A Taxonomic Revision of the Endemic Hawaiian Lysimachia (Primulaceae) Including Three New Species

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ABSTRACT: A taxonomic revision of the endemic Lysimachia of the Hawaiian Islands was undertaken with the goal of clarifying species boundaries, especially within the L. hillebrandii/L. remyi complex of the previous taxonomic treatment. The endemic species appear to be monophyletic with Malesian affinities. The revision presented here is based upon observations of morphological characters. Sixteen species are recognized, of which three are probably extinct. Most species have narrow ecological preferences and are endemic to a single island. Species differ from each other most notably in the size, shape, and venation of the leaves; the size, shape, and pigmentation of the calyx and corolla lobes; and the presence or absence of viscid stems and leaves. Three new species, L. iniki, L. pendens, and L. scopulensis, are described. A key to species, species descriptions, and distribution maps are provided.

Lysimachia, one of the largest genera of the Primulaceae, consists of approximately 180 species of upright or sprawling perennial or annual herbs, shrubs, or subshrubs. Southwest China, with 122 (110 endemic) species, is the center of diversity (Chen and Hu 1979). Species also occur in temperate areas of the Northern Hemisphere, the Southeast Asian Tropics, South America, Africa, and Australia (Bennell and Hu 1983).

The infrageneric classification of the genus consists of six subgenera and 18 sections and is based primarily on the work of Handel-Mazzetti (1928), who emphasized floral structure, particularly the androecium. This classification was modified somewhat by Chen and Hu (1979).

Two subgenera occur in the Hawaiian Islands: subgen. Palladia (Moench) Hand.—Mazz., represented by the indigenous coastal Lysimachia mauritiana Lam. and subgen. Lysimachiopsis (Heller) Hand.—Mazz., which consists of species endemic to the Hawaiian Islands.

The endemic species are perennial, scandent or upright, woody shrubs with alternate leaves, regularly dehiscent capsules, axillary flowers, filaments connate and adnate to the lower third of the corolla, basifixed anthers with lateral dehiscence, and a 5–10 merous perianth. Species differ from each other in vestiture, viscidness, phyllotaxy, and the size, shape, and color of leaves and calyx lobes. Corollas of L. glutinosa Rock are white to cream, whereas they are green with a red base in L. forbesii Rock and L. kala­lawensis Skottsbg. and red at the base becoming white halfway toward the tip in L. iniki Marr, sp. nov. Corollas of the remaining species are red. The protogynous (Marr 1995), hermaphrodite flowers are sweetly fragrant, especially in the evening.

Endemic species have tetracolporate pollen grains that are the largest in the genus, especially those of L. forbesii Rock (Huynh 1970, 1971). Non-Hawaiian species have tricolporate pollen, although some species occasionally produce tetracolporate grains (Huynh 1970, 1971, Bennell and Hu 1983).

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Species grow from 250 to 2300 m in montane bogs, subalpine mesic shrublands, montane dry and wet forests, and lowland mesic shrublands (as classified by Gagné and Cuddihy 1990), and on wet vertical cliffs. Species occur on all of the larger islands except Kaho‘olawe, Ni‘ihau, and Hawai‘i in scattered populations and generally have allopatric distributions. Two exceptions are upper Kalalau Valley on Kaua‘i where the ranges of L. glutinosa, L. kalalauensis, and L. scopulensis Marr, sp. nov. overlap and the southern Wai‘anae Range on O‘ahu where L. hillebrandii Hook. f. ex. A. Gray and L. waianaeensis St. John occur together. Populations usually consist of fewer than 100 individuals.

An investigation of the fertility of artificial interspecific F₁ hybrids is incomplete because of the absence of flowers on greenhouse-grown L. daphnoides (A. Gray) Hillebr., L. scopulensis Marr, sp. nov., L. pendens Marr, sp. nov., L. inik Marr, sp. nov., and L. hillebrandii. However, F₁ hybrids that could be produced generally had pollen stainability as high as their parents with the exception of some (but not all) progeny of L. glutinosa and L. kalalauensis, which had very low stainabilities (Marr 1995).

Chromosome numbers of \( n = 36 \) are known for Lysimachia glutinosa (mistakenly identified as L. kalalauensis) and L. hillebrandii Hook. f. ex. A. Gray (chromosomes were observed from a plant now classified as L. remyi subsp. remyi) (Carr 1978). Skottsberg (1953) reported a count of \( 2n = ca. 54 \) for L. hillebrandii from O‘ahu. That count, because it is reported as an approximate one, should be regarded as suspect. It seems unlikely, though not impossible, that there would be more than one chromosome number among the endemic species.

**Taxonomic History**

The first description of Lysimachia from the Hawaiian Islands was that of Gray (1862), followed by treatments of Hillebrand (1888), Heller (1897), and Knuth (1905). All of those works provided keys and descriptions as additional species were discovered. St. John (1987) described 44 new endemic species and made four new combinations, bringing to 54 the total number of names published, but provided no key. The revised and expanded treatment of Wagner et al. (1990) referred many of the species of St. John (1987) within their circumscription of either L. hillebrandii or L. remyi.

Heller (1897) concluded that the shrubby habit and urceolate, red corollas of the Hawaiian Islands species warranted the creation of a new genus, Lysimachiopsis Heller, to include the endemic species alone. Knuth (1905) returned them to Lysimachia, but created section Fruticosae Knuth, again to include only the endemic Hawaiian species. Handel-Mazzetti (1928) combined sect. Fruticosae Knuth with sect. Rosulatae Champ. (containing a single Asian species, L. alpestris Champ.) to form subgenus Lysimachiopsis (Heller) Handel-Mazzetti. However, Handel-Mazzetti synonymized Fruticosae under a prior name, Cilicina Klatt published in 1866. This is confusing and may have been in error. In an overview of the infrageneric classification Ray (1956), who revised the North American species, included only part of Cilicina in subgen. Lysimachia. This suggests that Cilicina was a heterogeneous group that included non-Hawaiian species. Therefore, synonymy of Cilicina with Fruticosae was unwarranted because Fruticosae Knuth clearly included only the endemic Hawaiian species.

The unique (i.e., tetracolporate) pollen of Hawaiian Lysimachia led Huynh (1970) to split subgen. Lysimachiopsis along sectional lines and to elevate the sections to subgeneric status: sect. Fruticosae became subgen. Sandiwicensia Huynh and sect. Rosulatae became subgen. Nullicaulis Huynh (typified by L. alpestris). Sandiwicensia was an illegitimate name (mistakenly retained by Bennel and Hu [1983]) because Lysimachiopsis sensu Heller (1897) was already available and included only the endemic Hawaiian species. Furthermore, Chen and Hu (1979) formally transferred species in sect. Rosulatae from subgen. Lysimachiopsis to subgen. Lysimachia. To summarize, the endemic Hawaiian Lysimachia are properly classified in subgen. Lysimachiopsis (Heller) Handel-Mazzetti.

Knuth) St. John, *L. remyi* Hillebr., and *L. venosa* (Wawra) St. John. *Lysimachia iniki* Marr, sp. nov. and *L. scopulensis* Marr, sp. nov. were discovered after 1990. Most of these taxa are clearly distinct in a number of characters and present no taxonomic difficulties. However, a number of metric characters vary among and sometimes within populations of *L. hillebrandii* and *L. remyi* sensu Wagner et al. (1990), such that those authors noted (p. 1077) that *Lysimachia* is “greatly in need of careful monographic work, especially the *Lysimachia hillebrandii*–*L. remyi* complex on the younger islands” (i.e., Maui and Moloka‘i), which “virtually form a broad continuum of variation” (p. 1081).

As delimited by Wagner et al. (1990), *L. hillebrandii* included plants from Kaua‘i, O‘ahu, Moloka‘i, Lāna‘i, and Maui with corolla lobes 10–20 mm long and petiolate, elliptic to ovate leaves greater than 10 mm wide. *Lysimachia remyi* included plants from Moloka‘i and Maui with corolla lobes 9–11 mm long and linear or narrowly elliptic leaves 1–8(15) mm wide. Based on these characters alone, plants with very broad leaves or very narrow ones could be assigned to *L. hillebrandii* or *L. remyi*, respectively. However, many plants were intermediate in these features and were not easily classified into either of these species. In addition, some populations contained some individuals that would be classified as *L. hillebrandii* using leaf dimensions, but *L. remyi* using corolla dimensions.

Plants classified as *L. lydgatei* also had broadly elliptic leaves but differed from *L. hillebrandii* primarily in having densely tomentose leaves and stems (Wagner et al. 1990). Populations of *L. lydgatei* have, to date, always been found intermixed with *L. remyi* as well as plants intermediate between these two in characters such as leaf width and the extent of tomentum. This brought into question whether or not *L. lydgatei* was a distinct species or simply part of a morphologically variable taxon including plants classified as *L. remyi*.

*Lysimachia filifolia* was also a somewhat variable species as circumscribed by Wagner et al. (1990). It comprised plants with leaves 0.3–1.8 mm wide from the headwaters of the Wailua River and upper Olokele Valley on Kaua‘i and from Waiahole Gulch on O‘ahu. Further collections from the Wailua River indicated that plants there typically have leaves up to 4 mm wide.

**Geographical Affinities**

A monophyletic origin for the endemic species is supported by several lines of evidence. The most parsimonious explanation for the presence of tetracolporate pollen in all species is that it was a character that evolved once, presumably from an ancestor with tricolporate pollen. In characters such as the shrubby habit and variable perianth number, the endemic Hawaiian species also have more in common with each other than they do with any non-Hawaiian species. The indigenous *L. mauritiana* is a somewhat fleshy perennial herb with 2n = 20 (Carr 1978), distinct filaments with versatile anthers, and an irregularly dehiscent capsule. None of these characters is found in the endemic species.

The closest relative of the endemic *Lysimachia* is not known. Handel-Mazetti (1928) suggested that *L. alpestris*, a yellow-flowered prostrate herb from South China was “nearly allied to the shrubby red-flowered [i.e., endemic Hawaiian] species.” Studies of pollen (Huynh 1970, 1971) and other morphological characters (Chen and Hu 1979) did not support this relationship. Wagner et al. (1990) and St. John (in an unpublished monograph on *Lysimachia* in Hawai‘i [hereafter referred to as unpubl. ms.]) suggested that Malesia (the Malay Peninsula and all islands north of Australia and east to the easternmost Solomon Islands) was the source region. Eight species (Van Steenis 1972) are found in that area: *L. capillipes* Hemsl., *L. decurrens* Forst. f., *L. japonica* Thunb., *L. laxa* Baudo, *L. mauritiana*, *L. montana* (Reinw.) Bakh, *L. peduncularis* Wall ex. Kurz, and *L. sikokiana* Miq. All are herbaceous with alternate leaves and axillary inflorescences. The corolla of *L. decurrens* is white or red, whereas that of *L. mauritiana* is white or pink. The other species have yellow corollas. St. John (unpubl. ms.) and Hu Chi Ming (pers. comm.) suggested that *L. laxa*, in subgen. *Idiophyton*, is the closest relative of the Hawaiian species. Of the above, *L. laxa* is the only species that has in common with the Hawaiian ones basified anthers with lateral dehiscence and connate filaments adnate to the corolla. All species of subgen. *Idiophyton* have...
basifixed anthers and some have ligneous stems (Chen and Hu 1979), further support for a connection between a species similar to *L. laxa* and the Hawaiian species. Although *L. decurrens* has a red corolla, in common with the endemic Hawaiian species, it has versatile anthers and distinct filaments.

*Lysimachia thyrsiflora* L., the only species from the west coast of North America, is unlikely to be the ancestor of the Hawaiian species. It is herbaceous with opposite or whorled leaves and short, dense, pedunculate, axillary racemes of yellow flowers with $2n = 40, 54$ (Hickman 1993).

Sporophytic chromosome numbers from 37 species are of little aid in elucidating the nearest relative of the Hawaiian species; these include $2n = 16, 18, 20, 24, 28, 30, 32, 34, 36, 40, 42, 54, 60, 84, 92, 98, 100, 102, 108, 112$ (Ornduff 1967, 1968, Federov 1974, Moor 1974, 1977, Goldblatt 1981, 1984, 1985, 1988, Goldblatt and Johnson 1990, 1994). No counts have been reported for *L. laxa*. The count of $2n = 36$ is for *L. nummularia*, a European species with yellow flowers and opposite leaves. These characters make it highly unlikely that that species is closely related to the Hawaiian ones, though chromosome doubling would yield the same number as the two Hawaiian species that have been counted.

### MATERIALS AND METHODS

The taxonomic revision presented here includes all of the endemic Hawaiian Islands species but focuses on the *L. hillebrandii–L. remyi* complex (including *L. lydgatei*) using characters that had not been evaluated previously by Wagner et al. (1990).

