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A MORPHOMETRIC ANALYSIS AND TAXONOMIC  
APPRAISAL OF THE HAWAIIAN SILVERSWORD  
ARGYROXIPHIMUM SANDWICENSE DC. (ASTERACEAE)

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## ABSTRACT

A difference of opinions presumably related to a paucity of critical field observations has led to a persistent uncertainty regarding the taxonomic status of the Haleakala and Mauna Kea silverswords, Argyroxiphium sandwicense s.l. In order to assess the differentiation of these silverswords, morphometric techniques were used to examine the pattern of variation of 45 characters between the two populations. Also, qualitative features were evaluated. A framework for a priori comparisons between the two populations of A. sandwicense was provided by including two additional species in the study, i.e. 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 and A. sandwicense ssp. sandwicense.

Argyroxiphium virescens var. paludosa and A. kauense are as distinct from each other as each is from A. sandwicense in many quantitative and qualitative characters.

The correlation analyses of different pairs of characters show that the more useful characters are: inflorescence proportions, leaf proportions, number of ray florets per capitulum, and capitulum diameter. Individuals of either subspecies can be recognized by the proportion of the inflorescence. However, to separate all four taxa, based on quantitative characters, at least three of the foregoing features are needed.

An affinity index based on the number of times a given combination of populations exhibited adjacent mean values for the vegetative and inflorescence characters analyzed suggests a linear pattern of relationships as follows: A. virescens var. paludosa-A. sandwicense ssp. macrocephalum-A. sandwicense ssp. sandwicense-A. kauense. However, the capitulum characters do not support this pattern of relationships. They indicate a closer affinity between A. virescens var. paludosa and A. kauense. This situation suggests the possibility of convergent evolution of reproductive features adapted to similar reproductive modes in similar extreme environments. Furthermore, the intermediate morphological and ecological position of A. kauense raises the possibility that hybridization between A. sandwicense ssp. sandwicense and a greensword was involved in the origin of A. kauense.

## RESOURCE MANAGEMENT RECOMMENDATIONS

1. This taxonomic revision of the Hawaiian silverswords demonstrates that Haleakala, Mauna Kea and Mauna Loa each have their own unique species or subspecies. These silverswords will cross with one another. Therefore, a given kind of silversword should not be introduced to areas where it was not known to be in nature.
2. The Mauna Kea silversword population is extremely small and threatened by mouflon sheep. The Ka'u silversword populations (there are two) are small and currently heavily disturbed by pigs or mouflon sheep. The Haleakala silversword, though numbering in the thousands and partially protected, is still threatened by goats and human vandalism. All populations of silverswords should be managed as though they were officially listed as Endangered because they are so vulnerable to predation.
3. Conservation of these species should concentrate on habitat restoration. Cultivation should be avoided wherever possible and only used as a last resort.

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## INTRODUCTION

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 complex (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 herbs 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 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 silverswords A. sandwichense s.l. and A. kauense, and a greensword, A. virescens var. paludosa. 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. sandwichense s.l. at the subspecies level. Hereafter, to avoid confusion, the Mauna Kea silversword will be referred to as Argyroxiphium sandwichense ssp. sandwichense and the Haleakala silversword as Argyroxiphium sandwichense ssp. macrocephalum.

#### LITERATURE REVIEW

##### Systematic Disposition and Evolutionary History of Argyroxiphium and its Relatives

Gray (1852), on the basis of capitulum characters, was the first to link the genus Argyroxiphium (and indirectly also Wilkesia) to the subtribe Madiinae (subtribe designation according to Keck 1968), tribe Heliantheae of the family Asteraceae. Members of this subtribe are also known in California as tarweeds. Bentham and Hooker (1873) followed Gray's treatment and placed Argyroxiphium and Wilkesia in the subtribe Madiinae, and Dubautia in the Galinsoginae, the immediately preceding subtribe. However, they placed Railliardia in the Senecioneae, a different tribe. In 1897, Hoffmann placed Dubautia and Railliardia together in the subtribe Galinsoginae, and retained Argyroxiphium and Wilkesia in the Madiinae. Skottsberg (1956) suggested affinities between Dubautia and Railliardia and different genera of Senecioneae from the southern and southwestern Pacific. Sherff (1935), in his monograph, treated Dubautia and Railliardia as related, but separate genera, making no comment about their derivation. Keck (1936) submerged Railliardia into Dubautia, and Wilkesia into Argyroxiphium. He pointed out that Dubautia and Argyroxiphium are closely related genera. However, he placed them in the Galinsoginae, and speculated on their derivation from the southern and southwestern Pacific.

Carlquist (1957, 1959a, 1959b), based on the morphological and anatomical characteristics of glandular trichomes, certain features of the leaves, floral bracts and style, demonstrated that Dubautia (including Railliardia), Argyroxiphium, and Wilkesia are closely related genera. The occurrence of

intergeneric hybrids between species of Dubautia and Argyroxiphium eliminated any doubt about their close relationship. Degener (1948) found hybrids of A. grayanum X Dubautia on the Mt. Eke plateau which were described and named by Sherff (1944) as Argyrautia degeneri. Also, another intergeneric hybrid was recognized by Kobayashi (1973a) in Haleakala which, by morphology and location, appears to be a hybrid between the Haleakala silversword and D. menziesii.

Keck's treatment of Dubautia (including Railliardia) (1936) was well received by taxonomists (Carlquist 1957, Carr 1978), but Keck's treatment of Argyroxiphium (including Wilkesia) has not gained acceptance. Keck (1936) placed Wilkesia grayana Hillebrand (1888) in Argyroxiphium and assumed that Wilkesia gymnoxiphium Gray (1852) was derived from the former taxon. Skottsberg (1944, quoted by St. John 1971b) said, "After the removal of W. grayana, Wilkesia stands out as a well-marked genus, not only as a subgenus (Keck l.c.) of Argyroxiphium." According to Carlquist (1957), the derivation of Wilkesia from Argyroxiphium is not possible, because the highly specialized type of leaf structure found in Argyroxiphium could not give rise to the generalized type found in Wilkesia. He also cited differences in inflorescence and capitulum structure to support his contention. Later, St. John (1971b) described a new species of Wilkesia, W. hobdyi, and presented in a table a list of morphological characters which separate Argyroxiphium from Wilkesia. These characters include leaf, capitulum, phyllary, and achene features. Thus, based on leaf characters, wood anatomy, and inflorescence types, the genera Dubautia, Argyroxiphium, and Wilkesia are clearly distinct (Carlquist 1957, 1959a, 1959b).

Fosberg (1948) postulated that a single immigrant gave rise to sixty-one entities of these three related genera. The extensive study on the comparative anatomy and cytology of the different species and genera of Madiinae by Carlquist (1959a) supports the viewpoint of Gray (1852) regarding the origin of the Hawaiian taxa. Many capitulum characteristics are shared by the Madiinae in California and the Dubautia-Argyroxiphium-Wilkesia complex of Hawai'i (Carlquist 1959a).

Some shrubby species of Californian Madiinae from the genera Hemizonia (offshore California islands) and Adenothamnus (northern Baja California) evolved from continental herbaceous annuals into several species characterized by loss of seasonal growth in the milder maritime climate (Carlquist 1974). This is part of the reason Carlquist (1970) suggested that among these genera may likely be found the ancestor of the perennial Hawaiian Madiinae.

Carr (1978) found a striking trend in the geographical distribution of Dubautia spp. with chromosome numbers of  $n=14$  and Dubautia spp. with chromosome numbers of  $n=13$  (Railliardia type). Only species with  $n=14$  are known from the island of Kaua'i, which

is the northwesternmost and geologically oldest major island (McDonald and Abbott 1970). The progressively younger islands to the southeast have concomitantly higher frequencies of species with  $n=13$  (Hawai'i: 71% have  $n=13$  and only 29% have  $n=14$ ) (Carr 1978). According to the same author, the widest ranging and most highly differentiated species have  $n=14$ , while species with  $n=13$  tend to be poorly differentiated and are highly restricted in distribution. Carr (1978) concluded that  $n=14$  is the ancestral chromosome number in the Hawaiian Madiinae and that species with  $n=13$  have evolved recently by aneuploid reduction. Moreover, Carr (1978) speculated that Dubautia scabra (Railliardia type, but  $n=14$ ) is the most likely immediate ancestor of 13-paired species. Also, he suggested that the Pacific Coast tarweed Adenothamnus validus (Brand.) Keck ( $n=14$ ) is a reasonable ecological, morphological, and cytological prototype for a putative ancestor of the Hawaiian tarweeds.

According to Carlquist (1974), in Dubautia, the leaf size is a sensitive indicator of mesomorphy and xeromorphy. Leaf size in this genus is also correlated with the volume of vessel elements such that species with large vessel elements and large leaves ( $n=14$  cytotype) occupy comparatively wet sites, whereas species with small vessel elements and small leaves ( $n=13$  cytotype) usually occupy comparatively dry sites (cf. Carlquist 1974, Carr 1978).

From the papers of Carlquist (1974) and Carr (1978), it can be concluded that the original Hawaiian tarweed immigrant probably diverged early into Argyroxiphium ( $n=14$ ), Wilkesia ( $n=14$ ), and Dubautia ( $n=14$ ), with the two former genera occupying upland dry sites and Dubautia ( $n=14$ ) occupying mesic sites. In latter stages of evolution, Dubautia ( $n=14$ ) gave rise to Dubautia ( $n=13$ ) which advanced into drier areas. The evolution within Argyroxiphium in relation to adaptation to different ecological conditions will be discussed in a following section of this paper.

#### The Different Entities of Argyroxiphium

The genus Argyroxiphium is commonly divided (somewhat imperfectly) into two more-or-less easily recognized groups. Species that are glabrous or merely pubescent are called greenswords, whereas species that are densely pubescent are called silverswords.

GREENSWORDS: Seven entities have been considered greenswords. These include A. virescens Hbd. (Hillebrand 1888), A. virescens var. paludosa St. John (1971a), A. forbesii St. John (1971a), and A. grayanum (Hbd.) Deg. (Degener 1932 et seq.) (formerly considered Wilkesia grayana--Hillebrand 1888). Although A. caligini Forbes (Forbes 1920) is densely pubescent, it is reasonable to consider it as ecologically related to

greenswords (Degener 1945). Such an assumption is supported by the anatomical evidence of Carlquist (1957). St. John (1973) made an emendment to the scientific name calling it A. caliginis, because "caliginis" is the genitive of the Latin noun "caligo" which means fog. The intergeneric hybrid A. grayanum X Dubautia called Argyrautia degeneri by Sherff (1944) can be considered in the greensword group. Also in the same group belongs the debated entity A. caliginis var. kai of Forbes (1920), called A. kai by Degener (1930, 1932 et seq.), and considered a hybrid between A. grayanum and A. caliginis by Keck (1936).

SILVERSWORDS: Species in the silversword group include A. sandwichense DC. (De Candolle 1836) and A. macrocephalum Gray (1852), which was also referred to as A. sandwichense var. macrocephalum by Hillebrand (1888). The two entities mentioned above have been merged by Keck (1936) and, taxonomically, they are not well defined. This aspect will be discussed in detail in a following segment of this paper. Another species considered in the silversword group is A. kauense (Rock & Neal) Deg. & Deg. (Degener 1932 et seq., Degeners and Sunadas 1976), formerly considered A. sandwichense var. kauense by Rock and Neal (1957). Of intermediate status is a hybrid between A. macrocephalum Gray of Haleakala and A. virescens, which was mentioned by Rock and Neal (1957), and Keck (1936), from Pu'u Nianiau Crater, on the northwestern slopes of Haleakala, Maui.

#### General Description of the Genus Argyroxiphium

The genus has been considered to comprise subcaulescent to caulescent perennial herbs, the trunks of which are crowned with numerous crowded leaves forming compact, subspheric rosettes. Leaves are spirally arranged below and alternately disposed above (Degener 1932 et seq., Keck 1936). systems will be more fully characterized in a general way.

ROOT: The Haleakala silversword has a long, branched, yet comparatively shallow root (Degener 1932 et seq.). In loose, unconsolidated material, the plants often have a taproot exceeding eight feet in length (U. S. National Park Service 1968). Argyroxiphium kauense also has a taproot bearing few side roots and, according to the Degeners and Sunadas (1976), the species roots sparingly from short, creeping stems.

STEM: The robust stems may be slightly woody near the base. They have abundant pith in the center, and they are covered with a dark bark, shaggy with old leaf traces which, after about one year, decay to expose rough leaf scars (Degener 1932 et seq., Keck 1936). Carlquist (1957) reported that A. grayanum and A. caligini possess abundant cork in subepidermal layers, whereas little cork occurs in A. virescens and in the Haleakala

silversword. This cork formation is also found in A. virescens var. paludosa. The possible significance of cork formation in these species has not been suggested. In most of the species, the stems are simple, short, thick, and erect. However, there are species with creeping and branched stems (Degener 1932 et seq., Keck 1936).

