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Reevaluation of *Chamaesyce forbesii* (Euphorbiaceae)

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ABSTRACT

The species of *Chamaesyce* endemic to the Wai'anae Mountains, O'ahu, Hawai'i, has been known for several decades as *Euphorbia forbesii* (or *Chamaesyce forbesii*). However, the type and most of the collections referred to the species by Sherff, the author of *E. forbesii,* represent *C. clusiifolia* from the leeward Ko'olau Mountains. The Wai'anae plant, which is shown to be distinct from *C. clusiifolia,* is here described as *C. herbstii.* This distinctive species is related to *C. rockii,* a cloud zone species of the Ko'olau Mountains, and *C. celastroides,* a polymorphic dryland species, based on common possession of the derived features of short and erect gynophores. These 3 species are the only Hawaiian species with these characters. *Chamaesyce clusiifolia* appears to be more closely related to *C. remyi* and *C. halemanui,* both of mesic to wet habitats on Kaua'i, than to the species with erect gynophores.

INTRODUCTION

The genus *Chamaesyce* S.F. Gray is a cosmopolitan genus of about 250 species, the majority occurring in the New World, where the genus presumably originated; it is often treated as a subgenus of *Euphorbia* L. In Hawai'i, *Chamaesyce* is the largest genus of the Euphorbiaceae, with 15 endemic shrub or tree species, including the one described here, and 7 naturalized herbaceous species (Koutnik & Huft, in press).

The endemic Hawaiian species of *Chamaesyce* exhibit considerable adaptive radiation. Species habitats range from coastal and low elevation, dry shrubland to montane rain forest, diverse mesic forest, and even bogs. The topic of this paper is the 3 large-leaved O'ahu species with open, branched inflorescences: *Chamaesyce herbstii,* sp. nov., found in the Wai'anae Mts, *C. clusiifolia,* found in the leeward Ko'olau Mts, and *C. rockii,* found on windward slopes and crest of the Ko'olau Mts. They have been referred to collectively as the *Chamaesyce clusiifolia* complex, since they have been thought to be closely related.

The Wai'anae Mts species has been variously interpreted in the past. It was first described by Hillebrand in his *Flora of the Hawaiian Islands* (1888) as *Euphorbia clusiaefolia* var. *grandifolia.* He used this name because the Wai'anae plants have much longer, narrowly oblong leaves than those of *C. clusiifolia* of the leeward Ko'olau Mts, O'ahu, which are usually oblong-elliptic and shorter.

In 1936 Sherff described *Euphorbia forbesii* based on 2 nearly sterile collections of *Chamaesyce* from the Wai'anae Mts and 6 collections from the leeward Ko'olau Mts. Because the type specimen of *E. forbesii* is a Ko'olau collection, Koutnik (1982), during his study of the entire genus in Hawai'i, synonymized *E. forbesii* with *C. clusiifolia.* He separated the Wai'anae populations at that time, but treated them as a variety of *Chamaesyce rockii,* and later (Koutnik 1985) made the combination *C. rockii* var. *grandifolia* for them. His reasons for assigning varietal status were that vegetatively the Wai'anae populations and *C. rockii*

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were indistinguishable; according to Koutnik (1985), they differ only in that the capsules of the Wai'anae plants are green or pink and angular, whereas those of *C. rockii* are red and globose. Further, he stated that the capsules of both the Wai'anae populations and *C. rockii* are larger than those of *C. clusiifolia.* His taxonomy appears unaltered in his soon to be published revision of the Hawaiian species (Koutnik 1987).

