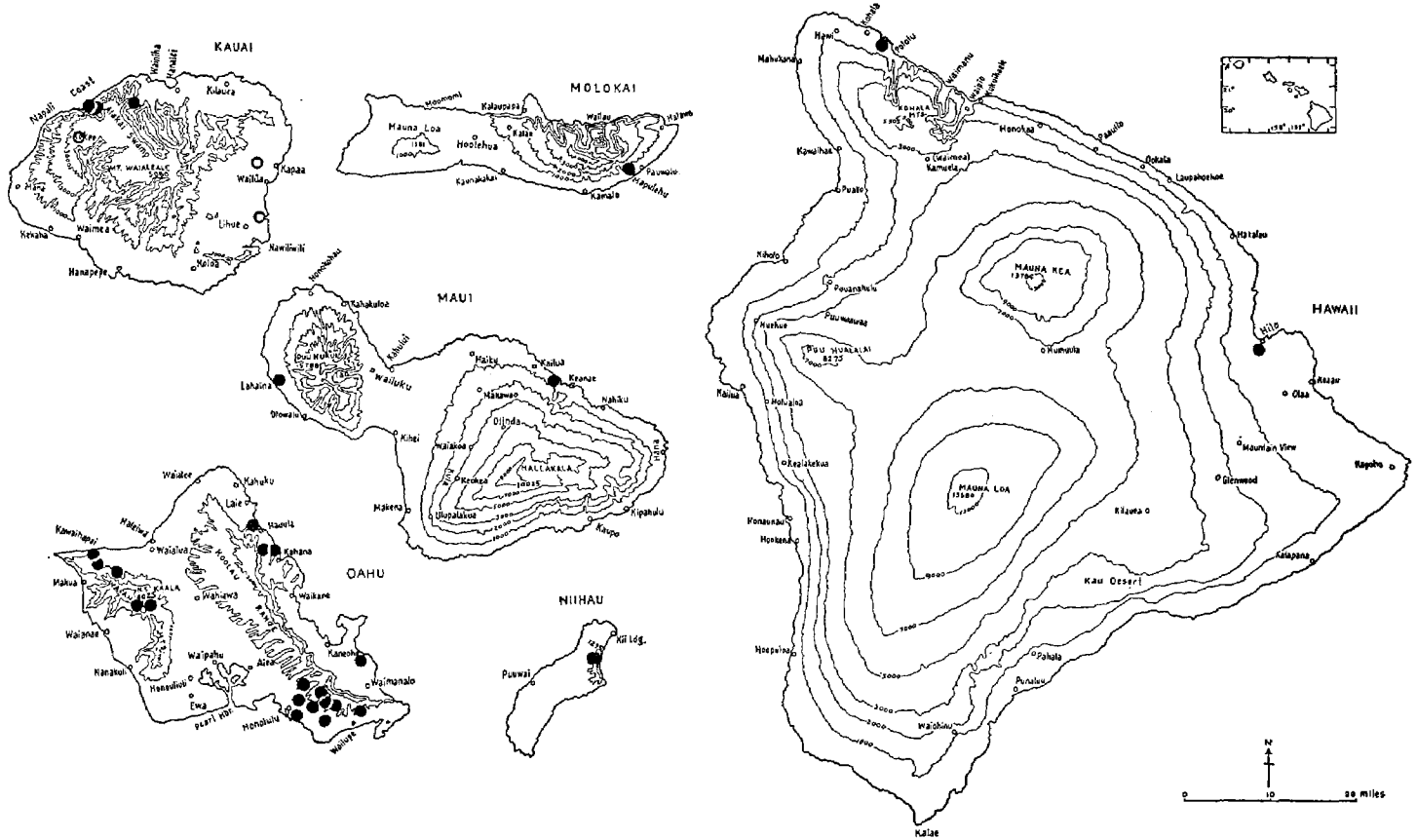

FIGURE 3.—Map showing the collection localities of *Lymnaea volutata*. (Solid dots indicate exact localities; circles, general localities.)

Hawaii: Kohala, no date, E. W. Thwing (25341); Hilo, no date, E. W. Thwing (25339); Kona, no date, E. W. Thwing (25340); Kohala, Niulii, bridge 406, east bank, *mauka* [mountainward], on wet rock bank, June 24, 1922, Marie C. Neal (59701).

This species is reported from streams, falls, swamps, and ditches but also from such hardly limnic biotopes as wet rocks, taro, and rice patches.

The shell of *L. volutata* is fairly close to that of the east Asiatic species *L. viridis* Quoy and Gaimard, but the spermathecal duct and the radula differ in the two species.

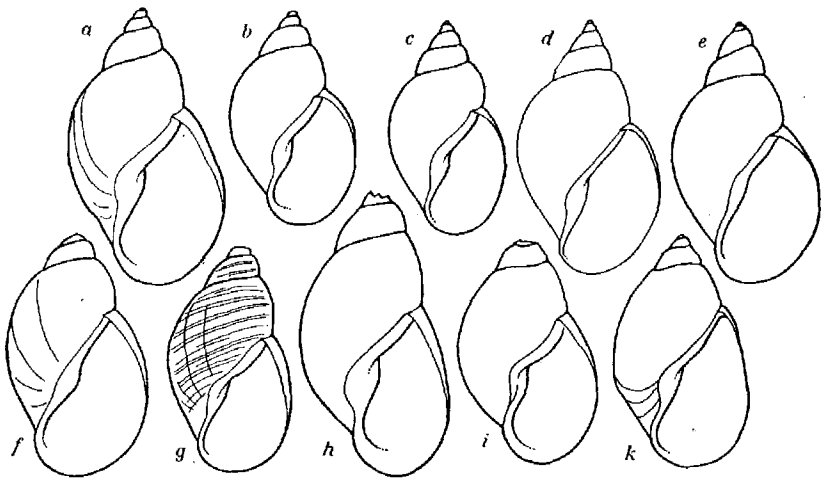

FIGURE 4.—Shells of *Lymnaea rubella:* **a-d,** from Waipio, Kauai (BBM 15499), shell heights 13, 10, 10, and 12 mm.; **e, f,** from Waimea Canyon, Kauai (BBM 48395), 9 and 8.5 mm.; **g,** from Kuliouou, Oahu (BBM 16016), 11 mm.; **h,** from Moanui, Molokai (BBM 14795), 10 mm.; **i,** from Kalihi, Molokai (BBM 33619), 8 mm.; **k,** from Mapulehu, Molokai (BBM 24271), 7 mm.

