A New, Dioecious Species of *Hedyotis* (Rubiaceae) from Kaua'i, Hawaiian Islands, and the Taxonomy of Kaua'i *Hedyotis schlechtendahliana* Resolved

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ABSTRACT. A new, cliff-dwelling species, *Hedyotis flynnii,* is described from the Hawaiian island of Kaua'i. It is distinguished by its conspicuously reticulate leaf venation, reduced leaves, and greenish yellow or sometimes white corollas. Based on morphological observations, it appears to be the first species in the genus known to have a dioecious breeding system. *Hedyotis flynnii* also expresses a strong corolla size dimorphism, with staminate flowers much larger than the pistillate. The taxonomy of the polymorphic species *Hedyotis schlechtendahliana* also is reconsidered recognizing the northwestern Kaua'i populations as *Hedyotis schlechtendahliana* subsp. *waimeae,* characterized by stiffly chartaceous to coriaceous reticulate leaves, open inflorescences, and subulate bracts and calyx lobes.

A distinctive, cliff-dwelling species of *Hedyotis* was first recognized as possibly a new species in Limahuli Valley by Tim Flynn and Moses Bergau in 1985. Additional collections from valleys along the Na Pali coast of Kaua'i, especially from Kalalau, established that it represented a new species. We now have ample material to ascertain that these populations represent a new species in the complex *Hedyotis* sect. *Wiegmannia* (Meyen) Fosberg. We also provide new analysis of a vexing problem in the complicated variation pattern in the related *Hedyotis schlechtendahliana* subsp. *schlechtendahliana,* treated as a very polymorphic variety in the most recent treatment by Wagner et al. (1990) and as four species by Fosberg (1943). We were able to clarify the taxonomy of this complex by study of numerous additional collections made during the past 10 years on Kaua'i, especially the northern half of the island. Our conclusion is that two morphologically distinctive subspecies with only partially overlapping ranges can be recognized.

HEDYOTIS FLYNNII

Hedyotis flynnii W. L. Wagner & Lorence, sp. nov. TYPE: Hawaiian Islands (U.S.A.). Kaua'i: Na Pali Coast, Hono o Na Pali Natural Area Reserve, Waiahuakua Valley, back of valley by main waterfall, on cliffs W of main falls, 1500 ft. (457 m), 24 Jan. 1993, *Perlman & Flynn 13270* (holotype, PTBG; isotypes, BISH, US). Figure 1.

Species *Hedyoti parvulae* affinis, sed foliis nervis tertiarius valde reticulatis, corolla cum tubo viridi vel viridi-flavo, corolla lobis albis vel viridi-flavis, corolla tubo 2- vel 3.1-plo lobis differt.

Compact shrubs (2–)3–7.5(–10) dm tall, many-branched; stems glabrous, young stems 4-costate, older stems 2-costate with bark weakly exfoliating. Leaves petiolate, usually closely spaced and overlapping, gradually reduced distally along the stem, coriaceous, lanceolate to ovate, rarely linear-lanceolate, 2–6 cm long, 0.5–1.5(–2.2) cm wide, the base cuneate, rounded or rarely truncate (Limahuli and Hanakapiai Valley collections), the apex long acuminate to long attenuate, often falcate, the lateral veins 2–4 on each side, strongly ascending, prominent on both surfaces, the tertiary venation prominently reticulate on both surfaces, the margins flat to occasionally weakly revolute, the petioles 0.2–0.8 cm long, glabrous, the petioles, stipules, and venation often with reddish purple tinge; stipules deltate, glabrous, aristate, the apex with a stiff awn 1.5–5 mm long. Flowers in dense, 7–15-flowered, corymbiform inflorescences subtended by a pair of ovate bracts, inflorescence branches and pedicels subtended by smaller bracts; flowers dimorphic and the plants apparently dioecious, the calyx lobes oblong or ovate to narrowly triangular-