Principal Components Analysis (PCA) of calyx lobe length, width and pubescence, leaf length, width and pubescence, petiole length, and internode length was utilized to search for breaks in the pattern of variation (Marr 1995). Scatterplots from this analysis, based on scores from the first two PCA axes, indicated considerable overlap among plants of *L. hillebrandii*, *L. remyi*, and *L. lydgatei*. This multivariate analysis confirmed the observations of Wagner et al. (1990) that variation is continuous in many metric characters. However, further examination indicated that populations of plants classified as *L. hillebrandii* or *L. remyi* (both sensu Wagner et al. 1990) consistently differed from each other in a number of other characters. These largely nonmetric characters form the basis for the taxonomic revision presented here.

The following observations were made of more than 300 specimens of the *L. hillebrandii–L. remyi* complex (including *L. lydgatei*): leaf shape and color, the angle of divergence between the primary and the secondary veins, translucence of tertiary veins, prominence of areoles, leaf color, calyx lobe color and shape, pedicel color and position, and vestiture. These specimens were plants grown in the greenhouse from seed or cuttings; pressed specimens from field collections done for this study in the summers of 1990, 1991, and 1992; and herbarium sheets borrowed from BISH, F, GH, K, MASS, MO, NY, PTBG, RSA, US, and W (abbreviations from Holmgren et al. 1990). Descriptions of all species are based upon the same sources of materials.

### RESULTS AND DISCUSSION

Categories recognized here as species are based entirely upon morphological characters. Because interspecific $F_1$ hybrids are highly fertile (Marr 1995), crossability cannot be used to assist in the delineation of species. Species are defined here as interbreeding groups of populations that share the same unique suite of morphological characters. These combinations of characters are not found in any other species and are taken as evidence that each species is monophyletic and reproductively isolated from all other species. Subspecies are considered to consist of geographically discrete populations within the overall distribution of the species; they differ in vegetative, but not floral characters.

*Lysimachia hillebrandii*, *L. remyi*, and *L. filifolia* are retained; however, several additional taxa are recognized at the specific or subspecific rank within the concept of these species sensu Wagner et al. (1990).

A number of nonmetric characters permit the recognition of four species within *L. hillebrandii*.
sensu Wagner et al. (1990) and four subspecies within *L. remyi* (Tables 1 and 2). In the following discussion, the most important characters used to distinguish among these taxa are emphasized.

There is considerable overlap in the dimensions and shape of leaves, calyx, and corolla lobes within and among populations of subspecies *L. remyi* (Table 1). However, groups of populations differ from each other in phyllotaxy, leaf shape, color, and vein translucence, and the angle of divergence between the primary and the secondary veins, especially those toward the tip of the leaf. The angle between the primary and the secondary veins in the leaves of *L. remyi* ssp. *remyi* is 20–30° for the lower veins, increasing to 45–60° for the upper veins. In the other subspecies, this angle is uniform for all veins.

*Lysimachia remyi* ssp. *remyi* is the most variable subspecies (Table 1). In some populations plants differ markedly from each other in the size and shape of leaves and calyx lobes and the degree of pubescence. In these populations leaves range from narrowly lanceolate and nearly glabrous to elliptic and densely tomentose, as in *L. lydgatei*. In other populations, leaves of nearly all plants are either lanceolate and glabrous or elliptic and tomentose. One possibility is that variable populations have resulted from hybridization between *L. lydgatei* and *L. remyi* sensu Wagner et al. (1990). On ridgetops on the southern side of West Maui, narrow-leaved plants grow on the more windswept, sparsely vegetated aspects, whereas broader-leaved plants are found on the adjacent, protected forested slopes. This suggests that ecological factors may contribute at least to a difference in phenotypic expression. In the “common garden” of the greenhouse, plants grown from wild seed of *L. lydgatei* included plants with nearly glabrous, narrow leaves, as well as plants with broader tomentose leaves. This observation and the fact that most populations from West Maui are morphologically variable argue in favor of treating these populations as belonging to a single phenotypically diverse taxon including plants previously classified as *L. lydgatei*.

Populations of *L. hillebrandii* sensu Wagner et al. (1990) are here reclassified as *L. ovoidea*, *L. waianaeensis*, and *L. hillebrandii*, each of

<table>
<thead>
<tr>
<th>TABLE 1</th>
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</thead>
</table>

<table>
<thead>
<tr>
<th>CHARACTER</th>
<th>ssp. <em>remyi</em></th>
<th>ssp. <em>caliginis</em></th>
<th>ssp. <em>kipahuluensis</em></th>
<th>ssp. <em>subherbacea</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf Length (mm)</td>
<td>20–55</td>
<td>30–45</td>
<td>20–30</td>
<td>45–60</td>
</tr>
<tr>
<td>Width (mm)</td>
<td>2–17</td>
<td>8–14</td>
<td>4–6</td>
<td>8–11</td>
</tr>
<tr>
<td>Color (upper)</td>
<td>Dark green/rusty brown</td>
<td>Dark green</td>
<td>Light green</td>
<td>Light green</td>
</tr>
<tr>
<td>Shape</td>
<td>Linear</td>
<td>Oblanceolate</td>
<td>Linear</td>
<td>Oblanceolate</td>
</tr>
<tr>
<td></td>
<td>Lanceolate, ovate, elliptic</td>
<td>Obovate</td>
<td></td>
<td>Ovate</td>
</tr>
<tr>
<td>Adaxial pubescence</td>
<td>Yes/no</td>
<td>No</td>
<td>No</td>
<td>No</td>
</tr>
<tr>
<td>Tertiary veins pellucid</td>
<td>No</td>
<td>Yes</td>
<td>No</td>
<td>No</td>
</tr>
<tr>
<td>Margins revolute</td>
<td>No</td>
<td>Yes</td>
<td>No</td>
<td>No</td>
</tr>
<tr>
<td>Shape of tip</td>
<td>Acuminate</td>
<td>Acuminate</td>
<td>Acute</td>
<td>Acuminate</td>
</tr>
<tr>
<td>Margins</td>
<td>Flat</td>
<td>Revolute</td>
<td>Flat</td>
<td>Flat</td>
</tr>
<tr>
<td>Calyx lobe Length (mm)</td>
<td>4–7</td>
<td>5.5–7</td>
<td>5–6</td>
<td>5–8</td>
</tr>
<tr>
<td>Phyllotaxy</td>
<td>Alternate</td>
<td>Alternate/whorled</td>
<td>Alternate</td>
<td>Alternate</td>
</tr>
<tr>
<td>Corolla lobe Length (mm)</td>
<td>8–13</td>
<td>10–11</td>
<td>8–10</td>
<td>11.5–14</td>
</tr>
<tr>
<td>Stems</td>
<td>Glabrate tomentose</td>
<td>Glabrate tomentose</td>
<td>Glabrate</td>
<td>Glabrate</td>
</tr>
<tr>
<td>Habitat</td>
<td>Montane mesic</td>
<td>Montane wet</td>
<td>Montane wet</td>
<td>Lowland mesic</td>
</tr>
<tr>
<td>Island</td>
<td>Maui, Lāna’i</td>
<td>Maui</td>
<td>Maui</td>
<td>Moloka’i, O’ahu</td>
</tr>
</tbody>
</table>
TABLE 2  
DISTRIBUTION OF CHARACTERS AMONG SPECIES PREVIOUSLY CLASSIFIED AS *L. hillebrandii* SENSU WAGNER ET AL. (1990)

<table>
<thead>
<tr>
<th>CHARACTER</th>
<th><em>L. hillebrandii</em></th>
<th><em>L. waianaeensis</em></th>
<th><em>L. ovoidea</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf</td>
<td>45-55</td>
<td>50-65</td>
<td>60-80</td>
</tr>
<tr>
<td>Length (mm)</td>
<td>12-24</td>
<td>16-24</td>
<td>25-36</td>
</tr>
<tr>
<td>Width (mm)</td>
<td>Yes</td>
<td>No</td>
<td>No</td>
</tr>
<tr>
<td>Pubescent</td>
<td>No</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>Tertiary veins pellucid</td>
<td>No</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>Areoles prominent</td>
<td>No</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>Angle between primary and upper secondary veins</td>
<td>35-55°</td>
<td>35-45°</td>
<td>35-40°</td>
</tr>
<tr>
<td>Calyx lobe</td>
<td>5-8</td>
<td>4-5</td>
<td>4-5.5</td>
</tr>
<tr>
<td>Length (mm)</td>
<td>Green</td>
<td>Green</td>
<td>Red</td>
</tr>
<tr>
<td>Color</td>
<td>Lanceolate</td>
<td>Ovate</td>
<td>Lanceolate</td>
</tr>
<tr>
<td>Shape</td>
<td>12-16</td>
<td>11-13</td>
<td>6-8.5</td>
</tr>
<tr>
<td>Corolla lobe</td>
<td>Green</td>
<td>Green</td>
<td>Red</td>
</tr>
<tr>
<td>Length (mm)</td>
<td>Erect</td>
<td>Erect</td>
<td>Pendulous</td>
</tr>
<tr>
<td>Pedicel</td>
<td>Montane wet</td>
<td>Lowland mesic</td>
<td>Lowland wet</td>
</tr>
<tr>
<td>Habitat</td>
<td>O'ahu, Moloka'i</td>
<td>O'ahu</td>
<td>Kaua'i</td>
</tr>
</tbody>
</table>

which is unique in a number of characters (Table 2). *Lysimachia waianaeensis* alone has well-defined leaf areoles. In *L. ovoidea* and *L. hillebrandii* the areoles are obscure. Calyx lobes of *L. waianaeensis* are ovate, whereas those of *L. hillebrandii* and *L. ovoidea* are lanceolate. The calyx lobes and pedicel of *L. ovoidea* are dark red for their entire length and the pedicel is pendulous. The calyx lobes and pedicels of *L. hillebrandii* and *L. waianaeensis* are green and the pedicel is upright. *Lysimachia ovoidea* and *L. waianaeensis* are entirely glabrous or nearly so, whereas the leaves, stems, calyx lobes, and pedicels of *L. hillebrandii* are moderately to densely pubescent.

The revised classification of *L. filifolia* (sensu Wagner et al. 1990) includes *L. filifolia* C.N. Forbes & Lydgate from Olokele Valley and Waiahole Gulch and the new species, *L. pendens* Marr, from the Wailua River. Leaves of *L. pendens* are broader and pubescent compared with those of *L. filifolia*, which are narrow and glabrous.

Sixteen species are recognized in the following key and species descriptions. The number of species per island is as follows: Kaua'i, 12 species (Figure 1); O'ahu, five species (Figure 2); Moloka'i, three species; Lāna'i, one species (Figure 3); and Maui, three subspecies of one species (Figure 4). Species on Kaua'i are endemic to that island except for *L. filifolia* and *L. hillebrandii*. Three of the five species on O'ahu are endemic to that island; *L. hillebrandii* also occurs on Moloka'i and Kaua'i; *L. remyi* subsp. *subherbacea* occurs on Moloka'i. One species on Moloka'i is restricted to that island. Three subspecies of *L. remyi* occur on Maui. Subspecies *remyi* is restricted to West Maui and Lāna'i; the other two subspecies from Maui occur on both East and West Maui.

**Genus Lysimachia L.**

Erect, ascending, or prostrate perennial herbs, sometimes subshrubs or shrubs. Leaves entire, opposite, whorled, or alternate, usually glandular-dotted. Flowers hypogynous, actinomorphic, 5(6-10)-merous, in terminal racemes, corymbs, panicles, or solitary in the leaf axils; calyx imbricate or valvate, persistent, deeply parted; corolla rotate to urceolate, deeply parted, tube very short, yellow, white, purple, reddish purple, or green, the lobes contorted in bud; staminal filaments slightly to nearly completely adnate to corolla, often more or less basally connate; anthers basifixed or versatile, opening by apical pores or longitudinal slits; ovary superior, placentation free-central; capsule 5-10-valved or irregularly dehiscent, ovoid to globose; seeds numerous, oblong, orbiculate or angular, testa crustaceous.