Lymnaea rubella Lea, Am. Phil. Soc., Trans. 9: 12, 1844.

Limnaeus sandwichensis Philippi, Arch. Naturgesch. 1: 63, 1845. (See figure 16, *a, b.*)

Lymnaea oahuensis Souleyet, Voy. Bonite, Zool. 2: 527, pl. 29, figs. 38-41, 1852.

Limnaeus sandwicensis Philippi, Küster in Martini and Chemnitz, Syst. Conch.-Cab. 1 (17 B): 26, figs. 25-26, 1862.

Limnaea ouahensis Souleyet, Sowerby in Reeve, Conch. Icon. **18:** sp. 90, pl. 13, 1872.

Shell (fig. 4). The general type of the shell resembles a very short-spired form of the group *Stagnicola*. The comparatively short or middle high spire has an apex, pointed to a greater or lesser extent, though often worn off. The spire is not distinctly set off from the body whorl, as in the preceding species, but its outlines merge gradually into those of the latter. The whorls are not at all truncate. The suture is much more steeply sloping than in the preceding species. The aperture is not considerably enlarged. The columella is generally twisted, usually less than in *L. volutata*. A distinct columellar fold and umbilicus are generally absent, but do sometimes occur. The brown or reddish-brown shell has a fine sculpture parallel to the peristome.

Anatomy. The proportion in length between penis sheath and praeputium varies, but the former is generally comparatively thick (fig. 5, *a-c*). Muscular pillars are feebly developed, sometimes almost lacking. Velum and sarcobelum are well-developed. The proximal chambers in penis sheath may be tubiform and narrow and separated by walls containing some muscular and connective tissue. A split may occur in the longitudinal muscle layer of the penis. Glandular cells seem to occur in the distal end of the penis. The prostate (fig. 5, *f, g*) has one large fold. The spermathecal duct is of the ordinary length. It widens considerably just before entering the vagina. The first laterals of the radula are bicuspid (fig. 5, *h*). A well-developed muscle runs on the ventral surface of the kidney.

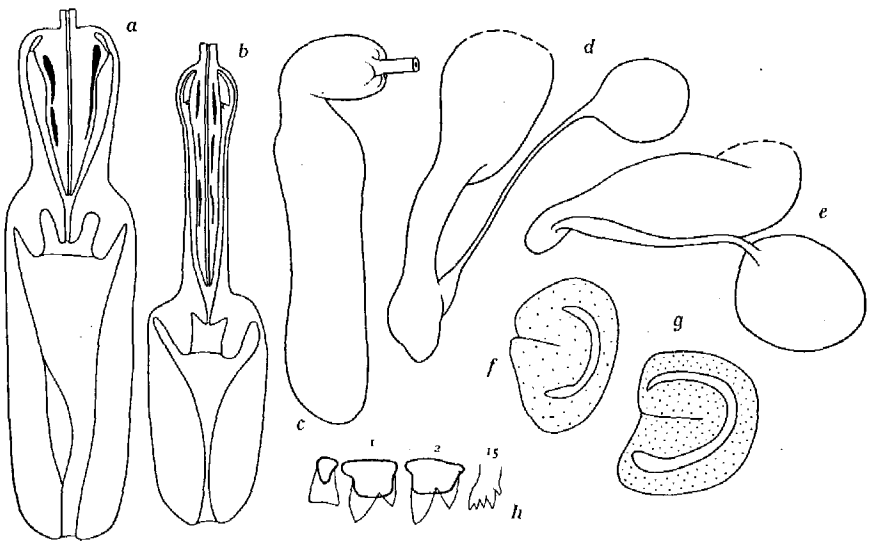

FIGURE 5.—Anatomy of *Lymnaea rubella:* **a, b,** longitudinally sectioned male copulatory organs (black areas indicate lacunae or splits in muscular tissue), about 35 ×; **c,** male copulatory organ, about 25 ×; **d, e,** spermathecal system and the most distal part of the female gonoduct, about 25 ×; **f, g,** schematic cross section through prostate, about 22 ×; **h,** central and some teeth from right side of a transverse row of radula, 300 ×. (For detailed explanation, see figure 8.)

Type: Oahu, *Nuttall.*

Range: Kauai, Oahu, Molokai, and Maui (fig. 6).

Kauai: Waipio, Nawaimaka Stream, July 7, 1907, C. M. Cooke, Jr. (15499); Kipukai, under Haopu, on wet leaves at foot of waterfall, C. M. Cooke, Jr. and C. A. Rice (36420); Halemanu Valley, in Faye's swimming pool just below house, August 11, 1919, C. M. Cooke, Jr. and C. M. Cooke III (48111); Waimea Canyon, Poomau Spring, August 20, 1919, A. Knudsen (48395); Olokele, 1.5 miles of the end of wagon road, near many small mango trees just above big boulder, June 29, 1925, W. Meinecke (79920); Olokele, above Rainbow Falls, July 2, 1925, W. Meinecke (124235).

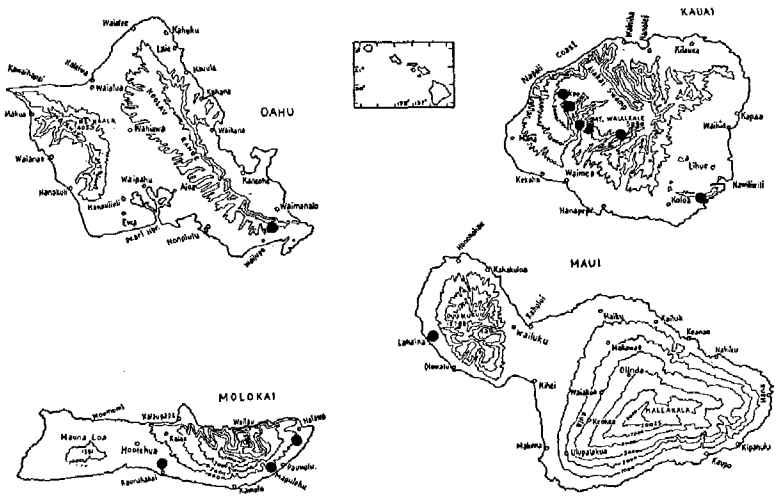

FIGURE 6.—Map showing exact collection localities of *Lymnaea rubella.*

Oahu (Koolau): Kuliouou, February 17, 1908, I. Spalding (16016).

