## A Reassessment of *Dubautia* (Asteraceae: Heliantheae—Madiinae) on Kaua'i

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ABSTRACT: Aggressive botanical exploration of Kaua'i has yielded nearly 200 collections and two new species of *Dubautia* since the last monograph of the genus was published about a dozen years ago. This paper presents an updated key to the 13 species of *Dubautia* found on Kaua'i, summarizes and discusses the importance and systematic impact of recent collection data, and provides new maps to reflect the current knowledge of species distributions.

An impressive amount of botanical field exploration has occurred on Kaua'i during the dozen years since publication of the most recent monograph of Dubautia (Carr 1985). The number of collections of this genus alone by Tim Flynn, David Lorence, Steve Perlman, and Ken Wood, largely under the aegis of National Tropical Botanical Garden, approaches 200. Significantly, many of these collections represent new locations and range extensions for the taxa involved. Moreover, the collections include two new species, D. syndetica and D. kenwoodii (Carr and Lorence 1998, Carr 1998), and demonstrate the existence of considerably greater infraspecific variation than previously recognized, especially in D. microcephala and D. plantaginea subsp. magnifolia.

The recent Kaua'i discoveries bring the total number of species recognized in the Hawaiian silversword alliance of *Argyroxiphium*, *Dubautia*, and *Wilkesia* to 30, including mat-forming subshrubs, monocarpic rosette shrubs, polycarpic shrubs, trees, and vines. Despite tremendous morphological and ecological differentiation, this assemblage has been demonstrated to be mono-

phyletic (Baldwin et al. 1991), and hybrids have been produced between some of the Hawaiian species and their apparent nearest mainland ancestors in the tarweed assemblage of western North America (Carr et al. 1996).

The availability of so much new information for the Kaua'i species of *Dubautia* prompted this reassessment, which includes keys and distribution maps for all taxa, additional descriptive information where appropriate, and citations of specimens not previously examined. Most of the information presented in the earlier monograph (Carr 1985) is still relevant and is not duplicated here. Rather, attention is called to changes in interpretation mandated by the new information.

## MATERIALS AND METHODS

Herbarium specimens used in this study were borrowed from or were studied at HAW, BISH, and PTBG (cf. Holmgren et al. 1990 for herbarium abbreviations and information). The same caveats expressed in the earlier monograph (Carr 1985) regarding specimen measurements, taxonomic philosophy, and the effect of hybridization in this group also apply in this treatment. Pollen fertility of selected individuals was estimated by the stain reaction of a sample of at least 300 pollen grains in cotton blue (Maneval 1936).

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## KEY TO KAUA'I SPECIES OF Dubautia

1.	Leaves with a short but distinct petiole about 5 mm long, blade conspicuously areolate-reticulate, areolae more or less isodiametric; vines. Sect. Venoso-reticulatae
1.	Leaves sessile, or blade tapering to a winged, petioloid base, blade with a single midvein, or more often with 3 or more conspicuous, more or less parallel veins, not visibly reticulate, or if so, areolae obviously longer than broad; shrubs or trees. Sect. <i>Dubautia</i>
2(1).	Receptacular bracts equaling number of florets, consistently found in center as well as at perimeter of head, usually not coalescent
2.	Receptacular bracts fewer than florets, or bracts confined to perimeter of head, often coalescent, at least basally, often forming a cup surrounding the florets 5
3(2).	Heads disposed in cymose-corymbose clusters, or if elongate-paniculiform (as in some <i>D. paleata</i> ) then pappus of ovate to lanceolate scales 1.5–2.5 mm long; leaves not areolate-reticulate.
3.	Heads disposed in elongate-paniculiform clusters, or if nearly corymbiform (some D. laevigata) then the leaves obviously elongate-areolate-reticulate; pappus of very narrow bristles 2–4 mm long
4(3). 4.	Corolla yellow, subequal to pappus of narrow bristles; leaves opposite laxa Corolla white, markedly exceeding pappus of ovate to lanceolate scales; leaves opposite or whorled
5(2) 5.	Leaves whorled 6 Leaves opposite 7
6(5). 6.	Leaves 1–3 cm long, closely imbricated; flowers yellow
7(5). 7.	Leaves with a slender attenuate-petioloid base, weakly 5–7-nerved, distally becoming conspicuously and uniformly elongate-areolate-reticulatelaevigata  Leaves weakly to prominently 5–11-nerved, not conspicuously and uniformly areolate-reticulate or if slightly so (D. kenwoodii), then lacking a slender attenuate-petioloid base
8(7).	Peripheral receptacular bracts basally coalescent, distal free portions broad and conspicuously overlapping; pappus of lanceolate scales much shorter than
8.	corolla
9(8). 9.	Heads disposed in erect or reflexed cymose-corymbiform clusters
10(9).	Ultimate peduncles often obscured by coarse, short-stalked or sessile purplish glands; flower clusters erect
10.	Ultimate peduncles glabrous to copiously hirtellous or puberulent in broad bands opposite bracts; flower clusters erect to reflexed
11(9). 11.	Peripheral receptacular bracts 2.5–6.5 mm long; florets mostly 2–11 per head 12 Peripheral receptacular bracts 6.5–8 mm long; florets mostly 12–18 per head
	kenwoouii

- 13. Receptacular bracts 2.5-4 mm long, often dark purple or black or in Kalalau specimens green with black glands; florets 4-7 per head ...... microcephala
- 1. Dubautia imbricata H. St. John & G. Carr Bull. Torrey Bot. Club 108:198, 1981.

## KEY TO SUBSPECIES

# 1a. *Dubautia imbricata* subsp. *imbricata* Figure 1

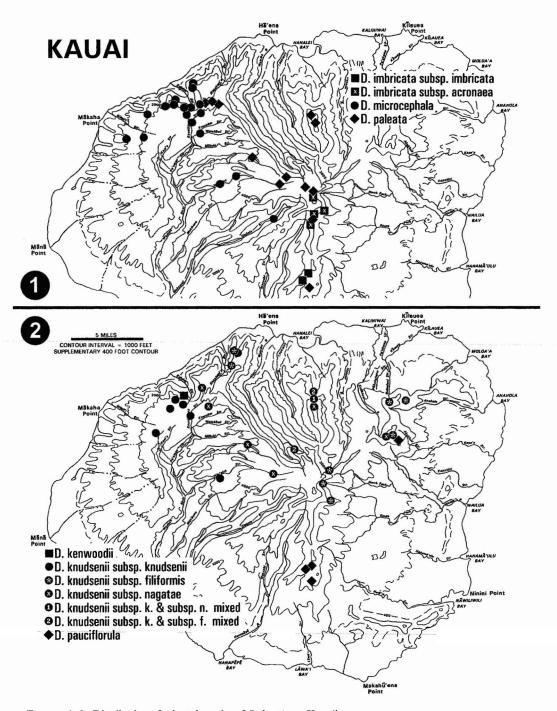
Dubautia imbricata subsp. imbricata is now known from several sites in the upper Wahiawa drainage basin, extending from the slopes adjacent to minor tributaries on the extreme west margin of the drainage to at least as far east as the upper headwaters of the main (NE) fork of Wahiawa Stream, due south of Kapalaoa Peak.