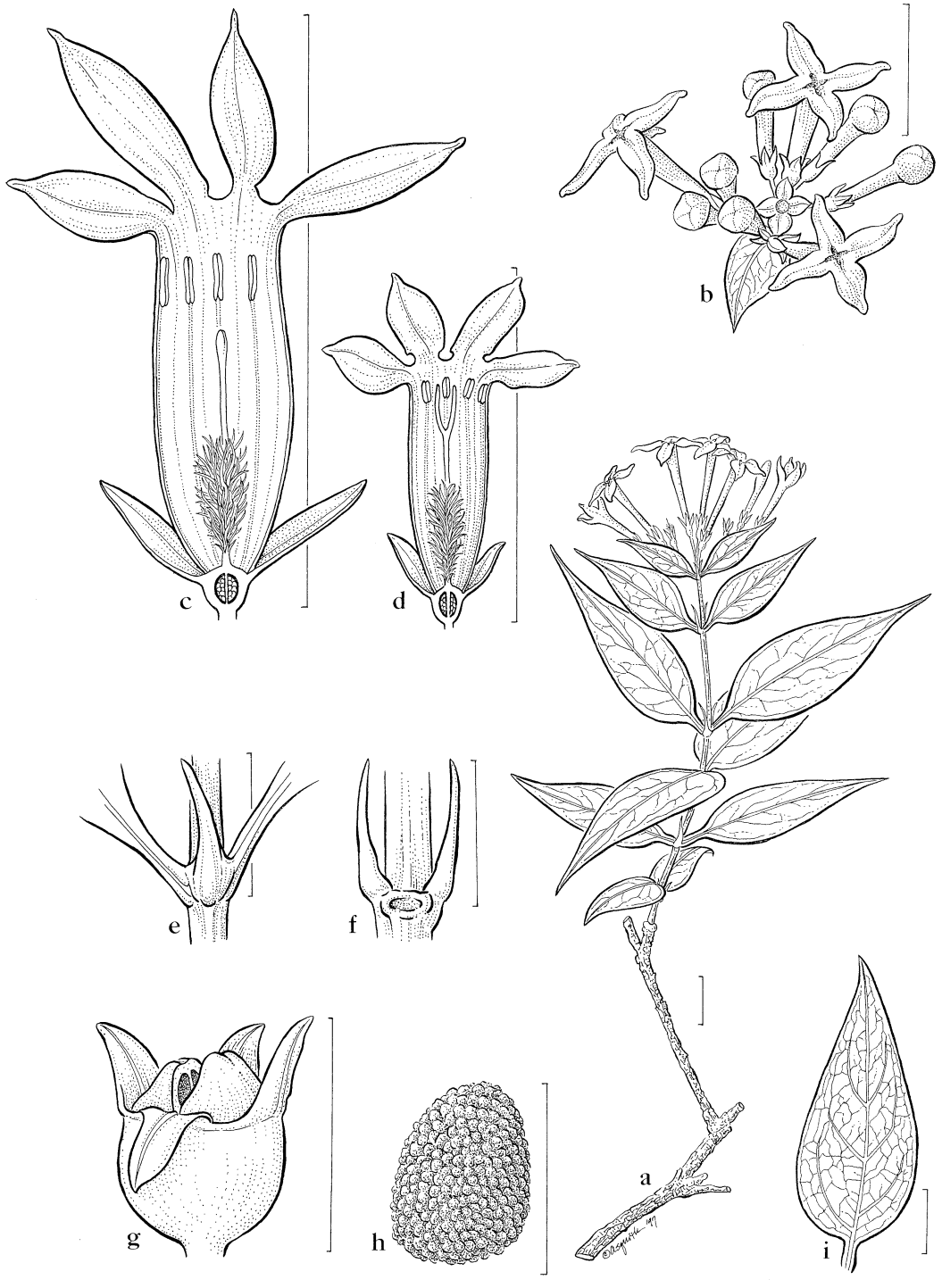

Figure 1. *Hedyotis flynnii* W. L. Wagner & Lorence. —a. Staminate flowering stem. —b. Inflorescence, top view. —c. Staminate flower, longitudinal dissection. —d. Pistillate flower, longitudinal dissection. —e. Stipule. —f. Stipule with petiole removed. —g. Dehisced capsule. —h. Seed. —i. Leaf, showing detail of venation. (a, e, f, i drawn from *Perlman & Flynn 13270,* the holotype; b from photo of *Lorence 6718*; c, d from *Wood 627*; and g, h from *Wood 1240.*) Bar scale = 10 mm in a, i; 24 mm in c; 13 mm in d; 6 mm in e, f; 8 mm in g; and 0.75 mm in h.

subulate, 2–6 × 0.5–2 mm, subequal, rigid, venose; corolla salverform, the valvate lobes conspicuously inflexed in bud, the apex depressed in bud, the tube greenish white or rarely with pink tinge, the lobes pure white or greenish white at anthesis; *staminate flowers* with the corolla tube 11–14 mm long, 2–2.5 mm diam., the lobes elliptic to oblong-lanceolate, 7.5–8 × 1.5–2 mm, the stamens inserted 2–4 mm below apex of tube, the anthers 1.8–2.8 mm long, the filaments 0.2–0.5 mm long, the style 5–8 mm long, 0.5–0.7 times the length of the tube, woolly-villous in lower ⅓–½, the stigma lobes poorly developed, coherent, ovules present at anthesis, but apparently never developing; *pistillate flowers* with the corolla tube 7–8 mm long, 1.2–1.5 mm diam., the lobes 2.5–4 × 0.8–1.5 mm, the stamens inserted 1–3 mm below apex of tube, the anthers 0.8–1.5 mm long, pollen not developing, the filaments 0.3–0.5 mm long, the style 6–8 mm long, 0.8–1.1 times the length of the tube, woolly-villous in lower ⅓–½, the stigma lobes ovate-elliptic, 1–1.5 mm long, free. Capsules subglobose, 5–6 mm long, 5–6.5 mm diam., dehiscing loculicidally across the disk, later weakly separating septicidally, the calyx lobes accrescent, erect, the disk raised, 1.5–2 mm long, the ovary ⅔ (rarely to ½) inferior; seeds irregularly ellipsoid-angulate or subglobose-angulate, 0.6–0.9 mm long, the testa dark brown or black, papillose.

Distribution, habitat, and ecology. Known only from northern and northwestern Kaua'i from the following valleys along the Na Pali coast: from Limahuli and Hanakapiai Valleys in the east (350–426 m elevation), to Kalalau Valley where the majority of collections have been made, and to Honopu, Pohakuao, Awa'awapuhi, Nualolo, and Kawaiula Valleys in the west (450–1100 m elevation).

