

A Morphometric Analysis and Taxonomic Appraisal of the Hawaiian Silversword *Argyroxiphium sandwicense* DC. (Asteraceae)¹

ALAIN MEYRAT,² GERALD D. CARR,³ and CLIFFORD W. SMITH³

ABSTRACT: Morphometric techniques were used to examine the pattern of variation of 45 characters between the Haleakala and Mauna Kea populations of *Argyroxiphium sandwicense*. Qualitative features were also evaluated. A framework for a priori comparisons between the two populations of *A. sandwicense* was provided by including two additional species in the study, that is, *A. kauense* and *A. virescens* var. *paludosa*. The *F* tests of one-way analysis of variance indicate that the means of each of 18 characters differ significantly ($P \leq 0.05$) between the two populations of *A. sandwicense*. Based on the presence of quantitative differentiation and geographical isolation and the near absence of qualitative differentiation between the two populations, it is proposed to recognize them as two different subspecies: *A. sandwicense* ssp. *macrocephalum* (Haleakala) and *A. sandwicense* ssp. *sandwicense* (Mauna Kea). The study also indicates that *A. virescens* var. *paludosa*, *A. kauense*, and *A. sandwicense* are distinct from one another in several quantitative and qualitative characters. Taxonomically useful quantitative characters include inflorescence proportions, leaf proportions, number of ray florets per capitulum, and capitulum diameter. The subspecies of *A. sandwicense* can be recognized on the basis of inflorescence proportions. However, to separate all four taxa, based on quantitative characters, a combination of at least three of the foregoing features appear to be needed. A taxonomic key and descriptions for common taxa of *Argyroxiphium* of the island of Hawai'i and of East Maui are presented.

THE GENUS *Argyroxiphium* INCLUDES some of the most interesting species of the flora of the Hawaiian Islands. Of the six species in the genus, the best known is the spectacular silversword of Haleakala, Maui (*A. macrocephalum* Gray or *A. sandwicense* DC. s.l.). *Argyroxiphium* belongs to the family Asteraceae, tribe Heliantheae, subtribe Madiinae, and together with the closely related genera *Dubautia* and *Wilkesia* forms the Hawaiian tarweed com-

plex (Carlquist 1957, 1959a, 1959b), which according to Carr and Kyhos (1981) is one of the most remarkable examples of adaptive radiation known to science.

The morphological and anatomical characteristics of *Argyroxiphium* suggest that it is one of the few examples of adaptation to tropical alpine conditions (Carlquist 1957, 1974, Hedberg 1964, Coe 1967). The species are all endemic to particular habitats of very limited areas on high volcanoes of Maui and Hawai'i. Some of the species called *silverswords* grow on volcanic rock and cinder in areas that are virtual deserts. Other species called *greenswords* occur in boggy areas kept continually wet by precipitation and fog. The genus comprises subcaulescent or caulescent perennial shrubs crowned with an attractive rosette of crowded silvery or green leaves. After several years of growth as a rosette, they finally produce an elongated inflorescence of many

¹ Supported in part by contract CX 8000 8 0001 from the National Park Service and by NSF Grant DEB-7822819 to the second author. This paper is adapted from part of a thesis submitted to the Graduate Division of the University of Hawaii in partial fulfillment of the requirements for the M.S. degree in Botanical Sciences. Manuscript accepted 1 March 1983.

² Present affiliation: Facultad de Ciencias Agropecuarias, UNAN, Apartado 453, Managua, Nicaragua.

³ University of Hawaii, Department of Botany, 3190 Maile Way, Honolulu, Hawaii 96822.

radiate capitula. Many individuals of silverswords have a single axis and are monocarpic in habit. However, if branching occurs prior to bolting, as is often the case in greenswords, only the fertile axes die after flowering.

The type species of this genus, *Argyroxiphium sandwicense*, was described by De Candolle (1836) from specimens collected on Mauna Kea, Hawai'i (cf. Wilson 1922). *Argyrophyton douglasii* of Hooker (1837a) was also based on material from Mauna Kea. Hooker (1837b) later acknowledged that his own name for the Mauna Kea material was superfluous, and in fact correctly applied De Candolle's earlier binomial.

In 1852, Gray described a silversword collected in Haleakala Crater, Maui, and named it *Argyroxiphium macrocephalum*. However, Hillebrand (1888) treated the same taxon as *A. sandwicense* var. *macrocephalum*. Keck (1936), in his monographic revision of the genus, merged the silverswords of the two different islands in the single taxon *A. sandwicense*. The recognition of two discrete taxa by both Gray and Hillebrand was based on some morphological differences between the populations of Haleakala and Mauna Kea silverswords. Gray, Hillebrand, and Keck obviously had different opinions regarding the taxonomic importance of these mostly quantitative morphological differences. These different opinions and a paucity of new observations have led to a persistent uncertainty regarding the taxonomic status of the Haleakala and Mauna Kea silverswords.

However, the taxonomic resolution of these populations of silverswords is especially important because the only known population of the Mauna Kea silversword is extremely small. Only 27 to 150 plants have been reported to remain in the Wailuku River drainage (Bryan 1973, Landgraf 1973). A clarification of the taxonomic status of the Mauna Kea population is a prerequisite to the development of effective plans for its management or recovery.

In the present study, morphometric techniques were used to assess the pattern of variation of 45 vegetative and reproductive characters among populations of the silver-

swords *A. sandwicense* s.l. and *A. kauense* (Rock & Neal) Deg. & Deg., and a greensword, *A. virescens* Hbd. var. *paludosa* St. John. An analysis of these patterns provides a framework to reexamine the classification of the Mauna Kea and Haleakala populations. Based on the results of this analysis it seems most appropriate to recognize both populations of *A. sandwicense* s.l. at the subspecies level. Hereafter, to avoid confusion, the Mauna Kea silversword will be referred to as *Argyroxiphium sandwicense* ssp. *sandwicense* and the Haleakala silversword as *Argyroxiphium sandwicense* ssp. *macrocephalum*.

MATERIALS AND METHODS

Morphological characters of five populations of *Argyroxiphium* were assessed (Table 1). A total of 49 flowering plants was studied. These provided a basis for analyzing 45 quantitative characteristics. Some vegetative features were observed in 36 additional non-flowering individuals. A limited number of vegetative and reproductive features were also observed in 16 incomplete individuals in various stages of decline. Altogether, 101 individuals provided data for the study (Table 2).

Of the 45 quantitative characters (Table 3), 8 were assessed in the field in every complete individual studied. Some floral parts were collected in plastic bags for later measurement in the laboratory. No magnification was used for 14 laboratory measurements, and 23 measurements were made using magnification (Table 3). The measurements were made with a measuring tape or a ruler, whichever was most suitable for the plant part being measured. For rigid structures that could not be straightened—for example, achenes—the measured distance was a straight line from one extreme to the other, curvature not being considered. The width was determined at the midpoint of the long axis of a given structure. In order to avoid repetition, the counted capitula were marked with ink. The number of ray and disk florets were determined by counting the number of their respective achenes, because some corollas abscised early.

For six field measurements there is only one

TABLE 1
POPULATIONS OF *Argyroxiphium* STUDIED

TAXON	LOCATION
<i>A. kauense</i>	Kahuku Ranch, Mauna Loa, ca 1830 m elev.
<i>A. kauense</i>	In a kipuka east of Power Line Road, Saddle Road, Hawai'i, ca 1650 m elev.
<i>A. sandwicense</i> ssp. <i>sandwicense</i>	Origin of Wailuku drainage, Mauna Kea, Hawai'i, ca 2850 m elev.
<i>A. sandwicense</i> ssp. <i>macrocephalum</i>	Haleakala Crater, Maui, ca 2100–2700 m elev.
<i>A. virescens</i> var. <i>paludosa</i>	Ridge between Kipahulu and Kuhiwa Valleys, Hana Forest, Maui, ca 1650–1900 m elev.