Note: To save space, only a partial list of cited specimens is included under “Specimens Examined” following the description of each species. K.L.M. should be contacted for a complete listing of all specimens viewed and annotated for this study.
FIGURE 2. Distribution of Lysimachia on the island of O'ahu: ▲, L. forbesii; ◆, L. remyi subsp. subherbacea; ■, L. waianaeensis; ▼, L. hillebrandii; ●, L. filifolia.
Figure 3. Distribution of *Lysimachia* on the islands of Lāna'i and Moloka'i: ▼, *L. hillebrandii*; ◆, *L. maxima*; ●, *L. remyi* subsp. *subherbacea*; ■, *L. remyi* subsp. *remyi*. 
FIGURE 4. Distribution of Lysimachia on the island of Maui: ◆, L. remyi subsp. remyi; ▶, L. remyi subsp. kipahuluensis; ♦, L. remyi subsp. calligynis.
KEY AND DESCRIPTIONS OF ENDEMIC HAWAIIAN *Lysimachia*

1a. Corolla green on upper portion, red at base; leaves elliptic, petiolate, dark green above often tinged with purple, much lighter below, calyx lobes lanceolate, usually more than 12 mm long .......................................................... 2

1b. Corolla creamy white or reddish purple; leaves linear, ovate, obovate, lanceolate, oblanceolate, or elliptic, petiolate or sessile, dark or light green above, calyx lobes ovate to linear, usually less than 12 mm long, or if longer than 13 mm, then usually at least 5 mm wide and ovate .......................................................... 3

2a. Leaves (80)160–200(260) mm long, (20)55–65(95) mm wide; upper and lower surface densely tomentose, the hairs multicellular; calyx and corolla lobes more than 20 mm long. O‘ahu ........................................................................... 3. *L. forbesii*

2b. Leaves (50)60–80(100) mm long, (15)25–32(45) mm wide; upper and lower surface glabrous or glabrate, the hairs unicellular; calyx and corolla lobes less than 20 mm long. Kaua‘i ........................................................................... 9. *L. kalalauensis*

3a. Corolla white, (15)19–24(30) mm long; leaves shiny, light green above, slightly lighter below, glabrous, (50)80–120(160) mm long; entire plant usually viscid, especially young shoots. Kaua‘i ........................................................................... 4. *L. glutinosa*

3b. Corolla red, or base red and upper 5–7 mm white, (5)6–18(20) mm long; leaves dull, light or dark green, glabrous or pubescent, (15)20–80(100) mm long; plants not viscid or if viscid, then viscid-hirsute to viscid-hirtellous ........................................... 4

4a. Leaves less than 2 mm wide, or if 2–4 mm wide, then narrowly lanceolate and stems pendulous, hanging from cliffs .......................................................... 5

4b. Leaves more than 2 mm wide; stems upright, not hanging from cliffs .......................... 7

5a. Leaves 2–4 mm wide, narrowly lanceolate. Kaua‘i ....................................................... 12. *L. pendens*

5b. Leaves less than 2 mm wide, usually 1 mm wide, filiform ......................................... 6


6b. Plants upright, streamsides and bogs. East Maui .......................... 13b. *L. remyi* subsp. *kipahuluensis*

7a. Leaves, stems, and pedicels densely viscid-hirsute to viscid-hirtellous; leaves sometimes glabrate but the margins remaining viscid-hirsute ........................................... 8

7b. Leaves, stems, and pedicels glabrous or pubescent but not viscid ............................... 9

8a. Leaves (25)35–38(42) mm wide, broadly ovate to orbicular, cupped upward; upper portion of corolla cream to white. Kaua‘i ......................................................... 7. *L. iniki*

8b. Leaves (7)10–13(23) mm wide, oblanceolate; upper portion of corolla salmon pink to dark red. Kaua‘i .............................................................. 1. *L. daphnoides*

9a. Calyx lobes lanceolate, 13–16 mm long, 4–6 mm wide; leaves obovate (50)75–80(100) mm long; plants glabrous. Kaua‘i .................................................... 15. *L. venosa*

9b. Calyx lobes ovate to lanceolate, 3–11 mm long, 1.5–4 mm wide or if greater than 4 mm wide, then ovate; leaves various (15)20–60(95) mm long; plants glabrous or pubescent .................................................. 10

10a. Leaves whorled, 3–4 per node, more than 20 mm wide, obovate or elliptic; stems rusty tomentose, glabrate with age. Moloka‘i ................................................... 10. *L. maxima*

10b. Leaves alternate or if whorled, then less than 20 mm wide, shape various; stems glabrous or pubescent .............................................................................. 11

11a. Leaves elliptic, ovate, or obovate and usually more than 16 mm wide, apex acuminate, often abruptly so ........................................................................ 12

11b. Leaves linear, lanceolate, or oblanceolate and mostly less than 16 mm wide; if elliptic, then less than 16 mm wide or densely rusty tomentose, apex attenuate, acuminate, or sometimes acute .................................................. 14

12a. Pedicel and calyx lobes dark red for entire length; pedicel pendulous; calyx lobes linear, 1.5–2 mm wide; petioles (6)7.5–12(15) mm long. Kaua‘i ......................... 11. *L. ovoidea*
12b. Pedicel and calyx lobes entirely or mostly green; pedicel erect; calyx lobes lanceolate to ovate, 2–5 mm wide; petals (2)3–8(15) mm long ................................. 13

13a. Leaves with poorly defined areoles (tertiary veins obscure); calyx lobes lanceolate, (4)5–8(9) mm long; pedicel, calyx lobes, stem, and lower leaf surface densely dark brown pilose to tomentose. Kaua’i, O’ahu, Moloka‘i ............................ 6. L. hillebrandii

13b. Leaves with well-defined areoles, (tertiary and higher-order veins prominent); calyx lobes usually broadly ovate, (3)4–5(8) mm long; plants nearly glabrous. O’ahu .......................... 13. L. hillebrandii

14a. Leaves with prominent glands when dried, elliptic. Kaua‘i ....................... 5. L. haupuensis

14b. Leaves without internal glands that are prominent when dried, shape various .......................... 15

15a. Young leaves and stems pulverulent (powdery appearance due to fine wax crystals), otherwise glabrous; leaves dark green, the tips recurved; calyx lobes glabrous, broadly ovate. Kaua‘i .......................... 14. L. scopulensis

15b. Leaves and stems not pulverulent, slightly to densely pubescent; leaves light or dark green, the tips flat; calyx lobes glabrous or pubescent, lanceolate, occasionally ovate .................. 16

16a. Angle of divergence of secondary leaf veins acute, nearly parallel to primary vein; calyx lobes 9–11 mm long; leaves narrowly obovate, 35–50 mm long. Kaua‘i .......................... 8. L. kahiliensis

16b. Angle of divergence of secondary leaf veins more obtuse; calyx lobes usually less than 10 mm long; if longer than 10 mm, then the leaves more than 50 mm long, leaves various. O’ahu, Lāna‘i, Maui, Moloka‘i .......................... 13. L. remyi


Lysimachia longa St. John, Phytologia 64:46, 1987.—Type: Kauai, bog at head of Wahiawa stream, 19 Oct., 1895, Heller 2736 (holotype: BISH; isotypes: BISH, F!, GH!, photo at K!, MASS!, MO!, NY!, p[3]!, US!).

Erect, upright shrubs usually less than 1 m tall, branching from the base, rarely so; younger stems green becoming dark reddish brown, densely viscid-hirtellous, sometimes glabrate. Leaves alternate, (0.5)3–7(11) mm apart, sessile or nearly so; blades oblanceolate, thickly coriaceous, (18)30–35(52) mm long, (6)10–13(23) mm wide, base cuneate, apex acuminate, margins slightly revolute; upper surface light green, viscid-hirtellous, rarely glabrous, the hairs white in younger leaves becoming brown, lower lighter than upper, densely viscid-hirtellous; base of lamina, primary vein, and sometimes secondary veins red; secondary veins often obscure. Flowers solitary in leaf axils, 6–8-merous, campanulate; pedicels (20)25–35(110) mm long, erect, densely reddish brown viscid-hirtellous; calyx lobes green, sometimes red at base, sparsely viscid-hirtellous, lanceolate, (6)7.5–11 mm long, (2)3–4(5) mm wide; corolla lobes dark maroon to salmon pink, obovate, (13)15–18(21) mm long, (7)11–13(16) mm wide; filaments (7)8.5–11(14) mm long, anthers 2–2.5 mm long; style (8)10.5–13(14) mm long. Capsules globose, 7–10 mm long. Seeds dark brown, irregularly shaped, 1–1.4 mm long.

DISTRIBUTION: Kaua‘i: Montane wet sedge-lands of Alaka‘i Swamp on low hummocks slightly higher than the surrounding vegetation, 1230–1400 m. Growing with Oreobolus, Rhynchospora, Carex, Panicum, Metrosideros, Cheirodendron, Melicope, Dubautia, Cibotium, Dicranopteris, Adenophorus, Vaccinium, Staphelia, Viola, Lycopodium, and Coprosma.

NOTE: This and L. iniki are the only species with densely viscid-hirtellous leaves, stems, and pedicels.

Specimens labeled Heller 2736 were collected on different dates and from different locations. Specimens at BISH, F, and US dated 19
October 1895 and specimens at MASS and F dated 12 August 1895 were collected “in and near a bog at the head of the Wahiawa.” A specimen at GH was collected on 14 August 1895, “along the Hanapepe River, near the falls.” A specimen at MO was collected on 24 August 1895 “between Hanapepe and Wahiawa Rivers.” Heller (1897) noted that these collections came from 800 m, higher than the 480-m elevation of Wahiawa Bog, but somewhat lower than the Alaka'i Swamp. A recent inventory of Wahiawa Bog failed to find this species (Tim Flynn, pers. comm.). Given these considerations, it seems most likely that *Heller 2736* did not come from Wahiawa Bog and instead came from the eastern part of the Alaka'i Swamp, or no longer occurs in Wahiawa Bog.

In the Hawaiian language *L. daphnoides* is identified as “lehua makanoe” or “kolokolo kua­kiwi” (Hillebrand 1888).

**SPECIMENS EXAMINED:** Kaua'i: eastern Alaka'i Swamp (“Sincocks Bog”), Perlman 10631 (MO,PTBG), Davis 133 (BISH); western Alaka'i Swamp, Forbes 888.K (BISH,US,W), Herbst 2175 (F,GH,MO,NY,PTBG,W), Hillebrand s.n. (GH), Selling 2905 (BISH), Marr 250 (UBC), Marr 505 (OS), Marr 507 (HAST), Marr 508 (IBSC), Marr 512 (MIC), Marr 513 (MASS), Marr 514 (P), Marr 515 (RSA), Marr 521 (COLO), Lorence 5700 (MO,PTBG), Wawra s.n. (W), Sinclair s.n. (K).


*Lysimachia waiaholeensis* St. John, Phytologia 64:50, 1987.—Type: Oahu, Waiahole gulch, 250 m, 26 July 1926, Degener 17666 (holotype: NY!).

*Lysimachia funkiae* St. John, Phytologia 64:44, 1987.—Type: Oahu, Waiahole gulch, 250 m, 24 Jan. 1984, Funk 211 (holotype: BISH!).

Pendulous delicate shrubs; stems up to 60 cm long, reddish brown to green, glabrate, branching profusely. Leaves alternate, (1)3–5(9) mm apart, petioles 0.1 mm long; blades filiform, coriaceous, (12)25–40(50) mm long, 0.5–1.2 mm wide, base attenuate, apex attenuate; upper surface dark green, glabrous, lower dark green, pilose when young, glabrate; secondary veins obscure. Flowers solitary in leaf axils, 5–7-merous, campanulate; pedicels 17–27(32) mm long, pendulous, green, occasionally red toward calyx, glabrous or minutely pilose; calyx lobes green, occasionally red at base, linear to lanceolate (4)5(6) mm long, (1)1.5–2(2.5) mm wide; corolla lobes dark red, lighter at tips, widely obovate, (5.5)6–8(10) mm long, 4.5–6 mm wide; filaments (2.5)4–5 mm long, anthers 1 mm long; style 3.5–4.5(5) mm long. Capsules globose, 3.5–5 mm long. Seeds dark brown, irregularly shaped, 1–1.5 mm long.

**DISTRIBUTION:** Kaua'i: Collected once in 1912 from upper Olokele Valley. O'ahu: Known only from three small subgulches of Waiahole Gulch, 250 m, growing with a pendulous habit on wet cliffs with *Isachne, Eragrostis, Machaerina, Bidens,* and *Selaginella.*

**NOTE:** Further collections from Olokele Valley would be most useful to verify that plants there are the same in all regards as those from O'ahu. The land is privately owned and access is not available. The collection location on the label of the type specimen, “far mauka, Olokele Valley” (mauka means “toward the mountain”), implies that the collection was made in upper Olokele Valley, possibly from wet cliffs similar to those where the O'ahu population is found. It is not stated in the original description whether the plant is upright or pendulous. The type specimen has a stem 0.4 cm wide, wider than that of O'ahu plants, thus it may have been more upright. St. John (unpubl. ms.) stated that *L. filifolia* (the type specimen) has viscid leaves. Wagner et al. (1990: 1080) stated that the Wailua River plants (here classified as *L. pendens*) and O'ahu plants are sparsely puberulent, whereas the type is viscid. We did not detect viscid leaves in specimens of *L. filifolia* or *L. pendens,* nor is this mentioned in the type description. If plants from Olokele are viscid and upright, they differ from the O'ahu plants.
SPECIMENS EXAMINED: Kaua’i. Type specimen only. O‘ahu: Wai‘ahole Gulch, O‘bata 90-689 (BISH), Perlman 11149 (PTBG), Marr 246 (UBC), Marr 792 (US), Marr 793 (COLO), Marr 794 (k), Marr 795 (NY), Marr 796 (BISC), Marr 797 (F), Marr 798 (MO), Marr 799 (OS).


