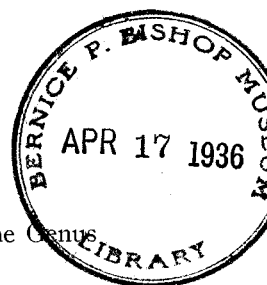


**THE HAWAIIAN SILVERSWORDS**  
**Systematics, Affinities, and Phytogeographic**  
**Problems of the Genus *Argyroxiphium***

By  
**DAVID D. KECK**

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## THE HAWAIIAN SILVERSWORDS:

Systematics, Affinities, and Phytogeographic Problems of the Genus  
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### INTRODUCTION

Theories as to the origin of the Hawaiian islands and the derivation of their flora and fauna have appeared with frequency and aroused the greatest interest among biologists. Probably no other region in the world has developed so extraordinary a degree of endemism, which, according to Hillebrand (9)<sup>1</sup>, for the indigenous vascular plants is 75.93 percent. Much more recent figures for the indigenous flowering plants given by Campbell (5) reach the remarkable figure of 90.4 percent! This endemism is directly connected with the fact that the Hawaiian Archipelago is the most isolated area of equal size in the world.

There have been many advocates of the theory that the Hawaiian islands are of oceanic origin, that they were elevated from the bottom of the ocean by volcanic action, and that they have always been completely isolated. Others have taken the opposing view that the islands have not always been so isolated, but may even be considered of continental origin. Those with the latter viewpoint believe that the present archipelago represents but the tips of volcanic mountain masses superimposed upon a large block that has undergone subsidence. For instance, Campbell (4) believes there may have been a more or less direct connection with other parts of Polynesia by means of one or several large land masses that possibly approached continental dimensions. Pilsbry (12) adds important support to this view by his study of the land snails, and there are many other faunistic data that give credence to it. A great weight of plant evidence favors a Polynesian-Australian and Indo-Malaysian origin for almost all of the Hawaiian flora. However, a Hawaiian land connection with America has been suggested upon occasion and an

<sup>1</sup> Numbers in parentheses refer to Literature cited, p. 29.

American derivation of the Hawaiian flora has had its advocates. Brown (3) has gone the farthest in proposing an American origin for the bulk of the flora through the agency of ocean currents, and Guppy (8) looked to America for the source of the Hawaiian endemic genera, which he supposed were chiefly spread through the agency of birds. The views of Brown have been strongly challenged by Skottsberg (14), and those of Guppy by Campbell (4) and by Skottsberg.

It will doubtless appeal to the great majority of botanists that the peculiar autochthonous flora of Hawaii could only have developed to its present degree of morphological isolation over a long period of time. Skottsberg (15) emphasizes that the Hawaiian flora has the characteristics of great age. Not only is the number of endemics large, but many species appear to be on the verge of extinction because of their lack of plasticity. Even the flora of the youngest Hawaiian mountains is very old, with 91 percent of the species endemic. This is not easily explained by those who regard the Hawaiian islands as purely oceanic in origin and the flora as carried there from great distances across the ocean, for these alpine regions ought to present favorable conditions for the establishment of new arrivals. But the fact is that, aside from the influence of man, overseas migration has practically ceased altogether. The question arises whether the flora at any time came from a great distance via overseas migration, or whether it dates from a time when the islands were much less isolated than they are now. The flora may not have been developed entirely on the existing islands, pioneering again and again on the upbuilding lava, but it may have existed for eons on adjacent soils that have since become submerged.

#### FLORISTIC CONNECTIONS BETWEEN HAWAII AND AMERICA

All botanists agree that there is an American element present in the Hawaiian flora, but most would admit that it composes a very small percentage of the whole. The plants assigned to American origin by most authors may be divided into two classes: first, a recent element that is represented by endemic species of genera common to Hawaii and the New World, but not found elsewhere; and second, a group of endemic genera in the Hawaiian Archipelago whose nearest affinities have appeared to be in the New World, but whose connections have often been quite obscure. The second group

must be older than the first, because its affinities have become obscured by the widening differences between its present day representatives and the ancestral stock, and because the species within the genera are usually well-marked, rather static, and senile in character. Campbell (4) has pointed to the comparative youth of the American Compositae that supposedly represent the ancestral stock of several Hawaiian endemic genera as an indication that this latter element in the Hawaiian flora is relatively modern. The present study has made it clear to me that these Hawaiian Compositae are probably not of American origin, which relieves us of the responsibility of attributing youth to these genera, which, by their peculiar development of unique features, as well as by their distribution upon the islands, apparently reflect a great age. From cutting the supposed phylogenetic ties that link the very ancient Hawaiian endemics with the New World and retying them elsewhere, an advantage accrues not only to our phylogenetic system but to the clarification of problems concerning the derivation of the Hawaiian flora. In short, it is possible to follow one's inclinations and agree with Campbell (4, 5), Skottsberg (14, 15), and others that the endemic element in the Hawaiian flora, at least so far as the flowering plants are concerned, is for the most part of great age, and that it may have had its beginnings on nearby land masses in the Pacific even before the present archipelago became habitable. As a corollary to this statement it may be added that the only wave (or ripple) of invasion from the New World seems to have occurred not earlier than the late Tertiary, doubtless long after the islands had attained isolation.

The ancient group of endemic genera supposedly of American origin is composed largely of Compositae. I have confined myself to a study of some of these genera and do not wish to offer critical judgments beyond this family; but as the remaining controversial cases are few, I shall point out possible explanations here also, which it is hoped will attract the critical attention of specialists in these groups.