SPECIMENS EXAMINED: Kōloa: W side of Wahiawa Drainage, below ridge between Hulua and Pu'uau'uka, 650 m, Wood et al. 1354 (BISH, PTBG); W of main Wahiawa Stream, NE of Hulua, 730 m, Perlman & Wood 12373 (BISH); gulch off Hanapēpē-Wahiawa dividing ridge, N of Hulua, 794 m, Perlman & Gemmel 13676 (PTBG); ridge adjacent to main (NE) fork of Wahiawa Stream, due S of Kapalaoa Peak, 720 m, Morden et al. 1369–1376 (BISH).

Dubautia imbricata subsp. acronaea
 G. Carr
 Allertonia 4:76, 1985.

## Figure 1

Though still represented by only a few collections, D. imbricata subsp. acronaea is now much better vouchered than when first characterized. It is now known to occur on the summit ridge extending south from Wai'ale'ale and Kawaikini and also on the slopes east of this ridge at elevations of 550-1525 m. It is described as locally abundant on the ridge between Hanapepe and 'Iole Valleys (Perlman & Wood 14387) and is characterized as a shrub or diffusely branching tree to 2 m tall. Leaves on some of the material (notably Wood & Perlman 3596) exceed 20 cm in length, well beyond the range of 6-15 cm cited by Carr (1985) for D. imbricata, based largely on material of subsp. imbricata. The new material also demonstrates that the expanded corolla is about 3.5 mm long and that mature achenes may reach 4 or sometimes even 5 mm in length in D. imbricata subsp. acronaea. This taxon hybridizes in nature with D. waialealae and also may have participated in the putative hybridization between D. laevigata and D. imbricata reported earlier (Appendix).



FIGURES 1-2. Distribution of selected species of Dubautia on Kaua'i.

SPECIMENS EXAMINED: District unknown: *Rock Oct 1916 s.n.* (BISH 35910, 74747, 467285).

Hanalei: Wai'ale'ale summit area, ca. 1524 m, *Wood 3890* (HAW, PTBG).

Kōloa/Līhu'e: Kāhili-Kawaikini ridge between Hanapēpē and 'Iole Valleys, 1055 m, *Perlman & Wood 14387* (PTBG).

Līhu'e: Back of 'Ili'ili'ula Valley below Kawaikini, 585 m, *Perlman & Wood 14432* (PTBG, HAW); 'Ili'ili'ula drainage S of Kamanu and Kalalea, 550–625 m, *Wood & Perlman 3596* (BISH, HAW, PTBG); above 'Ili'ili'ula and 'Iole drainage on ridge extending S

from Kawaikini, 915–1005 m, *Wood et al.* 3540 (HAW, PTBG).

2. Dubautia kenwoodii G. Carr Novon 8:8, 1998. Figure 2

This species is still known only from the type collection of a single sheet (*Wood & Query 1004*) (PTBG) from the Kalalau rim, north of Kahuama'a Flat at 800 m elevation.

3. *Dubautia knudsenii* Hillebrand Fl. Hawaiian Isl. 223, 1888.

#### KEY TO SUBSPECIES

- 1. Larger heads with 4–6 florets; capitulescences erect or partly pendulous to moderately reflexed.....
- 2. Capitulescences stout, erect; receptacular bracts often separating upon drying; leaves rather closely and uniformly puberulent abaxially ... 3c. D. knudsenii subsp. nagatae

# 3a. *Dubautia knudsenii* subsp. *knudsenii* Figure 2

Several recent collections of Dubautia knudsenii contribute to a better understanding of the overall pattern of variation in this species and also considerably expand the known geographic range of all three of the subspecies. Recognition of these subspecies has become a bit more difficult as local sites of sympatry and occasional intermediate forms have been detected in the field. However, the subspecies still appear to represent regional facies that can generally be readily identified by the key characters provided. Specimens from Mt. Nāmolokama are likely to be among the most confusing because all three subspecies intermingle in this area (cf. Lorence et al. 7279A, 7279B, and 7289). Dubautia knudsenii subsp. knudsenii, D. knudsenii subsp. filiformis, and potential intermediates are also found together in the area southwest of Mahinakēhau Ridge (cf. Lawrence et al. 7320, 7350). Dubautia knudsenii subsp. knudsenii is found basically on the western and northwestern part of the range of the species at elevations from about 450 to 1260 m. This taxon hybridizes in nature with D. laevigata and D. raillardioides (Appendix).

SPECIMENS EXAMINED: Hanalei: Upper N fork of Honopū headwaters, gulch of dividing ridge of Kalalau and Honopū, 1070–1130 m, *Wood 4977* (PTBG); upper Honopū drainage (N side), 1080–1125 m, *Wood 4925* (PTBG); Kōke'e State Park, Kaluapuhi Trail, ca. 1220 m, *Flynn & Decker 3281* (BISH), Hwy. 550 near mile 18.3, on Kalalau side of road, 1260 m, *Flynn 1195* (PTBG), Kahuama'a Flat Trail, *Flynn 159* (PTBG); head-

waters of Wainiha River, NE Fork, just SW of Mahinakēhau Ridge, 680–825 m, Lorence et al. 7320 (BISH, PTBG); Wainiha drainage S of Mahinakēhau, 700–800 m, Wood et al. 2341 (PTBG); upper Wai'oli Valley, N face of Mt. Nāmolokama, transect no. 2, 740–820 m, Lorence et al. 7291 (PTBG); upper Wai'oli Valley, below and E of main waterfall, 280–470 m, Lorence 7279A (PTBG).

3b. *Dubautia knudsenii* subsp. *filiformis* G. Carr Allertonia 4:84, 1985. Figure 2

Originally known only from the Makaleha Mountains, this subspecies has now been collected from several locations, primarily along the northern and eastern part of the species range, at elevations from about 350 to 860 m. Its occasional occurrence in the vicinity of the other two subspecies is discussed under *D. knudsenii* subsp. *knudsenii*. The data from several collections now suggest that flowering may occur throughout the year.