TABLE 2
NUMBER AND CONDITION OF SAMPLES OF EACH POPULATION OF *Argyroxiphium* ASSESSED

POPULATION	NUMBER OF FLOWERING PLANTS		NUMBER OF VEGETATIVE OR DRY PLANTS		TOTAL
	1977	1978	1977	1978	
<i>A. kauense</i> , Power Line kipuka bog	1	0	13	6	20
<i>A. kauense</i> , Kahuku Ranch	0	10	17	1	28
<i>A. sandwicense</i> ssp. <i>sandwicense</i>	1	4	5	0	10
<i>A. sandwicense</i> ssp. <i>macrocephalum</i>	4	25	4	0	33
<i>A. virescens</i> var. <i>paludosa</i>	4	0	2	0	6
TOTALS	10	39	41	7	97

NOTE: The inflorescence and height measurements of four individuals of *A. sandwicense* ssp. *sandwicense* that flowered in 1982 are also included in the analysis.

value per individual. Because of variation in leaves with respect to their position in the rosette, measurements were repeated nine times in each individual. Thus, three measurements were taken at the top, three at the middle, and three at the bottom part of the rosette. The measurements for the remaining characteristics were repeated at least five or six times per individual. An attempt was made to avoid bias in obtaining measurements.

After quantitative data were collected, a mean of the variation within each individual was obtained. This mean was considered as a single observation for a given individual. A group of observations for a given character pertaining to a given population constitutes a treatment for the statistical tests.

The variation of each morphological char-

acter among five populations was evaluated by one-way analysis of variance. An a priori comparison of the Haleakala and Mauna Kea silversword populations was inherent in this analysis. The *F* tests of individual characters, taken collectively, provided a basis to assess the total morphological differentiation of these populations. In addition, an a posteriori test, Tukey's studentized range test, was used to compare the means of each character for each of the populations of *Argyroxiphium*. For the statistical methods, the procedures outlined in Sokal and Rohlf (1981) were followed. To facilitate the statistical calculations, the 1982 SAS Statistical Programs were run on the University of Hawaii IBM 370 computer. None of the data sets used in the analyses were balanced so that considerable caution has

TABLE 3

LIST OF CHARACTERS ASSESSED AND RESULTS OF ANALYSIS OF VARIANCE IN FIVE POPULATIONS OF *Argyroxiphium*

Field measurements	20. Receptacle diameter ^c
1. Plant height	21. Number of peripheral receptacular bracts ^c
(including branched plants) ^b	22. Number of inner receptacular bracts*
(excluding branched plants) ^c	
2. Rosette height	Laboratory measurements with magnification
3. Rosette width ^c	23. Involucral bract length
4. Inflorescence length	24. Involucral bract width*
(including branched plants) ^b	25. Inner receptacular bract length*
(excluding branched plants) ^c	26. Inner receptacular bract width*
5. Inflorescence width	27. Ligule length
(including branched plants) ^c	28. Ligule width
(excluding branched plants) ^a	29. Ray floret tube length ^b
6. Number of capitula per inflorescence	30. Number of ligule lobules*
7. Leaf length ^a	31. Number of main veins per ligule ^c
8. Leaf width ^c	32. Ray floret style length
	33. Ray floret style branch length
Laboratory measurements without magnification	34. Ray achene length ^b
9. Capitulum length	35. Ray achene width
10. Capitulum diameter ^b	36. Number of ray achene ribs*
11. Number of ray florets per capitulum ^c	37. Disk floret length
12. Number of disk florets per capitulum ^b	38. Disk floret width*
13. Peduncle length ^a	39. Disk floret style length ^a
14. Peduncle width ^a	40. Disk floret style branch length
15. Bract length	41. Stamen filament length ^b
16. Bract width	42. Anther length
17. Number of bractlets per peduncle	43. Disk achene length
18. Bractlet length	44. Disk achene width
19. Bractlet width*	45. Number of disk achene ribs*

NOTE: Characters that do not differ significantly ($P \leq 0.05$) among populations of *Argyroxiphium* as determined by the F test from one-way analysis of variance are indicated by an asterisk *. Characters that differ significantly between *A. sandwicense* ssp. *sandwicense* and *A. sandwicense* ssp. *macrocephalum* as determined by the F test from one-way analysis of variance are designated with a superscript as follows: a, $0.05 \geq P > 0.01$; b, $0.01 \geq P > 0.001$; c, $P \leq 0.001$.

been exercised in the interpretation of the results. All data were tested for normalcy prior to statistical analysis.

The variation of qualitative morphological features such as type, shape, color, and indumentum of structures of traditional taxonomic importance was also studied in each of the populations.

In those instances where a character is limited to a single measurement per individual, the mean value is identified by \bar{x} in the taxonomic section. However, where multiple measurements per individual were made, the mean of mean values is reported as $\bar{\bar{x}}$. Each of the quantitative characters of the species *Argyroxiphium sandwicense* is described by using an average of the mean values of the subspecies, and these are identified in the taxonomy section by \bar{x}_{ab} or $\bar{\bar{x}}_{ab}$.

Voucher specimens for this study have been deposited in the University of Hawaii herbarium (HAW).

RESULTS

The F tests from one-way analysis of variance of 45 characters indicate that the means of 36 differ significantly ($P \leq 0.05$) at least between two of the five populations of *Argyroxiphium* examined. Of special interest here is the fact that the means of each of 18 characters differ significantly ($P \leq 0.05$) between *A. sandwicense* ssp. *sandwicense* and *A. sandwicense* ssp. *macrocephalum* (Table 3). Of those 18 characters, 6 differ significantly at $P \leq 0.001$, 5 differ significantly at $0.01 \geq P > 0.001$, and 4 differ significantly at $0.05 \geq P > 0.01$ (Table 4). The means of three charac-

TABLE 4

POPULATION STATISTICS AND RESULTS OF TUKEY'S STUDENTIZED RANGE TEST FOR CHARACTERS VARYING AMONG FIVE POPULATIONS OF *Argyroxiphium*

CHARACTER	POPULATION STATISTICS				
	K1	K2	SM	SS	VP
Plant height (m)					
including branched plants	1.43 ± 0.24 AB 1.08 – 1.76 7	2.15 ± 0.43 C 1.48 – 3.01 18	1.46 ± 0.34 AB 0.90 – 2.32 31	1.88 ± 0.61 BC 0.98 – 2.80 11	1.18 ± 0.28 A 0.75 – 1.49 6
excluding branched plants	1.43 ± 0.24 A 1.08 – 1.76 7	2.15 ± 0.43 B 1.48 – 3.01 18	1.51 ± 0.32 A 1.02 – 2.32 28	2.54 ± 0.26 B 2.25 – 2.80 4	1.18 ± 0.28 A 0.75 – 1.49 6
Inflorescence length (m)					
including branched plants	1.17 ± 0.21 A 0.9 – 1.38 6	1.48 ± 0.30 A 1.08 – 2.21 18	1.10 ± 0.26 A 0.65 – 1.52 31	1.46 ± 0.50 A 0.74 – 2.50 13	0.57 ± 0.08 B 0.49 – 0.70 6
excluding branched plants	1.17 ± 0.21 A 0.9 – 1.38 6	1.48 ± 0.30 A 1.08 – 2.21 18	1.11 ± 0.24 A 0.65 – 1.52 28	1.97 ± 0.32 B 1.70 – 2.50 5	0.57 ± 0.08 C 0.49 – 0.70 6
Inflorescence width (cm)					
including branched plants	21.0 ± 1.4 A 20.0 – 22.0 2	23.1 ± 3.9 A 15.0 – 29.0 11	43.7 ± 12.4 B 23.0 – 77.5 29	26.2 ± 4.4 A 16.0 – 33.0 13	33.3 ± 4.1 AB 30.0 – 40.0 6
excluding branched plants	21.0 ± 1.4 A 20.0 – 22.0 2	23.1 ± 3.9 A 15.0 – 29.0 11	44.4 ± 12.4 B 28.5 – 77.5 26	29.8 ± 1.9 AB 28.0 – 33.0 5	33.3 ± 4.1 AB 30.0 – 40.0 6
Peduncle length (cm)	9.5 ± 1.0 A 6.5 – 12.5 2	9.5 ± 1.9 A 3.1 – 14.3 10	16.3 ± 4.1 B 3.5 – 40.0 29	11.5 ± 2.0 AB 5.0 – 18.5 5	10.7 ± 5.3 AB 1.0 – 19.5 4
Bract length (cm)	8.9 ± 2.8 A 3.5 – 15.0 3	10.4 ± 1.8 AB 2.0 – 26.0 10	14.0 ± 2.2 B 4.5 – 26.0 29	13.0 ± 2.4 B 5.5 – 28.7 5	10.1 ± 3.0 AB 6.0 – 15.3 4
Number of capitula per inflorescence	171.7 ± 33.0 AB 120 – 202 6	268.0 ± 63.7 A 154 – 350 11	265.2 ± 101.1 A 99 – 637 31	193.4 ± 128.5 AB 52 – 395 5	135.2 ± 41.0 B 75 – 200 6
Number of disk florets per capitulum	144.6 ± 43.3 A 114 – 221 1	142.8 ± 32.1 A 45 – 214 10	320.1 ± 69.6 B 120 – 600 29	216.2 ± 71.0 AB 47 – 471 5	165.4 ± 26.7 A 100 – 271 4
Number of ray florets per capitulum	6.8 ± 1.5 A 5 – 8 1	8.2 ± 1.4 A 3 – 11 10	23.6 ± 5.4 B 11 – 42 29	12.5 ± 3.0 A 5 – 20 5	2.4 ± 1.3 A 1 – 8 4