The endemic Hawaiian genera which have been considered of American origin include *Charpentiera* of the Amaranthaceae, *Iso-dendron* of the Violaceae, *Nothoecstrum* of the Solanaceae, *Kadua* of the Rubiaceae, and *Argyroxiphium*, *Wilkesia*, *Dubautia*, *Railiardia*, and, of a more doubtful American relationship, *Lipochaeta*, *Campylotheca*, and *Remya*, all of the Compositae. *Charpentiera* is

placed by Schinz (13), in his recent treatment of the family, between several Old World genera. *Isodendron* combines capsular fruit and actinomorphic flowers which, with other features, leaves it a genus distinct unto itself. In Melchior's treatment (11), it is placed in a monotypic subtribe following a subtribe with berry fruit that has a New Zealand-Australian distribution. But it is perhaps closer akin to the subtribe of slightly zygomorphic South American forms that Melchior places after it. This genus, together with the Hawaiian shrubby species of *Viola*, points as strongly toward an American relationship as any example, and yet the connections are so indistinct here that an American origin for these forms probably cannot be proved. *Nothoestrum* is placed by Wettstein (17) adjacent to *Withania* of the Old World tropics and *Physalis* of the New World. Since it agrees with the former in woody habit, there seems no reason for continuing to suppose this genus is of American origin. *Kadua* has a recognized affinity with *Oldenlandia* through the latter's section *Hedyotis*, which occurs in the Malaysian region. *Argyroxiphium*, *Wilkesia*, *Dubautia*, and *Raillardia* I shall discuss in more detailed fashion below, but it may be noted here that their affinities are considered Pacific rather than American. *Lipochaeta*, *Campylothecca*, and *Remya* I have not examined, but the origin of the first two named appears to be quite as likely in the Old World as in the New, through their affinities with *Wedelia* and *Bidens* respectively. The latest treatment of *Lipochaeta*, by Sherff (16), lists 26 species, of which one is from the Galapagos Islands, another from New Caledonia and adjacent islands, the remainder being Hawaiian. The genus is therefore scattered across almost the entire width of the Pacific Ocean. *Remya* seems to be a genus so thoroughly distinct that the tracing of its phylogeny has become too much a matter of speculation. It occupies a dubious position in the Astereae-Solidagininae next to the American genus *Grindelia*, from which it might well be displaced by a later monographer.

This narrows the group of ancient Hawaiian endemics with New World affinities to those old species of genera common only to both. I have but a single example in this category, *Vallesia* of the Apocynaceae. This genus has six described species; one in the Hawaiian islands, two endemic in Mexico, one in Mexico and Guatemala, one in Santa Domingó, and one that extends from Florida and Lower California to Peru. Such a distribution indicates that the genus is not

young. Possibly the Hawaiian species is a relatively young member of the genus, and its origin was in America. But on the other hand it is significant that the genera related to *Vallesia* are Polynesian, Australian, Hawaiian, or Asian, and so the theory must be considered that this genus had its origin in the region where its affinities occur, that it has undergone eastward migration, and that the Hawaiian representative never started from America.

The remaining Hawaiian species with undoubted American affinities I judge are of an appreciably younger age than the preceding cases, at least of later arrival in the islands. *Asplenium fragile* Presl, *Pellaea ternifolia* Fée,<sup>2</sup> and *Fragaria chilensis* Duchesne are species indigenous in America and Hawaii. The following are Hawaiian representatives of otherwise American genera: *Sisyrinchium acre* Mann, *Hesperocnide sandwicensis* Weddell, *Sanicula sandwicensis* Gray, *Nama sandwicensis* Gray, *Sphacelle hastata* Gray, and *Aster divaricatus* variety *sandwicensis* Gray. It is possible that other cases have been overlooked, but the preceding data indicate that the total American element in Hawaii is very inconsequential in a flora of some 1,100 species of flowering plants, and that such representatives as have bridged the tremendous expanse of water between did so in accidental manner, probably in most instances since the present highest Hawaiian mountain peaks have become habitable.

#### RELATIONSHIPS OF ARGYROXIPHIMUM

Asa Gray (7a) was the first to point out some similarities between *Argyroxiphium* and the Madinae, a subtribe of the Helianthoideae, as follows:

The genus [*Argyroxiphium*] should be referred to the division Madieae (a group which belongs entirely to the western side of America, principally to California, and of which the radical leaves of some California species exhibit a somewhat similar silky covering) on account of the nearly obsolete pappus of the ray-achenia, and their inclosure in the involute scales of the involucre, and because there is an inner series of scales interposed between the ray-flowers and those of the disk.

Succeeding authors have subscribed to Gray's view and have placed *Argyroxiphium* in the subtribe Madinae. The present writer, engaged with others in a detailed investigation of the Madinae, undertook the systematic revision of *Argyroxiphium*, which here is under-

<sup>2</sup> Additional data from the Cryptogams has not been sought.

stood to include *Wilkesia*, with the expectation of treating it in the monograph on the Madinae in preparation. For reasons detailed below, *Argyroxiphium* is excluded from the Madinae and, consequently, is here presented in a detached treatment.

*Argyroxiphium* is understood by me to have no direct connection with the Helianthoideae-subtribe Madinae. Those characters mentioned above, by which Gray placed it in the Madinae, are outweighed by the dissimilarities between the two. On the other hand, the evident similarity between *Argyroxiphium* as here circumscribed and *Dubautia* and *Railliardia* of Helianthoideae-subtribe Galinsoginae has not received more than cursory mention. Bentham (2) followed Gray's disposal of *Wilkesia* and *Argyroxiphium*, placing them as the first two genera in his tenth subtribe, Madieae. These followed *Dubautia*, the last genus in his ninth subtribe, Galinsogaeae. Bentham neglected to note the very evident similarities and relationship between *Dubautia* and *Railliardia*, placing the latter genus in a remote position in the Senecionideae, three tribes away. This disposal of *Railliardia* was changed by Hoffmann (10), who returned it to the subtribe Galinsoginae as the last genus, following *Dubautia*. Hoffmann retained Bentham's order for *Wilkesia* and *Argyroxiphium* at the head of the Madinae.

I propose to insert *Argyroxiphium*, which is here defined to include *Wilkesia*, into the Galisoginae in front of *Dubautia*, with which it has more points in common than with *Railliardia*. This does not obscure the line through *Dubautia* and *Railliardia* to the Senecioneae, a transition suggested by Hoffmann (10), and plausible from a consideration of pappus and involucre, to which there is reason to suppose the connection may be less remote than from *Argyroxiphium* to the Madinae.