SPECIMENS EXAMINED: Hanalei: Hanalei Valley, 675-715 m, Flynn et al. 5320 (PTBG); headwaters of Hanalei River below Pohakupele, 670 m, Wood et al. 2459 (PTBG); headwaters of Wainiha River, NE fork, just SW of Mahinakehau Ridge, 680-825 m, Lorence et al. 7328 (BISH), Lorence et al. 7336 (PTBG), Lorence et al. 7350 (BISH); Limahuli Valley, E side of ridge separating Limahuli and Hanakāpī'ai Valleys, along main stream, 770 m, Wood et al. 1112 (BISH, PTBG); Limahuli Valley, W side of ridge separating Limahuli and Hanakāpī'ai Valleys, 490-630 m, Flynn et al. 2166 (BISH, PTBG), Flynn et al. 2175 (PTBG); Wainiha drainage S of Mahinakēhau, 700-800 m, Wood et al. 2342 (HAW, PTBG), Wood et al. 2344 (HAW, PTBG); upper Wai'oli Valley, below and E of main waterfall, 280-470 m, Lorence et al. 7279B (PTBG); W side of upper Wai'oli Valley, 400-490 m, Wood et al. 2553 (PTBG), Wood et al. 2565 (PTBG); back of Wai'oli Valley, 300-370 m, Wood & Perlman 1492 (BISH, PTBG), 550 m, Wood & Query 1584 (PTBG).

Hanalei/Kawaihau: Along stream bed,

610–860 m, Flynn et al. 5259 (BISH, PTBG); Makaleha Mountains, N-facing steep slopes below Kekōiki, 665–845 m, Wood 2852 (PTBG).

Kawaihau: Makaleha Mountains, transect no. 2A from S of Mālamalamaiki Peak to S of Leleiwi Peak, 500–600 m, *Lorence et al.* 7367 (PTBG); along unnamed tributary of N Fork of Wailua River, 425–595 m, *Flynn et al.* 4795 (BISH, HAW, PTBG).

Līhu'e: Back of 'Ili'ili'ula Valley, below Kawaikini, 560 m, *Perlman & Wood 14427* (HAW, PTBG).

Līhu'e/Kawaihau: "Blue Hole," headwaters of N Fork of Wailua River, just N of Kawaikini and SE of Wai'ale'ale, 600–700 m, Wood et al. 101 (PTBG), 610–670 m, Wood et al. 773 (PTBG), below "Blue Hole," 710 m, Wood et al. 1124 (PTBG).

3c. *Dubautia knudsenii* subsp. *nagatae* (H. St. John) G. Carr Allertonia 4:83, 1985. Figure 2

Previously known only from the Alaka'i Swamp, outlying populations of this subspecies have now been documented from Mt. Nāmolokama and the Makaleha Mountains and from sites ranging in elevation from about 875 to 1375 m. The close puberulence on the abaxial (lower) leaf surface that helps to distinguish D. knudsenii subsp. nagatae was erroneously ascribed to the adaxial (upper) surface in the key to subspecies presented earlier (Carr 1985). As with earlier collections, the recent flowering specimens were taken from September to December except for the Makaleha Mountains material, which was flowering in July. Data now available suggest that the seasonality of flowering in D. knudsenii subsp. nagatae is another feature that helps to distinguish it from conspecific

The occasional sympatry of *D. knudsenii* subsp. *nagatae* with the other two subspecies and the potential for intermediate specimens is discussed under *D. knudsenii* subsp. *knudsenii*. One specimen cited here, *Medeiros 497* (BISH), seems to combine certain features of all three subspecies. However, more speci-

mens from this location are needed to assess the significance of this observation.

SPECIMENS EXAMINED: Hanalei: N Kalalau rim, Keanapuka, 990–1190 m, Wood 1277 (PTBG), Wood 1282 (BISH, PTBG); ridge E of Pihea Peak toward Kilohana, 1250–1280 m, Flynn & DeLappe 3200 (BISH, PTBG); near Pihea, 1242 m, Takeuchi & Pyle 3692 (BISH); upper Wai'oli Valley, N face of Mt. Nāmolokama, 740–820 m, Lorence et al. 7289 (PTBG); Mt. Nāmolokama, 1200–1350 m, Wood et al. 0174 (BISH, PTBG); Wood et al. 0187 (BISH, PTBG).

Kawaihau: Makaleha Mountains, forested slopes and drainage ESE of Makaleha Peak, 800–830 m, *Wood et al. 2645* (PTBG), transect 3, central plateau ESE of Makaleha Peak, N of Makaleha Stream, 840–914 m, *Lorence et al. 7406* (PTBG).

Waimea: Along the trail from Pihea to the NE corner of the Alaka'i Swamp, 1220–1305 m, *Croat 44913* (PTBG); Pihea Trail from Pihea S to Alaka'i Swamp Trail, 1100–1200 m, *Lorence et al. 5599* (BISH, PTBG); Kōke'e Plateau, Koai'e Stream drainage, 1220 m, *Medeiros 497* (BISH).

4. Dubautia laevigata A. Gray Proc. Am. Acad. Arts 5:135, 1861. Figure 4

Though not particularly common, this is the most widespread of all the species of *Dubautia* on Kaua'i. Only a few new locations in the Kōke'e area have been added since the previous account (Carr 1985). However, the flowering time indicated by recent specimens is May to August rather than the earlier indication of December to August. This species hybridizes in nature with *D. laxa* subsp. *hirsuta*, *D. knudsenii* subsp. *knudsenii*, and possibly also with *D. imbricata* (Appendix).