Hedyotis flynnii is usually restricted to north- and northeast-facing cliffs and steep, narrow ridge crests and outcrops, less commonly occurring on steep rocky slopes and the upper portions of basalt cliffs. It generally occurs in windswept areas in small populations of 30 to 50 scattered plants or more in relictual lowland and montane diverse mesic forest and shrubland. Associated tree species include *Metrosideros polymorpha* Gaudichaud-Beaupré, *Acacia koa* A. Gray, *Diospyros sandwicensis* (A. DC.) Fosberg, *Psydrax odorata* (J. R. Forster) A. C. Smith & S. Darwin, *Myrsine linearifolia* Hosaka, *Eurya sandwicensis* A. Gray, *Exocarpus luteolus* C. N. Forbes, and *Alphitonia ponderosa* Hillebrand. Associated shrubby taxa include *Chamaesyce eleanoriae* Lorence & W. L. Wagner, *Alyxia oliviformis* Gaudichaud-Beaupré, *Dodonaea viscosa* Jacquin, *Nototrichium divaricatum* Lorence, *Coprosma* sp., *Dubautia* sp., *Vaccinium* sp., *Lobelia niihauensis* H. St. John, *Lysimachia* spp., *Sida* sp., *Hibiscus kokio* Hillebrand ex Wawra subsp. *saintjohnianus* (M. J. Roe) D. M. Bates, *Styphelia tameiameiae* (Chamisso & Schlechtendal) F. v. Mueller. Associated herbaceous taxa include *Bidens sandvicensis* Lessing subsp. *sandvicensis*, *Eragrostis* spp., *Poa mannii* W. Munro ex Hillebrand, and *Stenogyne campanulata* S. Weller & A. Sakai, (K. R. Wood, pers. comm., 1997).

Conservation status and threats. The major threats to *Hedyotis flynnii* are browsing and the resulting erosion, habitat degradation, and landslides provoked by the large feral goat populations in Kalalau Valley and adjacent areas on the Na Pali coast. Feral pigs are also a threat in some areas. In addition, invasion by numerous alien plant species, primarily *Erigeron karvinskianus* DC., *Kalanchöe pinnata* (Lamarck) Persoon, *Psidium guajava* L., *Schinus terebinthifolius* Raddi, *Lonicera japonica* Thunberg, *Passiflora mollissima* (Kunth) L. H. Bailey, *Rubus argutus* Link, and *Lantana camara* L., also threatens this species.

Morphology. Collections from lower elevations, i.e., from Limahuli and Hanakapiai Valleys, tend to have truncate to broadly rounded leaf bases, whereas those from higher elevations in localities to the west are characterized by having obtuse to cuneate bases.

Paratypes. HAWAIIAN ISLANDS (U.S.A.). **Kaua'i:** Hanalei District: Limahuli Valley, on exposed rock face on ridge extending into valley on W side, N exposure, 1200 ft. (366 m), 16 Dec. 1985, *Flynn & Bergau 1442* (PTBG); Limahuli Valley, E side of valley near Pohaku Kane, NE-facing cliff, 1400 ft. (427 m), 17 Oct. 1996, *Perlman & Wichman 15631* (BISH, PTBG, US); Hanakapiai Valley, W side of valley, cliffs below Pohakea, 1150 ft. (350 m), 27 June 1996, *Perlman 15448* (BISH, PTBG, US, WU); Na Pali Kona Forest Reserve, Kalalau valley, below Pu'u O Kila Lookout, 3400 ft. (1067 m), 23 Sep. 1989, *Montgomery s.n.* (BISH); Kalalau rim, Kalahu, cliff, 1 Feb. 1950, *Degener & Hatheway 24353* (BISH, US); Kalalau Valley, W side of valley N of Pu'u O Kila lookout, 3200 ft. (975 m), 5 Oct. 1994, *Perlman & Wood 14451* (PTBG, WU); Kalalau, drainage W of Pu'u O Kila, *Exocarpus* ridge, 3000 ft., 22 May 1991, *Wood & Sloan 876* (PTBG); Kalalau rim, NE below Pu'u O Kila and down to peach tree ridge, 1100–1200 m, 9 Oct. 1991, *Wood et al. 800* (PTBG), *Wood et al. 810* (PTBG, US); Kalalau rim, N, below Pu'u O Kila, 1030 m, 5 Aug. 1991, *Wood et al. 1090* (PTBG); Kalalau Valley, in back of valley, 750–800 m, 11 June 1992, *Wood et al. 1967* (PTBG); Kalalau rim, N of Kahuama'a Flat, 990–1020 m, 3 Mar. 1991, *Wood et al. 627* (BISH, PTBG), 4 Dec. 1991, 800 m, *Wood & Query 1018* (PTBG, US); S rim of Kalalau Valley, N of Kahuama'a Flat and Hwy. 550, 900 m, 6 Mar. 1991, *Lorence et al. 6718* (GH, PTBG, US), *Wood 638* (PTBG); Kalalau rim, Kalahu side below and W of first Kalalau look-