The large, nodding heads of *Argyroxiphium* are not at all closely duplicated in the Madinae, while its purple ray-flowers, hardened pappus scales, and involucre bracts are of types likewise foreign to the Madinae. The following tabulation indicates the distribution of the most important characters between these genera and shows that *Argyroxiphium* has more points of agreement with *Dubautia* and *Railliardia* than with the Madinae.

| MADINAE  | ARGYROXIPHIMUM<br>(Including WILKESIA)  | DUBAUTIA AND<br>RAILLIARDIA   |
|--|---|---|
| Heads heterogamous   | Heads heterogamous<br>or homogamous   | Heads homogamous  |
| Ray-akenes enclosed<br>by their enfolding<br>bracts  | Ray-akenes (when<br>present) merely<br>subtended by con-<br>cave but not<br>enfolding bracts    | Ray-akenes none   |
| Herbs (mostly<br>annuals); few<br>shrubby species  | Shrubs or small trees   | Shrubs or small trees   |
| Leaves not clustered at<br>ends of stems in<br>perennial species                                     | Leaves clustered at<br>ends of woody stems,<br>which are marked<br>with prominent<br>leaf-scars | Leaves often clustered<br>at ends of woody<br>stems, which are<br>marked with prom-<br>inent leaf-scars |
| Involucral and recep-<br>tacular bracts unlike,<br>not adnate, often<br>connate                      | Involucral and recep-<br>tacular bracts alike,<br>± adnate; receptac-<br>ular bracts connate    | Involucral (and recep-<br>tacular) bracts alike,<br>usually in one series,<br>± connate                 |
| Filaments not pustu-<br>late-thickened at<br>base of anthers   | Filaments pustulate-<br>thickened at base of<br>anthers   | Filaments pustulate-<br>thickened at base of<br>anthers   |
| Style-branch appen-<br>dages not abruptly<br>differing from<br>stigmatic portion,<br>long, attenuate | Style-branch appen-<br>dages thickened and<br>short, acute                                      | Style-branch appen-<br>dages usually very<br>short, acute   |
| Habitat in western<br>North America, one<br>species extending<br>south through Chile<br>to Patagonia | Habitat in Hawaiian<br>islands  | Habitat in Hawaiian<br>islands  |

Tracing further the connection between *Argyroxiphium*, on the one hand, and *Dubautia* and *Railliardia*, on the other, it must be admitted that differences in inflorescence, head size, and pappus are so pronounced as to indicate an ancient separation between the groups. But the agreement in shape, texture, venation, arrangement and fall of leaves in *Argyroxiphium Grayanum* and *Dubautia plantaginea*, for example, is certainly suggestive, although not conclusive evidence, of relationship. Similarities in the androecium and gynoecium are of more importance in this connection. Both *Argyroxiphium* and *Dubautia* have at least some rosette-tree life forms. The



connection between the habitats of the three genera should also be pointed out, *Argyroxiphium* being chiefly alpine, *Dubautia* and *Railliardia* montane with alpine representatives.

Bentham (1, p. 446) has pointed out that the Madinae is a transition group between Helianthoideae and Helenioideae and that the members of the Galinsoginae have formerly been classed under the Helenioideae. To be sure, the numerous transitions and recombinations of key characters make it very difficult to maintain clear-cut tribes in this phylogenetically unified portion of the great family Compositae. The problem often becomes more acute when the boundaries of the subtribes are to be set. Synantherologists, without hesitation, link many genera together which have an evident relationship regardless of the fact that exceptions to the key characters must be admitted; and they likewise apply group names to these assemblages, such as the subtribal one, in spite of the necessity for fallible definitions of the groups. These facts should be borne in mind in weighing this realignment of the Galinsoginae and Madinae. I feel that the Madinae becomes a definitely more natural subtribe by the exclusion of the Hawaiian species, and certainly no violence is done by placing the latter with their Hawaiian neighbors in the Galinsoginae.

*Argyroxiphium*, *Dubautia*, and *Railliardia* would appear to constitute an insular group unto themselves, all being endemic, and probably without close relatives. I admit no evident relationship between the first of these and the Madinae, nor am I able to concur at all with Asa Gray's view that *Railliardia* and *Raillardella* are so closely related that the latter may be treated as a section of the former. It would seem Gray was placing too much emphasis on parallel variation in style-appendages and pappus, and too little on the tremendous dissimilarities of habit, inflorescence, and distribution, when this proposal was made. If the affinities of these genera are totally within the Helianthoideae, it is possible that their origin is American; but if, on the other hand, their relationship lies with the Senecioneae, a possibility by no means excluded at present, their ancestral line may extend toward a southwestern, rather than an eastern, origin.

In checking Bentham's placement of *Railliardia* adjacent to *Robinsonia* and *Rhetinodendron*, closely related endemic genera of Juan Fernandez and universally regarded as members of the Senecioneae, one finds there is a strong resemblance between *Robinsonia* and some

species of *Dubautia* in growth form (both being small rosette-trees), foliage, inflorescence, androecium, etc., but other differences are so profound as to discourage the claim of an intimate connection between the two. In the case of such relict genera it is not to be expected that always morphological similarities can be discovered in organ after organ, even in the next of kin, or that always satisfactory phylogenetic connections can be traced. With this in mind we may ponder Skottsberg's suggestion (15, p. 56) :

By way of *Dubautia* these genera [*Argyroxiphium* and *Wilkesia*] are perhaps connected with *Raillardia* and this with *Robinsonia* of Juan Fernandez, which has a recently discovered close relative in the mountains of New Guinea, *Brachionostylum* Mattfeld.

This resemblance, or one with such a genus as *Bedfordia* of Australia, is sufficiently arresting to indicate that the affinities of these genera are to be found to the south or southwest in the Pacific. Certainly the morphological gaps are at least as large or larger between these and any of their suggested American affinities. By thus divorcing *Argyroxiphium* from the American genera to which it has been thought related, the most persistently proposed connection between the ancient element in the Hawaiian flora and the New World has been shattered.