Molokai: Moanui, about 1903, D. Thaanum (14795); Mapulehu Valley, subridge, July 30, 1912, C. M. Cooke, Jr. (24271); Kaunakakai, Kalihi, pipeline trail below spring, January 26, 1913, H. A. Pilsbry and C. M. Cooke, Jr. (33619).

Maui: Lahaina, Mt. Retreat, no date, D. D. Baldwin (25338).

This species is reported from streams and from swimming pools,

but also from wet leaves at the foot of a waterfall and from a pipeline trail below a spring.

Lymnaea aulacospira Ancey, Le Naturaliste **11**: 290, 1889.

Limnea aulacospira Ancey, Sykes in Malac. Soc. London, Proc. 3(5): 275, pl. 13, fig. 19, 1899.

Limnaea hawaiensis Pilsbry, Acad. Nat. Sci. Philadelphia, Proc. **55**: 790, 1903.

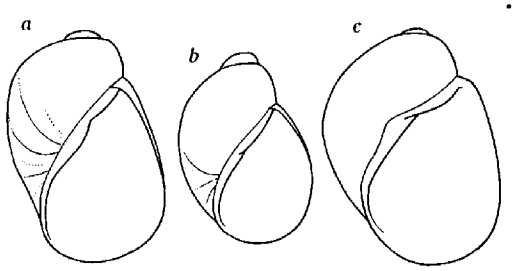

FIGURE 7.—Shells of *Lymnaea aulacospira:* **a, b,** from Waialae River, Kauai (BBM 107444), shell heights 7 and 6 mm.; **c,** from Akaka Falls, Hilo, Hawaii (BBM 39138), 4.5 mm.

Shell (fig. 7). The spire is extremely short and the shell is almost entirely made up of the body whorls. (The obtuse spire consists of one and a half whorls.) Broadly speaking, the body whorl is rectangular. The comparatively large aperture is fairly regularly pyriform, the columella and the upper portion of the peristome are almost straight and connected to each other below by the rounded lower (or frontal) portion of the peristome. The inner lip is not expanded or broadly reflected over the body whorl. Sometimes it is not even densely appressed to the latter, thus leaving a narrow umbilical chink. There is no columellar fold. The pale brown shell has an extremely faint sculpture of, generally, interrupted lines parallel to the peristome.

Anatomy. The comparatively thick penis sheath is shorter than the praeputium and distinctly delimited from the latter (fig. 8, *a, b*). The muscular pillars are comparatively small but velum and sarcobelum are of the ordinary size. The proximal chambers in the penis sheath are separated by thin walls. The penis has a wide split in its proximal portion and in the same region the vas deferens and its nearest surrounding tissue are coiling within the split. There is no fold in the prostate (fig. 8, *d*). The spermathecal duct is long and slender and thickens slightly in its distal end (fig. 8, *c*). The first laterals of the radula are bicuspid (fig. 8, *e*). The centrals are asymmetrical as in all other lymnaeids, having one small lateral cusp. The centrals of *L. aulacospira* are not unicuspid as Pilsbry (13, p. 791),[1] maintains.

[1] Numbers in parentheses refer to Bibliography, page 328.

Type: Maui. The type specimen probably in Bishop Museum. On the label written by Ancey is the following, "*Errina* ? *aulacospira* Ancey, type, Maui, ex D. D. Baldwin" (BBM 19093, in Bishop Museum).

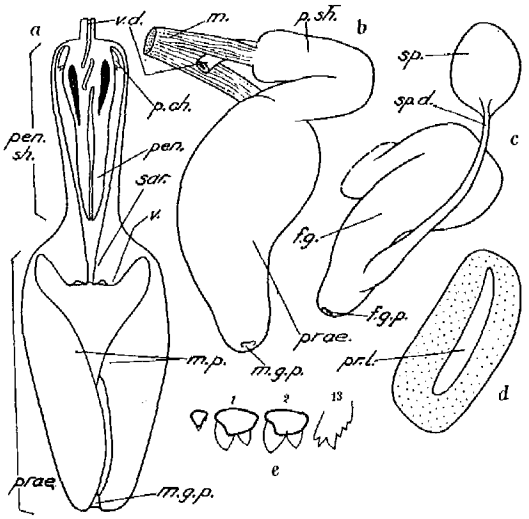

FIGURE 8.—Anatomy of *Lymnaea aulacospira:* **a,** longitudinally sectioned male copulatory organ (black areas indicate lacunae or splits in muscular tissue), about 25 × (*m.g.p.*, male genital pore; *m.p.*, muscular pillars; *p. ch.*, wall between proximal chambers; *pen.*, penis; *pen. sh.*, penis sheath; *prae.*, praeputium; *sar.*, sarcobelum; *v.*, velum; *v.d.*, vas deferens); **b,** male copulatory organ, about 22 × (*m.*, muscles; *m.g.p.*, male genital pore; *prae.*, praeputium; *p. sh.*, penis sheath; *v.d.*, vas deferens); **c,** spermathecal system and most distal part of female gonoduct, about 20 × (*f.g.*, female gonoduct; *f.g.p.*, female genital pore; *sp.*, spermatheca; *sp. d.*, spermathecal duct); **d,** schematic cross section through prostate, about 30 × (*pr. l.*, lumen of prostate); **e,** central tooth and some teeth from right side of a transverse row of radula, 300 ×.

Range: Kauai, Molokai, Maui, and Hawaii (fig. 9).

Kauai: Hanakoa, near Halulu Falls, July 16, 1907, W. F. Frear and A. Knudsen (15612); Haena, Manoa, head of valley on sides of waterfall, June 16, 1914 (36395); Waialae River, September 27, 1931, d. A. Welch (107444).