LEAF: The leaves are rigid, entire, and ensiform, from linear to linear-lanceolate; thick, flat, or, in cross-section, somewhat triangular or rhomboidal. They are longitudinally from 1 to 12-nerved. The leaves are never connate into a basal sheath except in A. grayanum where they may be so for less than 1 mm (Degener 1932 et seq.). Species with glabrous green leaves or sparsely pubescent vesture are called greenswords. On the other hand, species with densely pubescent leaf vesture, from gray to brilliantly silver in appearance, are called silverswords. Consequently, they were called Ahinahina and Pohinahina by Hawaiians which, translated to English, means "very or extremely gray" (Degener 1945). When De Candolle (1836) described Ahinahina, based on the leaf shape and vesture, he constructed "argyroxiphium" from the Greek roots for "silver" and "sword", hence the generic name.

RACEME: Under natural conditions, usually after several years of development, the subspheric rosette plant produces a bulky, spindle-like structure protected by helicoidally arranged bracts which rapidly elongates into an erect inflorescence, whereupon the plant flowers and sets seeds. In the simple-stemmed species (or individuals) the entire plant dies after seeding, but in branched species (or individuals) only the fertile branch dies. This die back may be progressive in certain species so that separate branches may become independent plants (Degener 1932 et seq.).

The inflorescence has been described as a simple raceme of capitula (with one capitulum per peduncle) in all species (Hillebrand 1888, Forbes 1920, Degener 1932 et seq., Keck 1936, Rock and Neal 1957, St. John 1971a, Degeners and Sunadas 1976). However, in A. sandwicense, besides the simple raceme, panicles with more than one capitulum per peduncle (racemose branches) have been reported by Hillebrand (1888) and Keck (1936). Carlquist (1959b) established that Argyroxiphium has a bidirectional (simple) raceme in which most of the maturation is acropetal, but some heads younger than those in the middle of the axis occur at the base. He also found that in most of the species the terminal head is bigger and blooms precociously.

The raceme stalk is hollow. The inflorescence has an oblong delineation, and it can be from 2 dm long in A. forbesii (St. John 1971a) to 20 dm long in some individuals of A. macrocephalum (Degener 1932 et seq.). The inflorescence can bear from 15 capitula in A. caliginis (Degener 1932 et seq., Keck 1936) to 500

capitula in some individuals of A. macrocephalum (Degener 1932 et seq.). The size of the inflorescence and the capitulum in Argyroxiphium species suggests gigantism which may be related to the monocarpic habit of these species (Carlquist 1974).

**BRACT, PEDUNCLE, AND BRACTLET:** At the base of every peduncle there is a lanceolate bract. The largest bracts are at the lower part of the raceme, and the shortest bracts are at the top. The lower bracts are glandular-pubescent on the basal half and have a vesture similar to that of the leaf of the respective species on the distal part. The bracts at the middle and at the top of the raceme are glandular and yellowish (Degener 1932 et seq., Degeners and Sunadas 1976). The peduncle is rigid, hollow, and flattened, with a glandular-pubescent vesture. There are one to many bractlets per peduncle. The bractlet is persistent, lanceolate, yellowish, and glandular-pubescent (Degener 1932 et seq.).

**INVOLUCRE:** The involucre is broadly campanulate to hemispheric with a diameter from 1 cm in A. forbesii (St. John 1971) to 3.5 cm in A. macrocephalum (Degener 1932 et seq.). The terminology applied by Carlquist (1959b) will be used to describe the bracts of the capitulum. The involucre bracts form a single outer series equal in number to, and subtending, the ray florets. The involucre bracts are linear to oblanceolate with attenuate bases and acute to acuminate apices. They are pale green, glandular-pubescent without, and glabrous and shiny within. They are incurved along their margins, partly enclosing the ovary of the subtended ray floret, and sometimes they are adnate toward the base to the inner bracts (Degener 1932 et seq.). These inner bracts constitute a single row of longitudinally connate, outer receptacular bracts forming a receptacular cup. With a paucity of ray florets (absent in Dubautia and Wilkesia), the true involucre is more-or-less lacking, and its function is taken over by a similar structure, the receptacular cup (Degener 1932 et seq., Keck 1936, Carlquist 1959b).

**RECEPTACLE:** The receptacle can be concave, convex, or conical (Gray 1852, Hillebrand 1888, Degener 1932 et seq., Keck 1936, St. John 1971a, Degeners and Sunadas 1976), and is naked (Hillebrand 1888, Keck 1936).

**RAY FLORET:** Ray florets, when they are present, vary from few to several, and are arranged in a single row. They are pistillate and fertile and have a tube from 1 to 7 mm long with a broad, spreading to reflexed ligule. The ligule can be from 3 to 7 mm long and 2 to 5 mm wide. It may be yellow to purple in color and from 2- to 4-dentate distally, but is most frequently 3-dentate.

The ray achene is linear, curved due to the peripheral position, and is usually 4- to 5-ribbed, glabrous, and blackish. The pappus, when present, is short-truncate and coroniform or reduced to a single scale or totally reduced to an erosulate margin on the cartilaginous areola (Degener 1932 et seq.).

DISK FLORET: The number of disk florets varies from 75 to 400 per capitulum depending on the species (Degener 1932 et seq., Keck 1936). They have a tubular corolla 4-6 mm long with an elongated limb barely widened and 5-toothed. The distal part is yellow to lavender depending on the species. The tube is glabrous to pubescent on the outer surface. The style is as long as, or longer than, the corolla. The style branches are linear, flat, and widened at the conical end. The anthers are obtuse at the base and are appendaged (Degener 1932 et seq., Keck 1936, St. John 1971a).

The disk achene is more-or-less 5-ribbed and straight if from near the center of the capitulum, but curved if from near the periphery. They are similar to ray achenes in size. The pappus is persistent or deciduous, of 3-6 short, broad, unequal, acute scales (Degener 1932 et seq.).

#### Distribution and Habitat of *Argyroxiphium*

The genus *Argyroxiphium* is endemic to the islands of Hawai'i and Maui, and the distributions of species, varieties, or even populations of a particular species are severely restricted. The Mauna Kea silversword (*A. sandwicense* s.s.) has been reported on Mauna Kea, Mauna Loa, and Hualalai, Hawai'i at elevations ranging from 2134 to 3658 m (Hillebrand 1888). However, it is now known that even specimens referred to by Keck (1936) as *A. sandwicense* actually represent *A. kauense* (cf. Rock and Neal 1957). Hillebrand (1888), Wilson (1919), and later authors have probably based their conclusions regarding the occurrence of *A. sandwicense* on Mauna Loa on Douglas' observation of January 28, 1834, during his ascent of Mauna Loa: "I proceeded for an hour longer, to what might be called the Line of Shrubs, and at two miles and a half further on, encamped for the night. We collected some small stems of a heath-like plant, which, with the dried stalks of the same species of Compositae which I observed on Mouna Kuah, afforded a tolerably good fire."

It is quite probable that Douglas, like Keck, saw only vegetative specimens of the silverswords from Mauna Loa and mistakenly considered them the same as specimens from Mauna Kea, when actually they represented the still undescribed (at that time) taxon, *A. kauense*. Although Hillebrand (1888) lists Hualalai as a location where *A. sandwicense* occurs, apparently no specimens of any silversword from there have been preserved. Furthermore, even if Hillebrand had had first-hand observations, it is probable that he, like Douglas and Keck, would have confused it with related taxa such as *A. kauense*.



Argyroxiphium sandwicense s.s. has been observed growing mostly near or on elevated volcanic rocks on areas of twenty to thirty percent slope (Meyrat unpublished). Currently, the Mauna Kea silversword is known only from the Wailuku drainage, at an elevation of 2820 m, on Mauna Kea.

Also on Hawai'i, there are, presently, three widely separated populations of A. kauense known. One is located near Kahuku Ranch in the Ka'u Forest Reserve on Mauna Loa at an elevation of 1829 m (Rock and Neal 1957, Degeners and Sunadas 1976). The second population is located in a kipuka found east of Power Line Road going to Kipuka 'Ainahou, at an elevation of 1646 m (James Jacobi personal communication). Both areas are bog-like, but the topography of the former is more irregular and more steeply inclined than the latter which is almost flat. The third known population occurs at an elevation of 2195 to 2744 m, at Kapapala on Mauna Loa (Landgraf 1973, U. S. National Park 1974).

Argyroxiphium macrocephalum is a taxon very similar to the Mauna Kea silversword and is confined to Haleakala Crater, east Maui, from elevations of 2134 to 2743 m. According to Kobayashi (1973b), this species grows mostly on the outer slopes of dark cinder cones and breached cones, or on the outer and inner slopes of red cinder cones. Plants are also concentrated at the foot of elevated boulders from breached cones and on the windward edges of red lava flows.

Two species of the greensword complex grow on eastern Maui. Argyroxiphium forbesii occurs on the northeastern slope of Haleakala Crater, across the divide from Kipahulu Valley (St. John 1971a). Hillebrand (1888) reported A. virescens var. virescens from elevations of 2438 to 2743 m on cliffs of Ko'olau Gap of the northwestern slope of Haleakala Crater, but this taxon appears to be no longer extant (Fosberg and Herbst 1975). Argyroxiphium virescens var. paludosa grows on the ridge between Kipahulu and Kūhiwa valleys, at elevations of 1235 to 1950 m, on small, flat, boggy areas below Wai Anapanapa Lake (St. John 1971a).

The other species of greenswords are found in flat, boggy areas on the mountains of West Maui. Argyroxiphium caliginis grows at an elevation of about 1646 m on Mt. Eke and Pu'u Kukui and shares its habitat with A. grayanum which has been reported from elevations of 1219 to 1950 m (Keck 1936).

From the foregoing it can be observed that the habitat of greenswords is somewhat different than that of the silverswords. However, one feature that characterizes both habitats is the absence or paucity of an overstory. Argyroxiphium apparently cannot survive under a closed canopy.

Adaptations of Argyroxiphium to its Environment

ADAPTATIONS OF ARGYROXIPHIMUM TO AN ALPINE ENVIRONMENT--Germination: Only about five to twenty-five percent of the seeds of the Haleakala silversword are viable (U. S. National Park Service 1968, Kobayashi 1973b). They describe living embryos of Argyroxiphium as white and succulent, and non-living embryos as flat and brown. In the right conditions, germination is obtained within eight days, and after six weeks may reach seventy-five percent (U. S. National Park Service 1968).

Although light has been claimed to inhibit germination (U. S. National Park Service 1968), Siegel et al. (1970) interpret this inhibition as the result of local heating. Siegel et al. (1970) and Kobayashi (1973b) found that germination is adversely affected when the temperature exceeds 30°C, suggesting that silversword seeds are not as resistant to high temperatures as might be expected considering ground temperatures within the Crater. However, Kobayashi (1973b) found that ground temperatures never exceed 32°C within cinder fragments even during the hottest and driest days of summer. Also, he found that in winter time, when the wind disperses the seeds and at the same time consolidates the surface fragments, the maximum temperature never exceeds 23°C within any type of fragment. However, loose cinder and bare sand had temperature maxima ranging from 31° to 47°C. From experimental data, Kobayashi (1973b) found that four year old seeds are still able to grow. However, there is a marked reduction in viability each year. Kobayashi, in his extensive experimental studies, also found that in substrates whose moisture content is below one-half field capacity, there is a sharp drop in germination. Thus, the quantity of water is obviously a very important factor for the germination of this species. In this regard, it is probably pertinent to recall the report of the U. S. National Park Service (1968) that water in which silversword seeds have been soaked for twenty-four hours strongly inhibits germination and early growth of radish seeds. Moreover, Siegel et al. (1970) found in silversword seeds a monophenolic aldehyde or ketone which inhibits germination of seeds of lettuce and five other species with non-selective action upon composites or non-composites. Possibly, under field conditions, silversword seeds would germinate only if this inhibitor is washed out from the seeds and leached away by rainfall.

Seedling: The seedlings of Argyroxiphium differ from the adult stages in two main aspects. First, the seedling and juvenile leaves of the Haleakala silversword apparently do not contain pectic material filling the intercellular spaces of the mesophyll parenchyma as found in the adult stages. Nevertheless, the resistance of young seedlings to desiccation is impressive, since plants grown at Hawaii Volcanoes National Park have been known to recover fully from a wilted, prostrate condition when watered after a period of desiccation (U. S. National Park Service 1968). The second way in which seedlings differ from

adults is that the former have their leaves arranged in pairs (opposite) whereas the latter have them arranged spirally. Opposite leaves have been observed in seedlings of A. macrocephalum, A. sandwicense s.s., A. virescens var. paludosa, and A. kauense (Carlquist 1957, Méyrat unpublished).