The Wai'anae populations differ from both *C. rockii* and *C. clusiifolia* in a number of features, especially inflorescence size, portion of the gynophore exserted from the involucre, capsule size, color, and shape, and modally in habit and leaf texture. Moreover, their geographic distributions and habitats are also quite different. The level of differentiation of the Wai'anae populations is similar to or greater than that of other *Chamaesyce* in Hawai'i recognized as species. Therefore, they are best treated as a separate species. Since there is currently no name available at the species level, I am describing them as *C. herbstii.*

TAXONOMY

Key to the Species of the *Chamaesyce clusiifolia* Complex

1. Gynophores recurved, straightening just prior to capsule dehiscence, exserted from involucre 3–9 mm, glabrous; leaves decussate or the pairs spirally arranged, uncommonly some pairs distichous, oblong-elliptic or oblong-oblanceolate; involucral glands dark purple . . . (leeward Ko'olau Mts) ..... ***C. clusiifolia***

   Gynophores erect, exserted from involucre 1–4 mm, puberulent; leaves distichous, narrowly oblong to narrowly oblong-oblanceolate or narrowly oblong-elliptic; involucral glands yellowish green, green, or red 2

2. Inflorescences 7–17 cm long; capsules green or sometimes reddish purple tinged, especially on angles, angled, 5–10 mm long; gynophores exserted ca. 1 mm from involucre; trees 3–8 m tall; leaves thinly coriaceous; petioles (1.5–)2–5 mm long . . . (Wai'anae Mts) . . .. ***C. herbstii***

   Inflorescences 2–6(–7) cm long; capsules brilliant red, globose, 14–25 mm long; gynophores exserted 1–4 mm from involucre; usually compact shrubs or sometimes small trees 0.5–2 m tall, sometimes up to 4 m tall; leaves coriaceous; petioles 0–1(–2) mm long . . . (windward slopes and crest of Ko'olau Mts) ..... ***C. rockii***

Chamaesyce clusiifolia (Hook. & Arnott) Arthur, Torreya 22: 30 (1922), as "*clusiaefolia.*" *Euphorbia clusiaefolia* Hook. & Arnott, Bot. Beechey Voy. 95 (1832). TYPE: HAWAIIAN IS: O'AHU: 1826–1827, *G.T. Lay & A. Collie s.n.* (K, holotype). Fig. 1

Anisophyllum nodosum Klotzsch & Garcke, Abhl. Königl. Akad. Wiss. Berlin 1859(1): 22 (1860). TYPE: HAWAIIAN IS: without further locality, 1817–1820, *C. Gaudichaud-Beaupré s.n.* (B, holotype, presumably destroyed; P, isotype, not located).

Euphorbia forbesii Sherff, Bot. Gaz. (Crawfordsville) 97: 582 (1936). *Chamaesyce forbesii* (Sherff) Croizat & Degener in Degener & Croizat, Fl. Hawaiiensis, fam. 190. *Chamaesyce,* part 4 (1936). TYPE: HAWAIIAN IS: O'AHU: Wahiawa Ditch Trail, *C.N. Forbes 2218.0* (F, holotype; BISH!, F, K, MO, isotypes).

Sprawling to erect shrubs 0.5–3 m tall, glabrous throughout. Leaves decussate, or the pairs spirally arranged, uncommonly some pairs distichous, often red or purple tinged, coriaceous, oblong-elliptic or oblong-oblanceolate, sometimes oblong, (3.5–)5–11(–14) cm long, (1–)2–4.5 cm wide, margins entire, apex obtuse to rounded, sometimes minutely emarginate, base cuneate to rounded, oblique, petioles 2–4 mm long, stipules deltate, 1–2 mm long, erose. Cyathia (1–)3–10(–12) in branched, open cymose inflorescences 2–7(–9) cm long, peduncles 6–23 mm long, sparsely puberulent; involucre broadly campanulate, 2–2.5 mm high, 3–4 mm wide, puberulent, the glands 4–5, dark purple, upper surface glabrous, lower surface puberulent. Capsules green or yellowish green and purple tinged