TABLE 4 (Cont.)

CHARACTER	POPULATION STATISTICS				
	K1	K2	SM	SS	VP
Number of peripheral receptacular bracts per capitulum	41.2 ± 7.4 A	36.0 ± 2.4 A	70.8 ± 13.1 B	50.7 ± 6.6 AB	31.7 ± 2.3 A
	33 - 53	22 - 42	32 - 115	31 - 75	24 - 46
	1	10	29	5	4
Rosette diameter (cm)	56.3 ± 6.7 AB	59.5 ± 11.3 A	58.7 ± 12.8 AB	38.9 ± 18.0 C	44.5 ± 5.3 BC
	43.0 - 66.0	33.0 - 83.0	37.0 - 90.0	19.0 - 80.0	36.0 - 52.0
	12	16	33	10	6
Rosette height (cm)	29.5 ± 9.9 A	28.6 ± 13.5 A	33.1 ± 11.3 AB	29.8 ± 10.2 A	45.5 ± 17.0 B
	10.0 - 46.0	12.0 - 55.0	18.0 - 66.5	18.0 - 49.0	26.0 - 71.0
	13	18	29	10	6
Leaf length (cm)	30.3 ± 4.5 AB	31.6 ± 3.8 A	22.7 ± 3.8 CD	25.8 ± 4.5 BC	18.8 ± 3.7 D
	12.0 - 42.0	23.2 - 39.5	13.0 - 32.5	18.0 - 39.0	6.5 - 28.0
	12	20	31	9	6

NOTE: The first line of each entry includes mean, standard deviation, and one or more letters; means sharing one or more of the same letters are not significantly different. The second line of each entry gives the range; the overall range is given even where a mean of means is provided in the first entry. The last line in each entry indicates the number of individual plants that provided measurements; a single plant may provide a number of measurements (see Methods). K1 = *A. kauense* (Kahuku Ranch); K2 = *A. kauense* (Power Line Road); SM = *A. sandwicense* var. *macrocephalum*; SS = *A. sandwicense* var. *sandwicense*; VP = *A. virescens* var. *paludosa*.

ters—that is, plant height, inflorescence length, and inflorescence width—differed significantly at different levels depending on whether observations from branched plants were included or excluded from the data sets.

Tukey's studentized range test indicates that none of the means of characters are significantly heterogeneous among all five populations. The means of 12 characters differ significantly among only some of the five populations (Table 4). Furthermore, the means of five of these characters differ significantly between the Mauna Kea and Haleakala populations of *A. sandwicense*. However, branching of plants affects the outcome of the test in three of these characters, that is, plant height, inflorescence length, and inflorescence width. The Tukey test does not reveal significantly heterogeneous means for the remaining 33 characters.

A graphic summary of pairwise comparisons of all of the populations for the 12 characters found to vary by the Tukey test aids in visualizing the results (Figure 1). Based solely on these characters *A. sandwicense* ssp. *macrocephalum* is more similar to ssp. *sandwicense* than to the other taxa. By the same criteria, however, *A. sandwicense* var. *sandwicense* is more similar to the populations of *A. kauense* than to *A. sandwicense* var. *macrocephalum*. The highest degree of similarity found was between the two populations of *A. kauense*, which differ significantly only in plant height (Figure 1, Table 4).

Although comparison of one or two characters at a time often permits distinction of two or more of the four taxa considered here, simultaneous comparison of three features appears to be required for complete resolution of all four. For example, perhaps the best resolution is attained when the individuals are plotted as a function of leaf length–width ratio, inflorescence length–width ratio, and ray floret number in three dimensional fashion (Figure 2).

Qualitative features such as leaf indument, ligule color, and pappus condition also aid in the recognition of *Argyroxiphium sandwicense*, *A. kauense*, and *A. virescens* var. *paludosa*. The style of *A. kauense* differs from that of the other two species. *Argyroxiphium sandwicense*

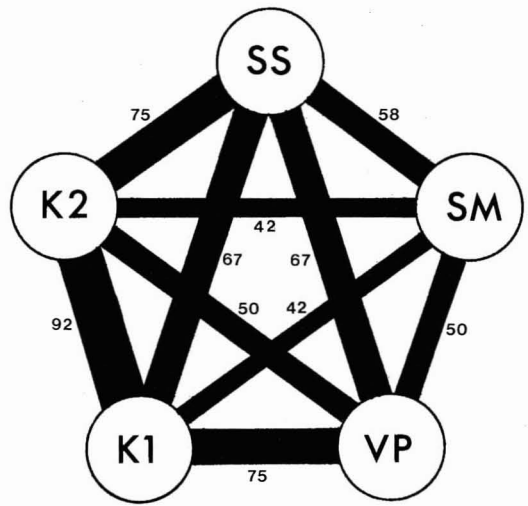


FIGURE 1. Similarity index of five populations of *Argyroxiphium* based on the 12 variable characters identified in Table 4. The numbers indicate the percent of quantitative characters in each pairwise comparison that do not differ significantly according to the Tukey test. The widths of the lines between populations are proportional to their similarities. Population abbreviations are explained in Table 4.

ssp. *sandwicense* has a higher frequency of partially paniculate inflorescences and sessile capitula at the base of the inflorescence than other taxa. These and other qualitative characters are dealt with more fully in the taxonomic section.

DISCUSSION

All five of the characters indicated as being significantly different between the two subspecies of *Argyroxiphium sandwicense* by the Tukey test (Table 4) were also identified as differing significantly between the two subspecies of *A. sandwicense* by the *F* test (Table 3). These were rosette diameter, inflorescence width, inflorescence length, plant height, and the number of ray florets per capitulum. The results of both tests were affected by inclusion of data from branching plants for three characters, that is, plant height, inflorescence length, and inflorescence width. No attempt