From experimental data and field observations, Kobayashi (1973b) found that the seedlings of the Haleakala silversword survive best in a substrate comprising a sandy layer overtopped by a layer of tabular fragments at a slope of thirty-five degrees. This inclination is low enough to stabilize a sandy layer, yet steep enough to be slightly unstable which maintains a layer of tabular fragments not thicker than 5 cm. Generally, the seedlings have their roots oriented toward the top of the slope.

Adult Plant: The alpine Argyroxiphium found in Haleakala has a simple, short (3-10 cm), thick (2-5 cm), and erect stem (Degener 1932 et seq.). Coe (1967) explains that the root, at low temperatures, absorbs water very slowly. Thus, it is an advantage for alpine plants to develop short stems, not only because of the reduced distance that water must be transported to the leaves, but also because the danger of freezing may also be lowered. The thickness of the stem may be explained on the basis of continual cambial activity because of small seasonal temperature variation (Carlquist 1966a). Argyroxiphium species do not produce thick layers of bark. However, they do accumulate thick sheaths of dry, dead leaves, an adaptation which has been reported as an insulation mechanism in other alpine plants by Hedberg (1964).

Argyroxiphium species present their numerous leaves helicoidally arranged in a compact spherical rosette. This arrangement of leaves is likely an adaptation to the alpine environment by retention of juvenile characteristics (Carlquist 1974). Little elongation of the stem results in crowded leaves at its distal extreme and in the suppression of any axillary buds. This is an advantage for the monocarpic plant in that it provides protection from frost and dessication for a single terminal bud. It has been reported by Hedberg (1969) that Senecio keniodendron shows an annual increase in height of only 2.5 cm.

The advantages of rosette plants in alpine environments have been demonstrated by different authors. Coe (1967) reports that the humidity of the air in alpine conditions changes violently from ninety percent early in the morning to below twenty percent in bright, unobscured sunlight. He points out that the leaves of a rosette plant would lie within a sphere of high and more constant humidity and, as a result, water loss from the plant by transpiration would be greatly reduced.

Carlquist (1974) mentioned that all Senecios and Lobelias are able to close their leaf rosettes at night and open them

during the day. Argyroxiphium species may also respond in this manner as is suggested by the observation of the U. S. National Park Service (1968) that the leaves of A. kauense would droop while the sun was shining directly on them, but in the afternoon when the plant was in the shade, the leaves would straighten up again. Although the rosettes may open and close in this manner, the central growing point of the rosette is always tightly ensheathed by young leaves which remain folded until the inflorescence is formed.

In African rosette plants, Hedberg (1964) observed that on cold mornings, when the ambient air temperature was below freezing ( $-4^{\circ}\text{C}$ ), the temperature inside rosettes of Senecio keniodendron and Senecio brassica was above freezing ( $+1.8^{\circ}$  and  $+1.5^{\circ}\text{C}$ , respectively). Furthermore, Coe (1967), working with Lobelias and Senecios, reported that when the ambient air temperature fell to  $-5^{\circ}\text{C}$ , the temperature amongst the outer leaves was  $-1^{\circ}\text{C}$  while the central leafy cylinder remained at up to  $2^{\circ}\text{C}$  above freezing throughout the night.

Many alpine plants share the characteristic of having leaves covered by very dense vestiture. Carlquist (1957) assumed that the special vestiture of alpine Argyroxiphium species is an adaptation to high light intensity at these elevations. He brought out the fact that the Haleakala silversword leaves have thick-walled richomes with flattened ends. These flattened hairs are possibly the cause of the unusual sheen of the leaves which may function as a protective mechanism by reflecting excessive sunlight. According to Hedberg (1964), Carlquist (1974), and Coe (1967), hairy vestiture insulates alpine plants against sub-zero temperatures. The hairs may also be important in the water economy of these plants, for where a layer of relatively immobile air is trapped above the leaf surface, transpiration losses will be considerably reduced (Coe 1967).

The leaves of Argyroxiphium in alpine sites possess a prominent cuticle and thick-walled epidermal cells. These species also have three layers of palisade cells on the adaxial part of the leaf and two layers of palisade cells on the abaxial portion. In the Dubautia-Argyroxiphium-Wilkesia complex only Argyroxiphium and some Dubautia spp. such as D. menziesii growing in the same alpine environment have adaxial and abaxial palisade cells. It was also found that Argyroxiphium has three sets of vascular bundles in the leaf. The upper and the middle sets are normal, but the lower is inverted with respect to the orientation of xylem and phloem. Thus, the highly specialized palisade layers and vascular bundles, and their close relationship lead to the conclusion that these plants possess a highly efficient photosynthetic apparatus (Carlquist 1957).

Carlquist (1957) found that every Argyroxiphium he studied had loosely-arranged mesophyll parenchyma with intercellular spaces completely or partly filled with hydrophilic pectic gel. As these materials are present in channels of the mesophyll which

run the length of the leaf between the vein sheath extensions, they were termed "pectic channels." These pectic channels are a xeromorphic adaptation which allows water storage from one rainy season to the next (Carlquist 1957).

ADAPTATIONS ASSOCIATED WITH ECOLOGICAL SHIFTS IN ARGYROXIPHIMUM: Argyroxiphium grayanum has been reported at an elevation of 1219 m, and the other species of the genus have been reported above this altitude to about 3050 m. It is possible that A. sandwicense DC. s.s. extends to higher elevations, but such reports are at best poorly documented. In comparison, the altitudinal gradient occupied by Wilkesia is about 305 to 1067 m, while that of Dubautia is about 305 to 3110 m.

The presence of pectic channels, the presence of adaxial and abaxial palisade with multiple layers of cells, and the inverted lower vascular bundles in the leaf in all the species of Argyroxiphium studied so far, point to a common ancestor adapted to a dry alpine habitat (cf. Carlquist 1957, Carlquist 1974). All Argyroxiphium species have short vessel elements which is another xeromorphic characteristic, and the fact that bog species have only slightly longer vessel elements suggests that Argyroxiphium species from the bogs represent only a recent shift from drier areas (Carlquist 1974). Species which appear in wetter areas, below the inversion layer (2134 m), are almost glabrous with the exception of A. caliginis, which in contrast to the Haleakala silversword, has a thin cuticle, thin-walled epidermal cells, and trichomes which are not flattened at the end. Another contrasting feature in A. caliginis is the presence of hydathodes in the leaves which permit expulsion of excess water.

Argyroxiphium virescens var. virescens is a weakly branching taxon with certain features similar to the Haleakala silversword, its putative ancestor. However, (if still extant) it occurs in wetter cloudswept sites of Ko'olau Gap, and differs from its putative ancestor in having less pubescent leaves (Degener 1930) with two, rather than three, layers of palisade cells on the adaxial portion (Carlquist 1957). It is possible that A. virescens var. virescens gave rise to A. forbesii and A. virescens var. paludosa (St. John 1972), and also possibly gave rise to A. grayanum (Carlquist 1957). In comparison, A. grayanum and A. virescens var. paludosa have broader and flatter leaves and are more highly branched than A. virescens var. virescens.

Coe (1967) observed that Senecio keniophytum shows an increase of hairiness and epidermal pigmentation concomitant with altitude. Two plants of Mauna Kea silversword exhibited high epidermal pigmentation (possibly anthocyanin) in a population of about thirty-five plants at 2866 m (Meyrat unpublished). However, Haleakala silverswords growing at 2134 m exhibited pigmentation only in drying leaves and bracts from plants which were flowering, or in damaged leaves of vegetative plants.

Generally, Haleakala and Mauna Kea silverswords have short stems. However, a few plants observed in Silversword Loop, Haleakala, are exceptions to this rule, having stems 30 to 50 cm long (Meyrat unpublished). This may be related to the presence of more moisture in this area due to the daily ingression of clouds into Ko'olau Gap. The other species of Argyroxiphium in wetter habitats have mostly longer stems. Another characteristic of Haleakala silverswords is that they are normally unbranched and die after flowering. When the rosette of the main stem is damaged, branching may be observed even in the Haleakala silversword. On the other hand, some other species of Argyroxiphium, especially the greenswords, produce branches which continue to grow after the main stem flowers and dies. Moreover, in these species, the stem may elongate considerably. In A. caliginis the rosettes branch at the base and these prostrate shoots root in the bog. This presumably is an advantage, because few plants have been seen flowering, and vegetative reproduction is perhaps an adaptation to lack of suitable pollination conditions in the bog (Carlquist 1957, 1974).

Argyroxiphium species at lower elevations show a decrease in the number of capitula per inflorescence and in the number of ray florets per capitulum as compared to those of higher elevations. Also, the color of the ligules becomes lighter at lower elevations. That this correlation may be due to certain changes in the reproductive strategy of these plants is inferred by Carlquist (1974), who suggested that the loss of ray florets can occur easily in Asteraceae and that the conspicuousness of ray florets in species of higher altitudes may be correlated with an alpine pollinator. Carlquist (1974) also pointed out that Argyroxiphium species in boggy areas have nutant capitula comparable to those of some Espeletias of South America and some Senecios of Africa in similar habitats. He suggested that nutant heads are readily accessible to pollinators yet are not likely to fill with water which would wash pollen away and otherwise hinder visiting insects.

#### Loss of Dispersibility in Argyroxiphium and its Allies

The dispersal of American Madiinae has depended on bristles and hairs on small achenes or sticky involucrel and receptacular bracts which envelop the achene. These special structures are adaptations of the plant that enhance dispersal by animals. The tarweed immigrant which gave rise to the Dubautia-Argyroxiphium-Wilkesia complex may have arrived by means of any of the above described structures. However, the Hawaiian representatives of tarweeds have some of the largest achenes in the Madiinae and few of their achenes are enveloped by sticky bracts. Furthermore, the achenes have only a few, small pappus scales, and no hairs (Carlquist 1970). Carlquist (1966b) speculates that if an immigrant arrives in an oceanic island setting, and if it evolves without contact with the agent responsible for its dispersal, then the dispersal mechanism may

become of neutral value in its new location. It may even be a hindrance, because energy must be expended for the production of dispersal devices such as hairs, bristles, or sticky bracts. This could explain the apparent loss of the dispersal mechanism in the Argyroxiphium complex.

#### THESIS PROPOSAL

Macrae climbed Mauna Kea, Hawai'i in 1825 and collected some specimens of a "superb plant" (Wilson 1922) which were described and classified by De Candolle (1836) as Argyroxiphium sandwicense, the type species for the genus Argyroxiphium. Nine years later, David Douglas also ascended Mauna Kea and collected specimens of the same species (Douglas 1914, Wilson 1919, Degener 1945) which in the hands of Hooker (1837) were described and classified as Argyrophyton douglasii. Today, the latter name is recognized only as a synonym of Argyroxiphium sandwicense (Degener 1932 et seq., Keck 1936).

In 1852, A. Gray described a plant collected in Haleakala Crater, Maui and named it Argyroxiphium macrocephalum. However, Hillebrand (1888) considered it as A. sandwicense var. macrocephalum, and Keck (1936), in his monographic revision of the genus, merged the plants from Hawai'i and Maui, recognized single taxon A. sandwicense, and relegated A. macrocephalum and A. sandwicense var. macrocephalum to synonymy.

Before Keck's monograph, Degener (1930) distinguished two species from different islands. Later, in his *Flora Hawaiiensis* (1932 et seq.), he considered the two species as one, possibly following Keck's point of view (cf. U. S. National Park Service 1968). However, in his last publication about Argyroxiphium (Degeners and Sunadas 1976), he again considered the plants of different islands as different species. Hence, it can be seen that taxonomists do not have a uniform opinion regarding these two entities of Argyroxiphium.

Asa Gray (1852) differentiated his new taxon A. macrocephalum from A. sandwicense DC. on the basis that the former has larger capitula (38 mm in diameter), conical receptacles, and lacks pappus. Hillebrand (1888) disputed the lack of pappus in A. macrocephalum Gray. However, he accepted the notion that it has larger capitula (25 to 38 mm in diameter) and added that the taxon, as he recognized it (A. sandwicense DC. var. macrocephalum (Gray) Hbd.), has twenty to thirty ray florets in contrast to twelve to sixteen ray florets in typical A. sandwicense. Hillebrand (1888) also noted that in A. sandwicense var. macrocephalum, the ligules are shorter than in A. sandwicense var. sandwicense. The description of A. sandwicense by Degener (1932 et seq.) is a mixture of characteristics of both entities, but possibly comes closer to reflecting the characteristics of the Haleakala silversword due to the better

accessibility of Haleakala material. Comparing the description of A. sandwichense by Gray (1852, 1861, ined.) or Hillebrand (1888) with the description of A. sandwichense by Degener (1932 et seq.) or A. sandwichense by Keck (1936), reveals slight differences in leaf length, leaf width, inflorescence type, inflorescence length, peduncle length, involucre diameter, and the number of ray florets per capitulum. These slight differences, in addition to the general lack of accord among the authorities working with these plants, indicate the possibility that Mauna Kea silverswords are recognizably distinct from Haleakala silverswords.