SPECIMENS EXAMINED: Hanalei: Awa'awapuhi Valley, ridge on N side of trail, 1000–1050 m, Wood & Query 1806 (BISH, PTBG); Kalalau rim, N of Kahuama'a Flat, 990–1020 m, Wood et al. 637 (PTBG), 990–1190 m, Wood & Perlman 1248 (PTBG), Wood & Perlman 1249 (PTBG); rim of Kalalau Valley near Kaluapuhi Trail Head be-

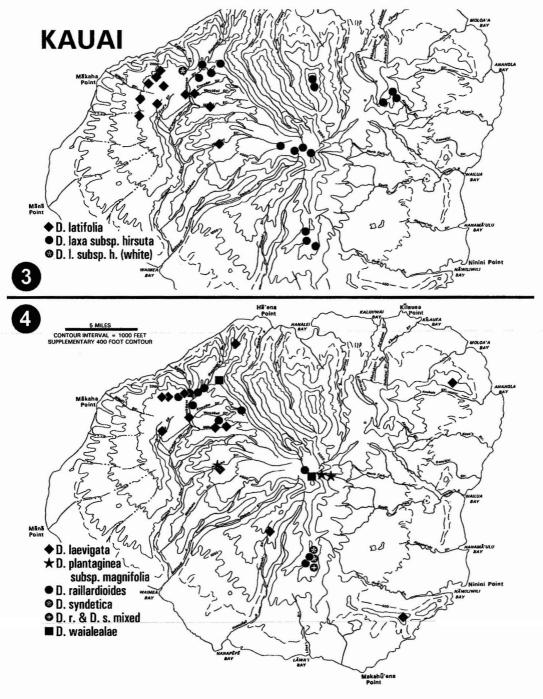
tween Kalalau and Pu'u o Kila Lookouts, 1220 m, *Baldwin 671* (BISH), *Baldwin 777* (BISH); Kōke'e State Park, Kalalau Valley, Hwy. 550 near mile 18.3, ca. 1220 m, *Flynn 1170* (PTBG), near mile 18.6, SE corner of valley, 1160–1220 m, *Flynn et al. 2246* (BISH, PTBG), *Flynn et al. 2247* (BISH, PTBG).

Waimea: Kōke'e, Kauaikananā Stream below Mōhihi Road, 990 m, Flynn et al. 2264 (PTBG); Nu'alolo, Ku'ia Natural Area Reserve, 1110–1195 m, Wood & Perlman 2712 (PTBG); Nu'alolo Valley below transect end within main gulch area, 950–1050 m, Wood & Perlman 1064 (BISH), Wood & Perlman 1065 (PTBG); Mōhihi Stream near start of Mōhihi-Wai'alae Trail, ca. 1065 m, Wood & Perlman 2542 (PTBG); Mōhihi Trail from Camp 10 road, 960–1100 m, Flynn et al. 5030 (PTBG); Wai'alae Valley, ridge between Wai'alae and Nāwaimaka Valleys, above Wai'alae Falls, 950–1050 m, Wood et al. 0846 (BISH).

5. Dubautia latifolia (A. Gray) Keck Occas. Pap. Bishop Mus. 11:26, 1936. Figure 3

Recent field explorations in the Kōke'e region have added five new locations of this rare and endangered species. However, the total number of individuals known is still quite low because a site often has only one or very few plants. The new data still indicate strong seasonality of flowering from September to November. The elevational range of the species as currently understood is about 850–1200 m.

SPECIMENS EXAMINED: Waimea: Awa'awapuhi Trail, off side of trail to N, 980 m, Wood et al. 12309 (PTBG); Kauhao Ridge, near gauging station and ditch, N-facing mesic forest, 927 m, Wood 3484 (PTBG); Kōke'e, cultivated in the yard of John Plews, Flynn 943 (PTBG), Plews 25 Oct 1990 s.n. (BISH 598086); Camp 10 road, 1/2 mile (0.8 km) from John Plews residence, Plews 23 Oct 1986 s.n. (BISH 523730, 524403); Mōhihi Road at junction with Camp Sloggett, Wagner et al. 5053 (BISH); Kumuweia Ditch Trail, 2 miles (3.2 km) in, 1135–1175 m, Wood



FIGURES 3-4. Distribution of selected species of Dubautia on Kaua'i.

2092 (BISH, PTBG); N slope of Mākaha Valley at 1.3 miles (2.1 km) W of Hwy. 550 along Mākaha Ridge Road by Koki'o Ke'oke'o picnic area, 800-900 m, Lorence & Gustafson 5593 (BISH, PTBG); Mākaha Valley, 1.5 miles (2.4 km) down Mākaha Ridge Road, 902 m, Flynn 1209 (PTBG), 914 m, Wagner 5617 (BISH); Mōhihi-Wai'alae Trail, across Mōhihi Stream from end of Camp 10 road (picnic area), heading E up ridge, 1050 m, Lorence et al. 7210 (PTBG, BISH); on N-facing slope of Nu'alolo Valley floor, boundary of Ku'ia Natural Area Reserve, 1036 m, Perlman & Wood 13231 (BISH, PTBG); Nu'alolo, Ku'ia Natural Area Reserve, 1005-1036 m, Wood & Perlman 2263 (PTBG); upper Nu'alolo Stream, N branch, 1130-1160 m, Wood & Boynton 4853 (PTBG); Wai'alae Valley, ridge W of Wai'alae Cabin, near State goat enclosure, 900-1000 m, Wood & Perlman 680 (BISH [2]).

6. Dubautia laxa Hook. & Arn. Bot. Beechey Voy. 87, 1832.

6a. Dubautia laxa subsp. hirsuta (Hillebrand)G. CarrAllertonia 4:67, 1985.Figure 3

Several new locations for this taxon are established by recent collections. The most notable in terms of range extension are the collections on Mt. Nāmolokama. Also noteworthy are additional collections of a whiteflowered form from the east rim of Kalalau Valley (Carr & Flynn 1330; Flynn 1171, 1352; Flynn & Lowrev 1874). These correspond to a suite of specimens cited by Carr (1985) from the same area with similar characteristics (Degener 23854, Forbes 1034K, Carlquist H12), but that were not known at the time to have white flowers. Besides the difference in flower color, these plants have less harsh pubescence on the leaves, slightly longer pappus, and slightly longer and less glandular corolla tubes than typical D. laxa subsp. hirsuta. There is also a tendency for the capitulescence in these variants to be more elongated than usual. With so few individuals known, it is uncertain that they represent a reproductively stable population. However, pollen samples from these plants have been 95–99% stainable, suggesting that they have normal fertility. Moreover, spontaneous hybridization between this unusual form of *D. laxa* subsp. *hirsuta* and the closely sympatric *D. laevigata* has been documented (Appendix). The typical, yellow-flowered form of *D. laxa* subsp. *hirsuta* hybridizes in nature with *D. paleata* and probably also with *D. pauciflorula* (Appendix).