NOMENCLATURAL NOTE: Lysimachia longisepala was preoccupied by a plant from China, therefore Forbes (1914) made the formal change to L. koolauensis. However Rock published L. forbesii earlier the same year (St. John 1933).

The original description cites flowering specimens collected in September 1908 and fruiting specimens collected 8 months later. The lectotype bears an immature flower and is labeled as a “type” but bears no date. This specimen may be the one upon which the type description was based because it matches the original description in having three flowers in the leaf axil and calyx lobes exceeding the corolla lobes (corolla lobes exceed the calyx in older flowers). The isolectotype is dated September 1908, elev. 2300 ft., as stated in the original description, but does not show floral features as well as the lectotype. The lectotype bears a note “Sheet no. 3.” We have not seen sheets no. 1 or 2.

Sprawling woody shrubs, usually unbranched; stems up to 1.5 m long, dark red, pilose with red hairs, glabrate. Leaves alternate, (3)5–23(40) mm apart, petioles (23)31–45(62) mm long; blades narrowly to broadly elliptic, chartaceous, (80)160–200(260) mm long, (20)55–65(95) mm wide, base attenuate, apex acuminata; upper sur-

face dark green, glandular punctate when young, glabrate, lower much lighter, pilose, the hairs red, multicellular, glandular punctate; primary, secondary, and higher-order veins prominent, especially on lower surface. Flowers 1–5 in leaf axils, (6)7–8(9)-merous; pedicels 16–25(32) mm long, pendulous, densely tomentose; calyx lobes green with red veins, pilose, lanceolate (18)20–22(27) mm long, (3)4–5(7) mm wide; corolla lobes green with red veins, narrowly elliptic, the margins erose 20–24(28) mm long, (6.5)7–10 mm wide; filaments (9)9.5–13.5(16.5) mm long, anthers 3 mm long; style (16.5)17–19(24) mm long, persistent in fruit. Capsules globose, 10.5–12(15) mm long. Seeds dark brown, irregularly shaped, 1.5–2.5 mm long.

DISTRIBUTION: O‘ahu: Known only from collections along the Castle ("Pig-God") Trail, 600–710 m. It is unclear whether all collections came from a single population. Some specimens were collected “near the top of the trail overlooking the Valley” (presumably Punalu‘u). Another was collected from a “small gulch at the head of Kaluanui,” a valley immediately west of Punalu‘u; the Castle Trail connects the two.

NOTE: In all characters, this was the world’s largest Lysimachia. No other Hawaiian species had multicellular hairs, punctate glands, and often more than one flower per axil. Of the extant species, L. kalalauensis is almost certainly the closest relative because these are the only species with a green corolla having erose margins and occasionally bearing two flowers per axil.

Lysimachia forbesii was last collected in 1934 and is presumably extinct. During the study reported here unsuccessful searches were made in the type location. The ecology of the area has been substantially altered by introduced species, yet many native species do persist.


Woody shrubs up to 2.5 m tall, branching primarily from the base, the entire plant viscid, often pulverulent; stems green to reddish brown. Leaves alternate, (1)3–13(35) mm apart, petioles (1)4.5–10.5(15) long; blades oblanceolate to broadly obovate, rarely oblanceolate to broadly obovate, rarely elliptic, coriaceous, (50)80–120(160) mm long, (15)25–35(49) mm wide, base attenuate, apex acuminate, sometimes abruptly so; upper surface light green, shiny, glabrous, lower slightly lighter than above, glabrous; secondary veins prominent. Flowers solitary in leaf axils, (5)6–7(8)-merous, campanulate; pedicels (23)33–47(60) mm long, erect, glabrous; calyx lobes green, the margins hyaline, glabrous, lanceolate to ovate, (8)10–12(17) mm long, (3)5.5–7(8) mm wide, base attenuate, apex acuminate, sometimes abruptly so; upper surface light green, shiny, glabrous, lower slightly lighter than above, glabrous; secondary veins prominent. Flowers solitary in leaf axils, (5)6–7(8)-merous, campanulate; pedicels (23)33–47(60) mm long, erect, glabrous; calyx lobes green, the margins hyaline, glabrous, lanceolate to ovate, often with prominent branching nerves, (8)10–12(17) mm long, (3)5.5–7(8) mm wide; corolla lobes white or cream, sometimes red at base, obovate, (15)19–24(30) mm long, (9)11–14(17) mm wide; filaments (6)8–11(12) mm long, anthers (2)2.5–4(5.5) mm long; style (6)8–9(10.5) mm long. Capsules globose, (9.5)10–11(14) mm long. Seeds dark brown, irregularly shaped, 1.2–1.7 mm long.

**DISTRIBUTION:** Kaua’i: Mostly restricted to the Kōkē’e area, 1090–1290 m. A single collection from Kāhili Ridge, SE Kaua’i (Fay 502), 550 m, is unusually low for the species. Exact location of the Olokele collection is unknown, but is also outside the principal range. Growing in lowland wet forest dominated by *Metrosideros, Dianella, Dicranopteris, Scaevola, Coprosma, Perrottetia, Psychotria, Myrsine, Styphelia, Nestegis, Ilex, and Cheirodendron.*

NOTE: This is the only species with white corollas and sessile glands that produce a viscid surface. “Viscidness” may be recessive, because hybrids with nonviscid species are not viscid (Marr 1995).

Putative F$_1$ hybrids between *L. glutinosa* and *L. kalalauensis* have been collected from two locations below Kalalau Lookout (Marr 615 [UBC], Wood 1417 [UBC]). These closely resemble artificial F$_1$ hybrids between these two species. Hybrids between this species and *L. scopulensis* have also been collected below Kalalau Lookout (Wood 1712, [PTBG], Wood 641, 805 [UBC]) and near Pu’u Ki’i (Wood 2396 [PTBG, UBC]).

**SPECIMENS EXAMINED:** Kaua’i: Kalalau Lookout, Carlson 3713 (F), Degener 22334 (BISH, MASS, PTBG), Herbst 1001 (PTBG), Fosberg 41467 (BISH), Wagner 5005 (BISH, G, RSA), Plews 129 (PTBG), Marr 616 (UBC), Marr 619 (COLO), Flynn 2769 (PTBG), Stern 2998 (BISH); Kalāhū, Degener 21465 (BISH, FNY); Kaluapuhi Trail, Flynn 160 (PTBG), Marr 254 (UBC); Honopū Trail, Marr 260 (UBC), Marr 561 (OS), Gagne 546 (BISH), Herbst 2154 (F, MO, NY, PTBG), Sohmer 6532 (NY); Kīholoana, Yuncker 3494 (F, NY), Degener 22334 (BISH, MASS, PTBG), St. John 19985 (BISH); road between Kīholoana and Pu’u o Kila, Marr 255 (UBC), Marr 593 (MICH), Marr 595 (HAST), Marr 596 (OS), Marr 599 (IBSC), Marr 600 (MASS); ridge between Pu’u o Kila and Pihea, Lamoureux 2846 (BISH, F), Carlquist 1317 (RSA, US); Kahuama’a Flat, Herbst 2055 (F); road opposite Awa’awapuhi trailhead, Gustafson 1715 (RSA), Lawrence 5798 (PTBG); Lehuanakani Trail, near road, Degener 23949 (W); Kōkē’e area, not specific, Forbes 786. K (NY, P, US, W), MacDaniels 810 (BISH), Stern 2998 (BISH, RSA), Wilder 446 (BISH), Shear s.n. (US), Degener 17667 (K, MO), Neill s.n. (MO), Rock s.n. (K).

5. *Lysimachia haupuensis* St. John, Phytologia 64:45, 1987.—Type: Kauai, Haupu Range, along base of cliff, 400 m, 26 Feb. 1927, MacDaniels 883 (holotype: BISH!).
Low branching shrub at least 50 cm tall; stems dark brown, pilose when young. Leaves alternate, 1-10 mm apart, petioles 2 mm long; blades elliptic, coriaceous, internal glands prominent upon drying, (25)36–45(50) mm long, (7)9-13(14) mm wide, base acuminate, apex acute; upper surface dark green, shiny, glabrous, lower lighter than above, brown glabrate; secondary veins prominent, tertiary veins obscure. Flowers solitary in leaf axils, 6-merous; pedicels 25 mm long, erect, densely pilose; calyx lobes pilose, lanceolate, 6 mm long, 2 mm wide; corolla lobes red, obovate, 10 mm long, 5 mm wide; filaments 4 mm long, anthers 2 mm long; style 7 mm long. Capsules and seeds not seen.

**DISTRIBUTION:** Kaua‘i: Possibly extinct. Known only from the single sheet from the type collection.

**NOTE:** This species is difficult to classify because of the limited collections. *Lysimachia haupuensis* and *L. scopulensis* are the only species with prominent (upon drying) internal foliar glands. The former species differs from the latter in being pubescent, not pulverulent, and has longer, lanceolate calyx lobes. *Lysimachia haupuensis* was probably collected within 1-3 km of *L. kahiliensis*. The leaf shape of *L. haupuensis* most closely resembles narrow-leaved individuals of *L. hillebrandii* from the Ko‘olau Range on O‘ahu, yet internal glands are not prominent in dried specimens of *L. hillebrandii*, whose leaves are thicker and much lighter green beneath than those of *L. haupuensis*.


**NOMENCLATURAL NOTE:** This species was originally published as var. a of *Lysimachia hillebrandii* Hook. f. ex A. Gray in Gray (1862), a description of collections made during the 1840 U.S. South Pacific Exploring Expedition. The description provided by J. D. Hooker, “*L. hillebrandii* Hook. f. in litt.-Oahu and Maui,” was apparently of a Hillebrand collection. Hillebrand, however, did not arrive in Hawai‘i until 1851. Thus, it is unlikely that Hooker based his description on specimens (US 2983211, NY s.n.) from the 1840 expedition. The lectotype designated here is part of a mixed collection. Branches on the lower part of the sheet are indicated as *Hillebrand 183*, received at Kew in 1865; on the upper part of the sheet, separated by a pencil line, are two branches bearing flowers and fruit, indicated as having been sent to Kew by Hillebrand in 1858. St. John...
annotated, but did not publish, *Hillebrand* 183 as
the lectotype. Because it was received at Kew
after Gray’s publication, this cannot be the mate­
rial viewed by Hooker. The branches sent in 1858
fit the description and likely was the material
viewed by Hooker.

*Hillebrand* (1888) restricted specimens col­
lected from the Ko‘olau Range of O‘ahu, on
“bare mountain ridges of Kalihi and Manoa” for
var. α. Knuth (1905) also restricted var. α typica
R. Knuth to O‘ahu citing *Hillebrand* s.n. and
Wawra 2211, 2380. However, Wawra 2211 is
*L. waianaeensis* St. John from the Wai‘anae Range.

Woody shrubs up to 2 m tall; stems dark
brown, densely reddish brown tomentose at the
tip, glabrate. Leaves alternate, (0.5)3–24(36)
apart, petioles (2)3–7(13) mm long; blades nar­
rowly to broadly elliptic or obovate, coriaceous,
(24)36–55(60) mm long, (6)12–24(40) mm
wide, base attenuate, apex acute to rounded,
often abruptly acuminate; upper surface usually
light green, pilose, red at base, lower slightly
lighter than above, pilose to rusty tomentose,
especially along the primary vein and petiole.

Flowers solitary in leafaxils, (6)7–8(9)–merous,
campanulate; pedicels (10)11–24(30) mm long,
erect, densely rusty tomentose; calyx lobes
green, often red toward base, pilose to tomen­
tose, lanceolate to narrowly ovate, (4)5–8(9) mm
long, (1.5)2–3.5(5) mm wide; corolla lobes red,
obovate, (9)12–16 mm long, (5)6–8(9) mm
wide; filaments (4)5–7.5(8.5) mm long; style
6–8(12) mm long. Capsules globose, (6)8–10
mm long. Seeds dark brown, irregular, 1.5–2.5
mm long.