Molokai: Moanui, about 1903, D. Thaanum (14796).

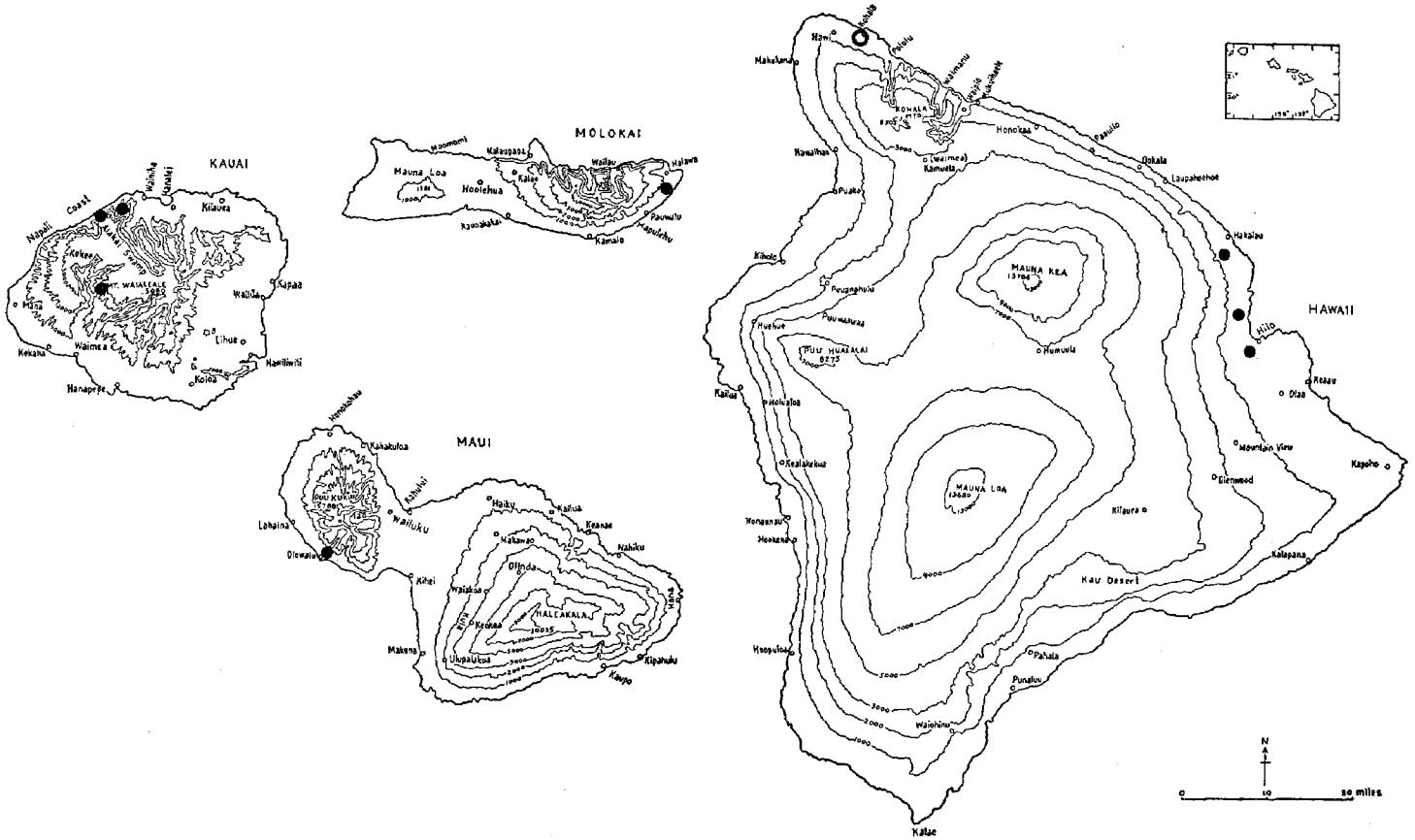

FIGURE 9.—Map showing collection localities of *Lymnaea aulacospira*. (Black dots indicate exact localities; circle, general locality.)

Maui: Olowalu, about 2 miles inland, on wet surface rocks of precipice, 1913, D. Thaanum (36903).

Hawaii: Kohala, no date, E. W. Thwing (25341); Hilo, Honolii River, no date, D. Thaanum (14797); Hilo, Akaka Falls, May 23, 1915, C. M. Forbes (39138); Hilo, Wailuku River, no date, D. Thaanum (19092).

This species is reported from rivers and falls, as well as from the wet surface rocks of a precipice.

Lymnaea newcombi (H. and A. Adams).

Erinna Newcombi H. and A. Adams, Zool. Soc. London, Proc. (23): 120, 1855. (See figure 16, *c*.)

Shell (fig. 10). The shell of *L. newcombi* resembles that of *L. aulacospira,* but the peculiarities of the latter are even more pronounced in *L. newcombi.* This species is quite neritiform, its spire being entirely reduced. Its apical region is surrounded by the body whorl. The pyriform aperture is as high as the body whorl, thus reaching the upper (or caudal) end of the shell. The columella is straight and there is no columellar fold but the lower (frontal) portion of

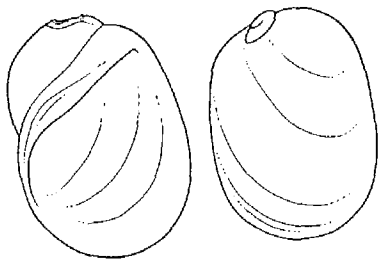

FIGURE 10.—Shells of *Lymnaea newcombi* from Hanakapiai Stream, Kauai (BBM 15571), shell-height 5 mm. The right specimen from above.

the columella is calloused with a bluish white color. The aperture is slightly funnel-shaped and the inner lip is, consequently, reflected over a small part of the body whorl. It is, however, not appressed toward it. A sort of umbilical chink occurs therefore. When the animal is creeping the apical region is directed obliquely backward to the right. The surface of the shell is smooth and dull but has an extremely faint sculpture parallel to the peristome.