SPECIMENS EXAMINED: Hanalei: Alaka'i, North Bog, NW of Kilohana overlooking Wainiha, 1220 m, Wood 3912 (PTBG); along the NE edge of the Alaka'i Swamp, at edge of lookout at Kilohana, 1220-1280 m, Croat 44988 (PTBG); ca. 1/2 mile (0.8 km) E of Pihea Peak, 1250-1280 m, Flynn & DeLappe 3201 (BISH, PTBG); Kōke'e State Park, rim of Kalalau Valley near Kaluapuhi Trail Head between Kalalau and Pu'u o Kila Lookouts, 1220 m, Carr & Flynn 1330 (BISH); Hwy. 550 near mile 18.3, at back of Kalalau Valley, 1220 m. Flvnn 1171 (BISH, HAW), Flvnn 1352 (PTBG); just below trail along Kalalau Valley rim, 1205 m, Flynn & Lowrey 1874 (BISH, PTBG); S end of summit of Mt. Nāmolokama. 1250-1350 m, Flynn et al. 3065 (PTBG), Flynn et al. 3066 (PTBG), Flynn et al. 3067 (PTBG); central pass of Mt. Nāmolokama, 1200-1350 m, Wood et al. 190 (PTBG); E rim of Mt. Nāmolokama, 1200-1350 m, Wood & Doyle 166 (PTBG).

Kawaihau: Makaleha Mountains, central plateau ESE of Makaleha Peak, N of Makaleha Stream, transect no. 3, 840–914 m, Lorence et al. 7408 (BISH, PTBG); Makaleha Mountains, N-facing cliffs and forested slopes between Pu'u 'Eu and Leleiwi, 840–890 m, Wood et al. 2671 (PTBG).

Köloa: Along trail from relay towers to Mt. Kāhili, *Flynn 529* (PTBG); Mt. Kāhili, steep windswept slope near TV relay tower, *Wagner et al. 5389* (BISH); along ridge between TV relay tower and first peak on W side of Mt. Kāhili, 853 m, *Wagner et al. 5223* (BISH).

Waimea: Alaka'i Swamp Wilderness Preserve, trail to Kilohana Lookout, 1120–1280 m, *Lorence et al. 5698* (BISH, PTBG); Alaka'i Swamp Wilderness Preserve, around Wai'ale'ale summit and 1 mile (1.6 km) to W, stream heading N toward Hinalele Falls,

1400–1600 m, *Wood & Doyle 154* (PTBG); Wai'ale'ale summit area, windswept slopes below Wai'ale'ale, 1555 m, *Wood 5920* (PTBG).

7. Dubautia microcephala Skottsb. Acta Horti Gothob. 2:277, 1926. Figure 1

A large number of recent collections have expanded the known range of this species and have also revealed a much greater amount of morphological variation than previously ascribed to it. Most notable in this regard are a large suite of specimens collected at lower elevations primarily on the rim of Kalalau Valley (cf. Perlman et al. 12694; Wood 626, 1153, 1186, 1190, 1235, 1236, 1397, 1436, 1599, 2385, 3612, 3616, 3639, 3856, 3933; Wood & Perlman 1247). These specimens share a tendency for dwarfed plant size, small leaves, reduced pubescence in the capitulescence, smaller than normal heads with greenish rather than purplish receptacular bracts, and conspicuous black glands in the capitulescence. However, this suite of specimens exhibits a considerable range in these features, and other collections sympatric with or adjacent to the dwarfed forms exhibit the "normal" range of morphology previously ascribed to this species (Carr 1985). The glands so conspicuous in the capitulescence of many of the dwarfed specimens were initially thought to be unique, but closer inspection revealed the existence of similar glands on virtually all specimens of D. microcephala, even though this feature was not reported earlier (Carr 1985). In most nondwarfed specimens the glands are light colored and are obscured by white-villous trichomes that are lacking in the nearly glabrous dwarfed forms. Though the extreme forms now included within D. microcephala are quite distinctive, formal taxonomic recognition of them at the level of subspecies is currently considered impractical because of the close spatial association of the extreme types together with the presence of many individuals of intermediate morphology.

The recent collections have increased the known range of elevation for the species to about 550–1275 m. Data from all of the recent collections, including the dwarfed Kala-

lau forms, indicate the same flowering time reported earlier (i.e., August to November). This species occasionally hybridizes in nature with *D. plantaginea* subsp. *magnifolia* (Appendix).

SPECIMENS EXAMINED: Hanalei: Honopū rim, 20 deg. N-facing cliffs, 500 m W of easternmost rim, 750-850 m, Wood et al. 1190 (BISH, HAW, PTBG); Kalalau rim, NW-facing aspect, below Pihea Peak, 990-1190 m, Wood 1138 (PTBG); below and a little S of Pihea Peak, collected on rappel to hanging valley, 1010 m, Wood 1344 (BISH, PTBG); SE edge of Kalalau Valley between Kalalau and Pu'u o Kila Lookouts along Hwy. 550 by entrance to Kahuama'a Flat Trail, 1250 m, Lorence et al. 5604 (PTBG); Kalalau rim, N of Kahuama'a Flat, 990-1020 m, Wood 626 (BISH, PTBG), Wood & Perlman 1247 (BISH, PTBG); Kalalau rim below Pu'u o Kila, 570 m, Wood et al. 1101 (BISH, HAW, PTBG), 600 m, Wood et al. 1103 (BISH, HAW, PTBG); Kalalau rim, drainage W of Pu'u o Kila, 885 m, Wood 3612, 3616 (HAW); Kalalau rim, Kalāhū side below and W of first Kalalau lookout, 1036 m, Wood 1599 (PTBG), 550-670 m, Wood 1436 (PTBG), 200 m E of plane crash site, 900-1000 m, Wood 1153 (BISH, HAW, PTBG), 950 m, Wood 1186 (BISH, HAW, PTBG), 300 mE of plane crash site, 790 m, Wood 1397 (BISH, PTBG); Kalalau, lower Kalāhū side, 610 m, Wood 3639 (HAW); Kalalau rim, N-S ridge below and E of first Kalalau lookout, 960-1100 m, Wood 1230 (BISH, HAW, PTBG), Wood 1231 (BISH, PTBG), Wood 1235 (HAW, PTBG), Wood 1236 (PTBG); Kalalau Valley, W side rim, N side of large dividing ridge between Kalalau lookouts, 1177 m, Perlman & Lau 14511 (PTBG); Kalalau rim, below and E of first lookout, 1190 m, Wood & Lau 3682, 3684 (HAW); Kalalau rim, NW-facing cliffs below and E of first Kalalau lookout, 1000-1100 m, Wood et al. 1224 (BISH, HAW, PTBG); N side of Kalalau below Alealau, near Pu'u Kī, 790 m, Wood 2385 (HAW); Pōhakuao, cliffs below Pu'u Kī and Manono Ridge, 640 m, Perlman et al. 12694 (BISH, PTBG).