out, 950 m, 3 Sep. 1991, *Wood 1185* (PTBG), 790 m, 20 Sep. 1991, *Wood 1400* (PTBG), 700–800 m, 22 Nov. 1991, *Wood 1418* (PTBG, US), 550–670 m, 4 Dec. 1991, *Wood 1460* (PTBG, US), 900–1000 m, 20 Aug. 1991, *Wood 1158* (PTBG), 2150–2350 ft., 14 Oct. 1994, *Wood 3641* (PTBG), 1900–2100 ft. (579–640 m), 27 Feb. 1994, *Wood & Perlman 3021* (PTBG); Kalalau Valley, slopes of Kalahu, 300 m E of Navy plane crash, 2500 ft. (762 m), 2 Aug. 1994, *Wood & Perlman 3387* (GH, K, MO, PTBG); Kalalau rim, N–S-running ridge below and E of first Kalalau lookout, 960–1100 m, 18 Sep. 1991, *Wood 1240* (BISH, PTBG, US[2]), *Wood 1243* (PTBG); Honopu [Valley] rim, N-facing cliffs, 500 m W of easternmost rim, 750–850 m, 5 Sep. 1991, *Wood et al. 1204* (US); Honopu [Valley] rim, 3000 ft. (914 m), 6 Nov. 1993, *Wood 2824* (PTBG), 2800 ft. (853 m), *Wood 2829* (BISH, PTBG, US); Pohakuao, hanging valley between Kalalau and Hanakoa, 400–600 m, 1 Apr. 1992, *Wood 1762* (PTBG), 600 m, 2 Apr. 1992, Pohakuao, cliffs below Pu'u Ki and Manoa Ridge, 2020 ft. (613 m), 2 Apr. 1992, *Perlman et al. 12692* (PTBG). Waimea District: Awa'awapuhi Valley, N-facing slopes above stream, 0.5 mi. in along trail, 3300–3500 ft. (1006–1067 m), 18 May 1994, *Wood et al. 3197* (K, PTBG, US), 3480 ft. 18 May 1994, *Perlman & Wood 14201* (PTBG, US). Nualolo Valley, 2800–3100 ft., 18 Dec. 1994, *Wood 3857* (CHR, PTBG). Kawaiula Valley, 2700–3300 ft., 5 Feb. 1994, *Wood & Lau 3695* (PTBG).

Affinities. *Hedyotis flynnii* keys out to *H. parvula* (A. Gray) Fosberg following the key in Wagner et al. (1990) and may be most closely allied to it, although the similarities may represent convergent adaptations to the cliff habitat. A more biogeographically parsimonious hypothesis is that both *H. flynnii* and *H. parvula* were derived from the polymorphic and widespread *H. schlechtendahliana* Steudel. This hypothesis is supported in that features of *H. flynnii* and *H. parvula* that are most similar are ones expected in an exposed cliff habitat, such as reduced leaf size and internode length and coriaceous blade texture. However, *H. flynnii* and *H. parvula* are quite distinct in floral morphology. Flowers of *H. parvula* are pure white or white tinted with pink or purple-pink or violet, whereas corollas of *H. flynnii* have a yellowish green or green tube and white to yellowish or greenish yellow lobes. The corolla tube: lobe length ratio in both staminate and pistillate flowers is somewhat greater in *H. flynnii*, 2:1 to 4.5:1 (rarely 1.6:1), with no difference between the sexes, compared to 1.6:1 to 1.8:1 in *H. parvula*.

Breeding system. Our study of the available collections suggests that *Hedyotis flynnii* has a dioecious breeding system. This is based on the morphology described above and microscopic examination of anthers and pollen from six collections. Staminate (larger) flowers have large anthers, which produce conspicuous and abundant, well-developed pollen grains and have poorly developed, coherent, apparently non-functioning stigma lobes. The ovules, although present at the flowering stage, do not develop. All but two of these collections had no developed capsules, providing further confirmation that they had staminate rather than perfect flowers. However, two otherwise normal staminate collections each had a single, abnormally small capsule (*Wood 1240, Wood 1418*). Seed production was not evident, as one capsule had dehisced and the other contained an insect pupa. Pistillate flowers, on the other hand, always display tiny, aborted stamens with no evidence of pollen development, whereas the stigma lobes were well developed and divergent. There is a similar pattern of style morphology in another Hawaiian species, *H. tryblium* Herbst & W. L. Wagner (*H.* sect. *Phyllozygia* W. L. Wagner & Herbst), and this was interpreted by Wagner et al. (1989, 1990) in the same fashion as for *H. flynnii*, but in that case there was not supporting information on ovules and fruit development. In *H. tryblium* functional (short-styled flowers) and non-functional (long-styled flowers) anthers were found. However, the distribution of the different types of flowers was different in *H. tryblium* with at least some of the two types occurring on the same plant, suggesting a gynomonoecious or monoecious breeding system. Another difference was that the larger corollas were found in the apparent pistillate rather than the staminate (or perfect) flowers.