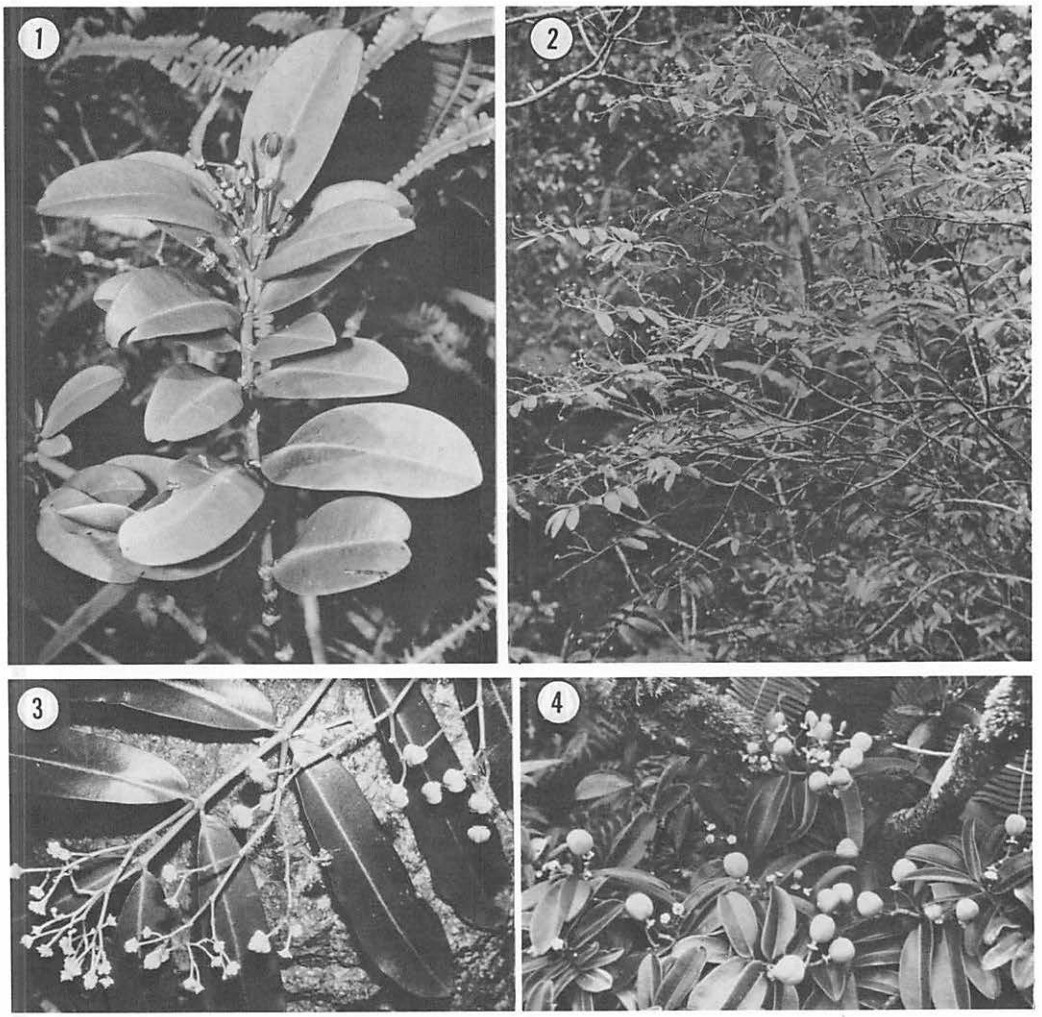