#### ARGYROXIPHIMUM VERSUS WILKESIA

Ever since its proposal as a genus, *Wilkesia* has been separated chiefly on the basis of its discoid heads from *Argyroxiphium*, in which the heads are radiate. In this case it has been generally assumed that the absence of ray-flowers represents a loss through reduction and that accordingly *Wilkesia* is the derived group. A series may be arranged on the basis of number of ray-flowers starting with *Argyroxiphium sandwicense*, which has the most, through *A. virescens* and *A. caligini* with progressively fewer, and *A. Grayanum* with an occasional radiate head, to *Wilkesia gymnoxiphium*, which has no trace of a ray-flower. It was very recently mentioned that *A. Grayanum* had ray-flowers. Degener called my attention to the fact and sent me some heads for substantiation. Since then I have discovered at least one or two ray-flowers on several sheets of this species; but in most heads there are none, and the inconspicuous ligule aids them in escaping detection. Before this

discovery it was apparent that the plant then called *Wilkesia Grayana* agreed with the species of *Argyroxiphium* in phyllotaxy, inflorescence, disk-flowers, pappus, and habitat. That it has ray-flowers, even though rarely, shows it rightfully belongs with the true *Argyroxiphiums* rather than with the isolated Kauai endemic, *Wilkesia gymnoxiphium*.

In addition to the ray-flower character, the distinctness of *Wilkesia* as a genus has been greatly weakened by a consideration of other characters of first importance. So, after taking into account its close connection with *Argyroxiphium* and its distant relationship elsewhere, the position of *Wilkesia* as a monotypic genus seems to have become untenable. I have followed the course of retaining *Wilkesia* as a section under *Argyroxiphium* by which the obvious genetic relationship that exists here is emphasized. Even with this inclusion, *Argyroxiphium* remains sufficiently small to reveal at a glance what is contained within it. After all, the strongest argument is that, considering the transitional position of *A. Grayanum*, there are no characters of generic value remaining on which to retain two genera.

Morphologically, *A. Grayanum* serves as a link to connect the other species of section *Euargyroxiphium* with section *Wilkesia*. Its rosette leaves on pressed specimens always appear to be arranged in a continuous close spiral; but Hillebrand (9) asserts that they are verticillate in young plants. In *Wilkesia* the leaves are verticillate throughout, while in *Euargyroxiphium* they are spiral, probably even in the youngest rosettes. In *A. Grayanum*, too, there is a tendency for the leaves to be connate at their very bases, and their blades are flat and veined, all of which are reminiscent of *Wilkesia*. In habit, the dwarf rosette-tree of *A. Grayanum* is intermediate between the much taller *A. gymnoxiphium* and the epigeous rosettes of the other species.

The specificity of habit in these plants has not been sufficiently emphasized. Degener (6, p. 308) notes that *A. caligini* “. . . is characterized by dividing and creeping profusely over the ground and progressively dying back at the base, thus isolating the branches into independent plants.” *Argyroxiphium sandwicense* and *A. virescens* do not creep. The former is almost without exception a monopodial hapaxanthic rosette-shrub; the latter is more frequently sympodial but limited in its branching to a second rosette (6). The rosette-

trees, *A. Grayanum* and *A. gymnoxiphium*, are apparently monopolial in the majority of cases.

#### MATERIALS

There have been available for this study the collections in the herbaria of the following institutions, indicated in citations by the abbreviations in parentheses: Bernice P. Bishop Museum, Honolulu (Bish); University of California, Berkeley (C); California Academy of Sciences, San Francisco (CAS); Field Museum of Natural History, Chicago (F); Gray Herbarium of Harvard University (GH); Missouri Botanical Garden, St. Louis (M); New York Botanical Garden (NY); Academy of Natural Sciences, Philadelphia (Ph); Dudley Herbarium of Stanford University (SU); United States National Herbarium, Washington (US). To the custodians in charge of these collections I wish to express my most sincere thanks for their assistance. In addition, I wish particularly to acknowledge the help given by Mr. Otto Degener, of Honolulu, whose private herbarium (Deg) contains much unduplicated material, and who supplied not only herbarium specimens but liquid material of three species and valuable notes based upon his field experience with these plants. For similar observations and material I owe my thanks to Mr. Ray Fosberg, of the University of Hawaii, Dr. Herbert E. Gregory, Director of Bernice P. Bishop Museum, and Dr. G. M. Smith, Stanford University, kindly helped me obtain the habit photographs used in illustration.

The genus *Argyroxiphium* is composed of narrowly endemic species that do not blossom regularly and consequently are poorly represented in the herbaria in flowering stages. This paucity of material tends to mask the complete intergradation of the variations that exist in many characters, as shown when full series of specimens are assembled. It is regrettable that there is no evidence to offer, either from breeding, cytology, or published field observations concerning hybridization, which is here considered to have taken place more than once between two pairs of species.

SYSTEMATIC ACCOUNT OF ARGYROXIPHIMUM

**Argyroxiphium** De Candolle, Prodr., vol. 5, p. 668, 1836.

*Argyrophyton* Hooker, Comp. Bot. Mag., vol. 2, p. 163, 1836;  
Icon. Plantarum vol. 3, pl. 75, 1836.

Subcaulescent to arborescent perennials; caudex stout, woody, medullary, simple or divided, not elongated, or forming more or less elongated creeping woody stems, or consisting of an erect trunk, crowned with a dense rosette of spirally or verticillately arranged ensiform entire rigid longitudinally nerved leaves, hapaxanthic, at length elongating to produce an ample erect raceme or panicle. Heads many, large, heterogamous or homogamous, nodding after anthesis. Involucre (or what corresponds to it) campanulate to hemispheric or urceolate; bracts of true involucre uniseriate or none, when present equal, herbaceous, narrow, the thin ciliate margins  $\pm$  enfolding the akene; bracts surrounding the disk (receptacular cup) united, uniseriate, the convex or conical receptacle otherwise naked and glabrous. Ray-flowers, when present, several or few, pistillate, fertile; ligules purplish or yellowish, 3-fid. Disk-flowers many, hermaphrodite, fertile; corolla tubular or somewhat flaring at throat, yellow, the 5 regular deltoid lobes about 0.5 mm long; style-branches with penicillate-tufted conical appendages. Ray akenes, when present, broadly linear, somewhat arcuate, 4- or 5-angled, blackish; areola slightly eccentric, calloused and surmounted with a corneous cyathiform pappus. Disk-akenes similar to ray akenes, prismatic, with or without a pappus of a few short fimbriate cartilaginous  $\pm$  united paleae. Type species: *A. sandwicense* De Candolle.