Anatomy. The penis sheath is distinctly shorter than the praeputium but it is almost as thick as the latter (fig. 11, *a, b*). Its connection with the praeputium is only slightly narrower than the praeputium. No distinct muscular pillars occur. Velum and sarcobelum are of about the ordinary size. Thin-walled proximal chambers occur in the penis sheath. The penis is rather short and has a comparatively wide lumen. The prostate is unfolded (fig. 11, *d*). The spermathecal duct is long and slender but increases considerably in thickness distally (fig. 11, *c*). The tentacles have the ordinary flat form. The mantle

border has the ordinary breadth. There is a straight kidney with two very slender superficial muscles in the comparatively small mantle cavity. The jaw is very weak and has a small point medially. In the radula (fig. 11, *e*) the centrals are asymmetrical and the first laterals are bicuspid. The visceral commissure contains only three or possibly four ganglia, pleural ganglia included.

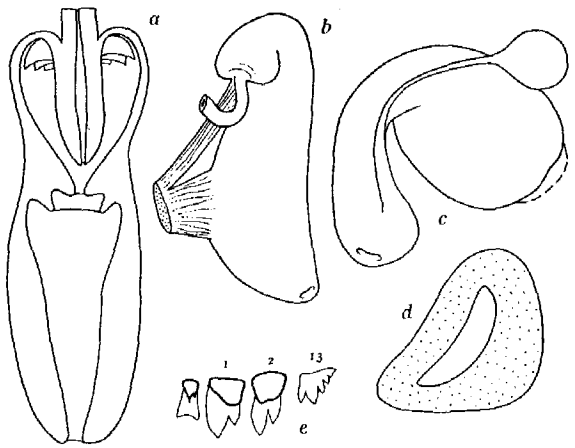

FIGURE 11.—Anatomy of *Lymnaea newcombi:* **a,** longitudinally sectioned male copulatory organ, about 30 ×; **b,** male copulatory organ, about 25 ×; **c,** spermathecal system and most distal part of female gonoduct, about 30 ×; **d,** schematic cross section through prostate, about 40 ×; **e,** central and some teeth from right side of a transverse row of radula, 300 ×. (For detailed explanation, see figure 8.)

Type: H. and A. Adams give "Heneta River, Kami, Sandwich Islands" as the type locality which is obviously incorrect. It is probably Hanalei River, Kauai, collected by Newcomb, the type in the British Museum of Natural History (fig. 16, *c*).

Range: Kauai (fig. 12).

Kauai: Hanakapiai, head of valley near waterfall, July 15, 1907, W. F. Frear and A. Knudsen (15600); Hanakapiai Stream, on overhanging rock near swift water, July 13-15, 1907, C. M. Cooke, Jr. (15571); Kalalau, July 17, 1907, C. S. Davies (15634); Hanakoa, near Halulu Falls, July 16, 1907, W. F. Frear and A. Knudsen (15613); Waipahi, valley above dam, 0.5 mile above valley mouth, October 17, 1925, C. M. Cooke, Jr., Mr. and Mrs. T. T. Dranga (80515).

The original inclusion of *L. newcombi* within the genus *Erinna*

by H. and A. Adams (1, p. 120) was based upon shell features which I cannot consider sufficient. In comparison with the general variation in shell structures in *Lymnaea,* the distinguishing shell characteristics in *Erinna* are merely of specific value. My dissections show that the visceral commissure has fewer ganglia in *Erinna* than in those other species of *Lymnaea* examined by me. This feature is undoubtedly of

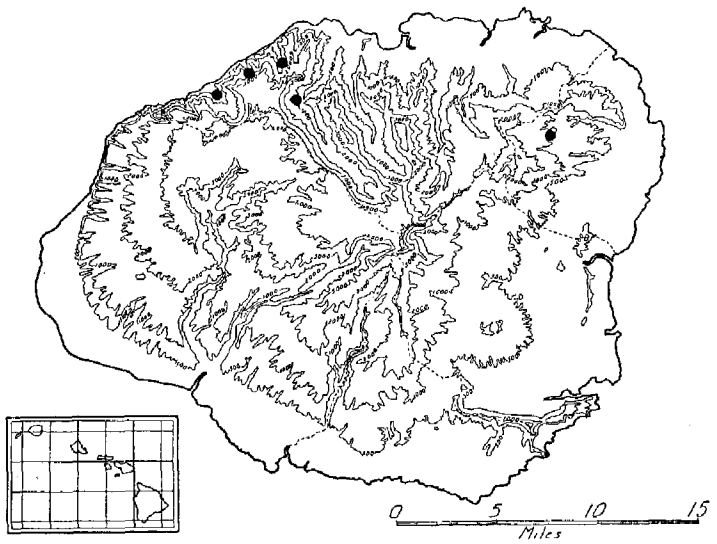

FIGURE 12.—Map of Kauai, showing collection localities of *Lymnaea newcombi.*

greater taxonomic importance than are the shell features. In my opinion, the far-reaching concentration of the nervous system in *L. newcombi* has certainly evolved in connection with the reduction of the spire; and it seems to me much more probable that the reduction in both spire and visceral commissure have occurred within *Lymnaea* than that a generic distinction exists as implied by the old separation of H. and A. Adams. Consequently, *Erinna* should be reduced to a subgeneric rank. The difficulty of delineating the distinguishing shell characteristics between *Lymnaea* and *Erinna* and, in addition, the possibility that the same structure may occur in the nervous system through parallel evolution in other species of *Lymnaea* not hitherto studied with this in mind, are reasons enough for including this species of *Erinna* in *Lymnaea.* In short, a taxonomic separation of *Erinna* does not seem possible.

L. newcombi is very similar to *L. onychia* Westerlund from Japan, which was earlier included in the group *Omia*. In *L. onychia*, however, the cusps of the lateral teeth are rounded, whereas this is not true of any other *Lymnaea* examined. It is, however, impossible to decide whether *L. onychia* and *L. newcombi* are closely related or have evolved independently.

Lymnaea reticulata Gould.