**DISTRIBUTION:** O‘ahu: Ko‘olau Range wet
forest at 400–710 m. Southern Wai‘anae Range
lowland mesic forest and cliffs 720–820 m,
growing with *Dubautia, Bidens, Hedyotis, Era­
grostis, Elaphoglossum, Peperomia, Carex,
Styphelia, Plantago, Hibiscus*, *Lysimachia wai­
aeensis*, and *Silene*. Moloka‘i: A single 1912
collection from Wailau. Kaua‘i: location unknown.

Leaves are mostly 12–40 mm wide; however,
a few collections (*Forbes 1255.O, Forbes s.n.,
Degener 17669, St. John 13004, Faurie 707*)
from the Ko‘olau Range have leaves 6–14 mm
wide. The distribution of these specimens over­
laps with that of broader-leaved specimens.

Some sheets (*Mann & Brigham 229, BISH, F*)
bear narrow- and broad-leaved branches. Plants
from O‘ahu have leaves less than 32 mm wide;
those from Moloka‘i have leaves up to 40 mm
wide.

The most recent collection from the Ko‘olau
Range was in 1980 (*Obata 434*). Before 1980,
*L. hillebrandii* had not been collected from that
range since 1937. No flowering specimens have
been collected from the Wai‘anae Range.

*Lysimachia hillebrandii* is identified as “pua­
heliki” in the Hawaiian language (*Hillebrand*
1888).

**SPECIMENS EXAMINED:** O‘ahu: Olympus­
Waimanalo Pali, *Rock s.n.* (BISH), *Garber 249
(BISH)*; Punalu‘u (Pig-God Trail), *Degener
17681 (GH,NY,US)*; Suehiro s.n. (BISH); *Nu‘uanu,
opposite King’s Falls, Mann & Brigham 229
(BISH,F,GH,MMA,MO,NY)*; Pu‘u o Kona (Crest of
Kuli‘ou’ou), *Obata 434 (BISH)*; Kalihi, *Hille­
brand 183 (F, photo at K)*; Kalihi Valley, top of
ridge, *Swezey s.n. (GH)*, *Christopherson 1270
(BISH), Forbes 229.O (BISH), Forbes 2291.O (K)*,
*Hillebrand s.n. (BISH), Faurie 707 (P)*; NE of
Palikea, *Wood 1812 (PTBG), Perlman 5404
(PTBG)*; Palawai Gulch, *Wilbur 622 (BISH)*; ridge
between Nānākuli and Lualualei, *Marr 1292
(MASS), Marr 1293 (UBC), Wood 1982
(PTBG,UBC)*; Middle Hālawa Ridge, *Degener
17669 (GH,NY)*; Kalauao-Waimalu Ridge, *St.
John 13004 (BISH)*; location not stated, *Wawra
2380 (w), U.S. South Pacific Exploring Expedi­
tion, 1838–1842, s.n. (NY,US)*. Moloka‘i: *Waiehu,
Wailau Valley, Forbes 559.Mo (BISH, MO,P,W)*.
Kaua‘i: location unknown, *Lydgate s.n. (BISH
586775)*.

7. *Lysimachia iniki* Marr, sp. nov.—Type:
Kaua‘i: headwaters of the north fork of the
Wailua River, 720 m, 30 Oct. 1992, *Lorence
7270 (holotype: PTBG)*.

Figure 5

*Lysimachiae daphnoidis* affinis a qua praecipue
different apice albo corollae minoris; foliis
lattioribus, plus orbiculatis, sursum versis, viridi­
bus, versum basem, non rubris.
Woody shrubs with pendulous branches 30–150 cm long; stems branching above, green, densely hirsute. Leaves alternate, 2–5(10) mm apart, sessile; blades obovate to orbicular, cupped upward, coriaceous, chartaceous when dry, (35)37–45(54) mm long, (25)35–38(42) mm wide, base cordate, apex rounded, abruptly acuminate; upper and lower surfaces light green, translucent viscid-hirtellous throughout, becoming glabrate; secondary and tertiary veins prominent, veins pellucid. Flowers solitary in leaf axils, 6–7-merous, funnelform; pedicels 15–25 mm long, erect, green, densely viscid-hirtellous; calyx lobes green, the margins hyaline, densely
translucent viscid-hirtellous, lanceolate, 8–10 mm long, 2–3 mm wide; corolla lobes with the upper 5–7 mm white, the lower portion dark red, the inner surface densely glandular-punctate, oblanceolate, 15–16 mm long, 5 mm wide; filaments 10 mm long, dark red, anthers 2.5 mm long; style 8–9 mm long. Capsules globose, 6–7 mm long. Seeds dark brown, irregularly shaped, 1 mm long.

**DISTRIBUTION:** Kaua‘i: Known only from two populations of at least 25 individuals growing on wet, mossy, or rocky cliffs of the headwaters of the north fork of the Wailua River, 720 m. Growing with Machaerina, Isachne, Bidens, Plantago, Hedyotis, Pipturus, Cyrtandra, Dubautia, Athyrium, and Metrosideros.

**NOTE:** The viscid-hirtellous leaves, stems, pedicels, and calyx lobes of *L. iniki* resemble those of *L. daphnoides*. *Lysimachia iniki* differs in having broader leaves cupped upward with pellucid veins, shorter calyx and pedicel, and narrower distally white corolla lobes.

Named after Hurricane Iniki, which struck Kaua‘i on 11 September 1992. The strong winds broke off branches from the cliffs above the headwaters of the Wailua River in the same area where *L. pendens* grows. These were discovered by Lorence et al., and seeds (from Lorence 7270) were sent to UBC, where the species was first seen in flower. In the Hawaiian language ‘iniki means sharp and piercing, as wind or pangs of love (Pukui and Elbert 1992).

**SPECIMENS EXAMINED:** Kaua‘i: headwaters of N fork of Wailua River, Flynn 5276 (PTBG), Perlman 13079 (PTBG), Marr 1535 (BISH, PTBG, UBC), Perlman 13079 (PTBG).


Upright shrub, at least 40 cm tall; stems reddish brown, glabrous. Leaves alternate, 1–10 mm apart, petioles 1–2 mm long; blades narrowly obovate, coriaceous, 35–50 mm long, 9–12(15) mm wide, base attenuate, apex acuminate; upper and lower surfaces glabrous; angle between primary and secondary veins narrowly acute, tertiary veins obscure. Flowers solitary in leaf axils, 6-merous; pedicels 6–17 mm long, erect; calyx lobes green, lanceolate, 9–11 mm long, 3 mm wide; corolla unknown. Capsules globose, 6 mm long. Seeds, dark brown, irregularly shaped, 1.5–3 mm long.

**DISTRIBUTION:** Kaua‘i: Possibly extinct. Collected only once from Kāhili Ridge, exact location unknown.

**NOTE:** This is a problematic species because it is known from a single collection without corollas. The leaves resemble those of *L. daphnoides* from which it differs in that the entire plant is nearly glabrous, the angle between the primary and secondary veins is more acute, the leaves are much less coriaceous, and the apex is more acuminate. Leaves of *L. kahiliensis* also resemble those of *L. remyi* subsp. *subherbacea*; however, its calyx is longer than that of the latter. *Lysimachia remyi* subsp. *subherbacea* has never been collected from Kaua‘i. The absence of corollas also cautions against inclusion of the type specimen within any other species.


*Lysimachia hanapepeensis* St. John, Phytologia 64:44, 1987.—Type: Kauai, ridge west of Hanapepe, 23 July 1895, Heller 2614 (holotype: photo at K!; isotypes: A!, P!, GH!, MO!, NY!, P!, US!). Note: St. John added an “A” to specimens he annotated (i.e., 2614A).
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Shrub with stems up to 4 m long, branching mostly from the base, with short lateral shoots; stems brown to dark red, densely rusty tomentose at the tips, glabrate. Leaves alternate, (1)3–23(40) mm apart, petioles (5)7.5–8.5(10.5) mm long; blades elliptic, obovate, rarely ovate, coriaceous, (50)60–80(100) mm long, (15)25–32(45) mm wide, base attenuate, apex acute or acuminate; upper surface dark green, tinged with red, glabrous, lower much lighter, lightly pilose, with scattered reddish streaks; primary and secondary veins prominent, higher-order veins often obscured by thick cuticle. Flowers solitary in leafaxils, (5)6–7(8)-merous, urceolate, the petals often tightly closed around the exserted style, even until corolla abscission; pedicels (12)16–33 mm long, green, often peniculous, rarely erect, lightly to densely tomentose; calyx lobes green, with red streaks, the margins slightly hyaline, nerves sometimes visible, glabrous, linear to narrowly lanceolate, (7)13–16(20) mm long, (2)3–3.5(5) mm wide; corolla lobes red at base becoming green in upper half, veins red to the tip, inner surface red farther distally than outer, the margins erose, obovate, (13)15–17 mm long, (6.5)7–9(9.5) mm wide; filaments 10–12 mm long, red, anthers (2.5)3–5 mm long; style 10–12(16) mm long, persistent in fruit. Capsules globose (7.5)8–10 (11) mm long. Seeds dark brown, irregularly shaped, 2–3.1 mm long.

**DISTRIBUTION:** Kaua‘i: Scattered populations in lowland diverse mesic forest of western and central Kaua‘i, 970–1260 m. Growing with *Metrosideros, Acacia, Zanthoxylum, Melicope, Tetraplasandra, Alyxia, Psychotria, Poteria, Wickstroemia, Stylphelia, Vaccinium, Antidesma, Wilkesia, Remya, Scaevola, Alphitonia, Dianella, Pleomele, Hedoytis, Dodonaeae, Dubautia*, and *Nestegis*.

**NOTE:** The description of the collection location must be in error. Kilohana Lookout is above Hanalei Valley; Kalalau Lookout is above Kalalau Valley. It is more likely that the type was collected below Kalalau Lookout, where the habitat is more typical for the species. The sheet of the lectotype bears two branches; one is *L. glutinosa*.

This is the only extant species whose corolla lobes are distally green with red veins and erose margins. The corolla lobes and often the exerted stamens tightly surround the exerted style. Leaves of seedlings and sometimes young leaves of older plants often are silvery.


NOMENCLATURE NOTE: Hillebrand (1888) first described plants from “Molokai! Pali of Pelekunu and smaller forms, quite glabrate, with sessile leaves from Maunahui; E. Maui! Haleakala; at heights of 3000 to 4000 ft.” as *L. hillebrandii* var. *A*, which was not validly published. Knuth (1905) named it var. *A maxima* citing the Pelekunu and Haleakalā collections. I have not seen any specimens from Maui labeled *L. maxima*; however, it is possible that the plant cited was *L. remyi* subsp. *caliginis*, which has densely tomentose stems and whorled leaves.

Sturdy upright shrubs; stems 1–2 m long, light brown or green, densely brown tomentose at tip, often retaining pubescence on older stems. Leaves 3(4) per node, sometimes alternate, (0.1)0.5–43(70) mm apart, petioles (1)2–3(5) mm long, red at base; blades ovate, obovate, or elliptic, coriaceous, slightly rugose, margins revolute, (38)55–60(95) mm long, (18)23–30(50) mm wide, base cuneate or attenuate, apex acuminate, upper surface dark green, sparsely pilose, lower slightly lighter, moderately pilose with red streaks; secondary and tertiary veins prominent, often pellucid. Flowers solitary in leaf axils, (5)6(7)-merous, campanulate; pedicels (16)25–30(35) mm long, erect, densely tomentose; calyx lobes green, pilose, lanceolate, 9–10.5(11) mm long, (3)3.5–4(4.5) mm wide; corolla lobes green, pilose at tips, obovate, 15–16(17.5) mm long, 9–10 mm wide; filaments (6.5)7.5–8.5(10) mm long, anthers 1.5–2(2.5) mm long; style 9–11 mm long. Capsules globose, 8–9 mm long. Seeds dark brown, irregularly shaped, 1–2 mm long.

**DISTRIBUTION:** Moloka‘i: A single population of 45–50 individuals on the northwestern rim of Pelekunu valley in lowland wet forest at 950 m. Growing with *Metrosideros, Dicranopteris, Vaccinium, Psychotria, Lycopodium, Machaerina, Hedyotis, Labordia, Cheirodendron, Dubautia, Sadelaria, Elaphoglossum, Broussaisia, Styphelia, Scaevola*, and *Cyrtandra.*

**NOTE:** *Lysimachia maxima* appears to be most closely related to *L. remyi*, in which the leaves are also occasionally ternately arranged. *L. maxima* differs from the latter in having much broader leaves, longer calyx and corolla lobes, and a more obtuse angle between the primary and the secondary veins.