### The Proposal

STATEMENT OF PURPOSE: This study is being undertaken to determine whether there are discernible qualitative or quantitative morphological differences between the Haleakala silversword (A. macrocephalum Gray) and the Mauna Kea silversword (A. sandwichense DC). However, other taxa of Argyroxiphium will also be studied with the same methods in order to gain a working knowledge of variation within the genus so that comparisons and evaluations will be more soundly based. The other taxa included in the study will be A. virescens var. paludosa and two populations of A. kauense (cf. Table 1, Materials and Methods).

HYPOTHESES: 1) There are enough morphological differences between the Haleakala silversword (A. macrocephalum Gray) and the Mauna Kea silversword (A. sandwichense DC.) to warrant their formal taxonomic recognition.

2) The Haleakala silversword (A. macrocephalum Gray) is the closest living relative of the Mauna Kea silversword (A. sandwichense DC.).

3) The Mauna Kea silversword (A. sandwichense DC.) is the closest living relative of the Ka'u silversword (A. kauense (Rock & Neal) Deg. & Deg.).

4) The two populations of A. kauense (Kahuku Forest Reserve vs. Power Line Road) are morphologically differentiated.

IMPORTANCE OF THE STUDY: Although extinction of organisms has been a natural adjunct to the process of evolution, man's activity has directly or indirectly greatly accelerated the demise of many organisms. Species restricted to islands are far more vulnerable to extinction than those of continental areas (Fosberg 1971). The various species of Argyroxiphium are endemic to the islands of Hawai'i and Maui, and due to their very localized, limited, and unique habitats, which have been disturbed by man's activity and by feral animals, some taxa are reported rare or endangered (cf. Fosberg and Herbst 1975, U.S.F.W.S. 1980).



A case in point is the greensword, Argyroxiphium virescens var. virescens. It was discovered by Hillebrand (1888) and collected on different expeditions to its habitat (Keck 1936). In 1930, Degener mentioned having visited a population of thirty plants. In 1970, Carlquist suggested that this taxon was close to extinction, and in 1975, Fosberg and Herbst listed it as possibly extinct. Apparently, it has not been seen in the field since Degener's observation (1930). The cause of its decline is not known; however, it is known that the habitat where it grew is highly disturbed by abundant feral pigs (Meyrat unpublished).

A second case concerns the Haleakala silversword whose plight was described poignantly by Degener (1948): "According to reliable accounts, the silversword in the early days was so abundant on the cinder cones in Haleakala as to make 'the hillside look like winter or moonlight.' The Hawaiians made silversword leis, but believed they must abide by certain rituals or their offended mountain gods would deluge them with rain. Later, tourists often uprooted the largest specimens just to watch them roll down the mountain slopes like giant snowballs. Until about 1915, these plants were gathered in great numbers, dried, and shipped to the Orient as ornaments. As a result of such vandalism by man, the ravages of hungry feral goats and of insect pests, the silversword was threatened with extinction."

In a following paragraph, Degener (1930) wrote: "In 1927, I made an intensive study of the silversword during a three-week's stay in Haleakala... the silversword population in Haleakala had dwindled to barely 100 plants!"

At present, the population of Haleakala silversword seems to be increasing (43,000 plants according to Kobayashi 1973b), because Haleakala National Park has been controlling feral goats and educating people about the uniqueness of the particular species. However, other closely related species which are part of the integrity of this genus are presently endangered, probably more so than the Haleakala silversword ever was.

One such example is the Mauna Kea silversword presently confined to the Wailuku drainage on Mauna Kea. Bryan (1973) reported that in 1951, he counted 27 good silversword plants growing in the area. He also mentioned a more recent counting of 40 plants and an estimation of 100 silversword plants for the whole area made by a State forester. Landgraf (1973) estimated the population at 150 plants, but only 35 plants were counted in 1978 (Meyrat unpublished). The extremely low number of individuals certainly places the Mauna Kea silversword in jeopardy.

In addition to the possible threat of outright extinction is the risk of gene pool dilution, alteration, or swamping by other species that could be transplanted to nearby locations. Certainly, transplanting of silverswords has been practiced, but fortunately not in the vicinity of the Wailuku River drainage.

For example, Haleakala silverswords have been planted by the Division of Forestry in Pu'u Kihe on Mauna Kea. Also, Haleakala, Mauna Kea, and Ka'u silverswords have been planted by the National Park Service on Red Hill and on the Mauna Loa Strip Road on Mauna Loa (Bryan 1973, Landgraf 1973, U. S. National Park Service 1974).

As a cooperative endeavor to help protect the Mauna Kea silverswords, the Division of Forestry, the Division of Fish and Game, and the U. S. Forest Service constructed a fenced enclosure adjacent to Wailuku canyon, in 1972 (Bryan 1973, Landgraf 1973). Although the walls of the canyon partially protect the silverswords and other native plants from browsing animals, additional areas along the canyon have also been fenced (Landgraf 1973). Bryan (1973) and Landgraf (1973) point out that the enclosure is for research purposes relating to vegetation regeneration, including silversword regeneration studies. However, there is no indication that Haleakala silverswords have been planted in this area.

The syndrome of morphological adaptations of Argyroxiphium to the alpine environment described earlier makes the genus one of the few living examples of such adaptations to tropical alpine conditions. In order to understand their morphological, anatomical, and physiological adaptations, and the evolutionary history of the genus, it is important to conserve every population in existence as the total and unique germ plasm for future scientific research. The careful study of groups such as this will undoubtedly provide invaluable information of wide application about plant modifications in stress environments.

The concern for conservation of silverswords expressed by scientists is augmented by the fact that the beauty of these plants attracts many visitors annually. Of perhaps far more significance is the conservation of every unique population of Argyroxiphium, each an evolutionary product requiring thousands or millions of years, on the basis that each is a component of the limited flora of the finely tuned and delicate ecosystem of the Hawaiian Islands. Extinction is forever.

This taxonomic study has the objective of determining whether the Mauna Kea and Haleakala silverswords are indeed unique, i.e., can they be considered recognizably distinct? This determination is extremely important from the standpoint of conservation and management of rare and endangered taxa and unique gene pools.

## MATERIALS AND METHODS

Morphological characters of five populations of Argyroxiphium were assessed (Table 1). A total of 49 flowering plants were 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 12 incomplete individuals in various stages of decline. Of the total of 97 individuals, 51 were observed in the summer of 1977 and 46 were observed in the summer of 1978 (Table 2).

Eight of the 45 quantitative characters (Table 3) were assessed in the field in every complete individual studied. Some floral parts were collected in plastic bags for later measurement in the laboratory. Fourteen laboratory measurements were made without magnification, 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, e.g. 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 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 character 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, the Duncan new

multiple 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 Snedecor and Cochran (1967), and Sokal and Rohlf (1969) was followed. To facilitate the statistical calculations, the BASIC Statistical Program of the HP2000 computer of the University of Hawaii was used.

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  $\mu$ . Each of the quantitative characters of the species A. sandwicense is described by using an average of the mean values of the subspecies, and these are identified in the taxonomy section by  $x_{ab}$  or  $\mu_{ab}$ .

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

## RESULTS

### Argyroxiphium sandwicense

The F tests from one way analysis of variance of 45 characters indicate that the means of 36 differ significantly ( $P < 0.05$ ) 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 ( $P < 0.05$ ) between A. sandwicense ssp. sandwicense and A. sandwicense ssp. macrocephalum (Table 4). Of those 18 characters, eight differ significantly at  $P < 0.001$ , six differ significantly at  $0.01 > P > 0.001$ , and four differ significantly at  $0.05 > P > 0.01$  (Table 4). When the branched plants were included in the analysis of variance, plant height was not significantly different between the two populations. However, when only non-branched plants were compared, plant height and also inflorescence differed significantly ( $P < 0.001$ ).

The Duncan new multiple range test indicates that the means of seven characters are significantly heterogeneous among all five populations (Table 5). The means of four additional characters, i.e. rosette height, peduncle length, bract length, and the number of bractlets per peduncle differ significantly among only some of the five populations. The Duncan test does not reveal significantly heterogeneous means for the remaining 34 characters.

When the data for individuals of all four taxa of Argyroxiphium are plotted together, correlations of leaf length with rosette diameter ( $r = +0.5242$ ) and peduncle length with inflorescence width ( $r = +0.7107$ ) are found (Figures 1,2). In each case the critical value for correlation coefficients indicates a highly significant relationship ( $P \leq 0.01$ ).

Likewise, the number of disk florets is found to be correlated with the following characters: receptacle diameter ( $r = +0.8985$ ), number of peripheral receptacular bracts per capitulum ( $r = +0.9137$ ), capitulum diameter ( $r = +0.9366$ ), and number of ray florets per capitulum ( $r = +0.9092$ ). In each, a strong relationship ( $P \leq 0.01$ ) is found. The relationship between the number of ray florets and capitulum diameter (Figure 3) is a good example of the relationship between any two capitulum features. Below the level of the genus, however, these features were found to be significantly correlated ( $P \leq 0.01$ ) only in A. sandwicense ssp. macrocephalum. In A. sandwicense ssp. sandwicense there is a tendency but no significant correlation, whereas in A. kauense and A. virescens var. paludosa, even the tendency of relationship of the features is very low.

In Argyroxiphium as a whole, there is a significant correlation ( $r = -0.3403$ ,  $0.05 > P > 0.01$ ) between leaf length and leaf width (Figure 4). Below the level of the genus, however, these features were found to be significantly correlated ( $P \leq 0.01$ ) only in A. sandwicense ssp. macrocephalum and A. kauense. In A. virescens var. paludosa there is a tendency but no significant correlation, and in A. sandwicense ssp. sandwicense, even the tendency is very low.

In contrast to the previous cases, there is no correlation between inflorescence length and inflorescence width ( $r = -0.0131$ ) when all the individuals of Argyroxiphium are considered (Figure 5). Below the level of the genus, these features were found to be significantly correlated ( $P \leq 0.01$ ) only in A. sandwicense ssp. macrocephalum and A. kauense. In A. sandwicense ssp. sandwicense there is a high tendency but no significant correlation and in A. virescens var. paludosa there is only a tendency of relationship between these features.

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 6).

Qualitative features such as leaf indument, ligule color, and pappus condition also aid in the recognition of A. sandwicense, A. kauense, and A. virescens var. paludosa. The

style of A. kauense differs from that of the other two species. Argyroxiphium sandwicense 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.

### Infrageneric Relationships

The F tests from one way analysis of variances indicate that of 45 characters, five differ significantly ( $P < 0.05$ ) between two populations of A. kauense. Of these characters, two differ significantly at  $P < 0.001$ , and three differ significantly at  $0.5 \geq P \geq 0.01$  (Table 6). The Duncan test indicates that among the means of 45 characters, eight are significantly heterogeneous (Table 5). This is three characters less than in the comparison between the two subspecies of A. sandwicense.

The means of 45 characters were ordered according to magnitude in order to determine the number of times that each pairwise combination of populations exhibited adjacent values (Table 7). Thus, A. sandwicense ssp. macrocephalum and A. sandwicense have adjacent means for 39 of the 45 characters, A. kauense and A. virescens var. paludosa 30, A. kauense and A. sandwicense ssp. sandwicense 21, A. sandwicense ssp. sandwicense and A. virescens var. paludosa 15, and A. sandwicense ssp. macrocephalum and A. virescens var. paludosa or A. kauense have adjacent means for only 13 characters.

With the data of Table 8 (Appendix), the coefficient of variation (C.V.) was calculated for each character of each of the four taxa. (Appendix tables not included in this report but can be obtained from M.S. thesis deposited in CPSU/UH library.) Argyroxiphium sandwicense ssp. sandwicense has the highest C.V. values in 17 characters out of 45. The mean C.V. for all the characters is 20.29. Argyroxiphium sandwicense ssp. macrocephalum has the highest C.V. values in 16 characters and an overall mean C.V. of 23.16. Argyroxiphium kauense has the highest C.V. values in six characters and an overall mean C.V. of 18.22. Argyroxiphium virescens var. paludosa has the highest C.V. values in only five characters and an overall mean C.V. of 16.48.

The qualitative features are tabulated in the Appendix (Tables 9, 10, 11). In all taxa some individuals with a terminal capitulum in the inflorescence are found. However, this character is highly frequent in A. kauense and seldom occurs in A. sandwicense ssp. macrocephalum (Appendix, Table 9). Sessile capitula at the base of the raceme are found only in A. sandwicense, always in ssp. sandwicense but seldom in ssp. macrocephalum (Appendix, Table 9). The shape of the receptacle was found to be strictly convex in A. virescens var. paludosa but strictly conical in A. kauense. In the two subspecies of A.

sandwicense, both receptacle shapes are found, in a few cases, even within single individuals.

The examination of ligule coloration (Appendix, Table 10) indicates that A. virescens var. paludosa has only yellow ligules, or rarely, they are tinged with wine red. Ligule color in A. sandwicense varies from wine red to rose pink, darker tones more usually present in ssp. macrocephalum, and lighter tones in ssp. sandwicense. In A. kauense the ligule color is a mixture of wine red, yellow, and white, tending to lighter tones. In fact, even plants with only white ligules were found in the population (Appendix, Table 10).