Waimea: Kōke'e, Mōhihi Road, past Sugi Grove, Flynn 635 (PTBG); Mākaha Valley, NE gulch of upper valley, 884 m, Wood & Lau 3803 (HAW, PTBG); Mākaha Valley, 692 m, Wood 3933 (PTBG); Nu'alolo Valley, N side of trail at 1036-m contour, 850–945 m, Wood 3856 (PTBG).

8. Dubautia paleata A. Gray Proc. Am. Acad. Arts 5:185, 1861. Figure 1

The most notable new collections of D. paleata are those from Mt. Nāmolokama. The known range of the species now extends in a narrow zone due north and south from the Wai'ale'ale summit area and northwest across the Alaka'i Swamp to Pihea. Recent flowering specimens were taken from May to November. The outlying occurrence in Kanaele (Wahiawa) Swamp cited earlier (Carr 1985) has still not been documented with flowering material. However, a collection of D. paleata from somewhat S of Kawaikini (Wood et al. 3532) was recently made, and the species was also reported to occur along the summit ridge as far south as Kapalaoa Peak, though apparently no vouchers were taken (see label data on Wood et al. 840D and Perlman & Wood 14387). Confirmation of these occurrences with voucher specimens would be desirable.

It now appears that the specimens cited by Carr (1985) as having vegetative features and stature intermediate to D. paleata and D. raillardioides (Rock 4865, 4997, 4998) represent the common form of D. paleata on the forested fringes of boggy areas. The combination of characters possessed by this morphotype is suggestive of introgressive hybridization between the more extreme bog form of D. paleata and D. raillardioides, which often occurs in nearby sites. This is precisely the conclusion of a preliminary study that employed RAPD molecular markers to assess the dynamics of these populations (Carino and Morden 1997). Formal taxonomic recognition of such apparently introgressed plants is impractical because their floral features are virtually identical to those of D. paleata and also because of the presence of numerous individuals with intermediate vegetative morphology. An apparently lesscomplicated pattern of natural hybridization

of *D. paleata* with *D. laxa* subsp. *hirsuta* and *D. waialealae* is indicated by a number of specimens (Appendix).

SPECIMENS EXAMINED: Hanalei: Alaka'i Swamp, Wainiha Pali, 1/2 mile (0.8 km) W of Hinalele Falls, on NNE-facing cliff face, 1433 m, Wood 33 (PTBG); Alaka'i Wilderness Preserve, around Wai'ale'ale summit and NW of rain gauge, 1400-1600 m, Wood et al. 1869 (PTBG); N bog along Wainiha Pali, 1310-1340 m, Wood & Perlman 3659 (PTBG); central pass of Mt. Nāmolokama, 1200-1350 m, Wood et al. 189 (PTBG); NW rim of Mt. Nāmolokama, 1200-1350 m, Wood & Doyle 178 (PTBG); summit plateau of Mt. Nāmolokama, 1280 m. Lorence et al. 6063 (HAW, PTBG), 1280-1347 m, Lorence et al. 6059 (PTBG); upper Hanakāpī'ai drainage and the N bog area along Wainiha rim (ridge to Hono'onāpali), 1125-1190 m, Wood 5286 (PTBG).

Hanalei/Waimea: Halehaha Bogs, 1310–1340 m, Wood & Perlman 3411 (PTBG).

Kōloa: SW edge of Kanaele (Wahiawa Bog), 640 m, Flynn et al. 2161 (PTBG), SW edge of bog, 640 m, Flynn et al. 2383 (PTBG).

Līhu'e: Ridge below Kawaikini, W of 'Ili'ili'ula and 'Iole, 855–975 m, *Wood et al.* 3532 (PTBG).

Waimea: Alaka'i Swamp, 1200 m, Herbst 2184 (PTBG), 1067 m, Stern & Herbst 2979 (PTBG), second bog past river, Flynn 567 (PTBG [2]), beginning of the first bog, Flynn 277 (PTBG); Alaka'i Swamp Wilderness Preserve, trail to Kilohana Lookout, 1120–1280 m, Lorence et al. 5703 (BISH, PTBG); ca. 1/2 mile (0.8 km) SE of Pihea on Pihea Trail, ca. 1220 m, Carr et al. 1374 (BISH), Carr et al. 1375 (BISH); Pihea Trail, Flynn 296 (PTBG); Alaka'i Wilderness Preserve, around Wai'a-le'ale summit and 1 mile (1.6 km) to W, on stream heading N toward Hinalele Falls, 1400–1600 m, Wood & Doyle 0145 (BISH, PTBG).

 Dubautia pauciflorula H. St. John & G. Carr Bull. Torrey Bot. Club 108:202, 1981. Figure 2

With one exception all of the recent collections of this rare species have been from near the type locality in the Wahiawa drainage basin. However, Flynn et al. 3448 is from the Makaleha Mountains about 17 km away. The recent and earlier collections indicate a flowering time of late July to November for D. pauciflorula. This species apparently hybridizes in nature with D. laxa subsp. hirsuta and/or D. raillardioides (Appendix).

SPECIMENS EXAMINED: Kawaihau: Keālia Forest Reserve, along ridge leading to Pōhakupili from just above Kahūnā Road, 640—790 m, *Flynn et al. 3448* (BISH, HAW, PTBG).

Kōloa: Small side stream to W of main Wahiawa Stream, 700 m (type locality), Perlman 13823 (PTBG); NW of Wahiawa Bog, along tributary NW of main Wahiawa Stream and SE of Hulua, 650-730 m, Obata 1989 (PTBG); Wahiawa Mountains, NE of Hulua, along stream banks to W of main Wahiawa Stream, 713 m, Perlman & Wood 12376 (PTBG); Wahiawa Stream and Mountains, along unnamed tributary E of main Wahiawa Stream headwaters (first tributary N of LZ-1), 700 m, Lorence et al. 6781 (PTBG); Wahiawa drainage, first gulch W of LZ-1, 660-780 m, Wood et al. 572 (PTBG); Wahiawa Mountains, NE of Hulua near Waimea District boundary, 700-740 m, Perlman et al. 12229 (PTBG [2]); road from Alexander Reservoir to microwave relay towers on Mt. Kāhili, 490-700 m, Flynn et al. 2384 (BISH, HAW, PTBG), Flynn et al. 2385 (PTBG).