Sprawling shrub mostly branching from the base; stems up to 3 m long, red-maroon to green, pilose at the tip, glabrate. Leaves alternate, (1)5–36(48) mm apart, petioles (6)7.5–12(15) mm long, dark red; blades elliptic, coriaceous, waxy, (45)60–80(105) mm long, (18)25–40(50) mm wide, base attenuate to rounded, apex acuminate to cuspidate; upper surface light green, glabrous, lower slightly lighter, glabrous; primary vein dark red, secondary veins prominent, tertiary veins obscure. Flowers solitary in leaf axils, 5–6-merous, barely open, almost urceolate; pedicels (20)24–30(40) mm long, pendulous, thicker toward calyx, dark red for full length, glabrous; calyx lobes dark red, glabrous, narrowly lanceolate, 4–5.5 mm long, 1.5–2 mm wide; corolla lobes, obovate, deep maroon, the margins lighter, 6–8.5 mm long, 4–5.5 mm wide; filaments (2)3–4 mm long, anthers 1–1.5 mm long; style (3)4–5(5.5) mm long. Capsules globose, 5–6 mm long. Seeds dark brown, irregularly shaped, 1–2 mm long.

**DISTRIBUTION:** Kaua‘i: Known from only two populations in lowland wet forest on the north side of the island, 615–680 m. Growing with *Metrosideros, Psychotria, Eugenia, Cyanea, Pittosporum, Dicranopteris, Diplopterygium, Ilex, Alyxia, Broussaisia, Xylosma, Scaevola, Dubaut-
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tia, Freycinetia, Bidens, Vaccinium, Melicope, and Cibotium.

NOTE: Only in this species are the calyx and pedicel entirely dark red.

SPECIMENS EXAMINED: Kaua‘i: Wainiha-Mānoa Ridge, Christensen 283, 316 (BISH), Wichman 253 (PTBG, UBC), Marr 1241 (UBC), Marr 1240 (F), Marr 1250 (MO), Marr 1251 (PTBG); Limahuli-Hanakāpī‘ai Ridge above Limahuli Falls, Perlman 18 (BISH), Flynn 2164 (MO, PTBG, RSA), Marr 525 (p, w), Marr 526 (NY, RSA, MASS), Marr 527 (HAST, MICH), Marr 528 (PTBG), Marr 529 (IBSC, UBC), Marr 530 (OS), Marr 531 (K, COLO), Marr 533 (US).

12. Lysimachia pendens Marr, sp. nov.—Type: Kaua‘i, headwaters of the north fork of the Wailua River, 720 m, 23 July 1987, Lorence 5349 (holotype: PTBG!).

Figure 6

Lysimachiae waiaholeensi affinis a qua praecipue differit foliis latioribus, lanceolatis, non linearibus; pagina inferiore foliorum brunnea manente et puberula ubi matura; pedicello longiore.

Small, many branched, delicately pendulous shrubs; stems 20–60 mm long, densely tan tomentose when young, glabrate. Leaves alternate, (0.1)0.5–3.5(5) mm apart, petioles 1(2) mm long; blades narrowly lanceolate, soft coriaceous, (20)25–30(45) mm long, 2–4 mm wide, base attenuate, apex attenuate, upper surface green, glabrous, lower green, brown pilose; secondary and higher-order veins obscure. Flowers solitary in leaf axils, 5–7-merous; pedicels (6)9–12(14) mm long, erect, green, occasionally red below calyx, densely tomentose; calyx lobes green, sometimes red toward base, narrowly ovate, 4–6 mm long, 2–2.5(4) mm wide; corolla lobes red, obovate, 7.5–8.5 mm long, 5–6 mm wide; filaments 3.5–4 mm long, red, anthers 1 mm long; style 3.5–4.5 mm long. Capsules globose, 5–6.5(7) mm long. Seeds dark brown, irregularly shaped, 1.2–1.8 mm long.

DISTRIBUTION: Kaua‘i: Known only from several small populations at the headwaters of the north fork of the Wailua River, 720 m. Growing on vertical wet, mossy, or rocky cliffs with Machaerina, Isachne, Bidens, Selaginella, Plantago, Hedyotis, Pipturus, Cyrtandra, Dubautia, Athyrium, and Metrosideros.

NOTE: This species is distinguished from L. filifolia by its broader leaves and tomentose leaves, stems, and pedicels.

SPECIMENS EXAMINED: Kaua‘i: Headwaters of the north fork of the Wailua River, Wood 344 (PTBG), Lorence 7253 (BISH), Perlman 13078 (BISH), Marr 261 (MO), Marr 262 (UBC), Marr 470 (COLO), Marr 481 (F), Marr 477 (HAST), Marr 500 (W), Marr 487 (RSA), Marr 489 (K), Marr 490 (OS), Marr 491 (US), Marr 496 (MICH), Marr 497 (IBSC), Marr 498 (P).


NOMENCLATURAL NOTE: Hillebrand (1888) cited six collections in his description of Lysimachia remyi: “Maoui! Haleakala, Waihee, Waiehu; Molokai! Halawa, Waikolu, collected also by Remy.” Hillebrand (1888) cited L. hillebrandii var. angustifolia Gray collected by Remy on Maui as a synonym. Sheets from GH and K, collected by Hillebrand, appear to be those cited from Hālawa and Waihe’e. One is labeled “Lysimachia hillebrandii H. f. var. linearis, W. Maui: Gulch of Waihee” and the other “Lysimachia hillebrandii Hook. f. var. angustifolia, Molokai: Gulch of Halawa.” (L. hillebrandii H. f. var. linearis was not validly published.) The Waihe’e collection lacks fruit and flowers. That from Hālawa bears fruit and a single flower but leaves are unusually narrow for plants from Moloka‘i. The specimen cited as “Haleakala” by Hillebrand may have been
Figure 6. Lysimachia pendens. A, flower; B, flowering branch.
from the Wilkes 1838–1842 Expedition (US 76574), labeled “Lysimachia hillebrandii Hook. f. verging to var. angustifolia”; however, no collection location is given. This specimen is *L. remyi* subsp. *caliginis*.

We have designated Remy 458 as the lectotype because it is a good flowering specimen and appears to be among the material cited by Hillebrand. The collection location is not stated on the sheet chosen as the lectotype; however, St. John (unpubl. ms.) viewed a duplicate from GH and listed the collection location as Waiehu in the description of *L. stene* St. John, which is based on the same specimen.

Sprawling to erect shrubs; stems up to 5 m long, red or green, glabrate or densely reddish brown tomentose. Leaves alternate or whorled, (0.1)0.5–30(55) mm apart, petioles (1)2–10(12) mm long; blades linear, oblanceolate, ovate, elliptic, coriaceous, sometimes undulate and rugose, margins sometimes revolute, (15)20–60(95) mm long, (1)4–17(33) mm wide, base acute to attenuate, apex acute or acuminate; upper surface light to dark green, glabrous, glabrate or tomentose, lower lighter, glabrous, pilose, or densely light brown tomentose sometimes with scattered red streaks, veins sometimes pellucid. Flowers solitary in leaf axils, 5–8-merous, campanulate, rarely urceolate; pedicels (3)10–30(70) mm long, erect, glabrous to tomentose; calyx lobes entirely green, or red at the base, linear, lanceolate or ovate, glabrous to densely tomentose (2.5)4–8(10) mm long, (1)1.5–3(4.5) mm wide; corolla lobes red, obovate, (5)8–14(17) mm long, (5)6–9(15) mm wide; filaments (3)4.5–7.5(11) mm long, anthers 1–3.5 mm long; style 3–6.5(7) mm long. Capsules globose (4)4.5–8(10) mm long. Seeds dark brown, irregularly shaped, 1.3–2.9 mm long.

**NOTE:** This species encompasses plants from O‘ahu, Moloka‘i, Lāna‘i, and Maui that are upright, with leaves (1)2–20 mm wide, red corolla lobes less than 15 mm long, and calyx lobes less than 15 mm long, and calyx lobes less than 10 mm long.

### KEY TO SUBSPECIES

1a. Angle between primary and secondary veins more obtuse in upper portion of leaf than lower; leaves dark green above, much lighter below, alternate. West Maui, Lāna‘i ... .......................... 13c. *L. remyi* subsp. *remyi*

1b. Angle between primary and secondary veins nearly uniform; leaves dark or light green above, slightly lighter below, alternate or whorled .......................................................... 2

2a. Leaf veins pellucid; leaves often whorled; stems often densely tomentose. East and West Maui .......................................................... 13a. *L. remyi* subsp. *caliginis*

2b. Leaf veins not pellucid; leaves alternate, rarely whorled; stems nearly glabrous .......... 3

3a. Leaf tip acuminate; leaves (20)45–60(95) mm long, distantly spaced, (0.1)1–22(55) mm apart, if closely spaced then nearly ternate, otherwise alternate; corolla lobes (6)11.5–14(17) mm long. Moloka‘i, O‘ahu .......... 13d. *L. remyi* subsp. *subherbacea*

3b. Leaf tip acute to acuminate, leaves (15)20–30(60) mm long, (0.5)1–6(20) mm apart, alternate; corolla lobes (6)8–10(13) mm long. East and West Maui .......................................................... 13b. *L. remyi* subsp. *kipahuluensis*


*Lysimachia kukuiensis* St. John, Phytologia 64:45–46, 1987.—Type: W. Maui, Puu Kukui, open bog, 1540 m, 18 Dec. 1928, Ewart 140 (holotype: BISH[1]).

Upright shrubs, sometimes sprawling, often
growing in dense clumps; stems up to 2.5 m long, light brown, often densely reddish brown tomentose. Leaves sometimes alternate, but often whorled, with up to 5 leaves per whorl, 0.5–19(35) mm apart, petioles (1)2–3(5) mm long, often dark red; blades lanceolate to ovate, coriaceous, undulate, rugose, the margins revolute, (18)30–45(70) mm long, (4)8–14(23) mm wide, base acute to attenuate, apex acuminate; upper surface dark green, glabrous, lower lighter, slightly pilose, scattered red streaks; veins pellucid, secondary and tertiary veins prominent. Flowers solitary in leaf axils, (5)6–7(merous, campanulate; pedicels (8)13–20(40) mm long, erect, green, often red toward calyx, pilose to densely tomentose; calyx lobes often dark red toward base, otherwise green with prominent red veins, (4)5.5–7(8) mm long, 2–3(4.5) mm wide; corolla lobes dark red, obovate (7)10–11(14) mm long, (5)7–8.5(12.5) mm wide; filaments (3)5–6(7) mm long, anthers 1.5–2 mm long; style (4)5–6(7) mm long, widely ovate. Seeds dark brown, irregularly shaped, 1.3–2.4 mm long.

DISTRIBUTION: East Maui: Montane wet forests, growing at or below treeline in Ko’olau Gap and Kaupō Gap, with Metrosideros, Blechnum, Vaccinium, Styphelia, Dubautia, Coprosma, Sterognyne, Cheirodendron, Machaerina, and Rubus, 1660–1970 m. West Maui: Montane wet shrublands and wet forest on summits, growing with Metrosideros, Dicranopteris, Dodonaea, Styphelia, Coprosma, Broussaisia, Sadleria, Lycopodium, Scaevola, Vaccinium, Dianella, and Sphenomeris, 1200–1760 m.

NOTE: Lysimachia remyi subsp. kipahuluensis and L. remyi. subsp. caliginis form hybrid swarms on East Maui in Kaupō Gap and near the old Waikau Cabin site in Ko’olau Gap. In those areas the range of leaf shape and size is continuous between subsp. caliginis and subsp. kipahuluensis. These two subspecies are not sympatric now, but may have been in the past. Decades of destruction of the native vegetation in Haleakalā by introduced animals has undoubtedly affected species distributions. Hybridization between L. remyi subsp. caliginis and subsp. remyi could account for some of the variation in leaf shape and spacing in some specimens from West Maui.