Physa reticulata Gould, Boston Soc. Nat. Hist., Proc. 2 : 214, 1847. (See figure 16, *d-f*.)
?Physa umbilicata Mighels, op. cit., 21, 1845.
?Physa producta Mighels, op. cit., 21, 1845.
Lymnaea affinis Souleyet, Voy. Bonite, Zool. 2 : 528, 1852.
Limnaeus volutatus, b. *sinistrorsus* Martens, Ann. Mag. Nat. Hist. III, **17** : 208, 1866.
Limnaea turgidula Pease, Am. Jour. Conch. 6 : 5, pl. 3, fig. 3, 1870.
Limnaea compacta Pease, op. cit., pl. 3, fig. 4, 1870. p. 6
Limnaea ambigua Pease, op. cit., pl. 3, fig. 5, 1870.
Physa peasei Clessin, in Martini and Chemnitz, Syst. Conch.-Cab. **1**(17) : 339, pl. 47, fig. 8, 1886.
Physa moreletiana Clessin, op. cit., 341, pl. 48, fig. 3, 1886.
Physa naticoides Clessin, op. cit., 341, pl. 48, fig. 5, 1886.
Physa sandwichensis Clessin, op. cit., 342, pl. 48, fig. 7, 1886. (See figure 16, *h*.)
Physa flavida Clessin, op. cit., 364, pl. 51, fig. 9, 1886.
Physa hartmanni Clessin, op. cit., 371, pl. 54, fig. 9, 1886.
Limnaea binominis Sykes, Fauna Hawaiiensis 2(4) : 391, 1900. (See figure 16, *g*.)

Shell (fig. 13). The sinistral shell (all other lymnaeids are dextral) has a medium high spire and a not very expanded aperture. The shell is very variable in all its features. The spire is slightly obtuse to pointed. Very often the apex is worn off. The suture is slightly to deeply impressed. The outline of the peristome sometimes forms a straight continuation of that of the body whorl but sometimes it forms an abrupt angle with the outline of the body whorl. The columella is generally barely twisted. A well-pronounced or a very small columellar fold is generally present but can also be absent. A very small, bluish-white callus is sometimes formed by the lower (frontal) part of the columella. An umbilical fold is generally absent. The brown, yellowish-brown or reddish-brown shell has a fine, sometimes interrupted, sculpture parallel to the peristome.

Anatomy. The penis sheath and penis are comparatively short (fig. 14, *a-f*), shorter in specimens from Kauai than in those from Oahu. Relatively small muscular pillars occur. Velum and sarcobelum are of about the ordinary size.

The proximal chambers are generally narrow. The penis is not very long, sometimes it is pyriform. A small split generally occurs in the musculature, and the vas deferens can be coiling within it. The prostate is unfolded (fig. 14, *k-n*). The spermathecal duct is long and slender (fig. 14, *g-i*). The first laterals in the radula (fig. 14, *o*) are bicuspid. The asymmetry of the centrals are the reverse of that in all dextral species.

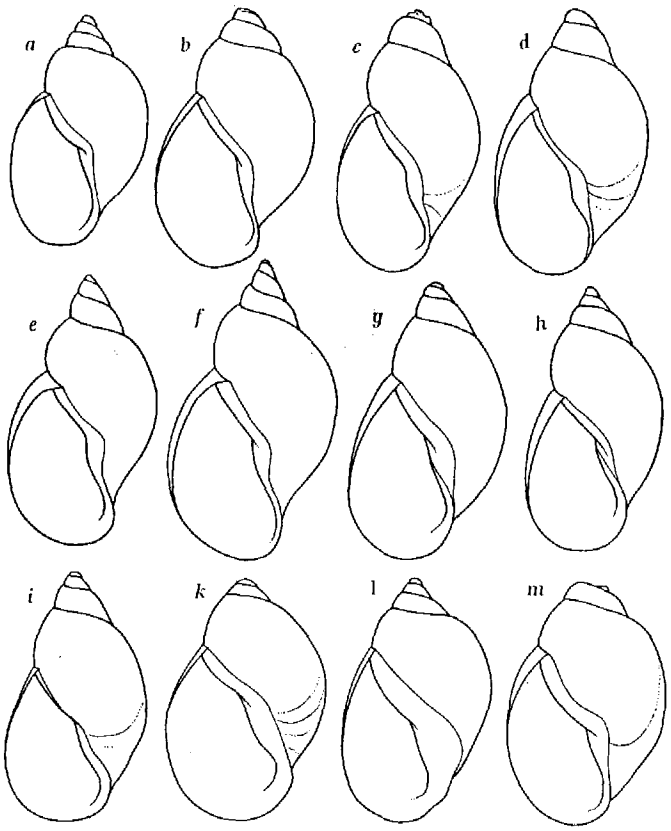

FIGURE 13.—Shells of *Lymnaea reticulata:* **a-c,** Kokee, Kauai (BBM 17782), shell heights 10, 11, and 12 mm.; **d,** Lihue, Kauai (BBM 19947), 8 mm.; **e, f,** Nawaimaka Stream, Waipio, Kauai (BBM 15498) 11 and 12 mm.; **g, h,** west valley, Makiki, Oahu (BBM 16505), 10 and 9 mm.; **i,** Makiki, Oahu (BBM 22089), 8 mm.; **k,** Nuuanu, Oahu (BBM 15014), 7 mm.; **l,** Punahou, Oahu (BBM 71121), 7 mm.; **m,** Kalihi Stream, Oahu (BBM 71118), 7 mm.

Type: Sandwich Islands, U. S. Exploring Expedition.

Range: Niihau, Kauai, and Oahu (fig. 15).