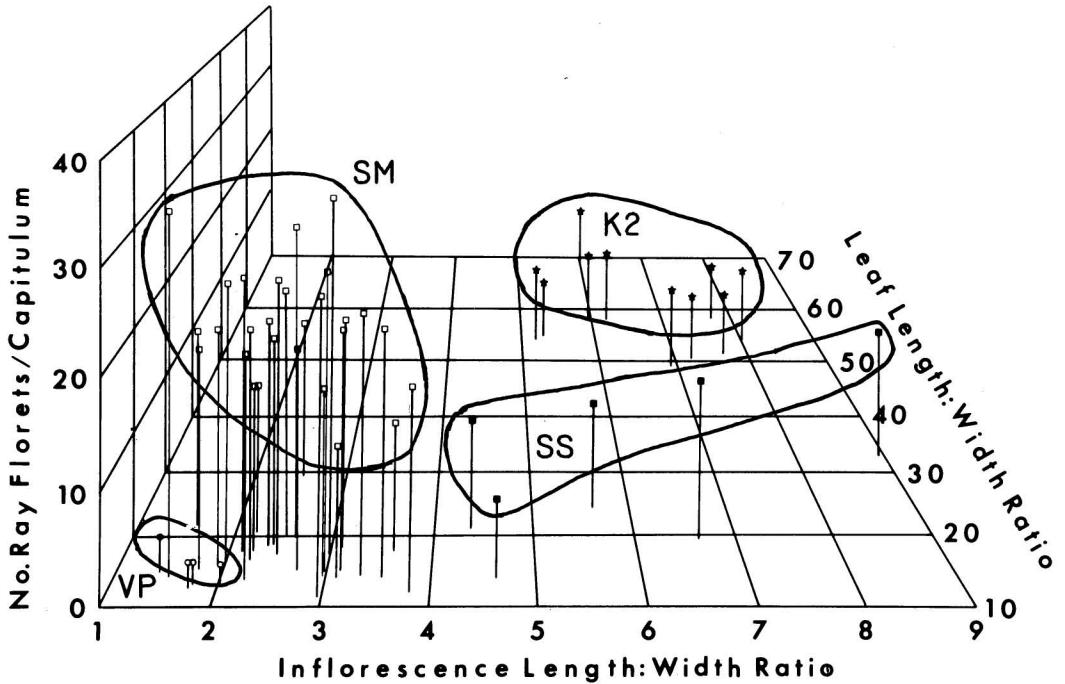


FIGURE 2. Scatter diagram of the relationship among inflorescence length : width ratio, leaf length : width ratio, and number of ray florets per capitulum of infrageneric taxa of *Argyroxiphium*. Symbols as in Table 4.

was made to determine to what degree these different responses may be due to changes in the sizes of inherently small samples as opposed to the possible effect of plant branching per se. Unfortunately, the very small size of the remaining population of the Mauna Kea silversword and the extremely low frequency of flowering precludes resolution of this question within a reasonable time frame.

The *F* test specifies 13 additional characters differing significantly between the Mauna Kea and Haleakala populations and as a result appears to be the best indicator of differentiation between the two subspecies of *Argyroxiphium sandwicense*. However, the conservatism of the Tukey test is especially desirable in this study because some of the sample sizes are quite small and there is considerable disparity between them. In addition, by identifying the characters that vary among the taxa, the Tukey test provided a framework to evaluate the taxonomic importance of the infraspecific

differences in each of the total of 18 characters specified as significant by the *F* test.

Among the 18 characters that differ significantly between the two subspecies of *Argyroxiphium sandwicense*, those taxonomically most useful appear to be inflorescence length, inflorescence width, and number of ray florets per capitulum. In fact, a given individual of either subspecies can be recognized by the proportion of its inflorescence. In *A. sandwicense* ssp. *macrocephalum* the length : width ratio of the inflorescence ranges from 1.5 : 1.0 to 3.8 : 1.0, whereas in *A. sandwicense* ssp. *sandwicense* this ratio ranges from 4.3 : 1.0 to 8.6 : 1.0. However, to separate all four of the taxa considered in this study based on quantitative characters, it seems that at least three features are needed, for example, inflorescence proportions, leaf proportions, and number of ray florets per capitulum (Figure 2).

Although few individuals were observed from the remaining population of *Argyroxiphium*

phium sandwicense ssp. *sandwicense*, other evidence also supports the taxonomic disposition proposed in this paper. The plates of plants from Mauna Kea presented independently by De Candolle (1838) and Hooker (1837b) show capitula with numbers of ray florets in the range found in this study for *A. sandwicense* ssp. *sandwicense*. Larger capitula of plants from Haleakala were reported by Gray (1852, 1861, Ms.) and Hillebrand (1888). Gray (1861) reported a capitulum diameter for the Mauna Kea silversword in the range found in this study. The number of ray florets per capitulum and the number of peripheral receptacular bracts of both populations were reported by Gray (1861, Ms.) and Hillebrand (1888). Leaf length and leaf width were reported by Gray (1861) and Hillebrand (1888) for Mauna Kea material. Inflorescence length and shape, peduncle length, number of bractlets, and achene length were also described by Hillebrand (1888) for Mauna Kea plants. In all of these cases the measurements of Mauna Kea and Haleakala silverswords fall within the ranges found for *A. sandwicense* ssp. *sandwicense* and ssp. *macrocephalum*, respectively, in the present study.

In addition, a specimen collected on Mauna Kea (Forbes 880H, BISH) has bract, peduncle, and capitulum measurements; peripheral receptacular bract, ray floret, and disk floret numbers; and ray and disk achene proportions in the respective ranges found for *A. sandwicense* ssp. *sandwicense* in this study. Moreover, a published photograph of a Mauna Kea silversword (Landgraf 1973) has inflorescence proportions similar to the individuals of ssp. *sandwicense* assessed in this study. An inflorescence length : width ratio of 4.5 : 1.0 is estimated from the photograph.

Although now severely restricted in size and numbers, the Wailuku River population of *Argyroxiphium sandwicense* ssp. *sandwicense* was once much more extensive. In fact, early accounts and collections of this taxon indicate that it was once a major widespread component of the alpine vegetation on the upper flanks of Mauna Kea (Carr and Meyrat 1982).

According to Davis and Heywood (1963), the subspecies category has been widely

accepted as a considerable segment of a species with a generally distinct geographical area and more or less distinct morphology. Many subspecies are often distinguished by several small and usually quantitative differences. Since the two major segments of *Argyroxiphium sandwicense*, one on Maui and one on Hawai'i, meet the foregoing criteria, the category of subspecies seems most appropriate. The two subspecies of *A. sandwicense* are less similar to each other than ssp. *sandwicense* is to *A. kauense* or *A. virescens* in the quantitative characters assessed (cf. Figure 1, Table 4). In fact, the average interspecific similarity index (0.59, calculated from Figure 1) is almost identical to the similarity index (0.58) of the two subspecies of *A. sandwicense*. However, *A. kauense*, *A. virescens*, and *A. sandwicense* are all quite markedly differentiated in a qualitative sense in addition to differing in a number of quantitative characters. The relatively small amount of qualitative differentiation between the Mauna Kea and Haleakala silverswords makes it imprudent to argue for their separation at the specific level.

A key to the subspecies of *Argyroxiphium sandwicense* and other common taxa of East Maui and Hawai'i is presented in the section on taxonomy. *Argyroxiphium forbesii* (St. John 1971) and *A. virescens* var. *virescens* (Hillebrand 1888) are excluded from this key because little information is available for these taxa. The former species is known only from the type specimen, and the latter species has apparently not been collected during the past 50 years.

TAXONOMY

Argyroxiphium DC. Prodr. 5: 668. 1836; Coll. Mem. 9. Pl. 8. 1838.

Argyrophyton Hook. Comp. Bot. Mag. 2: 163. 1837; Icon. Plant. Vol. 1, pt. 3, pl. 75. 1837.