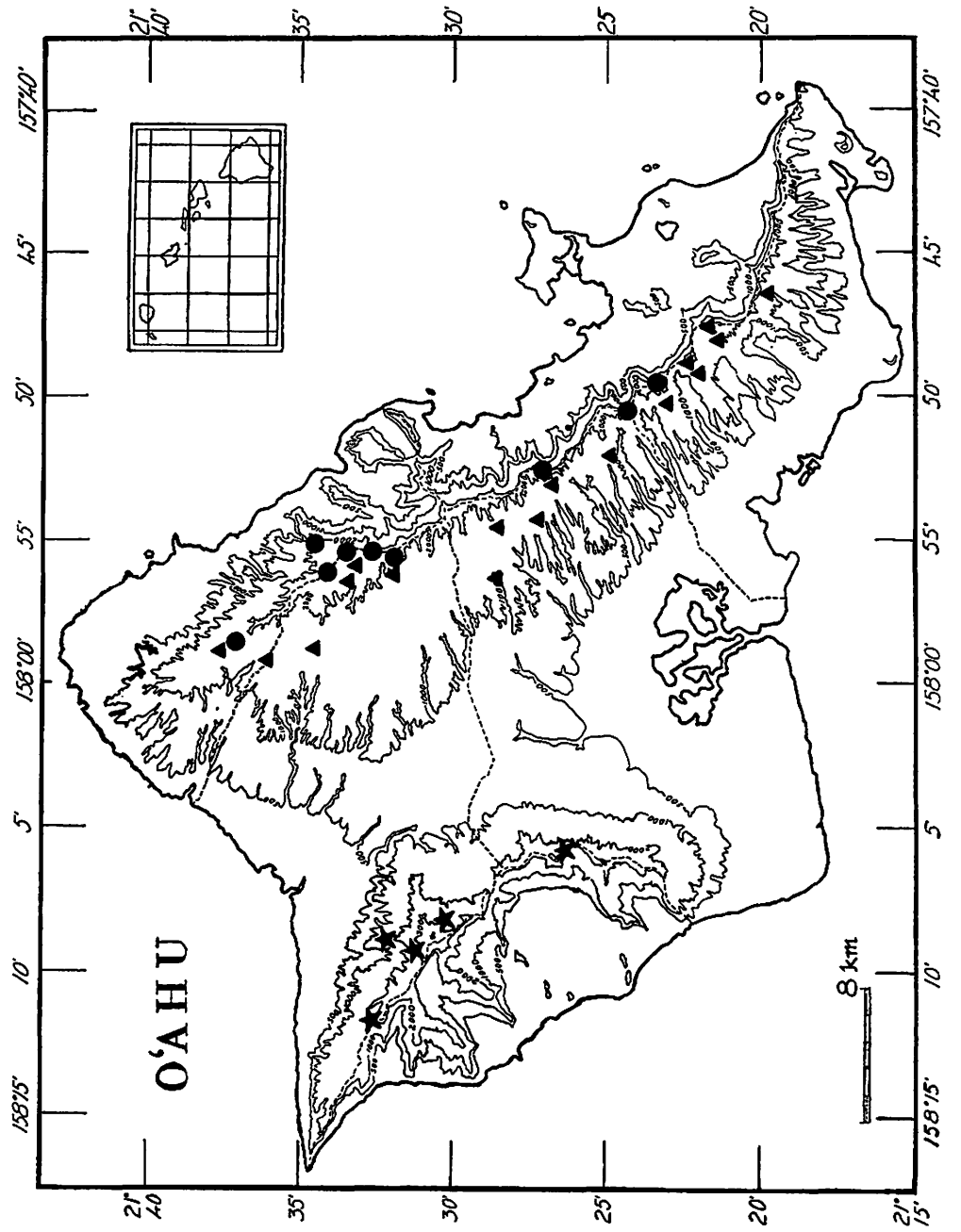