A genus endemic in the Hawaiian islands.

KEY TO SECTIONS

- A. Leaves spirally arranged, becoming alternate above, not united into a sheath at base; peduncles alternate, ascending; inflorescence racemose; involucre campanulate to hemispheric; ray-flowers present (usually none in *A. Grayanum*); akenes glabrous .....I. **Euargyroxiphium**
- AA. Leaves verticillate throughout, united into a sheath at base; peduncles verticillate, widely divaricate; inflorescence paniculate; involucre urceolate-campanulate; ray-flowers none; akenes pubescent .....II. **Wilkesia**

Section I. EUARGYROXIPHIMUM Keck, new section.

A section composed of four species that are confined to the islands of Maui and Hawaii.

Key to Species

- A. Caudex not elongated, rarely forked; heads large, involucre 12-35 mm in diameter; ligules of ray-flowers 6-8.5 mm long, purplish; rosettes 20-80 cm in diameter.

- B. Leaves silvery floccose, glistening, subtriquetrous; ray-akenes 5-angled, not geniculate apically.....1. **A. sandwicense**  
 BB. Leaves greenish, not floccose, thinner, ray akenes 4-angled, slightly geniculate apically .....2. **A. virescens**  
 AA. Caudex elongated, branching; heads smaller, involucre 10-15 mm in diameter; ligules of ray-flowers 4 mm or less long, or sometimes none; rosettes 6-20 cm in diameter.  
 C. Leaves silvery floccose, slender, thick; stems creeping with epigeous rosettes; ray-flowers always present, purplish.....3. **A. caliginis**  
 CC. Leaves green, broad, flat; stems erect, forming a dwarf rosette-tree; ray-flowers usually obsolete, yellow.....4. **A. Grayanum**

1. **Argyroxiphium sandwicense** De Candolle (pls. 1, *a-g*, 2, 3, 4, 5).  
*Argyroxiphium sandwicense* De Candolle, Prodr., vol. 5, p. 668, 1836; and De Candolle, Coll. Mem. IX. Comp., pl. 8, 1836.  
*Argyrophyton Douglasii* Hooker, Comp. Bot. Mag., vol. 2, p. 163, 1836, nomen subnudum; and Hooker, Icon. Plantarum, vol. 3, pl. 75, 1836.  
*Argyroxiphium macrocephalum* Gray, Am. Acad., Proc., vol. 2, p. 160, 1852; emend. vol. 5, p. 137, 1861. Type locality: "On the island of Maui, at the base of a high crater." This crater is Haleakala.

Gray distinguished *A. macrocephalum* from *A. sandwicense* on the basis of its larger heads, the total absence of pappus, and the conical receptacle. Hillebrand, in reducing this species to a variety of *A. sandwicense*, pointed out that his specimens from the type locality had perfectly developed pappus, but he stated that the variety differed from the species in having shorter ligules, and longer appendages of style-branches. The largest heads I have studied are on Forbes 880.H, from Mauna Kea, and are of the maximum size described for *A. macrocephalum*. Almost all cited specimens from Haleakala, on Maui, are from somewhat to very much smaller and well correspond with the description of *A. sandwicense*. These specimens show that on Haleakala some plants have abundant disk-pappus, some have no, or at most vestigial, pappus, and the evidence seems clear that such differences in pappus may exist in adjacent plants. The occurrence of pappus is so irregular as to number and size of the paleae that it is unwise to place taxonomic significance on the various degrees of its presence or absence. I have not found appreciable differences in the length of ligules or style-branch appendages. It is true that the extremely large heads of the Forbes 880.H collection had much more conical receptacles as a correlated feature.

But there is no correlation between head size and pappus, or between either of these characters and geographic distribution. So, *A. macrocephalum* would have to stand or fall on the basis of head size. A survey of the collections indicate that this character varies by gradual steps from one extreme to the other. Hence this name is necessarily relegated to synonymy without qualification.

**A. sandwichense** variety **macrocephalum** Hillebrand, Fl. Haw. Isls., p. 219, 1888.

Caudex 2-5 cm thick from a strong branched taproot, about 3-10 cm long, covered with dark-brown bark as much as 5 mm thick, the very rigid leaves forming a rosette 3-8 dm in diameter. Flowering stem 8-20 dm high, medullary, 4-8 cm thick at base, silvery tomentose below, glandular-pubescent and tawny above. Leaves of rosette arcuate-ascending, subtriquetrous, attenuate to the narrow but blunt tip, 10-40 cm long, 4-10 or 15 mm wide, very densely sericeous-floccose and silvery white; leaves of flowering stem similar, more horizontal, gradually reduced in size upward, the upper leaves viscid-pubescent at base, the very copious tomentum more and more confined to the apical portion. Raceme heavy, oblong, bearing 100-200 or more heads; peduncles 6-30 cm long, glandular-pubescent, with 2-6 or more equally spaced linear foliaceous bracts along their axes. Involucre hemispheric, 10-15 mm long, 15-35 mm broad; bracts linear, attenuate, 1.5-2.5 mm wide across the rounded back, densely glandular-pubescent, sometimes adnate toward base to inner bracts. Ray-flowers 10-30 or more; ligules moderately conspicuous, purple, about 6-12 mm long, 2-3.5 mm wide, oblong, the linear lobes up to 4 mm long; tube 3.5-6 mm long. Bracts of the disk somewhat exceeding the rays in number, connate about half way into a cup, each bract shallowly concave, thick, acuminate, viscid-pubescent without. Disk-flowers commonly more than 100, probably 300-400 in largest heads; corolla glabrous, or pubescent on tube, 5-6 mm long. Ray-akenes 7.5-12 mm long, usually 5-angled, not geniculate apically. Disk-akenes similar. Pappus of the ray-akenes coroniform, or of 1 or 2 minute paleae, or none; that of the disk-akenes none, or vestigial, or present and 1-5 mm long; paleae 5-10, more or less united, linear to quadrate, unequal, stramineous.