SPECIMENS EXAMINED: East Maui: Haleakala, Ko’olau Gap, Marr 327 (UBC), Marr 1019 (COLO), Marr 1026 (IBSC), Marr 1027 (RSA), Marr 1029 (OS), Marr 1039 (MIC), Degener 2553 (BISH,GH,MO,SY,US), Rock 8632 (GH,BISH), Herbst 1620 (BISH), Carquist 1933 (RSA), Forbes 1014.M (P), Hobdy 745 (BISH), St. John & Mitchell 21266 (BISH), Perlman 10769 (MO,PTBG); Haleakalā Crater, Degener 2554 (BISH,GH,K,MO,SY,US), Hitchcock 14960 (US), Woolford s.n. (BISH,GH); Pipeline Trail, Olinda, Degener 17686 (BISH,GH,MO,SY,UK); east of Ukulele, along edge of stream, Forbes 864.M (BISH); without locality, U.S. Exploring Expedition, under Captain Wilkes (as L. hillebrandii Hook. f., verging to var. angustifolia) (US). West Maui: Pu’u Kukui, Hitchcock 14820 (US), Degener 25074 (BISH,GH,K,MO,SY,US), Hitchcock 14820 (US), Degener 25074 (NY), Rock 8140 (GH,NY), Munro s.n. (BISH,NEAL s.n. (BISH); Mt. ‘Eke, Degener 2550 (GH,MO,SY,US), Forbes 389.M (BISH); Hanaka’ōō, Forbes 62.M (BISH).
1987.—Type: East Maui, NE of Lake Waianapanapa, 2120 m, 23 Nov. 1973, Harrison 488 (holotype: BISH!).

Upright shrubs mostly branching from the base, often growing in dense clumps several meters square; stems usually less than 1 m tall, but up to 2 m tall, light brown to red, glabrous to pilose. Leaves alternate, 0.5–6(20) mm apart, petioles (1)2–3(4) mm long; blades linear to oblanceolate or narrowly ovate, coriaceous (15)20–45(60) mm long, (1)2–6(14) mm wide, base attenuate, apex acute to attenuate; upper surface light green, glabrous, lower paler, slightly pilose; secondary veins pellucid in some, tertiary veins usually obscured by thick cuticle. Flowers solitary in leaf axils (5)6–7(8)–mers, sometimes urceolate, but usually campanulate; pedicels (5)11–17(31) mm long, erect, often red toward calyx, pilose; calyx lobes occasionally red at base, otherwise green, glabrous or pilose, linear to narrowly ovate, (3)5–6(9.5) mm long, (1)2–3(4.5) mm wide; corolla lobes red, much lighter toward margins, the veins red, obovate, (6)8–10(13) mm long, (5)6–7(9.5) mm wide; filaments (3)4.5–5.5(8) mm long, style (4)5–6.5(7) mm long. Capsules globose, 5–6(7) mm long. Seeds dark brown, irregularly shaped, 0.9–2.1 mm long.

**Distribution:** East Maui: Montane wet and montane mesic forests and subalpine mesic shrublands in and around Haleakalā Crater between the east side of upper Kaupō Gap and Lake Wai‘anapanapa and along streamsides or similar high-moisture environments in Kipahulu Valley, Waiho‘i Valley, and Hāna Forest Reserve from 690 to 2330 m. Growing with Metrosideros, Cheirodendron, Coprosma, Melicope, Myrsine, Blechnum, Elaphoglossum, Pemperomia, Astelia, Rubus, Dubautia, Vaccinium, Syphelia, Deschampsia, Lycophodium, Nephrilipis, Broussaisia, Selaginella, Machaerina, Dickranopteris, Acacia, Psychotria, and Clermontia from 690 to 1750 m. West Maui: Along streamsides growing with Pipturus, Bidens, Artemisia, Selaginella, Hedyotis, Coprosma, and Metrosideros from 370 to 900 m.

**Note:** Plants with leaves 1–3 mm wide are scattered along streamsides and in bogs in Kipahulu Valley, Waiho‘i Valley, and the Hāna Forest Reserve, as are plants with leaves more typical of the subspecies. Corolla lobes of plants from West Maui are more reflexed and somewhat longer (6–9 mm) than are those from East Maui (6–7 mm).

**Specimens examined:** East Maui: Trail from gulch SE of Palikū cabin and up to Kuiki Peak, Marr 281 (RSA), Marr 679 (UBC), Marr 683 (MICH), Marr 684 (HAST), Marr 685 (COLO), Marr 699 (IBSC), Marr 713 (W), Marr 689 (F), Marr 687 (PTBG), Degener 17670 (GH, MASS, MO, NY), Higashino 849 (BISH, US), Henrickson 3509 (BISH, RSA, US), St. John 21117 (GH, RSA, US); south of Kuiki, east side of Kaupō Gap, Degener 17671 (GH, MO, NY, US), Rock 8605 (BISH, GH, NY, PTBG, US), Olson 6 (BISH, photo at K, US); small gulch between Healani Gulch and Kaupō Gap, Gagne & Montgomery 605 (BISH); Hobdy 500 (BISH); W side Kaupō Gap, cliffs SE of Haleakalā Mtn., Degener 17755 (BISH, GH, MASS, MO, NY, US), Marr 292 (UBC); Kalapawili Ridge E of Pōhaku Pālahā to Lake Wai‘anapanapa, Marr 282 (UBC), Marr 646 (PTBG), Harrison 531 (BISH), Forbes 1195.M (K, US), Henrickson 3915 (BISH, US), Perlman 10517 (PTBG); upper Kipahulu Valley, Higashino 10190 (BISH), Marr 431 (UBC), Medeiros 8102 (UBC); S of Palikū cabin, Kaupō Gap, Henrickson 3884 (BISH, RSA, US); Waiho‘i Valley, Harrison 26 (BISH); Waihono Stream, Waiho‘i Valley, Nagata 1049 (BISH); Upper Hāna Forest Reserve “mid-camp,” stream bank, Harrison 567 (BISH), inner slopes of old cinder cone, Harrison 409 (BISH); Kipahulu Valley, Palikea Stream, Wood 3201 (PTBG), Marr 1281 (UBC), Marr 1280 (MO), Marr 1279 (P), below upper valley plateau, Marr 1287 (RSA), Kokowai Stream, Anderson s.n. (UBC). West Maui: Nākalaloa Stream, Marr 432 (UBC), Marr 438 (BISH); Black Gorge, Marr 1258 (UBC), Wood 0333 (PTBG).


Lysimachia lydgatei Hillebr., Fl. Hawaiian Isl., 284, 1888; Lysimachiopsis lydgatei (Hillebr.) Heller, Minn. Bot. Stud. 1:876, 1897.—Type: W. Maui, on slopes and in gulches back of Lahaina, Hillebrand s.n. (holotype: fragment of B at BISH!; isotype: GH, photo at K!).

Lysimachia occidentalis St. John, Phytologia 64:47, 1987.—Type: Maui, Hanaulaiki, 1000 m, 14 March 1972, Hobdy s.n. (holotype: BISH!).

Lysimachia pedicellata St. John, Phytologia 64:48, 1987.—Type: Lanai, ridge at head of Maunalei, 14 Oct. 1916, Munro 431 (holotype: BISH!).

Lysimachia pilosula St. John, Phytologia 64:48, 1987.—Type: Lanai, ridge at head of Maunalei, 14 Oct. 1916, Munro 431 (holotype: BISH!).

Lysimachia scansoria St. John, Phytologia 64:49, 1987.—Type: Lanai, Munro s.n. (holotype: BISH!).

Spreading shrub branching mostly from the base, often with very short axillary shoots; stems green, up to 1.5 m long, light brown or red, nearly glabrous to densely rusty tomentose. Leaves alternate, (0.1)0.5–30(50) mm apart, petioles (1)1.5–10(12) mm long; blades linear, lanceolate, oblanceolate, ovate, or elliptic, rarely orbicular, coriaceous, (15)20–55(90) mm long, (1)2–17(33) mm wide, base acute, attenuate, or rounded, apex acuminate, acute, or attenuate; upper surface dark green, glabrous to densely brown tomentose, lower much lighter, glabrate to densely brown tomentose, especially along the primary vein; secondary veins prominent or obscure, tertiary veins usually obscure. Flowers solitary in leaf axils, (5)6–8-merous, campanulate, sometimes rotate; pedicels (3)10–25(65) mm long, erect, densely tomentose; calyx lobes sometimes dark red at base, glabrous to densely tomentose, lanceolate (2.5)–(7)9 mm long, (1)1.5–3(3.5) mm wide; corolla lobes red, obovate (5)8–10(13) mm long, (4)5–7(9) mm wide; filaments (2.5)3–5(7) mm long, anthers 2–3 mm long; style (3)4–6(6.5) mm long. Capsules globose, (5)6–8(10) mm long. Seeds dark brown, irregularly shaped, 1.3–2.9 mm long.

DISTRIBUTION: West Maui: Montane mesic forest on the leeward side of the island from 670 to 1110 m. Growing with Metrosideros, Dodonaea, Styphelia, Sadleria, Vaccinium, Coprosma, Cheirodendron, Dubautia, Hedyotis, Myrsine, Pipturus, Alyxia, Astelia, Wikstroemia, Selaginella, Scaevola, and Lobelia. Lana‘i: Mountains, 650 m.

NOTE: This is easily the most variable taxon of Hawaiian Lysimachia. At one extreme are plants with nearly glabrous calyx lobes and glabrous leaves 15 mm long and 2 mm wide. These are L. remyi sensu Wagner et al. (1990). At the other extreme are plants previously classified as L. lydgatei such as a specimen from Lihau, Hobdy 519 (BISH), which has elliptic, densely tomentose leaves, stems, and calyx lobes and leaves 90 mm long and 30 mm wide. Lysimachia lydgatei is not recognized here because in many populations there is a continuum in form between tomentose plants with broad leaves to nearly glabrous plants with linear leaves.

The most important character that defines this L. remyi subsp. remyi is the angle between the primary and the secondary leaf veins, which becomes more obtuse toward the tip of the leaf whereas in other subspecies this angle is nearly equal for all secondary veins. This is evident in all but the most narrow-leaved plants. The contrast between the color of the upper versus the lower surface of the leaves is greater in L. remyi subsp. remyi than it is in other subspecies. Lysimachia remyi subsp. remyi has light brown tomentum, whereas it is dark red in the other subspecies.

SPECIMENS EXAMINED: West Maui: Ka‘u-la‘ula Canyon, Hobdy 1212 (BISH); Lihau, Marr...
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409 (UBC), Marr 408 (BISH), Marr 411 (PTBG), Hobdy 823 (BISH), Perlman 8425 (MO,PTBG, UBC); Manawainui Gulch (Hana‘ula), Degener 17687 (GH,NY,US,BISH), Gustafson 2069 (RSA), Forbes 114. M (BISH,MO,P,US,W), Nagata 961 (BISH,US), Hobdy 248 (BISH), Marr 356 (UBC); ridge north of Pohakea Gulch, Degener 2556 (US); Pōhākea Gulch, Gustafson 2075 (RSA), Hobdy 2671 (BISH), Nagata 1918 (BISH), Wood 1170 (PTBG); south of Hana‘ula, Wood 1176 (PTBG); left-hand side of Olowalu, Forbes 2300. M (BISH,W); Olowalu, right hand side of valley, Forbes 2368. M (NY,p), Forbes 2247. M (BISH,K); Kaho‘olewa Ridge, Perlman 10581 (PTBG); Waihe‘e Valley, Hillebrand s.n. (GH); Helu summit, Marr 1264 (UBC), Perlman 10729 (PTBG); Hale Pōhaku, Marr 934 (UBC), Marr 933 (OS), Marr 935 (US), Marr 939 (BISC), Marr 940 (f), Marr 951 (BISH), Marr 959 (HAST), Marr 970 (COLO), Marr 971 (PTBG), Marr 1001 (W), Marr 1000 (MO), Marr 1003 (MICH), Marr 1004 (NY); Pu‘u Lio, Degener 12909 (GH,NY,US); Black Gorge, Degener 23735 (GH,NY); between Kinihāpai and Ae streams, Gustafson 3300 (RSA); upper Ukumehame Canyon, Hobdy 1259 (BISH); Waiuku Pali, Forbes 2440. M (BISH); lowlands back of Kā‘anapali, Rock 81/64 (BISH); location uncertain, Forbes s.n. (BISH). Lāna‘i, Mtns., east end, Forbes 221.L (BISH,MO,NY,P,US); Kailholena, Forbes 387.L (BISH); Manaha, Rock 8096 (BISH,GH,K,NY); ridge above Maunalei, Munro 627 (BISH,W). type: BISH!, p!). (St. John changed the collection number on the p specimen to 705A).

*Lysimachia kalaupapaensis* St. John, Phytologia 64:45, 1987.—Type: Molokai, Kalaupapa Pali, 520 m, 23 May 1918, *Rock 14030* (holotype: BISH!).

*Lysimachia molokaiensis* St. John, Phytologia 64:47, 1987.—Type: Molokai, Hillebrand s.n. (holotype: photo at K!).


*Lysimachia munroi* St. John, Phytologia 64:47, 1987.—Type: Molokai, edge of Walialu Valley, 770 m, 23 June 1927, *Munro 127* (holotype: BISH!).