In all taxa the ray achene pappus differs from that of the disk achenes (Appendix, Table 11). In disk achenes pappus may be present, reduced, or absent. However, in ray achenes, only two conditions exist, reduced and absent. In A. virescens var. paludosa and A. kauense the disk achene pappus is always present. The ray achene pappus is always reduced in the former taxon, but absent in the latter. In the disk achenes of A. sandwicense ssp. macrocephalum the three pappus conditions exist. However, they are reduced or absent in most individuals. In A. sandwicense ssp. sandwicense they are present or absent. The reduced condition was not found. Both subspecies show similar pappus conditions of ray achenes.

## DISCUSSION

### Argyroxiphium sandwicense

Of 11 characters indicated as being significantly different among five populations of three species by the Duncan test, seven were also identified as differing significantly between the two subspecies of A. sandwicense by the F test. These were rosette diameter, inflorescence width, leaf length, number of ray florets per capitulum, number of disk florets per capitulum, peduncle length, and number of peripheral receptacular bracts per capitulum. It is apparent that the F test and the Duncan test give conflicting results for some characters. These differences result from the fact that although the Duncan test is stricter than the F test, it is not as sensitive as the F test to variation of individuals within and among populations. For this reason the F test appears to be the best indicator of differentiation between the two subspecies of A. sandwicense. However, by identifying the characters that vary among all of the taxa, the Duncan test provides 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.

Although plant height was initially considered an independent character, further analysis indicated that the

component contributed by the inflorescence was responsible for the significant differences in height detected in certain instances. Furthermore, it was noted that inflorescence length and number of capitula per inflorescence were affected by branching of the plant axis. None of the other characters were significantly affected by this factor.

The correlation of leaf length-rosette diameter and peduncle length-inflorescence width indicates that in each pair the dimension of the first is largely responsible for the dimension of the second. With respect to the relationship between capitulum diameter and number of ray florets (Figure 3), each taxon exhibits its own pattern. Argyroxiphium sandwicense ssp. macrocephalum has more ray florets as the capitulum diameter increases. Argyroxiphium sandwicense ssp. sandwicense also shows a similar tendency. Argyroxiphium kauense exhibits low variation of capitulum diameter but there is greater variation in the number of ray florets. In A. virescens var. paludosa the variation in capitulum diameter is more conspicuous than the variation in the number of ray florets.

The relationship between leaf length and leaf width shows a nearly continuous trend where taxa with larger leaves tend to have them narrower. However, within each taxon the relationship is reversed (Figure 4). In the relationship between inflorescence length and inflorescence width, A. sandwicense ssp. sandwicense and A. kauense overlap completely, and their slopes diverge from those of A. sandwicense ssp. macrocephalum and A. virescens var. paludosa (Figure 5).

Among the 18 characters that differ significantly between the two subspecies of A. sandwicense, the most useful are: inflorescence length, inflorescence width, leaf length, leaf width, number of ray florets per capitulum, and capitulum diameter. 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 to 3.8:1, whereas in A. sandwicense ssp. sandwicense this ratio ranges from 4.4:1 to 8.9:1. However, to separate all the four taxa considered in this study based on quantitative characters, at least three features are needed, e.g. inflorescence proportions, leaf proportions, and number of ray florets per capitulum (Figure 6).

Although few individuals were observed from the remaining population of A. 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, ined.) 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, ined.) 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 Argyroxiphium 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 is estimated from the photograph.

Although now severely restricted in size and number, the Wailuku River population of A. 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 unpublished).

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 A. sandwicense, one on Maui and one on Hawai'i, meet the foregoing criteria, the category of subspecies seems most appropriate.

The other species, A. virescens var. paludosa and A. kauense, are as distinct from each other as from A. sandwicense in many quantitative and qualitative characters. Although the two subspecies of A. sandwicense are differentiated by the same number of quantitative characters as the other species (Table 5), they are poorly differentiated in a qualitative sense. Thus, it seems imprudent to argue for specific status of the Mauna Kea and Haleakala silverswords.

A key to these subspecies of A. sandwicense and other common taxa of East Maui and Hawai'i are 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.

### Infrageneric Relationships

Although the Duncan test indicates eight characters with significantly different mean values between the two populations of A. kauense (Table 5), the F tests indicate that only five pairs of character means are significantly different between them (Table 6). Thus, there is an indication of differentiation between the two populations of A. kauense. However, because only a single complete individual of the Power Line Kipuka population has been evaluated, more studies are required before firm conclusions can be drawn.

The resemblance of A. sandwicense ssp. macrocephalum and A. sandwicense ssp. sandwicense in 11 of 15 vegetative characters and 28 of 30 capitulum characters (Table 7) indicates that they are very closely related taxa. Considering the geographical distributions, one might expect the Maui taxa A. virescens var. paludosa and A. sandwicense ssp. macrocephalum to resemble one another in a large number of characters. The same might be expected of the Hawai'i taxa A. sandwicense ssp. sandwicense and A. kauense. However, the results show that there are very low affinities between the two taxa of Maui, and although there is a high resemblance of characters between the two taxa of Hawai'i, there is still higher resemblance between A. kauense and A. virescens var. paludosa, even though they are from different islands. On the other hand, the similarity of A. sandwicense ssp. macrocephalum in vegetative and inflorescence characters to A. virescens var. paludosa, and of A. sandwicense ssp. sandwicense to A. kauense is great in relation to the rest of the pairwise comparisons. Vegetative and inflorescence characters suggest a linear pattern of relationship as follows: A. virescens var. paludosa-A. sandwicense ssp. macrocephalum-A. sandwicense ssp. sandwicense-A. kauense. This correlates well with the geographical distribution of these taxa, and A. sandwicense would be the link between the Argyroxiphium of East Maui and Hawai'i. However, the capitulum characters do not support this pattern of relationships. For example, they indicate a high resemblance of A. virescens var. paludosa and A. kauense in 25 of 30 characters. This situation may be due to convergent evolution of reproductive features adapted for similar reproductive modes in similar extreme environments (Carlquist 1974).

Also, it is possible that hybridization between A. sandwicense ssp. sandwicense and a greensword was involved in the origin of A. kauense. The resemblance of A. kauense and A. sandwicense ssp. sandwicense in 10 of 15 vegetative and inflorescence characters is high, considering that the two subspecies of A. sandwicense resemble one another in 11 out of 15 vegetative characters. Argyroxiphium kauense resembles A. sandwicense ssp. sandwicense in leaf and inflorescence proportions (Figures 4, 5). In addition, A. kauense is intermediate between A. sandwicense ssp. sandwicense and A. virescens var. paludosa in the number of ray florets per

capitulum, capitulum diameter (Figure 3), color of ligule, pappus condition, leaf indument, and length of stem below the rosette. Ecologically, A. kauense is also intermediate between the two latter mentioned taxa. Considering the observations made by Carr and Kyhos (1981) on hybridization in this group of plants, the morphological and ecological observations of this study suggest the possibility of the hybrid origin of A. kauense. Moreover, an artificial hybrid between A. sandwicense ssp. sandwicense and A. virescens var. paludosa grown at the Department of Botany of the University of Hawaii exhibits the number of ray florets, ligule color, capitulum size, leaf width, and leaf indument in the range of A. kauense. Other features such as leaf length and inflorescence proportions are dissimilar, but these characters have been observed to be out of normal ranges in other cultivated Argyroxiphium. One problem with this hypothesis is the fact that greenswords are not known from the island of Hawai'i. However, silversword-greensword hybrids have been reported from East Maui (Rock and Neal 1957).

Argyroxiphium virescens var. paludosa resembles A. sandwicense ssp. sandwicense and ssp. macrocephalum in about the same total number of features. However, the resemblance of the first pair is largely due to the smaller size of the capitulum of A. sandwicense ssp. sandwicense in comparison to that of ssp. macrocephalum.

Likewise, Argyroxiphium kauense resembles A. sandwicense ssp. macrocephalum and ssp. sandwicense in about the same number of capitulum features. However, the first pair resemble one another in only 3 of 15 vegetative and inflorescence characters. This is low in comparison to the resemblance of A. kauense and A. sandwicense ssp. sandwicense.

The two subspecies of A. sandwicense have the highest coefficients of variation in a greater number of characters compared to the other two taxa. This pattern suggests correlation between high character variation and populations of the alpine environment, and between low character variation and populations of the bog or bog-like conditions. It is known that Argyroxiphium adapted to bogs or bog-like conditions exhibit a high degree of vegetative reproduction. This might be partly responsible for the low character variation found in that habitat. However, more study of these populations and their environment is necessary before any conclusions may be drawn.

#### 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 diameter; 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 cm wide at the midpoint, 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 leaf-like 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; involucre 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 3 lobed, nearly white to yellow or to rose or wine red. Ray achenes linear, 4-14 mm long, arcuate, generally 4-5 ribbed, blackish; pappus present at the dorsal tip, 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 funnellform, sometimes campanulate, rarely suburceolate, distally flared into 5 deltoid lobes 0.5-1.0 mm long; anthers basally obtuse, terminally appendaged; the 2 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 4-5 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. A. 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, less than 35 times longer than broad; rosette nearly always sessile; ligule deep wine red to pale pink, not yellow.

3. A. sandwichense

3. Inflorescence 4.4-8.9 ( $\bar{x}$  = 6.0) times longer than broad; ray florets 5-20 ( $\bar{x}$  = 12.5); leaves 19.5-32.7 ( $\bar{x}$  = 25.5) times longer than broad (Hawai'i)

3A. A. sandwichense ssp. sandwichense

3. Inflorescence 1.5-3.8 ( $\bar{x}$  = 2.5) times longer than broad; ray florets 11-42 ( $\bar{x}$  = 23.6); leaves 12.3-21.1 ( $\bar{x}$  = 17.2) times longer than broad (Maui)

3B. A. sandwichense 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 cm 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 ( $\mu$  = 18.8) cm long, 0.9-2.0 ( $\mu$  = 1.4) cm wide at the midpoint, dark green, glabrate above, sparsely pilosulous below and more densely pilosulous-ciliate on the margin, 7-9 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 ( $\mu$  = 10.1) cm long, 0.8-1.8 ( $\mu$  = 1.4) cm wide; peduncles 1.0-19.5 ( $\mu$  = 10.7) cm long, 2-5 ( $\mu$  = 3.6) mm wide, branched or more often unbranched, bearing 0-4 smaller capitula in addition to the large terminal one; bractlets 1-11 ( $\mu$  = 4.4), 1.5-4.6 ( $\mu$  = 2.7) cm long, 0.2-0.7 ( $\mu$  = 0.4) cm wide. Capitula 1.4-2.0 ( $\mu$  = 1.6) cm long, 1.1-2.1 ( $\mu$  = 1.5) cm in diameter; receptacle conical, 0.5-0.8 ( $\mu$  = 0.7) cm in diameter; involucre bracts as many as ray florets, 0.9-1.3 ( $\mu$  = 1.2) cm long, 1-3 ( $\mu$  = 2.6) mm wide; peripheral receptacular bracts 24-46 ( $\mu$  = 31.7); inner receptacular bracts 0-1 ( $\mu$  = 0.2), 0.7-0.8 ( $\mu$  = 0.8) cm long, 0.5 mm wide. Ray florets 1-8 ( $\mu$  = 1.4); tube 0.2-0.4 ( $\mu$  = 0.3) cm long, 3-4 ( $\mu$  = 3.4) mm wide; ligule mimosa yellow and white, sometimes with wine red tinges, 0.6-0.7 ( $\mu$  = 0.62) cm long, 0.3-0.4 ( $\mu$  = 0.34) mm wide, 3-4 ( $\mu$  = 3.4) lobed, 4-6 ( $\mu$  = 4.9) veined; style 0.4-0.5 ( $\mu$  = 0.45) cm long, 2 branched, the branches slightly arcuate-descending 1-2 ( $\mu$  = 1.6) mm long. Ray achene 0.6-0.8 ( $\mu$  = 0.7) cm long, 1-2 ( $\mu$  = 1.3) mm wide, 4-5 ( $\mu$  = 4.5) ribbed; pappus reduced. Disk florets 100-271 ( $\mu$  = 165.4), glabrous, narrowly campanulate, sometimes suburceolate, 0.5-0.6 ( $\mu$  = 0.57) cm long, 1.0-2.0 ( $\mu$  = 1.6) mm wide; style 0.6-0.8 ( $\mu$  = 0.7) cm long, 2 branched, the branches 1-2 ( $\mu$  = 1.95) mm long; stamen filament 2.0 mm long; anther 2.0 mm long. Disk achene 0.6-0.7 ( $\mu$  = 0.67) cm long, 1.0 mm wide, 4-5 ( $\mu$  = 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., Aug. 21, 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, Aug. 2, 1977, Meyrat, Carr, & Stemmermann 52, 53 (HAW).