Known only from the islands of Hawaii and Maui. Type locality: ". . . in insulis Sandwicensibus ad Owyhee floridam mense junio legit cl. Macrae."

Hawaii, Mauna Kea: Wilkes Expedition (GH, Ph, US); 10,100 feet, Rock 8434 (Bish); source of Wailuku River, Forbes 880.H (Bish, C, F, M, SU, US); Kukaiau Ranch, 8,000-11,000 feet, Hitchcock 14280 (Bish, US).—Hawaii, (Mauna Loa): Kaa, Pohina, Kau, August 29, 1922, Meinecke (Bish); above Kapapala, Kau, Forbes 430.H (Bish). Also reported from Hualalai.

Maui, Haleakala Crater: Forbes 302.M (Bish, C, CAS, F, M, SU, US); 10,000 feet, Reed (C); Hitchcock 14949, 15570 (US); Rock

8608 (Bish, GH), 8608a, 10317 (Bish); Weaver 22 (Bish); Hillebrand and Lydgate (Bish); on cinder cone, Degener 3527 (Deg, SU); 8,100-10,000 feet, Mann and Brigham 370 (Bish, M); Sliding Sand Trail and lava beds at foot, on the side of a cinder cone, 2,450 meters, Fosberg 10002 (Bish, SU); Haleakala, Wilkes Expedition (US, type of *A. macrocephalum* A. Gray; isotype GH).

I have studied a few flowers taken by H. M. Hall in 1925 from the only sheet of the species in the De Candolle Herbarium. Hall considered this sheet the type and noted that there were no clear data with it. The type was taken in June by Macrae.

This species is among the most outstanding of the native flora. It is known to thousands by its common name, "silversword", who are as willing to seek for it in its mountain fastnesses as are those who cherished a glimpse of the edelweiss in Switzerland. A sight of the large, silvery-white, spherical rosettes of this species is a feature of the trip to the summit of the very barren and lava-strewn peaks, Haleakala, Mauna Loa, and Mauna Kea. The traditional beauty of the silversword was known to the native Hawaiians, who called it *ahinahina* (gray-headed), because they had never, before the coming of the white man, seen silver, and therefore could not apply to the plant the cognomen that is so appropriate.

This plant blooms from June to October. On the cinders and lava ledges of the alpine region where it grows, it is about the only plant life to be found.

## 2. *Argyroxiphium virescens* Hillebrand (pl. 6).

*Argyroxiphium virescens* Hillebrand, Fl. Haw. Isls., p. 219, 1888.

Caudex from a woody taproot, covered with a thin bark, densely clothed by the slender rush-like but rigid leaves which form a rosette 3-5 dm in diameter, occasionally branching to form a second rosette. Flowering stem 10-15 dm high, medullary, 2-4 cm thick at rosette, tawny and viscid-pubescent throughout. Leaves of rosette erect or ascending, subtriquetrous, attenuate to the very acute tip, 10-30 cm or more long, 3-7 or 8 mm wide, green, sericeous particularly marginally, glabrate beneath, lightly pubescent and viscid above; leaves of flowering stems recurved, gradually reduced in size upward, densely viscid-pubescent. Raceme heavy, bearing 30-100 or more large nodding heads; peduncles 6-15 cm long, glandular-pubescent, with 1 or 2 linear bracts along their axes. Involucre broadly campanulate, 10-18 mm long, 12-20 mm broad; bracts linear, attenuate, about 1.5-2 mm broad across the rounded back, adnate to the receptacular bracts for more than half their length, densely glandular-pubescent. Ray-flowers 6-20, unevenly spaced; ligules inconspicuous, pale purplish, about 6 mm long, about 2 mm wide, linear-oblong, the teeth about 1 mm long; tube 3 mm long, pubescent. Receptacle convex, puberulent or glabrate. Bracts of the disk about double the number of the rays, firmly con-



nate most of their length, each bract shallowly concave or plane, cartilaginous, acuminate, viscid-pubescent without. Disk-flowers about 200; corolla pubescent on the tube, 5-6 mm long. Ray-akenes 10-11.5 mm long, slightly geniculate apically, usually 4-angled; areola cup-shaped, the margin denticulate and occasionally bearing a short pappus-scale or two. Disk-akenes similar but not geniculate, 4- or 5-ribbed; areola bearing on the posterior rim a pappus of 2-6 fimbriate corneous unequal  $\pm$  fused paleae 2-4 mm long, and bearing on the anterior rim some irregular vestigial teeth, all soon deciduous.

Restricted to the island of Maui and known only from the region of Haleakala. Type locality: "northern slope of Haleakala, from 8,000 to 9,000 feet."

Maui: Remy 284 (GH); Wilkes Expedition (GH, US); Haleakala, Hillebrand (US, possibly isotype); Haleakala, 8,000-9,000 feet, Mann and Brigham 369 (Bish); Haleakala Crater: 6,000-10,000 feet, Hitchcock 14941 (US); Koolau Gap, on fog- and rain-swept moss-covered eroded lava, August 17, 1927, Degener and Topping 3528 (Deg, SU); Puunianiau Crater, Rock 8575 (Bish in part, C, F, GH, US), 8578 (US), 16036 (Bish); edge of Kipahulu, Forbes 1170.M (Bish, C, F, US); Keanae Gap, Forbes 1018.M (Bish, C), 1064.M (US); east of Ukelele, July 1919, Forbes (Bish); south-east of Ukelele, Forbes 1251.M (Bish).

### 3. *Argyroxiphium caligini* Forbes (pls. 7, 8).

*Argyroxiphium caligini* Forbes, B. P. Bishop Mus., Occ. Papers, vol. 7, no. 3, p. 38, 1920.