10. Dubautia plantaginea Gaudich Voy. Uranie, 469, pl. 84, 1830.

10a. Dubautia plantaginea subsp. magnifolia (Sherff) G. Carr Allertonia 4:80, 1985. Figure 4

A collection made in 1987 from cliffs at the headwaters of the north fork of the Wailua River (*Lorence et al. 5334*) appears to be the first specimen of *Dubautia plantaginea* taken on Kaua'i in more than 70 years. Several subsequent collections have been made at this locality. The Wailua River specimens have been almost exclusively a dwarf form of *Dubautia plantaginea* subsp. *magnifolia*,

which is otherwise known only from two collections, probably both from Wai'alae Stream near Kahōluamanu. As the subspecific epithet suggests, the Wai'alae specimens have large leaves and give the appearance of having come from large, robust plants. At first it was tempting to formally recognize the dwarf Wailua River forms as a new subspecies as was deemed appropriate for the distinctive West Maui cliff-dwelling dwarf analog, D. plantaginea subsp. humilis. However, as more collections of the Kaua'i taxon from Wailua River were made, a broader range of plant sizes was noted. One collection from well below the cliff area was reported to be a shrub 2.5 m tall. Specimens from this plant very closely match the Wai'alae material. Thus, based on current information, it seems advisable to treat the dwarf specimens as local variants of D. plantaginea subsp. magnifolia. It should be noted, however, that the dwarf form has been cultivated for several years and has flowered profusely while maintaining a dwarfed stature.

The three sites from which this taxon is known range in elevation from 470 to 1100 m. Flowering time appears to be July to November. This species occasionally hybridizes in nature with *D. microcephala* (Appendix).

SPECIMENS EXAMINED: Līhu'e/Kawaihau: "Blue Hole," headwaters of N fork of Wailua River, just N of Mt. Kawaikini and SE of Mt. Wai'ale'ale, 600–700 m, Lorence et al. 6790 (PTBG), 680–700 m, Lorence et al. 5334 (PTBG [2], BISH, HAW), 730 m, Wood 1127 (BISH, HAW, PTBG), 610–670 m, Wood et al. 763 (PTBG), below "Blue Hole," 730 m, Baldwin et al. 776 (BISH [2], HAW, MO [2], NY [2], OSC, PTBG, TEX, UC [2], US, WS, WTU), 470 m, Wood & Perlman 1347 (BISH, PTBG).

11. *Dubautia raillardioides* Hillebrand Fl. Hawaiian Isl. 224, 1888. Figure 4

The few new locations established for this species are mostly not particularly dramatic. In fact the species seems to be underrepresented in the recent collections. However, one collection from near the summit of

Wai'ale'ale (Wood & Doyle 148) is noteworthy in increasing the range of the species and also in extending its upper elevational limit to about 1450 m. Data from flowering specimens suggest that the flowering time should be extended to include the period from December to May or early June. Putative introgression of D. paleata with D. raillardioides is discussed under the former species. Dubautia raillardioides also hybridizes in nature with D. knudsenii subsp. knudsenii and possibly also with D. pauciflorula (Appendix).

SPECIMENS EXAMINED: Hanalei: Kalalau rim, below Pu'u o Kila, 950–1150 m, *Wood 1035* (BISH, PTBG [2]).

Kōloa: Along trail to Wahiawa Bog (Kanaele Swamp), 640 m, Flynn 372 (PTBG); Wahiawa Bog (Kanaele Swamp), 640 m, Stern & Herbst 2930 (PTBG); Mt. Kāhili, windswept slope near TV relay tower, Wagner et al. 5388 (BISH).

Waimea: Alaka'i Wilderness Preserve, around Wai'ale'ale summit and 1 mile (1.6 km) to W, on stream heading N toward Hinalele Falls, 1400–1600 m, *Wood & Doyle 148* (BISH, PTBG); Pihea Trail, from Pihea Lookout S along W edge of Alaka'i Swamp, 1300 m, *Lorence et al. 5152* (PTBG); Pihea Trail near Pihea, ca. 1220 m, *Carr et al. 1373* (BISH), *Carr et al. 1376* (BISH).

12. Dubautia syndetica G. Carr & D. LorenceNovon 8:4, 1998.Figure 4

The few recent collections that were not cited in the original publication do not expand the known range. However, consultation with the collectors has allowed more precise localization of the collection sites and indicates that the range given previously (Carr and Lorence 1998) exceeds the known distribution of this species. *Dubautia syndetica* now appears to be restricted to a narrow zone extending from the summit of Kapalaoa S along the banks of the main (NE) branch of Wahiawa Stream and beyond to as far south as Mt. Kāhili.

The origin of *D. syndetica* through hybridization between *D. laxa* and *D. raillar-dioides* as hypothesized by Carr and Lorence

(1998) was recently examined using molecular RAPD markers (Caraway 1997). The findings of the molecular study were consistent with the interpretation of a hybrid origin of *D. syndetica*, but additional sampling including more species is needed to rigorously assess this hypothesis and more fully evaluate the possible parentage.

SPECIMENS EXAMINED: Kōloa: Headwaters of the main (NE) fork of Wahiawa Stream, S of Kapalaoa, ca. 685 m, *Carr et al. 1499* (BISH), *Carr et al. 1500* (BISH), ca. 716 m, 720 m, *Lorence et al. 6405* (PTBG).

Līhu'e: Wahiawa, Kapalaoa Peak, 915–930 m, *Wood et al. 840-D* (PTBG).

13. *Dubautia waialealae* Rock Bull. Torrey Bot. Club 37:303, 1910. Figure 4

Recent collections document the occurrence of *D. waialealae* near Kilohana, about 14 km from the nearest plants in the summit area of Wai'ale'ale. Unfortunately, the Kilohana population may consist of only a single individual. More exploration of this area is desirable. The flowering time remains as previously given (i.e., August to November). The Kilohana site extends the range of elevations occupied by the species considerably to about 1150–1600 m. This species hybridizes in nature with *D. imbricata* subsp. *acronaea* and also with *D. paleata* (Appendix).

SPECIMENS EXAMINED: Hanalei: Upper Hanakāpī'ai drainage and the N bog area along Wainiha rim (ridge to Hono'onāpali), 1130—1190 m, *Wood 5295* (PTBG); Wai'ale'ale summit area, 1524 m, *Wood 3895* (PTBG).

Hanalei/Waimea: N of Kilohana, near Wainiha rim, open boggy areas, TNC survey of Hono'onāpali Natural Area Reserve, transect 11, 1183 m, *Perlman et al. 9203* (BISH, PTBG).

Waimea: Alaka'i Wilderness Preserve, around Wai'ale'ale summit and 1 mile (1.6 km) to W, 1400–1600 m, *Wood & Doyle 126* (PTBG).