Fig. 1–4. **1,** Photograph of upper flowering branch of *Chamaesyce clusiifolia.* Note that capsule becomes erect immediately before capsule dehiscence. Photograph taken by R. Gustafson on Aiea Ridge in 1986. **2,** Photograph of *Chamaesyce herbstii* showing diffusely branching habit (plant in foreground originating from lower right). Photograph taken by D. Herbst of plant from which holotype was taken. **3,** Photograph of upper flowering branch of *Chamaesyce herbstii.* Photograph taken by R. Gustafson in Pahole Gulch in 1985. **4,** Photograph of *Chamaesyce rockii.* Photograph taken by J. Obata on Castle Trail in 1985.

on the angles, becoming dark purplish green at maturity, angled, 6–9 mm long, up to 7 mm in diameter, glabrous, gynophores recurved, straightening just prior to capsule dehiscence, exserted 3–9 mm from involucre, glabrous. Seeds reddish brown, subglobose, 2.5–3 mm long, testa smooth.

Distribution (Fig. 5). This species occurs in scattered small populations in diverse mesic forest and low elevation rain forest, 300–650 m, on leeward slopes of the Ko'olau Mts, O'ahu.

Representative specimens examined. HAWAIIAN IS: O'AHU: Ko'olau Mts, Lā'ie-Mālaekahana Ridge, *St. John 11543* (BISH); Pūpūkea-Kahuku Trail, *Fosberg & Duker 9181*


O'AHU
8 km
21° 40'
35'
30'
25'
20'
21° 15'
157°40'
45'
50'
55'
158°00'
5'
10'
158°15'

(BISH); Kawailoa, *Bryan, Jr. 802* (BISH); S 'Ōpae'ula Gulch, *Hosaka 340* (BISH), *St. John 10629* (BISH); Wahiawā, *Forbes 1623.0* (BISH), *Degener 8083* (BISH); Kaukonahua, Wahiawā, *Rock 3037* (BISH); Kīpapa Gulch, S ridge, *Yamaguchi 1242* (BISH); Mānana, *Takeuchi Koolau-64* (BISH); Waimano, *Degener et al. 9964* (BISH); 'Aiea, CCC trail, *Degener et al. 11531* (BISH); Kalihi Valley, W ridge, *Degener et al. 19658* (BISH); Lanihuli Ridge, *MacDaniels 354* (BISH); Kōnāhuanui Trail, *Long et al. 3623* (BISH).

Chamaesyce herbstii W.L. Wagner, **sp. nov.** TYPE: HAWAIIAN IS: O'AHU: Wai'anae Mts, Peacock Flats Trail, in shallow gulch, beyond tin military shed, 560 m, 27 Dec 1969, *D.R. Herbst 1470* (BISH-509660!, holotype). Specimen formerly in HAW collection, transferred to BISH in March 1987. Fig. 2, 3

Euphorbia clusiaefolia Hook. & Arnott var. *grandifolia* Hillebr., Fl. Hawaiian Isl. 395 (1888). *Chamaesyce rockii* (C.N. Forbes) Croizat & Degener var. *grandifolia* (Hillebr.) Koutnik, Brittonia 37: 398 (1985). Hillebrand mentions "Makaleha in the Kaala range" [Makaleha, Wai'anae Mts]. The only Hillebrand material ever located of this entity was a sterile branch at B examined by E.E. Sherff (Bot. Gaz. [Crawfordsville] 87: 583 [1936]). This specimen was most likely the present taxon; however, it is now destroyed and Koutnik has designated a neotype (Brittonia 37: 398, 1985). TYPE: HAWAIIAN IS: O'AHU: Kukuiala Val, *E.H. Bryan, Jr. 820* (BISH-50175!, neotype; F, isoneotype).

Chamaesyce forbesii sensu auct., non Sherff (not as to type).

Arbor parva 3–8 m alta est, foliis distichis anguste oblongis vel interdum anguste oblongo-oblanceolatis vel anguste oblongo-ellipticis, (6–)8–19.5 cm longis, 1.6–3.8 cm latis, apice obtuse acuto vel late obtuso, petiolis (1.5–)2–4(–5) mm longis, cyathiis 3–15 in cymis apertis ramosis 7–17 cm longis, pedunculis 8–20 mm longis, puberulis, glandis involucris 5–6 luteo-viridibus plerumque cum appendice albo, capsulis viridibus vel interdum roseo-tinctis, angulosis, 5–9 mm longis usque ad 8 mm diametro, gynophorum viridibus erectis, ca. 1 mm longis, puberulis.

Small trees 3–8 m tall, diffusely branched in upper parts, glabrous. Leaves distichous, thinly coriaceous, narrowly oblong or sometimes narrowly oblong-oblanceolate or narrowly oblong-elliptic, (6–)8–19.5 cm long, 1.8–3.8 cm wide, glabrous or puberulent at base, margins entire, apex bluntly acute to broadly obtuse, usually minutely emarginate, base obliquely rounded or obliquely cuneate, petioles (1.5–)2–5 mm long, sparsely puberulent or glabrous, stipules deltate, 1.5–3 mm long, erose. Cyathia 3–15 in branched, open cymose inflorescences 7–17 cm long, peduncles 8–20 mm long, puberulent; involucre broadly campanulate, 1.5–2.5 mm high, 3.5–5 mm wide, puberulent, the glands 5–6, yellowish green, upper surface glabrous, lower surface puberulent, usually with a white appendage. Capsules green or sometimes reddish purple tinged, especially on angles, angled, 5–10 mm long, up to 8 mm in diameter, scarcely exserted from involucre, gynophores green, erect, exserted ca. 1 mm from involucre, puberulent. Seeds gray, broadly ellipsoid, 2.5–3 mm long, testa wrinkled.