2. Argyroxiphium kauense (Rock & Neal) Deg. & Deg. *Phytologia* 33(3):173-177. 1976.

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

Figures 7A, 8A, 9A

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 subspheric 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 ( $\mu$  =

31.7) cm long, 0.4-0.8 ( $\mu = 0.6$ ) 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 ( $\mu = 10.4$ ) cm long, 0.3-1.6 ( $\mu = 0.9$ ) cm wide; peduncle 3.1-14.3 ( $\mu = 9.5$ ) cm long, 1-3 ( $\mu = 2.2$ ) mm wide; bractlets 1-3 ( $\mu = 2.4$ ) per peduncle, 1.3-3.3 ( $\mu = 2.4$ ) cm long, 0.1-0.5 ( $\mu = 0.3$ ) cm wide. Capitula 1.5-2.2 ( $\mu = 1.9$ ) cm long, 1.0-1.8 ( $\mu = 1.5$ ) cm in diameter; receptacle convex, 0.6-0.9 ( $\mu = 0.7$ ) cm in diameter; involucre bracts as many as ray florets, 0.5-1.5 ( $\mu = 1.1$ ) cm long, 1-4 ( $\mu = 2.4$ ) mm wide; peripheral receptacular bracts 22-42 ( $\mu = 36$ ); inner receptacular bracts 0-3 ( $\mu = 0.1$ ), 0.8-1.1 ( $\mu = 0.9$ ) cm long, 0.3-1.0 ( $\mu = 0.8$ ) mm wide. Ray florets 3-11 ( $\mu = 8.2$ ); tube 0.2-0.4 ( $\mu = 0.3$ ) 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 ( $\mu = 0.6$ ) cm long, 0.2-0.5 ( $\mu = 0.3$ ) cm wide, 2-5 ( $\mu = 2.8$ ) lobed, 6-9 ( $\mu = 7.1$ ) veined; style 0.2-0.5 ( $\mu = 0.4$ ) cm long with sparsely dispersed hispidulous trichomes, 2 branched, the branches rolled, 2-2.5 ( $\mu = 2.0$ ) mm long and slightly truncate. Ray achene 0.7-0.9 ( $\mu = 0.8$ ) cm long, 1-2 ( $\mu = 1.4$ ) mm wide, 4-8 ( $\mu = 5.3$ ) ribbed; pappus absent. Disk florets 45-214 ( $\mu = 142.8$ ), funnel-form chrome yellow, usually with wine red tinges above and whitish below, 0.5-0.7 ( $\mu = 0.6$ ) cm long, 1.0-2.5 ( $\mu = 2.0$ ) mm wide; style 0.4-0.8 ( $\mu = 0.7$ ) cm long, 2 branched, the branches 1.5-2.5 ( $\mu = 2.0$ ) mm long; stamen filament 2.0 mm long; anther loosely connate 2.0-2.5 ( $\mu = 2.4$ ) mm long. Disk achene 0.6-1.0 ( $\mu = 0.8$ ) cm long, 0.7-2.0 ( $\mu = 1.6$ ) mm wide, 3-7 ( $\mu = 4.5$ ) 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., Aug. 20, 1977, Meyrat, Jacobi, Evenson, & Stemmermann 13, 14, 17 (HAW); Aug. 2, 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 ( $\mu_{ab} = 24.4$ ) cm long, 0.6-2.3 ( $\mu_{ab} = 1.2$ ) 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 ( $\bar{x}_{ab} = 1.7$ ) m long in unbranched plants, 16-78 ( $\bar{x}_{ab} = 34$ ) 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 ( $\mu_{ab} = 13.5$ ) cm long and 0.4-3.0 ( $\mu_{ab} = 1.3$ ) cm wide; peduncle 3.5-40.0 ( $\mu_{ab} = 13.9$ ) cm long, 2-10 ( $\mu_{ab} = 4.1$ ) mm wide; usually unbranched, but when branched bearing 0-10 smaller capitula in addition to the large terminal one; bractlets 1-28 ( $\mu_{ab} = 6.2$ ) per peduncle, 1.4-10.2 ( $\mu_{ab} = 4.4$ ) cm long, 0.1-0.9 ( $\mu_{ab} = 0.3$ ) cm wide. Capitula 1.2-3.5 ( $\mu_{ab} = 2.4$ ) cm long, 1.2-4.3 ( $\mu_{ab} = 2.4$ ) cm in diameter; receptacle conical or convex, 0.5-2.3 ( $\mu_{ab} = 1.3$ ) cm in diameter; involucre bracts as many as ray florets, 1-2.4 ( $\mu_{ab} = 1.6$ ) cm long, 1.0-8.0 ( $\mu_{ab} = 3.0$ ) mm wide; peripheral receptacular bracts 31-115 ( $\mu_{ab} = 60.8$ ); inner receptacular bracts 0-20 ( $\mu_{ab} = 1.3$ ), 0.9-2.5 ( $\mu_{ab} = 1.5$ ) cm long, 0.5-2.0 ( $\mu_{ab} = 1.2$ ) mm wide. Ray florets 5-42 ( $\mu_{ab} = 18.1$ ); tube 0.3-0.8 ( $\mu_{ab} = 0.5$ ) cm long, glandular-pilosulous above and non-glandular below; ligule wine red to rose pink, 0.6-2.0 ( $\mu_{ab} = 1.0$ ) cm long, 0.2-0.6 ( $\mu_{ab} = 0.4$ ) cm wide, 2-4 ( $\mu_{ab} = 2.9$ ) lobed, 5-11 ( $\mu_{ab} = 7.0$ ) veined; style 0.4-1.2 ( $\mu_{ab} = 0.7$ ) cm long, 2 branched, the branches arcuate descending 1-4 ( $\mu_{ab} = 2.6$ ) mm long. Ray achene 0.7-1.4 ( $\mu_{ab} = 1.0$ ) cm long, 1.5-3.0 ( $\mu_{ab} = 2.0$ ) mm wide, 4-7 ( $\mu_{ab} = 4.6$ ) ribbed; pappus usually absent, sometimes reduced. Disk florets 47-600 ( $\mu_{ab} = 268.2$ ), funnellform, rarely suburceolate, wine red to rose pink above, glandular pilosulous at the middle, white-yellowish and pilosulous below, 0.6-1.1 ( $\mu_{ab} = 0.8$ ) cm long, 1.0-2.5 ( $\mu_{ab} = 1.7$ ) mm wide; style 0.7-1.2 ( $\mu_{ab} = 1.0$ ) cm long, 2 branched, the branches 2-4 ( $\mu_{ab} = 2.8$ ) mm long; stamen filament 2-6 ( $\mu_{ab} = 3.3$ ) mm long; anther 2-4 ( $\mu_{ab} = 3.0$ ) cm long, disk achene 0.7-1.5 ( $\mu_{ab} = 1.0$ ) cm long, 1.0-3.0 ( $\mu_{ab} = 1.9$ ) mm wide, 4-8 ( $\mu_{ab} = 4.3$ ) 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 7B, 8B, 9B

DESCRIPTION: Rosette 18-49 ( $\bar{x} = 30$ ) cm high, 19-80 ( $\bar{x} = 39$ ) cm in diameter. Leaves linear lanceolate to linear, 18-39 ( $\mu = 26$ ) cm long, 0.6-1.5 ( $\mu = 1.0$ ) cm wide at the midpoint. Raceme simple or more frequently partially paniculate, oblong, 1.9-2.5 ( $\bar{x} = 2.2$ ) m long in unbranched plants, and 0.7-1.4 ( $\bar{x} = 1.1$ ) m long in branched plants, 16-29 ( $\bar{x} = 24.4$ ) 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 ( $\mu = 13.0$ ); peduncles 5.0-18.5 ( $\mu = 11.5$ ) cm long, 2.5-5.0 ( $\mu = 3.5$ ) mm wide, branched or more often unbranched; bractlets 2-12 ( $\mu = 5.1$ ). Capitula 1.2-3.5 ( $\mu = 2.4$ ) cm long, 1.2-3.2 ( $\mu = 2.1$ ) cm in diameter; receptacle usually conical or less often convex, 0.5-1.6 ( $\mu = 1.0$ ) cm in diameter; peripheral receptacular bracts 31-75 ( $\mu = 50.7$ ). Ray florets 5-20 ( $\mu = 12.5$ ); tube 0.3-0.6 ( $\mu = 0.5$ ) cm long; ligule wine red to pink, 5-8 ( $\mu = 6.3$ ) veined. Ray achene 0.7-1.4 ( $\mu = 1.0$ ) cm long. Disk florets 47-471 ( $\mu = 216.3$ ), funnelform; style 0.7-1.1 ( $\mu = 0.9$ ) cm long; stamen filament 2.5-6.0 ( $\mu = 3.5$ ) 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!; ISOTYPE: CGE-Lindley).

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

3B. Argyroxiphium sandwicense DC. ssp. macrocephalum comb. nov. et stat. nov.

Argyroxiphium macrocephalum Gary Proc. Amer. Acad. 2:160. 1852; Proc. Amer. Acad. 5:114-146. 1861.

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

Figures 7C, 8C, 9C

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 ( $\mu = 22.7$ ) cm long, 0.8-2.3 ( $\mu = 1.4$ ) 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 ( $\mu = 14.0$ ) cm long, peduncles 3.5-40.0 ( $\mu = 16.3$ ) cm

long, 2-10 ( $\mu = 4.7$ ) mm wide, usually unbranched; bractlets 1-28 ( $\mu = 7.2$ ) per peduncle. Capitula 1.4-3.5 ( $\mu = 2.3$ ) cm long, 1.4-4.3 ( $\mu = 2.7$ ) cm in diameter; receptacle convex or conical, 0.8-2.3 ( $\mu = 1.6$ ) cm in diameter; peripheral receptacular bracts 32-115 ( $\mu = 70.8$ ). Ray florets 11-42 ( $\mu = 23.6$ ); tube 0.3-0.8 ( $\mu = 0.6$ ) cm long, ligule wine red to rose pink, 5-11 ( $\mu = 7.6$ ) veined. Ray achene 0.7-1.1 ( $\mu = 0.9$ ) cm long. Disk florets 120-600 ( $\mu = 320$ ) funnelform, rarely suburceolate; style 0.7-1.2 ( $\mu = 1.0$ ) cm long; stamen filament 2-4 ( $\mu = 3.1$ ) 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, Aug. 3, 1977, Meyrat, Carr, & Stemmermann 1, 2, 3, 4 (HAW); Sliding Sand Trail, July 21, 1978, Meyrat & Funk 60, 62A-B, 63A-B, 64, 65A-B, 66A-B-C-D (HAW).

#### CONCLUSIONS

The fact that among 45 characters, the means of 18 differ significantly ( $P \leq 0.05$ ) between the Mauna Kea and Haleakala silverswords verifies that "there are enough morphological differences between them to warrant their formal taxonomic recognition," a hypothesis stated earlier. Based on the nature of the differentiation and the geographical isolation, it is proposed to recognize them as two different subspecies: A. sandwicense ssp. sandwicense and A. sandwicense ssp. macrocephalum. Because the two subspecies are poorly differentiated in a qualitative sense, and because they exhibit adjacent mean values for the largest number of characters of the relevant pairwise combinations of populations it appears that A. sandwicense ssp. macrocephalum is the closest living relative of A. sandwicense ssp. sandwicense.

The resemblance of A. kauense and A. sandwicense ssp. sandwicense in 11 of 15 vegetative and inflorescence characters suggests a close relationship between these taxa. However, the capitulum characters do not support this relationship. In fact, A. kauense resembles A. virescens var. paludosa in 25 of 30 capitulum characters. It is suggested that this situation may be due to convergent evolution of reproductive features adapted for similar reproductive modes in similar extreme environments. Also, the intermediate morphological and ecological position of A. kauense suggests the possibility that hybridization between A. sandwicense ssp. sandwicense and a greensword was involved in the origin of A. kauense.

There is an indication of differentiation between the two populations of *A. kauense*, because five pairs of character means are significantly different ( $P < 0.05$ ) between them. However, because only a single complete individual of the Power Line Kipuka population has been evaluated, more studies are required before firm conclusions can be drawn.

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TABLE 1. Populations of Argyroxiphium studied.