Another intriguing aspect of *Hedyotis flynnii* is the strong corolla size dimorphism, where the staminate flower is much larger than the pistillate. This agrees with the traditional view regarding sexual dimorphism in flower size where corollas on staminate flowers are always or nearly always larger those those on pistillate flowers (Delph, 1996). Delph (1996) has shown, however, that the traditional view stems from numerous temperate examples, but when tropical species are considered female flowers are about as likely to be larger than as smaller than males. In Rubiaceae, many genera and tribes have floral dimorphism, ranging from heterostyly (e.g., *Psychotria, Rondeletia*), to dioecy with non-functional stamens or pistils (e.g., *Randia*), to flowers that are highly differentiated morphologically (e.g., *Coprosma*). The syles of both sexes in *H. flynnii* are similar in length, and it is the corolla dimorphism that gives the appearence of heterostyly. The breeding system of this and related species of Hawaiian *Hedyotis* should provide valuable information on the evolution of breeding systems of Rubiaceae.

Hybridization. Two collections representing probable hybrids between *H. flynnii* and *H. schlechtendahliana* subsp. *schlechtendahliana* are

known from a population in Pohakuao Valley, where these two taxa grow sympatrically.

Specimens examined. HAWAIIAN ISLANDS (U.S.A.). Kaua'i: Hanalei District, Pohakuao, hanging valley between Kalalau and Hanakoa, 600 m, collected below Pu'u Ki, NW aspect, 2 Apr. 1992, *Wood et al. 1762* (PTBG) [this specimen is closer to *H. flynnii*], *Wood et al. 1766* (PTBG, US) [this collection was growing sympatrically with *H. flynnii*, but is closer to *H. schlechtendahliana*].

Etymology. We take particular pleasure in naming this attractive new species in honor of Timothy W. Flynn, Curator of the National Tropical Botanical Garden herbarium (PTBG), who has made extensive collections over nearly 20 years, especially of Kaua'i plants, contributing much new knowledge of the Hawaiian flora, and who has provided both of us with many new and significant insights.

Reevaluation of *Hedyotis schlechtendahliana* on Kaua'i

In the most recent treatment of Hawaiian *Hedyotis* by Wagner et al. (1990) both *Hedyotis glaucifolia* (A. Gray) Fosberg of Kaua'i and the O'ahu plants treated as *H. angusta* Fosberg were included in the polymorphic *H. schlechtendahliana.* Wagner et al. further stated that although these two subsumed taxa represented distinctive forms their most striking features, and those used to separate these taxa, appeared to vary independently and thus formed a continuum of variation rather than defining discrete taxa. Fosberg (1943), in his revision of the genus in the Pacific region, stated in several places that the differences among these and a number of other Hawaiian *Hedyotis* were "rather intangible" and that often the most distinctive features intergrade the most. Numerous new collections made on the island of Kaua'i since the Wagner et al. (1990) treatment have allowed us to reevaluate the taxonomy of this complex species. Our studies revealed that although there is considerable intergradation on Kaua'i between the widespread morphological form of *H. schlechtendahliana,* which occurs on Kaua'i, O'ahu, Moloka'i, Lana'i, and Maui, and the plants treated by Fosberg as *H. glaucifolia,* there are several correlated characters that delimit a taxon occurring in northern Kaua'i, which geographically overlaps only slightly with the widespread taxon, *H. schlechtendahliana* subsp. *schlechtendahliana.* Because of the intergradation we here adopt a taxonomy recognizing this entity as a subspecies of *H. schlechtendahliana.* The three recognized subspecies of *H. schlechtendahliana* can be separated by the following key. We have included nomenclature of *H. schlechtendahliana* subsp. *remyi* because a lectotypification was necessary to stabilize the name as it has been used since Fosberg's revision, and to call attention to current distribution information on this endangered taxon. We have not given full nomenclature for *H. schlechtendahliana,* but only those names with types from Kaua'i.

Key to the Subspecies of *Hedyotis schlechtendahliana*

1a. Leaves cordate, 3–6 cm long, the margin conspicuously revolute; inflorescences narrow, 2–3 nodes long; corollas cream-colored; Lana'i . . . . . subsp. *remyi*

1b. Leaves variously shaped, the base cuneate to truncate, occasionally cordate, usually over 5 cm long, the margins flat or very slightly revolute; inflorescences broad, usually more than 3 nodes long; corollas pale green to greenish yellow or greenish white; Kaua'i, O'ahu, Moloka'i, Maui.

2a. Leaves membranaceous to coriaceous, the lateral veins conspicuous, the tertiary venation inconspicuously reticulate; inflorescence axes elongate, the upper ones short; flowers produced in congested cymes, these sometimes elongating monochasially; bracts and calyx lobes usually foliaceous, the bracts usually partly obscuring the flowers; corolla pale green to greenish yellow; northern to eastern Kaua'i . . . . . subsp. *schlechtendahliana*

2b. Leaves stiffly chartaceous to coriaceous, lateral and tertiary venation equally prominent, the tertiary venation conspicuously reticulate; inflorescence axes spreading and elongate throughout, usually not elongating monochasially; bracts and calyx lobes not foliaceous, usually slender, subulate, not obscuring the flowers; corolla pale green to greenish yellow or greenish white; northwestern Kaua'i . . . . . subsp. *waimeae*