DESCRIPTION: Subcaulescent to caulescent perennials; mostly herbaceous, but with a short, erect, sometimes creeping woody stem crowned with numerous leaves spirally arranged into a subspherical rosette 5–90 cm in dia-

meter; axis branched or unbranched; inflorescence produced by rapid bolting process after long period of vegetative growth; unbranched plants monocarpic. Leaves rigid, entire, sessile, dilated at the base, linear to linear-lanceolate, flat, triangular, or rhomboid in cross section, 3–32 cm long, 0.2–2.0 cm wide at the mid-point, longitudinally nerved, brilliantly silver floccose-sericeous to gray tomentose-sericeous or glabrate and dark green. Inflorescence an erect raceme or panicle, oblong to lanceolate, essentially acropetal or bidirectional, comprising 5–630 more or less helicoidally arranged capitula; rachis hollow, 0.3–3.5 m long, 4–9 cm in diameter; peduncular bracts lanceolate, glandular-pilose, smaller above, large and more leaflike below; peduncle hollow, compressed, rigid, 4–40 cm long, bearing one large capitulum or less often up to 10 smaller capitula; bractlets yellowish, oblanceolate, glandular pilose. Capitulum 0.8–3.5 cm long, 1.0–4.3 cm in diameter; receptacle usually convex to conical, glabrous; involucre campanulate to hemispheric; involucral bracts oblanceolate with attenuate bases, acute or acuminate apices, glandular-pilose without and glabrous and shiny within, enfolding the ray achenes, arranged in a single row, basally adnate to the peripheral receptacular bracts, and where very numerous, sometimes also

basally connate; peripheral receptacular bracts glabrous, shiny at the base, glandular-pilose on the apical dorsa and margins, connate, usually in only one row, this constituting the receptacular cup; inner receptacular bracts few or absent, similar to peripheral bracts but narrower. Ray florets 1–42, pistillate, fertile; ligule 3–20 mm long, 2–5 mm wide, usually three lobed, nearly white to yellow or rose or wine-red. Ray achenes linear, 4–14 mm long, arcuate, generally four to five ribbed, blackish; pappus present at the dorsal tip, 0.0–2.0 mm long, truncate and coroniform or reduced to a single scale or absent. Disk florets 75–600, perfect, fertile, 4–7 mm long, mostly funnel-form, sometimes campanulate, rarely suburceolate, distally flared into five deltoid lobes 0.5–1.0 mm long; anthers basally obtuse, terminally appendaged; the two style branches linear, flat, widened at deltoid end with dense penicillate collecting hairs, rarely truncate. Disk achenes linear, slightly arcuate, 5–15 mm long, generally four to five ribbed; pappus of 1–11 short, broad, unequal, acute or obtuse scales, rarely absent or sometimes merely reduced, the reduction most pronounced on the ventral apex of the achene.

TYPE SPECIES: *Argyroxiphium sandwicense* DC.

KEY TO THE COMMON TAXA OF *Argyroxiphium* OF EAST MAUI AND HAWAI'I

1. Foliage glabrate, green; the leaves flat, conspicuously nerved; ray florets 1–8, nearly always less than 4 (Maui) 1. *Argyroxiphium virescens* var. *paludosa*
1. Foliage silvery sericeous, dull gray to brilliantly silvery; the leaves triangular to rhomboidal in cross section, not conspicuously nerved; ray florets 3–42, nearly always more than 5.
 2. Leaves silvery gray (dull in herbarium specimens), sericeous, but the hairs not totally occluding the surface, more than 45 times longer than broad, rosette often elevated on a short stem; ligules yellow to white, occasionally tinged with wine-red (Hawai'i) 2. *A. kauense*
 2. Leaves brilliantly silvery (even in herbarium specimens), copiously floccose-sericeous, the mat of hairs totally occluding the surface, mostly less than 45 times longer than broad; rosette nearly always sessile; ligule deep wine-red to pale pink, very rarely yellow 3. *A. sandwicense*
3. Inflorescence 4.3–8.6 (\bar{x} = 5.8) times longer than broad; ray florets 5–20 (\bar{x} = 12.5) (Hawai'i). 3A. *A. sandwicense* ssp. *sandwicense*
3. Inflorescence 1.5–3.8 (\bar{x} = 2.5) times longer than broad; ray florets 11–42 (\bar{x} = 23.6) (Maui). 3B. *A. sandwicense* ssp. *macrocephalum*

1. *Argyroxiphium virescens* Hbd. var. *paludosa* St. John Pac. Sci. 25: 70–73. 1971.

DESCRIPTION: Mostly herbaceous, but basally woody rosette plant, the woody basal portion below the leaves 3–50 (\bar{x} = 16.2) cm long, rarely up to 1.2 m long, 3.5–5.0 (\bar{x} = 4.2) cm thick, the open rosette 26–71 (\bar{x} = 45.5) cm long, 36–52 (\bar{x} = 44.5) cm in diameter; the axis usually branched. Leaves flexible, straight or recurved, flat and thick in cross section, ligulate, subcuneate toward the dilated base, the margin remote serrulate toward the acute apex, 6.5–28.0 (\bar{x} = 18.8) cm long, 0.9–2.0 (\bar{x} = 1.4) cm wide at the midpoint, dark green, glabrate above, sparsely pilosulous below and more densely pilosulous-ciliate on the margin, seven to nine parallel nerves raised and evident below, marked above by narrow furrows. Raceme simple or partially paniculate, broadly elliptic to lanceolate, 0.5–0.7 (\bar{x} = 0.6) m long, 30–40 (\bar{x} = 33.3) cm wide, bearing 75–200 (\bar{x} = 135.2) capitula, sometimes ending with a terminal capitulum; bracts 6.0–15.3 (\bar{x} = 10.1) cm long, 0.8–1.8 (\bar{x} = 1.4) cm wide; peduncles 1.0–19.5 (\bar{x} = 10.7) cm long, 2–5 (\bar{x} = 3.6) mm wide, branched or more often unbranched, bearing 0–4 smaller capitula in addition to the large terminal one; bractlets 1–11 (\bar{x} = 4.4), 1.5–4.6 (\bar{x} = 2.7) cm long, 0.2–0.7 (\bar{x} = 0.4) cm wide. Capitula 1.4–2.0 (\bar{x} = 1.6) cm long, 1.1–2.1 (\bar{x} = 1.5) cm in diameter; receptacle conical, 0.5–0.8 (\bar{x} = 0.7) cm in diameter; involucre bracts as many as ray florets, 0.9–1.3 (\bar{x} = 1.2) cm long, 1–3 (\bar{x} = 2.6) mm wide; peripheral receptacular bracts 24–46 (\bar{x} = 31.7); inner receptacular bracts 0–1 (\bar{x} = 0.2), 0.7–0.8 (\bar{x} = 0.8) cm long, 0.5 mm wide. Ray florets zero to eight (\bar{x} = 1.4); tube 0.2–0.4 (\bar{x} = 0.3) cm long; ligule mimosa yellow and white, sometimes with wine-red tinges, 0.6–0.7 (\bar{x} = 0.62) cm long, 0.3–0.4 (\bar{x} = 0.34) mm wide, three to four (\bar{x} = 3.4) lobed, four to six (\bar{x} = 4.9) veined; style 0.4–0.5 (\bar{x} = 0.45) cm long, 2 branched, the branches slightly arcuate-descending 1–2 (\bar{x} = 1.6) mm long. Ray achene 0.6–0.8 (\bar{x} = 0.7) cm long, 1–2 (\bar{x} = 1.3) mm wide, four to five (\bar{x} = 4.5) ribbed; pappus reduced. Disk florets 100–271 (\bar{x} = 165.4),

glabrous, narrowly campanulate, sometimes suburceolate, 0.5–0.6 (\bar{x} = 0.57) cm long, 1.0–2.0 (\bar{x} = 1.6) mm wide; style 0.6–0.8 (\bar{x} = 0.7) cm long, two branched, the branches 1–2 (\bar{x} = 1.95) mm long; stamen filament 2.0 mm long; anther 2.0 mm long. Disk achene 0.6–0.7 (\bar{x} = 0.67) cm long, 1.0 mm wide, 4–5 (\bar{x} = 4.5) ribbed; pappus of 2–3 acute scales.

TYPE: Hawaiian Islands, Maui Island, Haleakala, Kipahulu-Kuhiwa divide, among sedges in swamp, 6400 ft alt, 21 Aug. 1945, *H. St. John and A. L. Mitchell* 21000 (HOLOTYPE: BISH!).

SELECTED SPECIMENS EXAMINED: Hawaiian Islands, Maui Island, Hana Forest, bogs between Kipahulu and Kuhiwa Valleys, 2 Aug. 1977, *Meyrat, Carr, & Stemmermann* 52, 53 (HAW).

2. *Argyroxiphium kauense* (Rock & Neal) Deg. & Deg. Fl. Haw. 27 Dec. 1957.