Caudex woody, creeping, several decimeters long and 1-2.5 cm thick, often with several radiating elongated spreading woody stems at apex, consisting of a woody cylinder surrounding a large pith, the thick bark roughened with old leaf-traces, radiating stems rarely again forked, rooting to form isolated plantlets as the old stems die back. Flowering stems 3 or 4 dm high, not woody, slender, white-floccose throughout. Leaves linear, in dense epigeous rosettes 6-20 cm in diameter, plane or subtriquetrous, attenuate to the narrow but blunt tip, 3-13 cm long, 2-4 mm wide, very densely silvery sericeous-floccose; cauline leaves similar, erect, smaller, but prominent to apex of inflorescence, without reduction in the pubescence, not viscid. Raceme narrow, bearing 15-40 or more heads; peduncles 4-8 cm long, green and viscid-tomentose throughout or floccose at base, with a few linear-lanceolate floccose bracts along their axes. Involucre broadly campanulate, green, 8-10 mm long, 10-12 mm broad; bracts broadly linear, acute, about 1.5 mm broad across the rounded back, free, densely glandular-pubescent. Ray-flowers 10 or less, purplish; ligules inconspicuous, about 4 mm long, linear, the teeth less than 1 mm long; tube 1 mm long, glabrous. Bracts of the disk about double the number of rays, firmly united most of their length into a cup, cartilaginous, acuminate, viscid-pubescent without. Disk-flowers many less than 100; corolla glabrous, 4-5 mm long. Ray-akenes about 5 mm long; areola with short beak, shallow, the margin denticulate. Disk-akenes similar, 4- or 5-ribbed; pappus largely

posterior, of 4 to 6 ovate to lanceolate entire more or less united unequal paleae up to 1.3 mm long.

Common on the summits of Mount Eke (Mauna Eeke) and Puu Kukui, western Maui, doubtfully in eastern Maui. Type locality: "Type in the B.P.B.M. Herbarium, No. 391, M, collected on Eke, West Maui, T. H., October, 1917, by C. N. Forbes."

Maui: Mount Eke, Honokahau drainage basin, Forbes 391.M (Bish, type, 2 sheets; isotypes C, F, US); summit of Mount Eke, Degener 2557 (Deg, SU, US); Mauna Eke, Cox 10321 (Bish); Puu Kukui, December 1928, Bryan (Bish); Puu Kukui, in a bog near the summit, 5,400 feet, Yuncker 3484 (F); Haleakala, Rock 10317 (Bish, possibly a young *A. sandwicense*); without locality, Mann and Brigham 616 (Bish).

A clump of about five rosettes radiating on short stalks from a heavy taproot was found on the outer slopes of Haleakala, between the summit of the Halemau Trail and Puu Nianiaiu, by Fosberg, No. 9975 (Bish), who saw but the one specimen here. It is in the vegetative condition but is unmistakably of this species. The difference in habitat between this "dry brushy slope" and the swamps of Eke and Puu Kukui raises an ecological question difficult to answer. It might be considered that Fosberg's specimen was a waif that had chanced to survive in an environment quite unlike that of the species in West Maui. But on the other hand, certain short-leaved specimens with something of a caudex developed, which have been collected in the Haleakala region, are probably *A. sandwicense* in spite of certain characters of *A. caligini*. These may be the key to Fosberg 9975. It is to be hoped that future collectors can identify these short-leaved rosettes with flowering plants. Possibly it will be necessary to stake several such individuals and await their flowering several years in the future to properly clarify their identity.

Degener (6, p. 308) writes:

This Eke silversword, named *Argyroxiphium caligini* Forbes, is characterized by dividing and creeping profusely over the ground and progressively dying back at the base, thus isolating the branches into independent plants. It does not produce silvery spheres two or more feet through, as does the Haleakala plant. Instead, its mass of leaves is rarely six inches across. Of the many thousand plants growing, all of which could be easily seen, only one showed the remains of a flowering stalk in the late summer of 1927. This was about two feet high. Besides growing on Mount Eke, this plant may be found in small numbers on Puu Kukui, a higher mountain located across a deep ravine to the south.

4. **Argyroxiphium Grayanum** (Hillebrand) Degener.

*Argyroxiphium Grayanum* (Hillebrand) Degener, Fl. Hawaiiensis, 344: *Argyroxiphium Grayanum*, 1936.

*Wilkesia Grayana* Hillebrand, Fl. Haw. Isls., p. 220, 1888.

Plant to 2.5 m high; stem erect, 0.7-3 cm thick (described by Hillebrand as 3 inches thick at base), rarely forked, the thick bark persistent below, the continuous spiral node and often the fibery remains of leaf-traces prominent above, topped with a green rosette. Leaves in a continuous close spiral, almost free, connate for less than 1 mm, linear-lanceolate, attenuate to base and apex, plane, prominently longitudinally veined, reflexed after raceme elongates, the immature sericeous, the mature glabrous except for the hispid-ciliate margins, 10-25 cm long, 7-18 mm wide; leaves of inflorescence alternate and more remote, equaling the peduncles, glandular-puberulent, yellowish green. Raceme 2-6 dm long with numerous heads; rachis thick, longitudinally ridged, canescent and densely glandular; peduncles 5-15 cm long, densely glandular-pubescent, with 2-4 scattered linear bractlets. Involucre broadly turbinate to hemispheric, 9-12 mm high, 12-15 mm broad, outer (true) involucre nearly obsolete, when present similar and adherent to the inner involucre; bracts firmly connate, glandular-pubescent, the 20-30 free tips 2.5-5 mm long, lanceolate, ciliate, spreading after anthesis. Ray-flowers few, 3-5 per head, or commonly none, yellow; ligules inconspicuous, about 3 mm long, 2 mm wide, the lobes 0.6 mm long; tube 1.8 mm long, pubescent. Disk-flowers 100-200; corolla glabrous, or pubescent only on tube, 4-5 mm long; anthers included. Ray-akenes and disk-akenes similar, about 6 mm long, brown, glabrous, but ray-pappus vestigial. Pappus to 1.8 mm long; paleae 4-8, lanceolate to quadrate, variously fused, stramineous, fimbriate, the posterior 1 or 2 the longest, the anterior sometimes missing or all reduced to a single palea and a row of minute denticulations or some flowers of the head without pappus.