Hedyotis schlechtendahliana subsp. **remyi** (Hillebrand) Fosberg, Bernice P. Bishop Mus. Bull. 174: 40. 1943. *Kadua remyi* Hillebrand, Fl. Hawaiian Isl. 162. 1888. *Hedyotis schlechtendahliana* Steudel var. *remyi* (Hillebrand) Fosberg, Bernice P. Bishop Mus. Bull. 174: 40. 1943. *Hedyotis remyi* (Hillebrand) Fosberg, Brittonia 8: 165. 1956. TYPE: Hawaiian Islands.. Lana'i: on highest ridge, 1870, *W. Hillebrand s.n.* (lectotype, here designated, US-809302; isolectotypes, B, E, K, none seen). Fosberg mentioned this collection as the "type" in 1943, and we assume he selected the B sheet (now destroyed) effectively as the lectotype; he annotated the US collection here selected as lectotype as "isotype?". Because the B sheet is no longer extant we here select the US sheet of the Lana'i collection as the

replacement lectotype. The additional syntype, "Hamakua, East Maui" collected by J. Lydgate (photo of B sheet at BISH and BISH [with label by C. N. Forbes giving collectors as Hillebrand and Lydgate]), which is a collection of *H. schlechtendahliana* subsp. *schlechtendahliana*, was clearly segregated by Fosberg from his circumscription of *Hedyotis schlechtendahliana* subsp. *remyi*.

Distribution and habitat. *Hedyotis schlechtendahliana* subsp. *remyi* was historically known from several locations on the northwestern portion of Lanaihale, Lana'i, but currently because of habitat loss and degradation it is known from only six individuals from Kaiholeha-Hulupoe Ridge (Bruegmann, 1997) and therefore proposed for United States Endangered status. It occurs in mesic windswept shrubland habitat.

Hedyotis schlechtendahliana subsp. **waimeae** (Wawra) W. L. Wagner & Lorence, comb. et stat. nov. Basionym: *Kadua waimeae* Wawra, Flora 57: 264. 1874. *Hedyotis glaucifolia* (A. Gray) Fosberg var. *waimeae* (Wawra) Fosberg, Bernice P. Bishop Mus. Bull. 174: 43. 1943. TYPE: Hawaiian Islands. Kaua'i: Halemanu woods, 1869–1870, *H. Wawra 2087* (holotype, W not seen).

Kadua glaucifolia A. Gray, Proc. Amer. Acad. Arts 4: 318. 1859. *Hedyotis glaucifolia* (A. Gray) Fosberg, Bernice P. Bishop Mus. Bull. 174: 41. 1943. TYPE: Hawaiian Islands. Kaua'i: 1840, *U. S. Expl. Exped. s.n.* (holotype, US-42370; isotype, GH not seen).

Hedyotis glaucifolia (A. Gray) Fosberg f. *nealae* Fosberg, Bernice P. Bishop Mus. Bull. 174: 43. 1943. TYPE: Hawaiian Islands. Kaua'i: Halemanu, 3600 ft., 30 Apr. 1929, *M. C. Neal s.n.* (holotype, BISH-511673).

Hedyotis glaucifolia (A. Gray) Fosberg var. *subimpressa* Fosberg, Brittonia 8: 166. 1956. TYPE: Hawaiian Islands. Kaua'i: along road to Mohihi River, just NW of Kawaikoi Stream, steep grass and *Dicranopteris* slope, 13 Jan. 1952, *O. Degener & A. Greenwell 21746* (holotype, US-2062361; isotype, BISH).

Distribution and habitat. *Hedyotis schlechtendahliana* subsp. *waimeae* is restricted to central western Kaua'i west of the Alaka'i Plateau from the Koke'e area, Nualolo and Awa'awapuhi Valleys in the north to Kauhau Ridge, Mahanaloa and Makaha Valleys, and the more distant Hanapepe Valley in the south. It occurs in diverse mesic forest often with *Acacia koa, Metrosideros polymorpha,* and *Alphitonia ponderosa* dominant at elevations from 750 to 1220 m. This subspecies is known to overlap and intergrade with subspecies *schlechtendahliana* in Waimea and Koloa districts in the area bounded by and including the Nualolo Valley, areas in the vicinity of Mohihi and Kumuela, upper Koai'e Canyon, and Hanapepe Valley.