Distribution (Fig. 5). This uncommon species occurs in scattered populations as an understory tree in diverse mesic forest, (360–)500–760 m, northern and central Wai'anae Mts, O'ahu, with one population in the southern Wai'anae Mts in Pu'umaialau Gulch (between Pōhākea Pass and Pu'u Kaua).

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Fig. 5. Map of O'ahu showing distribution of *Chamaesyce herbstii*—stars (★); *C. clusiifolia*—triangles (▲); and *C. rockii*—dots (●).

Specimens examined. HAWAIIAN IS: O'AHU: Wai'anae Mts, Pahole Gulch, *Fosberg 13073* (BISH), *Nagata 1550* (BISH), *Herat & Herat 484* (BISH); mauka of Peacock Flats, *Degener & Degener 27927* (BISH); Peacock Flats Trail, *Herbst 1428* (HAW); Makaleha Val, *Degener 20699* (BISH), *Skottsberg 384* (BISH), *Russ s.n.* (BISH); Kukuiala Val, *Krauss s.n.* (BISH), *Swezey s.n.* (BISH); Mt Ka'ala, *Lamoureux et al. 2433* (BISH), *Herbst 1440* (*coll. Montgomery*) (BISH), *Herat & Herat 532* (BISH, HAW), *Forbes 1770.0* (BISH), *Gillett 1510* (BISH), *Young 19* (HAW); Pu'umaialau Gulch, between Pōhākea Pass and Pu'u Kaua, *Funk et al. 80* (BISH, HAW).

The specific epithet honors Derral R. Herbst, who discovered disjunct foliar veins in this species (Herbst 1971, 1972), and with whom I have collaborated on studies of the Hawaiian flora since 1982.

Chamaesyce rockii (C.N. Forbes) Croizat & Degener in Degener & Croizat, Fl. Hawaiiensis, fam. 190. *Chamaesyce,* part 4 (1936). *Euphorbia rockii* C.N. Forbes, Occas. Pap. Bernice P. Bishop Mus. 4(3): 38 (1909). TYPE: HAWAIIAN IS: O'AHU: Ko'olau Mts, Punalu'u Mts [now Castle Trail], *C.N. Forbes & J.F. Rock s.n.* (BISH-507784!, holotype; BISH!, CU, F, MO, isotypes). The sheet here indicated as the holotype is the one illustrated in the original publication. Fig. 4

Usually compact shrubs or sometimes small trees 0.5–2 m tall, in protected sites up to 4 m tall, glabrous throughout. Leaves distichous, coriaceous, narrowly oblong to narrowly oblong-elliptic, occasionally narrowly elliptic, (6–)8–14(–17) cm long, (1.5–)2–3.5(–4) cm wide, margins entire, apex obtuse to rounded, sometimes minutely emarginate, base obliquely subcordate, petioles 0–1(–2) mm long, stipules deltate, 2–3 mm long, weakly erose. Cyathia 3–10(–12) in branched, open to sometimes condensed cymose inflorescences usually 2–6(–7) cm long, peduncles 3–10(–12) mm long, sparsely to moderately puberulent; involucre broadly campanulate, 1.5–2.2 mm high, 3.5–4.5 mm wide, puberulent, sometimes very sparsely so, the glands 5–6, greenish yellow, green, or red, upper surface glabrous, lower surface puberulent, occasionally with a white appendage. Capsules brilliant red, sometimes pink and red tinged (and then perhaps not fully ripe), globose, 14–25 mm long and nearly so in diameter, glabrous, usually noticeably exserted from involucre, gynophores red, erect, exserted 1–4 mm from involucre, puberulent. Seeds brown to grayish brown, globose or broadly obovoid, 3.5–4 mm long, testa slightly wrinkled.