## LITERATURE CITED

BALDWIN, B. G., D. W. KYHOS, J. DVORAK, and G. D. CARR. 1991. Chloroplast DNA

- evidence for a North American origin of the Hawaiian silversword alliance (Asteraceae). Proc. Natl. Acad. Sci. U.S.A. 88:1840–1843.
- CARAWAY, V. 1997. Hybridization, introgression and speciation among *Dubautia* species (Asteraceae: Madiinae). M.S. thesis, University of Hawai'i at Mānoa, Honolulu.
- CARINO, D. M., and C. W. MORDEN. 1997. Identification of *Dubautia paleata* × *raillardioides* hybrids using RAPD markers. Newsl. Hawaii. Bot. Soc. 36:47–51.
- CARR, G. D. 1985. Monograph of the Hawaiian Madiinae (Asteraceae): Argyroxiphium, Dubautia, and Wilkesia. Allertonia 4:1–123.
- ——. 1998. Another new species of Dubautia (Asteraceae—Madiinae) from Kaua'i, Hawaiian Islands. Novon 8:8–11.
- CARR, G. D., and D. W. KYHOS. 1986. Adaptive radiation in the Hawaiian silversword alliance (Compositae—Madiinae). II. Cytogenetics of artificial and natural hybrids. Evolution 40:959–976.
- CARR, G. D., and D. H. LORENCE. 1998. A new species of *Dubautia* (Asteraceae—Madiinae) from Kaua'i, Hawaiian Islands. Novon 8:4–7.
- CARR, G. D., B. G. BALDWIN, and D. W. KYHOS. 1996. Cytogenetic implications of artificial hybrids between the Hawaiian silversword alliance and North American tarweeds (Asteraceae: Heliantheae—Madiinae). Am. J. Bot. 83:653–660.
- HOLMGREN, P. K., N. H. HOLMGREN, and L. C. BARNETT. 1990. Index Herbariorum. Part I. The herbaria of the world. Ed. 8. New York Botanical Garden, Bronx, New York.
- Maneval, W. E. 1936. Lacto-phenol preparations. Stain Technol. 11:9-11.

### APPENDIX

### NATURAL INTERSPECIFIC HYBRIDS

The following unstabilized hybrids among Kaua'i species of *Dubautia* are reported to occur in nature. The listing is strictly alphabetical according to formula name, and,

- where relevant, binomials are included as synonyms. Specimens are cited for hybrid combinations not previously reported and in those instances involving new material or new interpretations. Additional information and specimen citations may be found in Carr (1985).
- 1. Dubautia imbricata × D. laevigata × Dubautia media Sherff, Am. J. Bot. 20:617, 1933.
- Dubautia imbricata subsp. acronaea × D. waialealae
   Dubautia waialealae var. megaphylla Sherff, Am. J. Bot. 20:617, 1933.
- 3. Dubautia knudsenii subsp. knudsenii × D. laevigata
- 4. *Dubautia knudsenii* subsp. *knudsenii* × *D.* raillardioides

This material combines the peduncular glands of D. raillardioides with the trichomes and corolla glands of D. knudsenii subsp. knudsenii. The heads have a tendency to be slightly deflexed (a trait presumably inherited from D. knudsenii subsp. knudsenii). The corolla color is greenish yellow. In virtually all perceptible features these specimens appear to be intermediate to the putative parents. The cited material also closely matches artificially produced hybrids of the same parentage. Pollen stainability of this natural hybrid was 26% compared with 54% in the artificially produced hybrid, which exhibited a meiotic configuration of 12 pairs and a ring of four chromosomes (unpubl. data).

SPECIMENS EXAMINED: Waimea: Kōke'e State Park, Kauaikananā Stream, N of Mōhihi Road, 1050–1110 m, *Flynn et al. 4693* (BISH, HAW, PTBG).

5. Dubautia laevigata × D. laxa subsp. hirsuta × Dubautia mendax Sherff, Am. J. Bot. 20:617, 1933.

The cited specimens are intermediate in morphology to the putative parental species, with which they are closely associated. Pollen samples from two specimens contained 44% stainable grains. A cutting from *Carr 1370* was propagated and was maintained in cultivation for several years. Meiosis in this plant was characterized by the pairing configura-

tion of 12 bivalents and one chain of four chromosomes (unpubl. data).

SPECIMENS EXAMINED: Hanalei: Rim of Kalalau Valley near Kaluapuhi Trail Head between Kalalau and Pu'u o Kila Lookouts, 1220 m, *Carr 1370* (BISH, HAW, NY, UC, WS); Kōke'e, Kalalau Valley, just below trail along valley rim, ca. 1205 m, *Flynn & Lowrey 1875* (PTBG).

- 6. Dubautia laxa subsp. hirsuta × D. paleata specimens examined: Waimea: Near Wai'ale'ale, Brodie 4034 (BISH).
- 7. Dubautia laxa subsp. hirsuta × D. pauciflorula

Identification of the parents of this hybrid is problematic. An earlier collection closely matching the specimens cited here was denoted *Dubautia pauciflorula* × *D. raillardioides* (Carr 1985). However, none of these specimens possesses the peduncular glands so conspicuous in *D. raillardioides* and known hybrids with this species. Moreover, the leaves of these specimens, although largely glabrous, have coarse hairs along the midrib toward the base and are also proximally ciliate. These features are absent in *D. raillar-*

dioides and D. pauciflorula and, together with features of the receptacular bracts, suggest D. laxa subsp. hirsuta as one of the parents. The size of the heads and the prominence of the glands on the corolla tube and other features are consistent with the interpretation that D. pauciflorula is the other parent. Pollen samples of these plants have ranged from 26 to 50% stainable, and the meiotic pairing configuration includes a chain of four to perhaps a chain of six chromosomes in addition to bivalents (cf. Carr and Kyhos 1986).

SPECIMENS EXAMINED: Kōloa: Forested area NW of Wahiawa Bog, Flynn 586 (PTBG [2]), Carr et al. 1329 (BISH, HAW [2], PTBG, UC [2]); Wahiawa Bog, 640 m, Wagner et al. 5207 (BISH [2]).

- 8. Dubautia microcephala × D. plantaginea subsp. magnifolia
  Dubautia microcephala var. forbesii Sherff, Am. J. Bot. 20:617, 1933.
- 9. Dubautia paleata × D. waialealae
- 10. Dubautia pauciflorula × D. raillardioides See discussion under D. laxa subsp. hirsuta × D. pauciflorula (7).