*Lysimachia rockii* St. John, Phytologia 64:48, 1987.—Type: Molokai, Mapulehu, ridge to Kamakou, 770 m, 22 March 1910, *Rock 6146* (holotype: BISH!; isotype: BISH!, photo at K!, p!, US!, w!).


NOMENCLATURE NOTE: Four specimens, two at k and two at p are labeled “Moaui; voyage de M.J. Remy, 1851–1855 no. 458.” This is the collection number for the type specimen of *L. remyi*. One specimen from each of these herbaria is clearly *L. remyi* subsp. *subherbacea* and the letter “b” has been added after 458, perhaps by St. John, who annotated specimens in 1976 as *L. occidentalis* St. John. The other specimen from k is labeled 458a, and the second one from P remains 458. Both of these clearly came from West Maui.

Branching shrubs, acquiring an almost vine-like habit; stems brown to red, up to 5 m long, young stems rusty tomentose, older glabrate. Leaves alternate, sometimes almost ternate, (0.1)1–22(55) mm apart, petioles (1)2–3(7) mm apart.
long; blades linear, lanceolate, oblanceolate, or obovate, coriaceous, sometimes slightly undulate, (20)45–60(95) mm long, (3)8–11(20) mm wide, base acute to attenuate, apex acute to attenuate; upper surface olive green, glabrous, the veins slightly rugose, lower lighter, initially pilose, becoming glabrous, with scattered streaks of red; secondary veins prominent, tertiary veins obscure. Flowers solitary in leaf axils, (4)5–7-merous, campanulate; pedicels (11)20–30(70) mm long, erect, often red toward calyx, glabrous to densely tomentose; calyx lobes green, often red at base, glabrous to pilose, lanceolate to narrowly ovate, (3)5–8(10) mm long, (5)7.5–9.5(15) mm wide; filaments (4.5)6–7.5(11) mm long, anthers 2–3.5 mm long; style (5)6.5–8(11) mm long. Capsules globose, (5)6–8(9) mm long. Seeds dark brown, irregularly shaped, 1–2.1 mm long.


NOTE: Leaf and calyx size and shape are variable within and among populations. Plants in gulches generally have broader leaves and longer stems than those on drier hillsides.

SPECIMENS EXAMINED: Moloka’i: Pu’u Kolekole, Gustafson 3002 (RSA), Forbes 166.Mo (BISH), Davis 772, 806 (BISH), Anderson 514 (BISH), Marr 371 (UBC), Marr 372 (OS), Marr 373 (MASS), Marr 1140 (W), Marr 1146 (NY), Marr 1152 (P), Marr 1154 (US), Marr 1157, Marr 1169 (IBSC), Marr 1164 (PTBG); Kamalō, Rock 7024 (BISH); Makakupa’ia, Marr 378 (UBC); Wailau Valley, Faurie 706 (GH,P); Kaulahuki, Evans s.n. (BISH), Degener 17677 (GH); edge of Waihānau Valley, Degener 33500 (NY), Munro s.n. (BISH); Waikolu, Marr 402 (IBSC), Marr 391 (UBC), Carlquist 2216 (BISH,RSA), St. John 23437 (BISH), Degener 23734 (K), Gillett 1948 (US), St. John 12348 (NY); near Laianu, Degener 17678 (BISH,GH, NY); Hanalilolilo, Lorence 6324 (PTBG); ‘Ōnini Gulch, Mill 502 (BISH), Davis 846 (BISH), Marr 383 (F), Marr 385 (K), Marr 384 (UBC); Kalaupapa rim, Harrison s.n. (BISH), Southworth s.n. (BISH), Forbes 24.Mo (BISH, MO,US), Krajina 620612006 (UBC); Kawela, Perlman 6602 (PTBG,UBC), Lorence 5630 (BISH, MO,PTBG), St. John 19880 (PTBG), Warshauer 2317 (BISH), Marr 368 (HAST), Marr 367, Marr 369 (UBC), Marr 1178 (RSA,COLO), Marr 1182 (K), Marr 1184 (US), Marr 1187 (OS), Marr 1190 (P); ravine N of Pu’u Makali ‘ili’i, Degener 34499 (BISH, NY); ridge between Kaunakakai and Kūpā’i’a gulches, Davis 880 (BISH), Cuddihy 1244 (BISH), Marr 1066 (UBC), Marr 1093 (MO); Kahuaawii Gulch, Degener 33498 (GH, NY); Hālawa Gulch, Hillebrand s.n. (BISH), Rock 6146 (PTBG); Wailau Valley, ridge to Oloku’i along seacliff, Wood 1258 (MO,PTBG); no location given, Remy 457 (P), Remy 458b, (K,P), Hillebrand s.n. (US 809323). O’ahu: Wai’aane Range, Mākua Kea’au Forest Reserve, ‘Ohi‘ikolo area, Wood 2633 (UBC,PTBG).


Figure 7

*Lysimachiae waianaeensi* similis magnitudine et forma calycis, sed foliis paene sessilibus, areolis et venis secundariis obscuris. Folia atro-viridia et saepe pulverulenta, ad apicem deorsum curvata, caulibus semper pulverulentis.

Branching shrubs; stems up to 75 cm long, red or green, pulverulent when young. Leaves alternate, (0.5)2–7(8) mm apart, petioles (2)3–4.5(5) mm long; blades oblong, sometimes narrowly obovate, coriaceous, almost succulent, with internal glands, tips slightly to extremely recurved, (3)35–65(86) mm long, (5)8–11(23) mm wide, base acute, apex attenuate; upper sur-

face dark green, drying olive green, glabrous, pulverulent when young, lower dark green, drying lighter than above, glabrous; primary vein and petiole sometimes dark red, secondary veins prominent, tertiary veins obscure. Flowers solitary in leaf axils, (5)6(7)-merous, campanulate; pedicels 20–45 mm long, erect, green; calyx lobes green or red at the base, scarious margins, pulverulent, otherwise glabrous, widely ovate (2.5)4–5 mm long, (2)3–4(4.5) mm wide; corolla lobes red, obovate, 10–11 mm long, 6–7 mm wide; filaments 5 mm long, anthers 2 mm long; style 5 mm long. Capsules globose, 6.5–7.5(9) mm long. Seeds dark brown, irregularly shaped, 1.5–2.5 mm long.

**DISTRIBUTION:** Kaua‘i: Growing on steep cliffs of diverse lowland mesic forest in upper Kalalau Valley, 780–880 m. Associated with *Hedyotis, Chamaesyce, Hibiscadelphus, Nototrichium, Stenogyne, Poa, Melicope, Lobelia, Myrsine, Remya, Wilkesia, Dubautia, Lepidium,*
Lipochaeta, Metrosideros, Coprosma, Vaccinium, Rumex, and Exocarpus.

NOTE: The most distinct characteristics of this species are pulverulent young leaves and stems, the recurved leaf tips, and dark green, shiny upper leaf surface.

SPECIMENS EXAMINED: Kaua‘i: Kalalau rim, below Pu‘u o Kila, Wood 1008 (UBC,PTBG), Wood 798 (FNYUS,W, Mass,OS,MICH), Wood 2036 (MO,PTBG); Pu‘u Ki‘i, Wood 2397 (PTBG, UBC), Wood s.n. (BISH,K,PRSA, IBSC, COLO, MICH).


Shrubs at least 0.5–1 m tall; stems brown, pilose when young, glabrate. Leaves alternate, (3)10–15(25) mm apart, petioles 1–6 mm long; blades obovate, coriaceous (50)75–80(100) mm long, (12)20–35(48) mm wide, base attenuate, apex acuminate; upper surface dark green, glabrous, lower lighter than above, glabrous; secondary veins prominent, tertiary veins obscure. Flowers solitary in leaf axils, 6–7-merous; pedicels 15–27 mm long, erect, green; calyx lobes green with prominent dark veins, narrowly lanceolate, 13–16 mm long, 4–6 mm wide; corolla lobes dark red, obovate, 15–19 mm long, 10–11 mm wide; filaments 7 mm long, anthers 3 mm long; style 9–10 mm long. Capsules not seen.

DISTRIBUTION: Kaua‘i: Two collections, the type location and a second location from the type location in 1911. No further collections from there despite several recent visits by botanists. A broken branch collected in 1991 (Wood 784) from the headwaters of the Wailua River (NE corner of amphitheater) had fallen from the cliffs above, possibly from the summit area of Mt. Wai‘ale‘ale.

NOTE: The leaves of this species closely resemble those of L. glutinosa. Lysimachia venosa differs in having a dark red corolla, is not viscid, and has longer and narrower calyx lobes than L. glutinosa.

SPECIMENS EXAMINED: Kaua‘i: Summit of Mt. Wai‘ale‘ale, Rock 8881 (BISH, GH); Wood 784 (PTBG).

16. Lysimachia waianaeensis St. John, Phytologia 64:50, 1987.—Type: Oahu, Puu Kanehoa, Waianae Range, 830 m, 7 Jan. 1934, St. John 14012 (holotype: BISH; isotype: BISH!).

Sprawling shrubs with stems up to 4 m long and much shorter secondary shoots; stems green to light brown, usually pilose at tips, glabrate. Leaves alternate, (0.5)2–18(26) mm apart, petioles (2)5–8(15) mm long, often red; blades elliptic to slightly ovate or obovate, coriaceous, (30)50–65(100) mm long, (8)16–(24)39 mm wide, base rounded, apex abruptly acuminate; upper surface olive green, glabrous, lower slightly lighter, glabrous; areoles prominent, and all higher-order veins distinct. Flowers solitary in leaf axils, 5–6-merous, campanulate; pedicels (10)15–25(46) mm long, green, erect, glabrous; calyx lobes glabrous, green, usually widely ovate, rarely lanceolate, (3)4–5(8) mm long, (1)2.5–3.5(5) mm wide; corolla lobes red, obovate, (9)11–13(14) mm long, (6)7–9(10) mm wide; filaments (5)6–7·5(8) mm long, anthers 1.5–2 mm long; style (5)6–7(8) mm long. Capsules globose, (5)5–9(10) mm long. Seeds dark brown, irregularly shaped, 1.6–2.3 mm long.

NOTE: In the southern Wai‘anae Range this species grows sympatrically with *L. hillebrandii* in gulches NE of Palikea (800–870 m) and the ridge between Nānākuli and Lualualei (720–820 m). Hybrids between these species have not been found. This species typically lacks pigment on the calyx and pedicel, and the calyx is ovate. However, the calyx of a plant grown in the greenhouse from seed collected in Makaha Valley, on Kamaile’unu Ridge, was entirely red and lanceolate.

**SPECIMENS EXAMINED:** O‘ahu: Wai‘anae Range, Pu‘u Hāpapa, Degener 17672 (BISH, GH, MO, NY, US); Mākahā Valley, Kamaile’unu Ridge, N of Pu‘u Kawiwi, Marr 241 (UBC), Marr 453 (os), Marr 455 (IBSC), Marr 456 (COLO), Marr 460 (HAST), Marr 461 (p), Marr 466 (MIC), Marr 469 (RSA), Perlman 5053 (PTBG, BISH), Forbes s.n. (K, MO, US), Degener 4138 (BISH, GH, MO, NY, US), Nagata 1132 (BISH); Makaleha Valley, central ridge, Degener 21278 (GH, MO, NY, US), Obata 279 (BISH); Pu‘u Kaua, Marr 231 (PTBG), Marr 233 (UBC), Marr 778 (F), Marr 787 (MASS), Perlman 5103 (MO, PTBG), Degener 33507 (NY, W), Obata s.n. (BISH), Takeuchi 3719 (BISH), Nagata 1155 (BISH), Montgomery s.n. (BISH); Māku‘a Valley, Degener 17684 (GH, NY, US); Pu‘u Kāhekoa, Degener 17680 (GH); N slope Mt. Ka‘ala, Degener 19439 (GH, NY), Carlquist 2354 (RSA); E ridge Pu‘u Kalena, Hartung s.n. (BISH), Fosberg 13011 (BISH, GH), Kerr s.n. (BISH); Māku‘a Forest Reserve, ʻOhikilolo, Wood 2635 (PTBG), Ko‘i‘ahi, Wood 2494 (PTBG); Kukui‘ula Gulch, Fosberg 13072 (BISH); Kapuna Gulch, Marr 448 (UBC); Pahole gulch, Marr 769 (UBC); Maku‘le‘ia, Forbes 1775 (GH, US); Napapeiau ʻŌlelo Gulch, Marr 443 (UBC); ridge between Nānākuli and Lualualei, Marr 1295 (UBC); location unclear: Mtns., O‘ahu, U.S. Exploring Expedition 1838–1842 (US); Ka‘ala, Wawra 2211 (W).

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