Distribution (Fig. 4). This species occurs in scattered small populations as a shrub primarily along windswept cloud zone summit ridges and also, less commonly, as a large shrub or small tree in rain forest and along streams in rain forest, 600–830 m, along the crest and upper windward side of the Ko'olau Mts, O'ahu.

Representative specimens examined. HAWAIIAN IS: O'AHU: Ko'olau Mts, Ko'olau crest trail between Lā'ie and Kahuku summits, *Stemmermann & Higashino 1202* (BISH); Pūpūkea-Paumalū Forest Reserve, *Cowan & Pearsall 954* (BISH); Punalu'u, Castle Trail, *Herbst 1117* (BISH), *Sohmer 6052* (BISH); Waikāne-Schofield Trail, *Baker s.n.* (BISH); Waimano, *Degener 10292* (*coll. Potter*) (BISH); head of Ha'ikū Val, *Fosberg & Fosberg 13873* (BISH); Kalihi-Ft. Shafter Trail, *Kerr s.n.* (BISH).

The large, red capsules of *Chamaesyce rockii* are unique in the genus. The capsules scarcely exserted from the top of the cyathia is a characteristic shared only with *C. herbstii* and *C. celastroides.*

DISCUSSION

Chamaesyce herbstii has been misunderstood in the past primarily because few specimens of it were available for herbarium studies, and because those that were available were of

poor quality. More importantly, the taxonomic studies to date have been based only on herbarium specimens and have not incorporated studies of populations in the field, where it quickly becomes obvious how distinctive this species is among the Hawaiian *Chamaesyce.*

The confusion began when Sherff (1936) described *Euphorbia forbesii.* He described this species for plants primarily from the leeward Ko'olau Mts (6 collections of 8 cited) with leaves usually 7–16.5 cm long and 2.5–4.5 cm wide with veins conspicuous on the upper surface. He referred plants with leaves usually 4–9 cm long and 2–3.4 cm wide with obscure venation to *E. clusiaefolia,* which had a distribution similar to that of his *E. forbesii.* The 2 nearly sterile collections of *Chamaesyce herbstii* included by Sherff in *E. forbesii* (*Forbes 1770.0* and the type of *E. clusiaefolia* var. *grandifolia*) had leaves well over 9 cm long. Although the most common leaf size in *C. clusiifolia* is 5–11 cm long and 2–4.5 cm wide, plants with longer leaves, such as those assigned by Sherff to *Euphorbia forbesii,* occur sporadically throughout the range of *C. clusiifolia.* The leaf size coupled with the prominence of the venation clearly is an artificial basis for species delimitation. The latter feature appears to be related to the leaf thickness, which varies with site exposure. All 6 of the Ko'olau collections cited by Sherff as *E. forbesii* fall well within the range of variation of *C. clusiifolia* as delimited here and differ from the 2 Wai'anae collections cited by him as *E. forbesii* (that are here assigned to *C. herbstii*). The artificial nature of Sherff's concept of these entities is further evidenced by the fact that he also cited a Wai'anae collection (*Skottsberg 384,* BISH) under *C. rockii*; this collection actually is a specimen of *C. herbstii.*

Herbst (1972), Robichaux & Pearcy (1980), and other botanists who have collected or studied the Wai'anae species subsequent to Sherff have always applied the name *Euphorbia forbesii* (or *Chamaesyce forbesii*) to it, recognizing it as a very distinctive species. At the same time, they have consistently referred all populations of the leeward Ko'olau Mts to *Euphorbia clusiifolia* (or *Chamaesyce clusiifolia*). It is only since Koutnik's (1982, 1985) reexamination of all of the Hawaiian species that the misapplication of Sherff's original artificial concept, based solely on large leaves vs. small leaves and the prominence of venation, has become apparent.