Representative specimens. HAWAIIAN ISLANDS (U.S.A.). **Kaua'i:** Koloa District: [Hanapepe Valley], opposite Gay and Robinson's house, *A. A. Heller 2615* (NY); along the Hanapepe River, near the falls, 24–26 June 1895, *Heller 2442* (BISH, US); Waimea District: upper Nualolo Stream, N branch, 3700–3800 ft., 23 Nov. 1995, *Wood & Davis 4793* (PTBG); Kuia Natural Area Reserve, Nuololo, 3650–3920 ft., 17 Aug. 1993, *Wood & Perlman 2707* (PTBG); Kuia Natural Area Reserve, Kaunuohua Ridge W of and below Hwy. 550, 3560 ft., 15 Feb. 1989, *Flynn & Kawakami 3271* (BISH, PTBG, US); upper Kuia Valley, 3000–3200 ft., 6 Nov. 1994, *Wood & Lau 3702* (PTBG); Kuia Natural Area Reserve, Mahanaloa Valley, valley N of Milolii Ridge, above confluence with Paaiki Valley, 868–750 m, 22 Dec. 1994, *Lorence & Wood 7618* (BISH, PTBG, US); upper NE gulch of Makaha Valley, 2800–3000 ft., 8 Nov. 1994, *Wood 3742* (PTBG); Koke'e [State Park], Dec. 1960, *Degener 27226 (Coll. H. Hansen)* (BISH); Koke'e [State Park], E of Kumuweia Ridge, 3500 ft., *Degener 20491* (BISH, US); Koke'e State Park, in Awa'awapuhi trail just W of Hwy. 550, 1220 m, 2 Jan. 1989, *Lorence et al. 6321* (PTBG, US); Koke'e [State Park], 4000 ft., 22 Mar. 1972, *Herbst 2375* (BISH, PTBG); Kalalau trail, above Koke'e, 1150 m, Dec. 1935, *Fosberg 12718* (BISH, US); Makaha Valley, 0.9 mi. down Makaha Ridge road from Hwy. 550, 3180 ft., 31 July 1985, *Flynn 1158* (BISH, PTBG); Koke'e State Park, unnamed trail from Koke'e–Halemanu Trail to Highway 550, 1080–1100 m, 17 Feb. 1988, *Lorence et al. 5809* (PTBG); Koke'e State Park, along Elekeninui Strm., near crossing with Mohihi jeep tr., 1100 m, 25 May 1976, *Fay 594* (PTBG); Koke'e, Mohihi road 0.2 mi. W of Kumuwela Road, 3660 ft., 4 Mar. 1986, *Flynn 1584* (BISH, PTBG); Waiakoali, Aug. 1930, *Neal s.n.* (BISH); Kopakaka Ridge, 2900 ft., 23 Jan 1986, *Flynn & Lopez 1466* (BISH, PTBG); Waimea drainage basin, W side, Aug. 1917, *Forbes 802.K* (BISH, US), 3 July to 18 Aug., *Forbes 805.K* (BISH); Kaholuamamu, behind Waimea, Sep. 1909, *Forbes 385.K* (BISH), *Rock 5787 (145)* (BISH), 3–10 Mar. 1909, *Rock 1942(143)* (BISH); Halemanu, 14–26 Feb. 1909, *Rock 1887* (BISH), *Rock 1886 (143)* (US); Kauhau Ridge, near gauging station and ditch, 3220 ft., Wai'alae Valley, ridge between Wai'alae and Nawaimaka Valleys, above Wai'alae Falls, 950–1050 m, 16 Apr. 1991, *Wood et al. 852* (MO, PTBG, US); Koai'e Canyon, upper reaches of canyon, 2950–3080 ft., 31 Aug. 1994, *Wood & Perlman 3464* (BISH, US); Kauhau Ridge, near gauging station and ditch, 3100 ft., 12 July 1993, *Wood 2668* (US), 3220 ft. 3 Nov. 1994, *Wood 3478* (US), 3 Sep. 1994, *Wood 3482* (BISH, MO, NY, PTBG, US, WU), *Wood 3486* (US).

Hedyotis schlechtendahliana subsp. **schlechtendahliana** (on Kaua'i)

Kadua cordata Chamisso & Schlechtendal var. *pruinosa* Wawra, Flora 57: 262. 1874. *Kadua cordata* Chamisso & Schlechtendal var. *laxa* Hillebrand, Fl. Hawaiian Isl. 161. 1888, nom. superfl. TYPE: Hawaiian Islands. Kaua'i: Wai'ale'ale Plateau, 1869–1870, *H. Wawra 2202* (holotype, W not seen). Fosberg (Bernice P. Bishop Mus. Bull. 174: 38. 1943) selected the collection from Kaua'i, high plateau, s.d., *V. Knudsen s.n.* (B presumably destroyed) as the type of the Hil-

lebrand name, but because Hillebrand included Wawra's name, which Fosberg did not note, with his new taxon it is superfluous and automatically typified on the Wawra collection.

Kadua cordata Chamisso & Schlechtendal var. *opaca* Wawra, Flora 57: 262. 1874. *Hedyotis schlechtendahliana* Steudel var. *opaca* (Wawra) Fosberg, Bernice P. Bishop Mus. Bull. 174: 38. 1943. TYPE: Hawaiian Islands. Kaua'i: Pohakupili, 1869–1870, *H. Wawra 2041* (holotype, W not seen).

Distribution and habitat. *Hedyotis schlechtendahliana* subsp. *schlechtendahliana* is known from the northern to eastern parts of Kaua'i from the Koai'e Canyon and Nualolo Valley to Kalalau Valley around to Hanalei Valley, and also Mt. Haupu, the Wahiawa Mountains, and the ridges surrounding Hanapepe River Valley at elevations ranging from (360–)650 to 1200 m. It ranges from diverse mesic forest with taxa such as *Bobea, Metrosideros, Pleomele,* and *Perrottetia* to wet *Metrosideros–Dicranopteris* forest with taxa such as *Ilex, Melicope, Tetraplasandra, Psychtoria,* and *Syzygium.*