Argyroxiphium sandwicense DC. var. *kauense* Rock and Neal Occ. Pap. B. P. Bishop Mus. 22(4): 31–33. 1935.

Figures 3A, 4A, 5A

DESCRIPTION: Mostly herbaceous, but basally woody rosette plant, the woody portion below the leaves 3–70 (\bar{x} = 40) cm long and 3.5–7.5 (\bar{x} = 5.1) cm thick, the loose subspherical rosette 12–55 (\bar{x} = 28.6) cm high and 33–83 (\bar{x} = 59.5) cm in diameter; the axis usually unbranched and monocarpic, but sometimes branching. Leaves flexible, smoothly arcuate ascending or straight, succulent, linear, rhomboidal in cross section, 23.2–39.5 (\bar{x} = 31.7) cm long, 0.4–0.8 (\bar{x} = 0.6) cm wide at the midpoint, grayish silvery sericeous on a light green background. Raceme simple, or very rarely partially paniculate, narrowly elliptic, 1.1–2.2 (\bar{x} = 1.5) m long, 15–29 (\bar{x} = 23.1) cm wide, bearing 154–350 (\bar{x} = 268) capitula, usually with a terminal capitulum 1.7–2.2 (\bar{x} = 2.0) cm long and 1.6–2.2 (\bar{x} = 2.0) cm in diameter; bract 2–26 (\bar{x} = 10.4) cm long, 0.3–1.6 (\bar{x} = 0.9) cm wide; peduncle 3.1–14.3 (\bar{x} = 9.5) cm long, 1–3 (\bar{x} = 2.2) mm wide; bractlets 1–3 (\bar{x} = 2.4) per peduncle, 1.3–3.3

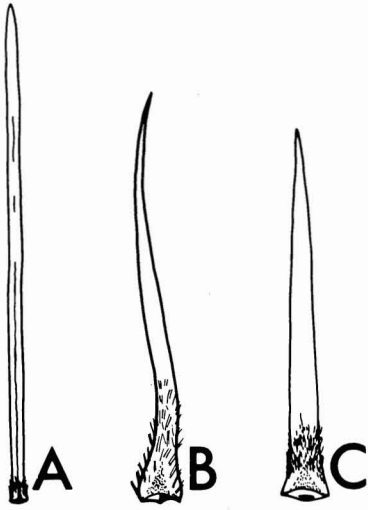


FIGURE 3. Leaves of three taxa of *Argyroxiphium*. A, *A. kauense*; B, *A. sandwicense* ssp. *sandwicense*; C, *A. sandwicense* ssp. *macrocephalum*. Note proportions and shapes. Reduced to ca 5/16.

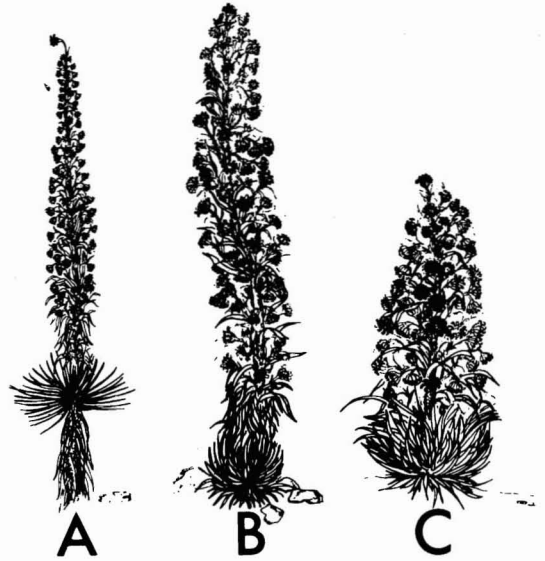


FIGURE 5. Habit of three taxa of *Argyroxiphium*. A, *A. kauense*; B, *A. sandwicense* ssp. *sandwicense*; C, *A. sandwicense* ssp. *macrocephalum*. Note inflorescence proportions and shape. Reduced to 1/25.

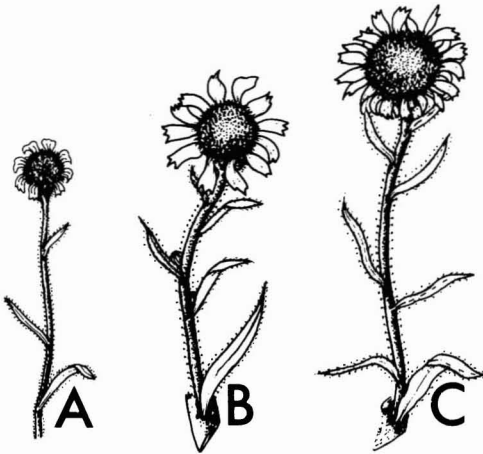


FIGURE 4. Capitulum and peduncle features of three taxa of *Argyroxiphium*. A, *A. kauense*; B, *A. sandwicense* ssp. *sandwicense*; C, *A. sandwicense* ssp. *macrocephalum*. Compare number of ray florets, capitulum diameter, and peduncle length. Reduced to 1/4.

(\bar{x} = 2.4) cm long, 0.1–0.5 (\bar{x} = 0.3) cm wide. Capitula 1.5–2.2 (\bar{x} = 1.9) cm long, 1.0–1.8 (\bar{x} = 1.5) cm in diameter; receptacle convex, 0.6–0.9 (\bar{x} = 0.7) cm in diameter; involucre bracts as many as ray florets, 0.5–1.5 (\bar{x} = 1.1) cm long, 1–4 (\bar{x} = 2.4) mm wide; periph-

eral receptacular bracts 22–42 (\bar{x} = 36); inner receptacular bracts 0–3 (\bar{x} = 0.1), 0.8–1.1 (\bar{x} = 0.9) cm long, 0.3–1.0 (\bar{x} = 0.8) mm wide. Ray florets 3–11 (\bar{x} = 8.2); tube 0.2–0.4 (\bar{x} = 0.3) cm long; ligule white, but more usually mixture of different tones of wine-red, rose, carmine, chrome-yellow, mimosa-yellow and white, sometimes pilosulous on the adaxial surface, 0.5–0.8 (\bar{x} = 0.6) cm long, 0.2–0.5 (\bar{x} = 0.3) cm wide, two to five (\bar{x} = 2.8) lobed, six to nine (\bar{x} = 7.1) veined; style 0.2–0.5 (\bar{x} = 0.4) cm long with sparsely dispersed hispidulous trichomes, 2 branched, the branches rolled, 2–2.5 (\bar{x} = 2.0) mm long and slightly truncate. Ray achene 0.7–0.9 (\bar{x} = 0.8) cm long, 1–2 (\bar{x} = 1.4) mm wide, four to eight (\bar{x} = 5.3) ribbed; pappus absent. Disk florets 45–214 (\bar{x} = 142.8), funneliform, chrome-yellow, usually with wine-red tinges above and whitish below, 0.5–0.7 (\bar{x} = 0.6) cm long, 1.0–2.5 (\bar{x} = 2.0) mm wide; style 0.4–0.8 (\bar{x} = 0.7) cm long, two branched, the branches 1.5–2.5 (\bar{x} = 2.0) mm long; stamen filament 2.0 mm long; anther loosely connate 2.0–2.5 (\bar{x} = 2.4) mm long. Disk achene 0.6–1.0 (\bar{x} = 0.8) cm

long, 0.7–2.0 ($\bar{x} = 1.6$) mm wide, 3–7 ($\bar{x} = 4.5$) ribbed; pappus of 3–9 truncate, fimbriate scales.

TYPE: Kahuku, above Kau Forest Reserve at Charlie Stone, 6700 ft alt, July 1956; *L. Williams Bryan* 25670 (HOLOTYPE: BISH!).

SELECTED SPECIMENS EXAMINED: Hawaiian Islands, Hawai'i Island, Mauna Loa, Kahuku Ranch, 1829 m alt, 20 Aug. 1977, *Meyrat, Jacobi, Evenson, & Stemmermann* 13, 14, 17 (HAW); 2 Aug. 1978, *Meyrat, Lamoureux, Stemmermann, & Higashino* 84, 87, 88, 89, 90, 91, 92, 93, 94 (HAW).