Koutnik (1982, 1985) correctly placed *Euphorbia forbesii* in synonymy under *Chamaesyce clusiifolia*; however, probably due to a lack of good flowering and fruiting specimens and no personal field observations, he did not recognize the distinctness of the Wai'anae plants. His information led him to assume that the only differences between *C. rockii* and the Wai'anae *Chamaesyce* species were in the angularity and color of the capsules and distribution. In fact, *Chamaesyce herbstii* is among the more distinctive species of Hawaiian *Chamaesyce* and differs from *C. rockii,* to which it is most closely related, in inflorescence and proportion of gynophore exserted from the involucre; capsule color, size, and shape; and modally in petiole length and habit—as outlined in the above key and descriptions.

To include *Chamaesyce herbstii* as a variety of *C. rockii* would make *C. rockii* a more heterogeneous species than most other Hawaiian *Chamaesyce.* Other than *C. celastroides,* which has 8 recognized varieties, the Hawaiian species of *Chamaesyce* are all characterized by a few unique characters or combinations of characters similar to those just discussed. The ecology of *C. rockii* and *C. herbstii* are likewise differentiated. *Chamaesyce rockii* is a shrub with coriaceous leaves that is found on windswept cloud zone summit ridges of the Ko'olau Mts, or sometimes in more protected rain forest. By contrast, *C. herbstii* is always a small tree with thinly coriaceous leaves that is found in gulches in the understory of diverse mesic forest in the drier Wai'anae Mts.

Is the *Chamaesyce clusiifolia* species complex monophyletic? The answer to this question appears to be no; however, the following comments are preliminary and based only on a few characters. More detailed analysis involving several lines of investigation are necessary to understand the phylogeny of this group. The present analysis suggests that the similarity

of *Chamaesyce clusiifolia* to both *C. herbstii* and *C. rockii* is based on similar, but independent, adaptations to wet or mesic habitats. The oblong-elliptic to oblong-oblanceolate leaf shape, decussate or spiral-paired leaf arrangement, open cymose inflorescences, and glabrous, recurved gynophores of *C. clusiifolia* suggest that it shares a common ancestor with Kaua'i species such as *C. halemanui* (Sherff) Croizat & Degener and *C. remyi* (A. Gray ex Boiss.) Croizat & Degener, which have similar but wider decussate leaves, inflorescences similar in structure but highly condensed, glabrous recurved gynophores, and similar capsules. These 2 Kaua'i species also occur in diverse mesic forest or rain forest.

Chamaesyce herbstii and *C. rockii* appear to share a common ancestor with *C. celastroides* rather than with the other mesic to wet habitat species (*C. clusiifolia, C. halemanui,* and *C. remyi*). This hypothesis is based on their possession of the derived features of short, erect, and puberulent gynophores. Among the Hawaiian species, only *C. herbstii, C. rockii,* and the less specialized *C. celastroides* possess erect gynophores. The Hawaiian *Chamaesyce* species appear to have derived from ancestors similar to the *C. atoto* (G. Forster) Croizat & Degener species complex (Degener & Croizat 1936; Koutnik 1982) of tropical Australia, Malesia, and many Pacific islands. Members of this complex have recurved, glabrous gynophores and inhabit coastal and low elevation dry sites. The less specialized Hawaiian species such as *C. degeneri* (Sherff) Croizat & Degener and *C. celastroides* occur in similar habitats, but only *C. degeneri* has the plesiomorphic feature of recurved gynophores. Thus, it appears that after colonization of Hawai'i, evolution led to one lineage that presently includes the polymorphic *C. celastroides, C. herbstii,* and *C. rockii.* The remaining species, all with recurved gynophores, belong to several lines of diversification, one of which made the adaptive shift to mesic and wet habitats and presently includes *C. remyi, C. halemanui,* and *C. clusiifolia.* In fact, this lineage may represent an early off-shoot from the common ancestor, since these species, like the members of the *C. atoto* complex, are glabrous. Most of the other Hawaiian species have at least the gynophores pubescent, a character that appears to be a derived feature in the Hawaiian species.

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