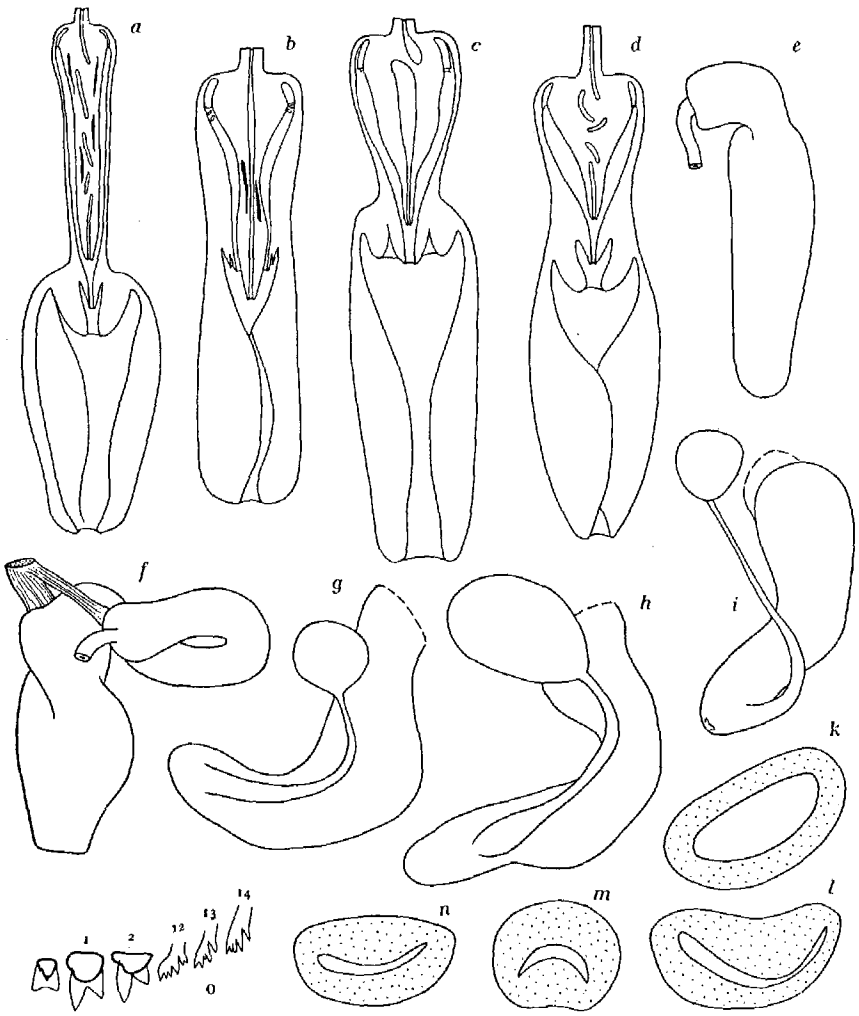

FIGURE 14.—Anatomy of *Lymnaea reticulata:* **a-d,** longitudinally sectioned male copulatory organs (black areas indicate lacunae or splits in the muscular tissue), 30-40 ×; **e, f,** male copulatory organs, about 30 ×; **g-i,** spermathecal system and most distal part of female gonoduct, about 30 ×; **k-n,** schematic cross sections through prostates, about 30 ×; **o,** central and some teeth from right side of a transverse row of radula, 300 ×. (For detailed explanation, see figure 8.)

Niihau: Kiekie, mountains, on damp rocks, January 1912, J. F. G. Stokes (37765); Kaali Spring, 750 ft., July 16, 1947, H. St. John and L. D. Tuthill (210502-210504).

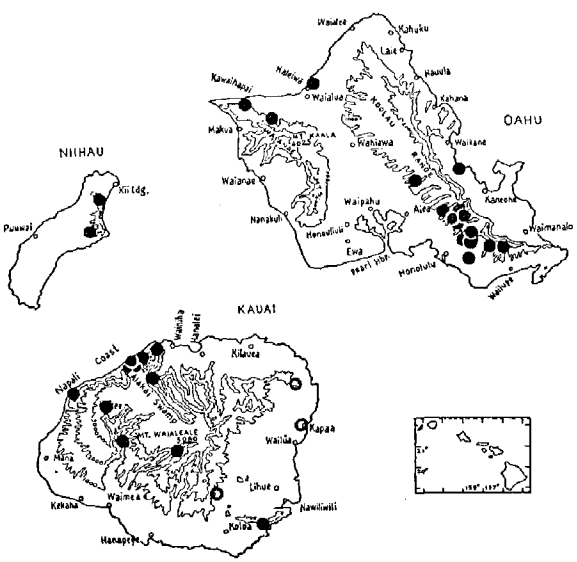

FIGURE 15.—Map showing collecting localities of *Lymnaea reticulata*. (Black dots indicate exact localities; circles, general localities.)

Kauai: Kipu, in front of Mt. Haupu, below cliffs, March 5, 1909, C. S. Dole and C. M. Cooke, Jr. (17830); Kapaa ?, gulch, July 14-29, 1919, D. Thaanum (47868); Waipio, Nawaimaka Stream, July 7, 1907, C. M. Cooke, Jr. (15498); Haena-Hanakapiai (near Haena), on damp rocks, July 13, 1907, C. M. Cooke, Jr. (15551); Hoolulu, west of Hanakapiai, July 4, 1927, W. Meinecke (124474); Hanakapiai, power ditch, near house, July 14, 1907, C. M. Cooke, Jr. (15573); Kokee (near camp), about February 1909, A. Knudsen (17782); Waimea, Paaiki branch, Milolii River system, about April 1909, A. Knudsen (17930); Lihue, stream near foot of Mt. Waialeale, 1909, C. N. Forbes (19946); Hii Mts., foot of Kahili, not near water, found growing on ground, October 1916, C. N. Forbes (42296); Anahola Valley, head of deep valley below high *pali* [cliff] full of *ti, ohia ae, kukui* [*Cordyline terminalis, Eugenia malaccensis, Aleurites moluccana*], over-run with cattle, October 19, 1925, C. M. Cooke, Jr., Mr. and Mrs. T. T. Dranga (80736, 80738); Nounou Mts., bottom of

valley, in pool, October 22, 1925, C. M. Cooke, Jr., Mr. and Mrs. T. T. Dranga (81020); Lihue, foot of Mt. Waialeale, about 1909, C. N. Forbes (169172); Wainiha Valley, 1 mile below intake, 600 ft., on rocks in stream, January 1, 1934, D. Anderson (184384).