3. *Argyroxiphium sandwicense* DC. Prodr. 5:668. 1836; Coll. Mem. 9, pl. 8. 1838.

DESCRIPTION: Mostly herbaceous, but basally woody rosette plant, the woody basal portion below the leaves 3–10 cm long, 3.5–7.0 cm thick; the compact subspheric rosette 18–67 ($\bar{x}_{ab} = 31.5$) cm high, 19–90 ($\bar{x}_{ab} = 50$) cm in diameter, composed of many spirally arranged leaves; the axis unbranched and monocarpic but sometimes branching in response to injury of the meristem. Leaves rigid, arcuate-ascending, succulent, linear to linear lanceolate, more or less three angled in cross section, 13–39 ($\bar{x}_{ab} = 24.4$) cm long, 0.6–2.3 ($\bar{x}_{ab} = 1.2$) cm wide at the midpoint, densely floccose-sericeous and remarkably silvery, except at the margin of the base lanate and dull. Raceme simple or partially paniculate, lanceolate to oblong, 0.7–2.5 ($\bar{x}_{ab} = 1.6$) m long in unbranched plants, 16–78 ($\bar{x}_{ab} = 35.0$) cm wide, bearing 145–637 ($\bar{x}_{ab} = 195.5$) capitula in unbranched plants; terminal capitulum sometimes present; sessile capitula sometimes present at the base of the raceme; bracts 4.5–28.7 ($\bar{x}_{ab} = 13.5$) cm long and 0.4–3.0 ($\bar{x}_{ab} = 1.3$) cm wide; peduncle 3.5–40.0 ($\bar{x}_{ab} = 13.9$) cm long, 2–10 ($\bar{x}_{ab} = 4.1$) mm wide, usually unbranched, but when branched bearing 0–10 smaller capitula in addition to the large terminal one; bractlets 1–28 ($\bar{x}_{ab} = 6.2$) per peduncle, 1.4–10.2 ($\bar{x}_{ab} = 4.4$) cm long, 0.1–0.9 ($\bar{x}_{ab} = 0.3$) cm wide. Capitula 1.2–3.5 ($\bar{x}_{ab} = 2.4$) cm long, 1.2–4.3 ($\bar{x}_{ab} = 2.4$) cm in diameter; receptacle conical or convex, 0.5–2.3 ($\bar{x}_{ab} = 1.3$) cm in diameter; involucrel

bracts as many as ray florets, 1.0–2.4 ($\bar{x}_{ab} = 1.6$) cm long, 1.0–8.0 ($\bar{x}_{ab} = 3.0$) mm wide; peripheral receptacular bracts 31–115 ($\bar{x}_{ab} = 60.8$); inner receptacular bracts 0–20 ($\bar{x}_{ab} = 1.3$), 0.9–2.5 ($\bar{x}_{ab} = 1.5$) cm long, 0.5–2.0 ($\bar{x}_{ab} = 1.2$) mm wide. Ray florets 5–42 ($\bar{x}_{ab} = 18.1$); tube 0.3–0.8 ($\bar{x}_{ab} = 0.5$) cm long, glandular-pilosulous above and nonglandular below; ligule wine-red to rose-pink, 0.6–2.0 ($\bar{x}_{ab} = 1.0$) cm long, 0.2–0.6 ($\bar{x}_{ab} = 0.4$) cm wide, two to four ($\bar{x}_{ab} = 2.9$) lobed, 5–11 ($\bar{x}_{ab} = 7.0$) veined; style 0.4–1.2 ($\bar{x}_{ab} = 0.7$) cm long, two branched, the branches arcuate-descending 1–4 ($\bar{x}_{ab} = 2.6$) mm long. Ray achene 0.7–1.4 ($\bar{x}_{ab} = 1.0$) cm long, 1.5–3.0 ($\bar{x}_{ab} = 2.0$) mm wide, four to seven ($\bar{x}_{ab} = 4.6$) ribbed; pappus usually absent, sometimes reduced. Disk florets 47–600 ($\bar{x}_{ab} = 268.2$), funnelform, rarely suburceolate, wine-red to rose-pink above, glandular pilosulous at the middle, white-yellowish and pilosulous below, 0.6–1.1 ($\bar{x}_{ab} = 0.8$) cm long, 1.0–2.5 ($\bar{x}_{ab} = 1.7$) mm wide; style 0.7–1.2 ($\bar{x}_{ab} = 1.0$) cm long, two branched, the branches 2–4 ($\bar{x}_{ab} = 2.8$) mm long; stamen filament 2–6 ($\bar{x}_{ab} = 3.3$) mm long; anther 2–4 ($\bar{x}_{ab} = 3.0$) cm long, disk achene 0.7–1.5 ($\bar{x}_{ab} = 1.0$) cm long, 1.0–3.0 ($\bar{x}_{ab} = 1.9$) mm wide, four to eight ($\bar{x}_{ab} = 4.3$) ribbed; pappus of 1–10 scales, sometimes reduced or absent.

3A. *Argyroxiphium sandwicense* DC. ssp. *sandwicense*

Argyrophyton douglasii Hook. Comp. Bot. Mag. 2:163. 1837; Icon. Plant. Vol. 1, pt. 3, pl. 75. 1837.

Figures 3B, 4B, 5B

DESCRIPTION: Rosette 18–49 ($\bar{x} = 30$) cm high, 19–80 ($\bar{x} = 39$) cm in diameter. Leaves linear lanceolate to linear, 18–39 ($\bar{x} = 26$) cm long, 0.6–1.5 ($\bar{x} = 1.0$) cm wide at the midpoint. Raceme simple or more frequently partially paniculate, oblong, 1.7–2.5 ($\bar{x} = 2.0$) m long in unbranched plants, and 0.7–1.6 ($\bar{x} = 1.1$) m long in branched plants, 16–33 ($\bar{x} = 26.2$) cm wide, bearing 225–395 ($\bar{x} = 310$) capitula in unbranched plants, and 52–157 ($\bar{x} = 116$) capitula in branched plants; terminal capitulum present or lacking; sessile

capitula usually present at the base of raceme; bracts 5.5–28.7 (\bar{x} = 13.0); peduncles 5.0–18.5 (\bar{x} = 11.5) cm long, 2.5–5.0 (\bar{x} = 3.5) mm wide, branched or more often unbranched; bractlets 2–12 (\bar{x} = 5.1). Capitula 1.2–3.5 (\bar{x} = 2.4) cm long, 1.2–3.2 (\bar{x} = 2.1) cm in diameter; receptacle usually conical or less often convex, 0.5–1.6 (\bar{x} = 1.0) cm in diameter; peripheral receptacular bracts 31–75 (\bar{x} = 50.7). Ray florets 5–20 (\bar{x} = 12.5); tube 0.3–0.6 (\bar{x} = 0.5) cm long; ligule wine-red to pink, 5–8 (\bar{x} = 6.3) veined. Ray achene 0.7–1.4 (\bar{x} = 1.0) cm long. Disk florets 47–471 (\bar{x} = 216.3), funnellform; style 0.7–1.1 (\bar{x} = 0.9) cm long; stamen filament 2.5–6.0 (\bar{x} = 3.5) mm long. Disk achene pappus of 1–6 scales or less often absent.

TYPE: Hawaiian Islands, Hawai'i Island, collected by James Macrae, June 1825 (LECTOTYPE: G-DC, microfiche!; ISOTYPES: CGE-Lindley! K!).

SELECTED SPECIMENS EXAMINED: Hawaiian Islands, Hawai'i, Mauna Kea, source of Wailuku River, 19 June 1915, *Forbes* 880H (BISH); origin of Wailuku drainage, 2800–2866 m alt, 21 Aug. 1977, *Meyrat, Jacobi, Evenson, & Stemmermann* 21, 22, 24, 25 (HAW); 19 July 1978, *Meyrat, Carr, & Palmer* 55A–B, 56A–B, 57A–B, 58A–B–C (HAW).