Representative specimens from Kaua'i. Hanalei District: Upper Hanalei Valley, back of valley below Pohakupele, 2300 ft., 22 Mar. 1993, *Perlman et al. 13462* (PTBG); Pu'u Ka Ele Strm. (Kilauea), Oct. 1916, *Forbes 566.K* (BISH); Wainiha Valley, back of valley on left (N side) fork, 2500 ft., 29 Jan. 1993, *Perlman et al. 13288* (PTBG); Namolokama plateau, steep slope on W side, 1265 m, 18 June 1991, *Hobdy et al. 3324* (BISH [2]); Na Pali Coast State Park, survey transect 4, Sta. 7.0, Hanakoa valley, on E side of Hanakoa Falls plunge pool, 1200 ft., 6 June 1989, *Perlman et al. 10358* (PTBG, US); Kalalau rim, Kalahu side below and W of first Kalalau lookout, 790 m, 13 Mar. 1992, *Wood & Perlman 1711* (AD, MO, PTBG, US); Pohakuao, cliffs above Kalalau tr., 14 June 1989, *Hobdy et al. 3060* (BISH), 600 ft., *Perlman et al. 10377* (US); upper Honopu drainage (N side), 3550–3700 ft., 28 Jan. 1996, *Wood 4936* (AD, MO, PTBG, US, WU). Waimea District: Nuololu, Kuia Natural Area Reserve, 3650–3920 ft., 17 Aug. 1993, *Wood & Perlman 2708* (PTBG); Koke'e State Park, Kauaikinana Stream below dam on Mohihi Road, 3400 ft., 10 July 1985, *Flynn 1142* (PTBG); Koke'e Strm., 30 June 1926, *Degener 30456* (BISH); Po'omau Canyon and northern ridge dropping into Po'omau, 900–950 m, 11 Oct. 1991, *Wood 1274* (PTBG); Waimea drainage basin, W side, 3 Jul. to 18 Aug. 1917, *Forbes 848.K* (BISH); Koai'e Canyon, upper reaches of canyon, 2950–3080 ft., 31 Aug. 1994, *Wood & Perlman 3472* (PTBG). Koloa District: Lihue-Koloa Forest Reserve, Wahiawa Mountains just NE of Wahiawa Bog, along N fork of Wahiawa Stream, NW of Mt. Kahili, 650–710 m, 7 Apr. 1988, *Lorence et al. 5934* (BISH, PTBG, US[2]); first N fork of Wahiawa Strm., 650–720 m, Apr. 1988, *Wagner & Imada 6013* (BISH, US); ridge W of the Hanapepe River, 22 Aug. 1895, *Heller 2615* (US). Lihu'e District: Ha'upu Range, Mar. 1909, *Rock 2454* (BISH), 700 m, Feb. 1927, *MacDaniels 869* (BISH), *MacDaniels 716* (BISH), 31 Dec. 1956, *St. John 26036* (BISH, US).

The following specimens from a limited area on Koke'e plateau where the two subspecies are sympatric are intermediate between *Hedyotis schlechtendahliana* subsp. *schlechtendahliana* and subspecies *waimeae.* These collections would be difficult to assign to either of the two Kaua'i subspecies. Other collections from the area of general sympatry are also somewhat intermediate, but are more similar to one of the subspecies, especially those assigned to subspecies *waimeae.* These collections exhibit broadly ovate and often cordate leaves, but have open inflorescences and conspicuous venation.

Hedyotis glaucifolia (A. Gray) Fosberg var. *helleri* Fosberg, Bernice P. Bishop Mus. Bull. 174: 44. 1943. TYPE: Koke'e Strm., June 1926, *Degener 11653* (lectotype, here designated, BISH-504151; isolectotype, BISH). Four syntype collections (all besides the lectotype represent *Hedyotis schlechtendahliana* subsp. *waimeae*) were cited from Kaua'i, the additional syntypes being: Kaua'i [Hanapepe Valley], opposite Gay and Robinson's house, *A. A. Heller 2615*; Kaholuamanu, *Rock 93,* and *Rock 1936.* There is at least one other collection made by Heller given this same distribution number of 2615, but collected at a somewhat different locality.

Additional intermediate specimens. HAWAIIAN ISLANDS (U.S.A.). **Kaua'i:** Waimea District: Koai'e Canyon, 0.75 mi. up stream, 2000 ft., 16 Apr. 1991, *Wood et al. 741* (PTBG); Koholuamanu, Sep. 1909, *Forbes s.n.* (BISH); head of Kumuwela Ridge, 28 Dec 1935, *Fosberg 12668* (BISH, US).

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Literature Cited

Bruegmann, M. 1997. Endangered and threatened wildlife and plants; Proposed endangered status for 10 plant taxa from Maui Nui, Hawaii. Fed. Reg. 62(94): 26757–26770.

Delph, L. F. 1996. Flower size dimorphism in plants with unisexual flowers. Pp. 217–237 *in* D. G. Lloyd & S. C. H. Barrett (editors), Floral Biology: Studies on Floral Evolution in Animal-pollinated Plants. Chapman & Hall, New York.

Fosberg, F. R. 1943. The Polynesian species of *Hedyotis* (Rubiaceae). Bernice P. Bishop Mus. Bull. 174: 1–102.

Wagner, W. L., D. R. Herbst & S. H. Sohmer. 1989. Contributions to the Flora of Hawai'i. II. Begoniaceae–Violaceae and the Monocotyledons. Bishop Museum Occas. Pap. 29: 88–130.

———, ——— & ———. 1990. Manual of the Flowering Plants of Hawai'i. 2 vols. Univ. Hawaii Press, Bishop Museum Press, Honolulu.