Oahu (Koolau): Waialae Iki, Kapakahi Valley, 1,500 ft., October 24, 1929, A. F. Judd and G. R. Ewart III (94297); Waialua, Anahulu Stream, no date, J. T. Gulick (71119); Punahou, no date, J. T. Gulick (71121); Palolo, second valley west, on damp rocks and leaves, November 19, 1919, C. F. Mant (49204); Tantalus, October 30, 1911, D. Thaanum (23521); Kahaluu Stream, no date, J. T. Gulick (71120); Nuuanu, Glen Ada, April 1, 1904, C. M. Cooke, Jr. (14761); Nuuanu Stream, opposite forester's house, near waterfall, November 28, 1906, C. M. Cooke, Jr. (15014, 15016); Nuuanu, Hillebrand's Glen, on lower waterfall, March 1907, C. M. Cooke, Jr. (15378); Nuuanu east, valley head of ridge VII, on cliff, May 5, 1908, C. M. Cooke, Jr. (16487); Nuuanu east, valley below ridge VII, October 25, 1910, C. N. Forbes and C. M. Cooke, Jr. (21724); Nuuanu west, waterfall cliff, January 4, 1912, A. Butt and C. M. Cooke, Jr. (23665); Makiki, west valley, just above waterfall, May 11, 1908, C. M. Cooke, Jr. (16505); Makiki, small valley west of dam, March 3, 1911, C. M. Cooke, Jr. (22089); Moanalua, lateral valley east, March 1910, C. N. Forbes (20806); Kalihi Stream, no date, J. T. Gulick (71118); Waimano, second side gulch above ditch intake, March 28, 1929, W. Meinecke (93145). Waianae: Back of Mokuleia, September 8, 1908, C. M. Cooke, Jr. (17365); Kawaihapai, on damp cliff, December 1913, C. N. Forbes and C. M. Cooke, Jr. (35672).

According to my observations, all shell features except one vary in the same way among populations from Kauai and from Oahu. Furthermore, the different characteristics are combined with each other in many different ways within both areas. The only shell feature which seems to occur exclusively in Oahu specimens is the small, bluish-white callus on the lower part of the columella, a feature which seems to be present in every specimen from Oahu. Its degree of development, however, varies greatly in different populations. The differences between specimens from Oahu and Kauai are apparently racial. *L. reticulata* has been split into two geographical races owing to the isolation between the populations of the two islands. (In the specimens from Niihau the callus is absent.)

The species is reported from pools, streams, and ditches but also

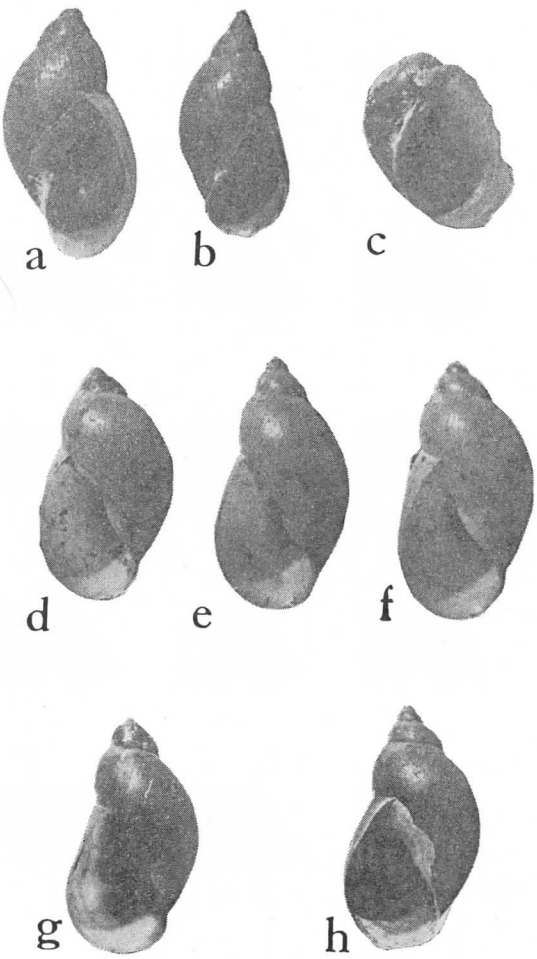

FIGURE 16.—**a, b,** type specimens of *Lymnaeus sandwichensis* (Brit. Mus. 1950-5-16. 2-4), 3 ×; **c,** type of *Errina newcombi* (Brit. Mus. 1950-5-19. 13-14), 5 ×; **d-f,** type specimens of *Physa reticulata* (Brit. Mus. 42-1-22. 509), 3.3 ×; **g,** type of *Limnaea binominis* (Brit. Mus. 1900-12-18. 1447-1449), 3.4 ×; **h,** type of *Physa sandwichensis* (Brit. Mus. 93-2-4. 1384-1386), 3.5 ×. [Brit. Mus. (N. H.) photographs.]

from damp cliffs and rocks and from the ground in a locality not near water.

CONCLUSIONS

The five species of *Lymnaea* inhabiting the Hawaiian Islands are endemic to the area. *L. newcombi* is similar to *L. onychia* from Japan, and in some respects *L. volutata* resembles *L. viridis* from eastern Asia. It is, however, quite impossible to prove a close relationship between the species, at least before a thorough examination of the chromosomes is made. It seems most probable that all the Hawaiian species have a common origin. The evolutionary process is favored by the geographical character of the area, that is a number of well-separated islands within a delimited range. It is easy to explain the evolution of a number of species within the genus but difficult to explain different independent migrations of species from any continent to this group of oceanic islands.

The different species are not restricted to different islands or different parts of the islands or even to different types of habitats. The species are sympatric. This, however, must be a secondary condition. An effective isolation must have preceded the formation of new species, just as the isolation of the populations of *L. reticulata* on Kauai from those of Oahu now seems to have led to the evolution of racial differences.

A striking feature of the Hawaiian lymnaeid fauna is the small size of all species. The mean size of the shells seems to be between 5 and 10 mm.; only a few specimens reach 13 mm. in length, and these rarely exceed 15 mm. Another peculiarity is the fact that all species occur in both real limnic habitats and in semi-terrestrial ones, such as swamps, wet rocks, wet leaves, and damp cliffs, even in habitats such as taro and rice patches and "on ground not near water." The small size and the wide ecological range of the species may possibly be related to one another.

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