3B. *Argyroxiphium sandwicense* DC. ssp. *macrocephalum* Meyrat stat. nov.

Argyroxiphium macrocephalum Gray Proc. Amer. Acad. 2:160. 1852; Proc. Amer. Acad. 5:114–146. 1861.

Argyroxiphium sandwicense var. *macrocephalum* Hbd. Fl. Haw. Isl. 219. 1888.

Figures 3C, 4C, 5C

DESCRIPTION: Taproot long and branched near the ground surface; the woody portion below the leaves rarely up to 40 cm long; the rosette 18–67 (\bar{x} = 33) cm high, 37–90 (\bar{x} = 60.5) cm in diameter, composed of 453–1150 (\bar{x} = 663) spirally arranged leaves. Leaves linear to linear-lanceolate, 13–33 (\bar{x} = 22.7) cm long, 0.8–2.3 (\bar{x} = 1.4) cm wide at the midpoint. Raceme simple or rarely partially paniculate, elliptic to lanceolate, 0.7–1.5 (\bar{x} = 1.1) m long in nonbranched plants, and

0.7–1.0 (\bar{x} = 0.8) in branched plants, 23–78 (\bar{x} = 43.7) cm wide, bearing 145–637 (\bar{x} = 275) capitula in unbranched plants and 99–258 (\bar{x} = 175) in branched plants; terminal capitulum rarely present; sessile capitula very rarely present at the base of raceme; bracts 4.5–26.0 (\bar{x} = 14.0) cm long, peduncles 3.5–40.0 (\bar{x} = 16.3) cm long, 2–10 (\bar{x} = 4.7) mm wide, usually unbranched; bractlets 1–28 (\bar{x} = 7.2) per peduncle. Capitula 1.4–3.5 (\bar{x} = 2.3) cm long, 1.4–4.3 (\bar{x} = 2.7) cm in diameter; receptacle convex or conical, 0.8–2.3 (\bar{x} = 1.6) cm in diameter; peripheral receptacular bracts 32–115 (\bar{x} = 70.8). Ray florets 11–42 (\bar{x} = 23.6); tube 0.3–0.8 (\bar{x} = 0.6) cm long, ligule wine-red to rose-pink, 5–11 (\bar{x} = 7.6) veined. Ray achene 0.7–1.1 (\bar{x} = 0.9) cm long. Disk florets 120–600 (\bar{x} = 320), funnellform, rarely suburceolate; style 0.7–1.2 (\bar{x} = 1.0) cm long; stamen filament 2–4 (\bar{x} = 3.1) mm long. Disk achene pappus of 1–10 scales, frequently reduced or sometimes absent.

TYPE: Haleakala, collected by Charles Pickering, Wilkes Expedition (U.S.E.E.) (LECTOTYPE: US! ISOTYPE: GH!).

SELECTED SPECIMENS EXAMINED: Hawaiian Islands, Maui Island, Haleakala Crater, Silversword Loop, 3 Aug. 1977, *Meyrat, Carr, & Stemmermann* 1, 2, 3, 4 (HAW); Sliding Sand Trail, 21 July 1978, *Meyrat & Funk* 60, 62A–B, 63A–B, 64, 65A–B, 66A–B–C–D (HAW).

ACKNOWLEDGMENTS

We thank Charles H. Lamoureux for reviewing earlier drafts of this manuscript. We are especially indebted to Jim Archie for a critical review of an earlier draft and suggestions that improved the statistical methods employed herein. We also gratefully acknowledge the assistance of Lani Stemmermann and Evangeline Funk in the field. Inflorescence measurements for four individuals of *A. sandwicense* var. *sandwicense* flowering in 1982 were kindly provided by Philip Rundel and Marti Witter. Finally, we thank Imelda Meyrat for preparing the plant illustrations and Barbara Carr for assistance in preparing the manuscript.

LITERATURE CITED

- BRYAN, L. 1973. Ahinahina. *Hawaiian Bot. Soc. Newsletter* 12(1):1-2.
- CARLQUIST, S. 1957. Leaf anatomy and ontogeny in *Argyroxiphium* and *Wilkesia* (Compositae). *Amer. J. Bot.* 44:696-705.
- . 1959a. Vegetative anatomy of *Dubautia*, *Argyroxiphium*, and *Wilkesia* (Compositae). *Pac. Sci.* 13:195-210.
- . 1959b. Studies on Madiinae: Anatomy, cytology, and evolutionary relationships. *Aliso* 4(2):171-236.
- . 1974. *Island biology*. Columbia University Press, New York.
- CARR, G. D., and D. W. KYHOS. 1981. Adaptive radiation in the Hawaiian silversword alliance (Compositae: Madiinae). I. Cytogenetics of spontaneous hybrids. *Evolution* 35(3):543-556.
- CARR, G. D., and A. MEYRAT. 1982. The status of the Mauna Kea silversword. Pages 34-39 in C. W. Smith, ed. *Proceedings, Fourth Conference in Natural Sciences, Hawaii Volcanoes National Park*. CPSU-UH, University of Hawaii, Botany Dept.
- COE, M. J. 1967. The ecology of the alpine zone of Mount Kenya. *Monogr. Biol.* 17. W. Junk, The Hague.
- DAVIS, P. H., and V. H. HEYWOOD. 1963. *Principles of angiosperm taxonomy*. Oliver Boyd, Ltd., Edinburgh.
- DE CANDOLLE, A. P. 1836. *Prodromus systematis naturalis regni vegetabilis*. Vol. 5. Treuttel et Wurtz, Paris.
- . 1838. *Coll. Mem.* 9, pl. 8. Treuttel et Wurtz, Paris.
- DEGENER, O., and I. DEGENER. 1957. *Flora Hawaiiensis*. Family 344. *Argyroxiphium*. Honolulu.
- GRAY, A. 1852. *Amer. Acad. Arts quarterly meeting*, 8 August 1949. *Sci. Proc.* 2:159-160.
- . 1861. Characters of some Compositae in the collection of the United States South Pacific exploring expedition under Captain Wilkes, with observations and... *Amer. Acad. Arts Sci. Proc.* 5:114-146.
- . Ms. United States exploring expedition under command of Charles Wilkes. Gray Herbarium Archives, Harvard University. (Photocopy at University of Hawaii Hamilton Library Pacific Collection.)
- HEDBERG, O. 1964. Features of afroalpine plant ecology. *Acta Phytogeogr. Suec.* 49:1-144.
- HILLEBRAND, W. 1888. *Flora of the Hawaiian Islands*. Vol. 1. Williams & Norgate, London.
- HOOKE, W. J. 1837a [1836]. A brief memoir of the life of Mr. David Douglas, with extracts from his letters. *Comp. Bot. Mag.* 2:79-182.
- . 1837b. *Icones plantarum*. Vol. 1, pt. 3. Williams & Norgate, London.
- KECK, D. D. 1936. The Hawaiian silverswords: Systematics, affinities, and phytogeographic problems of the genus *Argyroxiphium*. *B. P. Bishop Mus. Occ. Pap.* 11(19):1-38.
- LANDGRAF, L. 1973. Mauna Kea and Mauna Loa silversword: Alive and perpetuating. *Bull. Pac. Trop. Bot. Gard.* 3(4):64-66.
- ROCK, J. F., and M. C. NEAL. 1957. A new variety of silversword. *B. P. Bishop Mus. Occ. Pap.* 22(4):31-33.
- SOKAL, R., and J. ROHLF. 1981. *Biometry, the principles and practice of statistics in biological research*, 2d ed. W. H. Freeman and Co. San Francisco.
- ST. JOHN, H. 1971. Endemic plants of Kipahulu Valley, Maui, Hawaiian Islands. *Hawaiian Plant Studies* 36. *Pac. Sci.* 25(1):39-79.
- WILSON, W. F. 1922. With Lord Byron at the Sandwich Islands in 1825. Extract from the *Diary of James Macrae*, *Scottish Botanist*. Honolulu, Hawaii.