Taxon	Location
<u>A. kauense</u>	Kahuku Ranch, Mauna Loa, ca. 1830 m elev.
<u>A. kauense</u>	In a kipuka east of Power Line Road, Saddle Road, Hawai'i, ca. 1650 m elev.
<u>A. sandwicense</u> ssp. <u>sandwicense</u>	Origin of Wailuku drainage, Mauna Kea, Hawai'i, ca. 2850 m elev.
<u>A. sandwicense</u> ssp. <u>macrocephalum</u>	Haleakala Crater, Maui, ca. 2100-2700 m elev.
<u>A. virescens</u> var. <u>paludosa</u>	Ridge between Kipahulu and Kuhiwa Valley, 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	
A. <u>kauense</u> , Power Line Kipuka Bog	1	0	13	6	20
A. <u>kauense</u> , Kahuku Ranch	0	10	17	1	28
A. <u>sandwicense</u> ssp. <u>sandwicense</u>	1	4	5	0	10
A. <u>sandwicense</u> ssp. <u>macrocephalum</u>	4	25	4	0	33
A. <u>virescens</u> var. <u>paludosa</u>	4	0	2	0	6
Totals	10	39	41	7	97

Table 3. List of 45 characters assessed in individuals of five populations of Argyroxiphium.

Field Measurements		18. Bractlet length
1. Plant height		19. Bractlet width*
2. Rosette height		20. Receptacle diameter
3. Rosette width		21. Number of peripheral receptacular bracts
4. Inflorescence length		22. Number of inner receptacular bracts*
5. Inflorescence width		
6. Number of capitula per inflorescence		Laboratory Measurements With Magnification
7. Leaf length		23. Involucral bract length
8. Leaf width		24. Involucral bract width*
Laboratory Measurements Without Magnification		25. Inner receptacular bract length*
9. Capitulum length		26. Inner receptacular bract width*
10. Capitulum diameter		27. Ligule length
11. Number of ray florets per capitulum		28. Ligule width
12. Number of disk florets per capitulum		29. Ray floret tube length
13. Peduncle length		30. Number of ligule lobules*
14. Peduncle width		31. Number of main veins per ligule
15. Bract length		32. Ray floret style length
16. Bract width		33. Ray floret style branch length
17. Number of bractlets per peduncle		34. Ray achene length

TABLE 3.--Continued.

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35. Ray achene width	41. Stamen filament length
36. Number of ray achene ribs*	42. Anther length
37. Disk floret length	43. Disk achene length
38. Disk floret width*	44. Disk achene width
39. Disk floret style length	45. Number of disk achene ribs*
40. Disk floret style branch length	

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\* Characters that do not differ significantly ( $P < 0.05$ ) among populations of Argyroxiphium as indicated by the F test from one way analysis of variance.

TABLE 4. Characters that differ significantly between Argyroxiphium sandwicense ssp. sandwicense and A. sandwicense ssp. macrocephalum as determined by the F test from one way analysis of variance.

Character	F Calculated	Degrees of Freedom	Level of Significance
Plant height excluding branched plants	15.7721	1, 56	***
Rosette diameter	26.8872	1, 72	***
Inflorescence length			
including branched plants	7.8618	1, 61	**
excluding branched plants	33.7284	1, 55	***
Inflorescence width	16.3924	1, 48	***
Leaf length	4.1113	1, 73	*
Leaf width	25.2133	1, 73	***
Capitulum diameter	11.5901	1, 44	**
Number of ray florets per capitulum	26.3980	1, 44	***
Number of disk florets per capitulum	12.1072	1, 44	**
Peduncle length	7.2074	1, 45	*
Peduncle width	7.0565	1, 44	*
Receptacle diameter	34.9928	1, 44	***
Number of peripheral receptacular bracts per capitulum	15.0202	1, 44	***
Number of main veins per ligule	7.6906	1, 43	***

TABLE 4.--Continued.

Character	F Calculated	Degrees of Freedom	Level of Significance
Ray floret tube length	5.5789	1, 44	**
Ray achene length	7.4286	1, 44	**
Disk floret style length	2.7403	1, 44	*
Stamen filament length	8.0963	1, 44	**

NOTE: \* = probability of larger F value is lower than 0.05 but higher than 0.01, \*\* = probability of larger F value is lower than 0.01 but higher than 0.001, \*\*\* = probability of larger F value is lower than 0.001.

TABLE 5. Characters exhibiting significantly different means among five populations of Argyroxiphium as determined by Duncan's new multiple range test.

Character	Means of Populations				
Rosette height (cm)	28.6 K2	<u>29.5</u> K1	<u>29.8</u> SS	33.1 SM	45.5 VP
Rosette diameter (cm)	39.0 SS	44.5 VP	56.3 K1	59.5 K2	60.5 SM
Inflorescence width (cm)	21.0 K1	23.1 K2	24.4 SS	33.3 VP	43.7 SM
Number of capitula per raceme					
including branched plants	135.2 VP	171.7 K1	193.4 SS	265.2 SM	268.0 K2
excluding branched plants	135.2 VP	171.7 K1	268.0 K2	274.9 SM	310.0 SS
Leaf length (cm)	18.8 VP	22.7 SM	25.8 SS	30.3 K1	31.7 K2
Number of ray florets per capitulum	1.4 VP	6.8 K1	8.2 K2	12.5 SS	23.6 SM
Number of disk florets per capitulum	142.8 KS	144.6 K1	155.4 VP	216.3 SS	320.1 SM
Peduncle length (cm)	<u>9.5</u> K1	<u>9.5</u> K2	10.7 VP	11.6 SS	16.3 SM

TABLE 5.--Continued.

Character	Means of Populations				
Bract length (cm)	8.9 <u>K1</u>	10.1 <u>VP</u>	10.4 K2	13.0 SS	14.0 SM
Number of bractlets per peduncle	2.0 <u>K1</u>	2.4 K2	2.7 <u>VP</u>	4.2 <u>SS</u>	4.6 SM
Number of peripheral receptacular bracts per capitulum	31.7 VP	36.0 K2	41.2 K1	50.7 SS	70.8 SM

NOTE: Any two means underscored by the same line are not significantly different. Any two means not underscored by the same line are significantly different; VP = A. virescens var. paludosa, SM = A. sandwicense ssp. macrocephalum, SS = A. sandwicense ssp. sandwicense, K1 = A. kauense from Power Line Kipuka bog, K2 = A. kauense from Kahuku Ranch.

TABLE 6. Characters that differ significantly between the two populations of Argyroxiphium kauense as determined by the F test from one way analysis of variance.

Character	F Calculated	Degree of Freedom	Level of Significance
Plant length	16.6616	1, 62	***
Leaf width	10.1613	1, 73	***
Inflorescence length	4.7873	1, 61	*
Number of capitula per raceme	4.5574	1, 54	*
Involucral bract length	5.6122	1, 44	*

NOTE: \* = probability of larger F value is lower than 0.05 but higher than 0.01, \*\*\* = probability of larger F value is lower than 0.001.



TABLE 7. Number of occurrences of adjacent mean values of 45 characters in each possible combination of two populations of Argyroxiphium.

Populations Compared	Vegetative and Inflorescence Characters Total = 15	Capitulum Characters Total = 30	All Characters Total = 45
VP and SM	9	4	13
VP and SS	7	8	15
VP and K2	5	25	30
SM and SS	11	28	39
SM and K2	3	10	13
SS and K2	10	11	21

NOTE: VP = A. virescens var. paludosa; SM = A. sandwicense ssp. macrocephalum; SS = A. sandwicense ssp. sandwicense; K2 = A. kauense, from Kahuku Ranch.

FIGURE 1. The relationship between rosette diameter and leaf length in Argyroxiphium as indicated by data from four taxa. Open circles, A. virescens var. paludosa; stars, A. kauense; open squares, A. sandwicense ssp. macrocephalum; solid squares, A. sandwicense ssp. sandwicense.

FIGURE 2. The relationship between inflorescence width and peduncle length in Argyroxiphium as indicated by data from four taxa. Symbols explained in Figure 1.

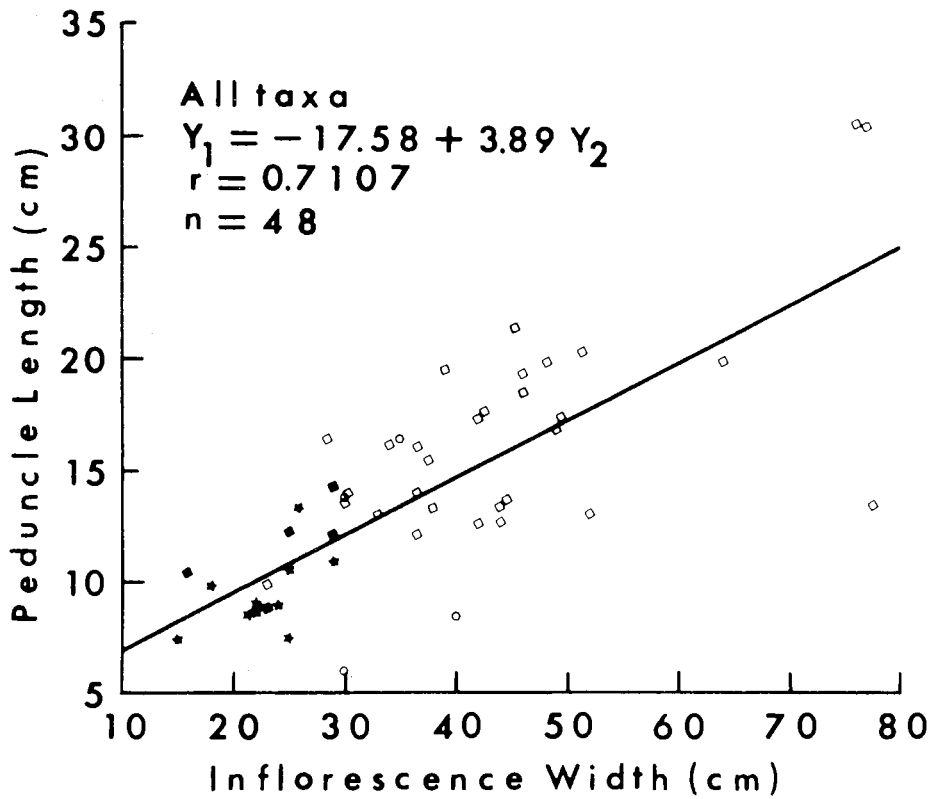
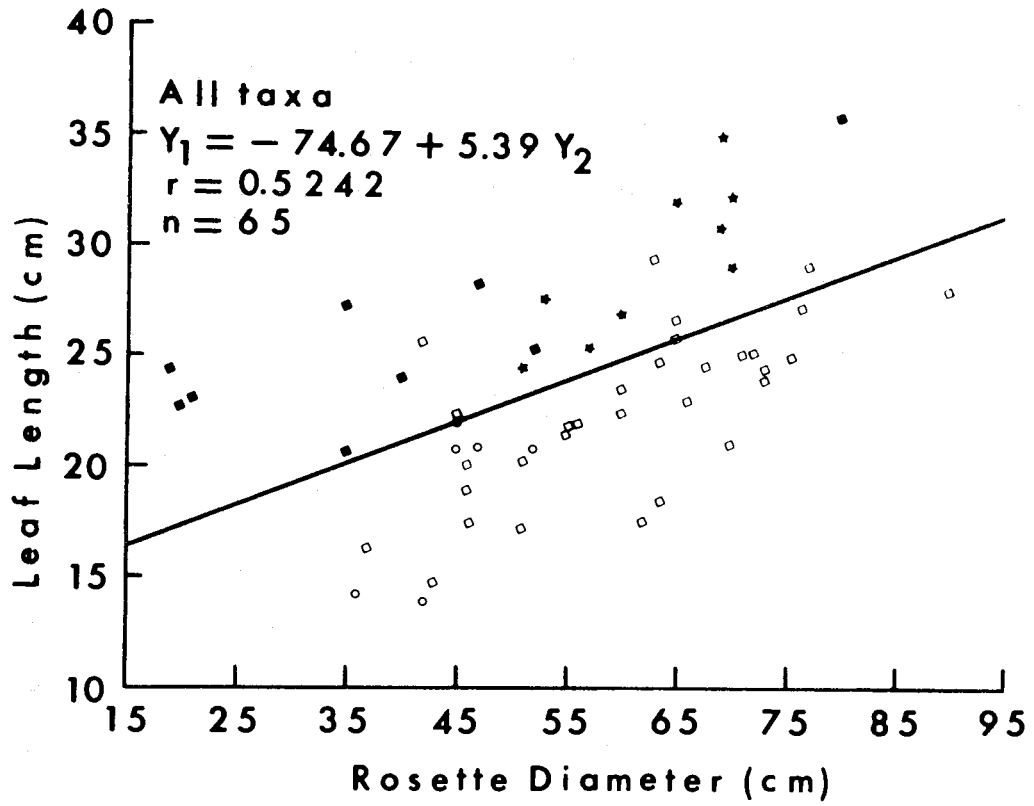


FIGURE 3. The relationship between number of ray florets per capitulum and capitulum diameter in the genus Argyroxiphium, and within infrageneric taxa. VP, A. virescens var. paludosa; K2, A. kauense; SM, A. sandwicense ssp. macrocephalum; SS, A. sandwicense ssp. sandwicense.

FIGURE 4. The relationship between leaf length and leaf width in the genus Argyroxiphium, and within infrageneric taxa. Abbreviations explained in Figure 3.

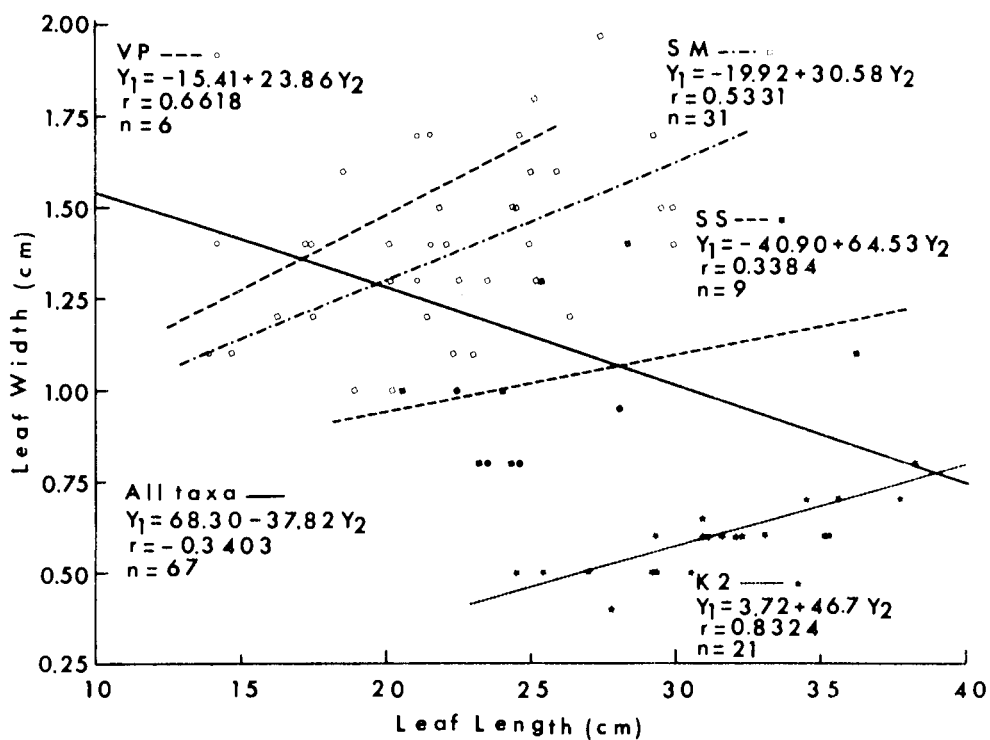
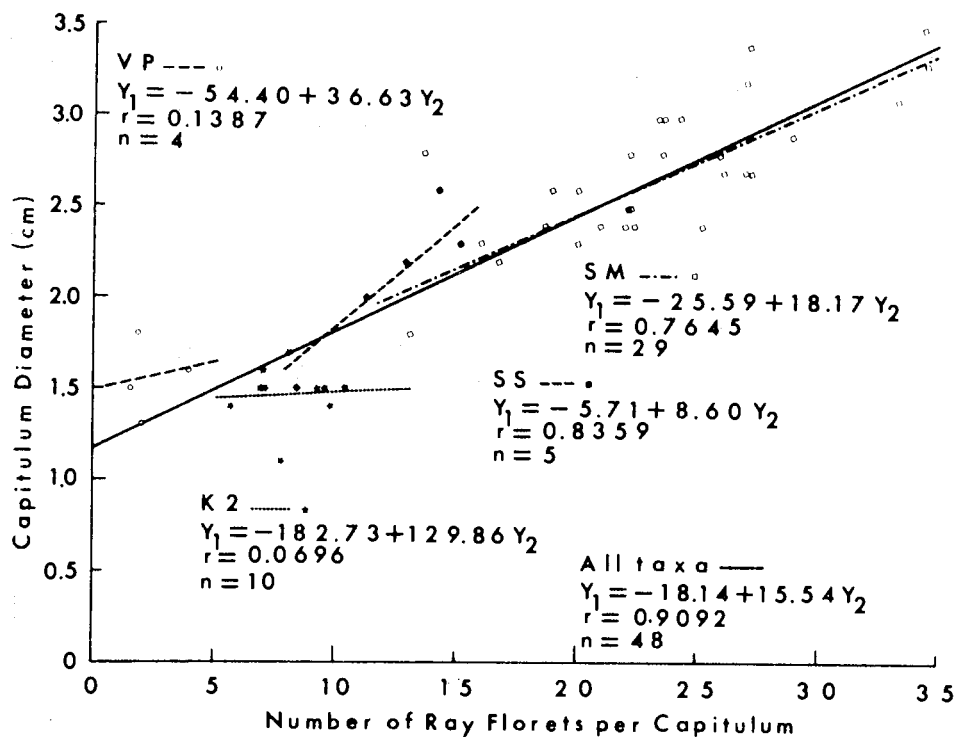


FIGURE 5. The relationship between inflorescence length and inflorescence width in the genus Argyroxiphium, and within infrageneric taxa. VP, A. virescens var. paludosa; K2, A. kauense; SM, A. sandwicense ssp. macrocephalum; SS, A. sandwicense ssp. sandwicense.

FIGURE 6. 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 Figure 5.

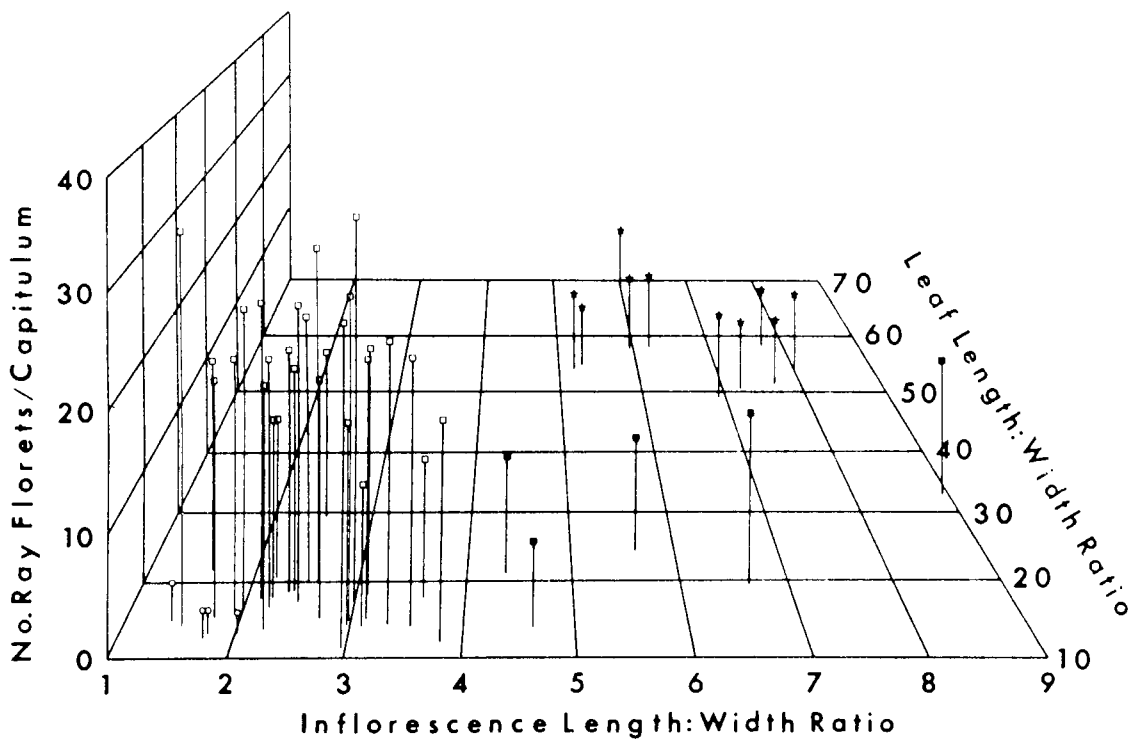
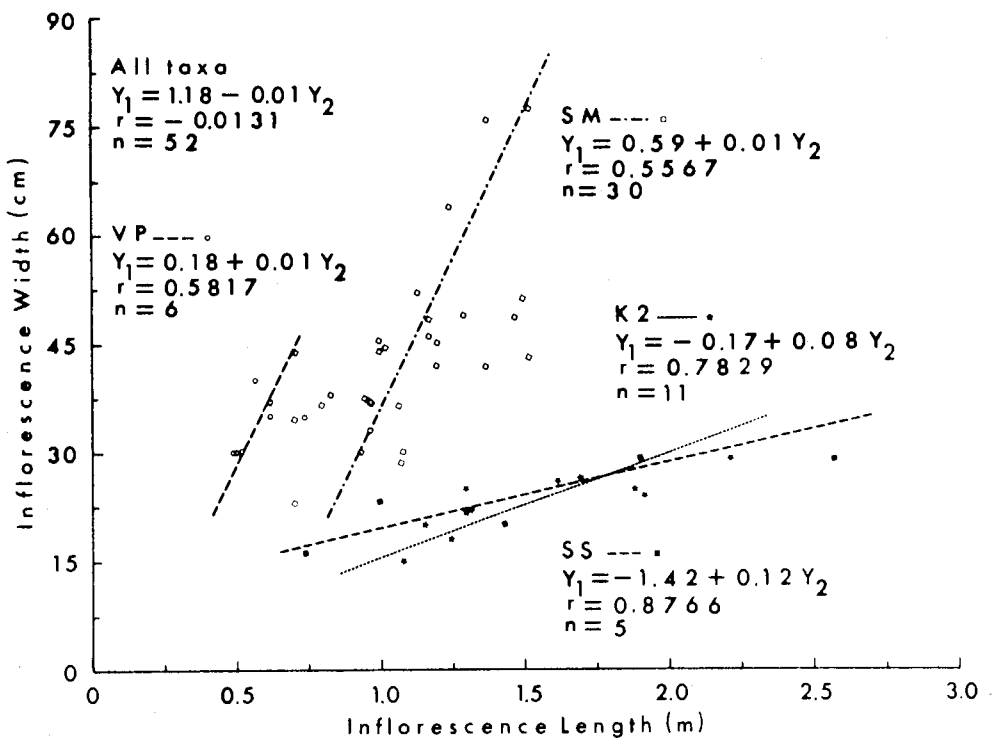


FIGURE 7. Leaves of three taxa of Argyroxiphium. A, A. kauense; B, A. sandwicense ssp. sandwicense; C, A. sandwicense ssp. macrocephalum. Note proportions and shapes. Reduced to ca. 5/16.

FIGURE 8. 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.



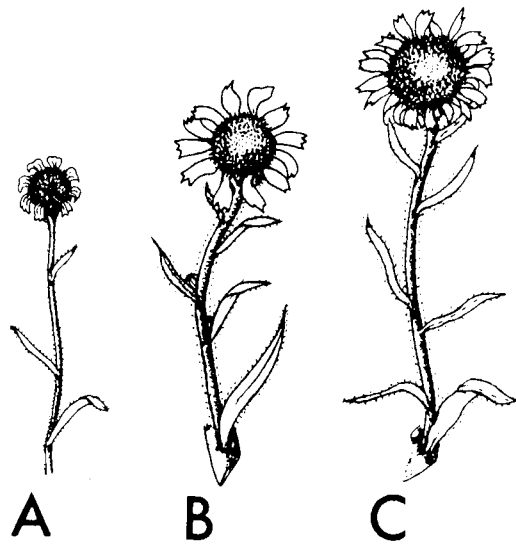
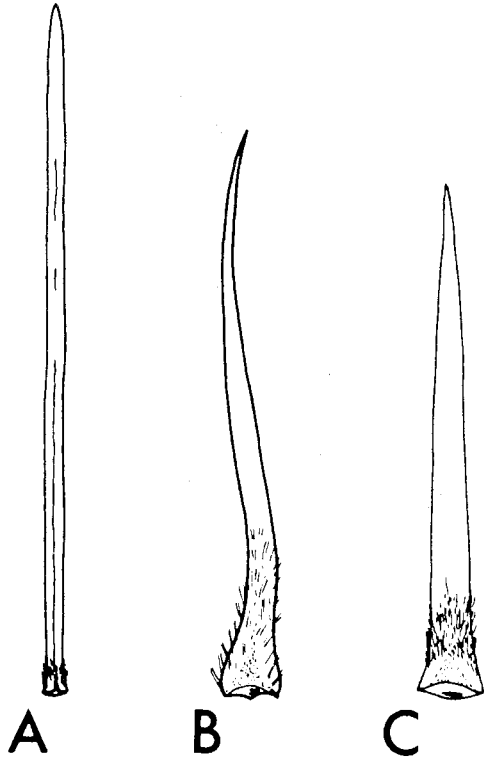




FIGURE 9. Habit of three taxa of *Argyroxiphium*. A, *A. kauense*; B, *A. sandwicense* ssp. *sandwicense*; C, *A. sandwicense* ssp. *macrocephalum*. Note inflorescence proportions and shape. Reduced to 1/25.