Endemic on the island of Maui. Type locality: "W. Maui; on the southern slope of Eeka at a height of 5,000 to 6,000 ft."

W. Maui: Mt. Eeka, Aug. 1870, Hillebrand (US, possibly isotype); Mt. Eeka, 4,000-6,000 feet, Hillebrand (GH, possibly isotype); Eke, Honokahau drainage basin, Forbes 392.M (Bish, F); northwest side of Mt. Eke, 50 feet below the summit, on an exposed, fog-swept, precipitous, clay bank, Degener 8011 (Deg, SU). Puu Kukui: 5,000 feet, Hitchcock 14845 (US); 3,000-5,000 feet, Hitchcock 14828 (Bish, US); fringe of open bog, Munro 625 (Bish, C, US); summit, Rock 8196 (Bish, C, GH, NY, US); Forbes 63.M (Bish); Bryan 682 (Bish), between Nakalalua and summit, open bog, Fosberg 10017 (Bish, SU); Haclaau-Puu Kukui trail, Ewart 52 (Bish). Bog below Wai Anapanapa, north slope of Haleakala, Forbes 1235.M (Bish).

Degener writes:

Don't be confused by Hillebrand's statement that the type locality of this species is Mount Eke! He apparently made an error and climbed Puu Kukui

from the town of Lahaina and mistook that mountain for Eke. He never reached Eke. I had great difficulty in doing so, and I had the advantage of crawling in tunnels through mountains to get near Eke. These tunnels had not been built in Hillebrand's time.

Certain sheets of Rock 8196 (Bish, NY, 1 sheet each) were collected to represent juvenile stages of this species. At the same time and under the same number adult specimens were taken. These young plants, with their fifty or more short wirey stems each bearing a rosette of leaves 1 or 2 cm long, appear too different from the adults. It is difficult to visualize them assuming an arborescent habit. It is plausible that these sheets represent this species and that intermediate stages of development were there to guide Rock in making the collection; but it also seems possible that these may represent some species of *Dubautia*.

#### HYBRIDS

Two interspecific hybrids are to be reported from the section *Euargyroxiphium*.

#### ***Argyroxiphium sandwicense* × *virescens*.**

This apparent hybrid has been collected twice on Haleakala, Maui, where both the parents occur. Each collection was made under the same field number as that given one or the other of the parents showing that it grows with both. A large basal rosette of this hybrid, from Puunianiau Crater, Haleakala, composes one sheet of Rock 8575 (Bish), the other material collected under this number being *A. virescens*. One of the sheets at Bishop Museum of Rock 8608, from the crater of Haleakala, collected for and with genuine *A. sandwicense*, is an exact match for the other specimen of this hybrid. Because it does not seem "useful or necessary" to name this hybrid, it is designated by a formula, in accordance with the International Rules of Botanical Nomenclature (1930). The following hybrid, however, is given a name because that name has already been applied to it as a variety.

#### × ***Argyroxiphium Kai* (*A. caligini* × *Grayanum*)** (pl. 9).

*Argyroxiphium caligini* variety *Kai* Forbes, B. P. Bishop Mus.,  
Occ. Papers, vol. 7, no. 3, p. 39, 1920.

This putative hybrid is known only from the bogs at the summits of Puu Kukui and Eke, western Maui, where it occurs with

both the parental species. Degener reports that it is much less frequent than the other two. This hybrid is considered a parallel to *Argyroxiphium sandwicense*  $\times$  *virescens* that is restricted to eastern Maui. Both are considered to be derived from crosses between a species with silvery leaves and one with greenish leaves; accordingly their resulting pubescence and color, of intermediate character, are closely similar. In habit,  $\times$  *A. Kai* duplicates *A. caligini*, creeping and branching along the ground with the terminal rosettes isolating into new plantlets as the woody stems die back. In foliar characters the hybrid combines characters from both the parents. Its leaves are considerably less crowded in the rosette than are those of *A. caligini* although they are of the same length and half again as wide. The texture, thinness, and shape of the leaves is similar to the condition in the smaller rosettes of *A. Grayanum*. No ray-flowers have been detected on the two flowering specimens of  $\times$  *A. Kai* seen, and the pappus of this hybrid is reduced to a solitary posterior tooth or an erosulate margin on the cartilaginous areola.

Because this has been reported as a more or less uniform and abundant type in its two localities, and since data are lacking as to its fertility and behavior of the offspring, the possibility must be considered that this is an allopolyploid species derived through hybridization with the parental species indicated.

Forbes, in describing *A. caligini* variety *Kai*, declared it was of wider distribution than the species. This was due to its discovery on Puu Kukui before *A. caligini* was known to occur there. The type is "No. 391, a. M., collected on Eke, West Maui, T. H., October, 1917, by C. N. Forbes."

Maui: Eke, Honokohau drainage basin, Forbes 391a.M (Bish, type, 2 sheets); northern summit of Mount Eke, rim only, in shrubless clay bog, Degener 3526 (Deg, SU); Puu Kukui swamp, 5,800 feet, Rock 10318 (Bish, GH).

#### Section 2. **WILKESIA** Keck, new combination.

*Wilkesia*, as a genus, A. Gray, Am. Acad., Proc., vol. 2, p. 160, 1852; emend. vol. 5, p. 136, 1861. Named in honor of Capt. Charles Wilkes, commander of the United States South Pacific Exploring Expedition.

A monotypic section, the single species endemic on the island of Kauai.

5. *Argyroxiphium gymnoxiphium* (A. Gray) Keck, new combination.

*Wilkesia gymnoxiphium* A. Gray, Am. Acad., Proc., vol. 2, p. 160, 1852.

Plant 1.5-4 m high including the panicle of 5-10 dm; stem erect, simple or (rarely?) verticillately branched, leafless below the crowning rosette, 1-3 cm thick, consisting of a thin wooden cylinder surrounding a firm pith, the brown bark longitudinally ridged, the prominent annular nodes 3-15 mm apart, glabrous or canescent. Leaves verticillate, 10-20 at a node, their bases connate into a sheath 2-6 cm long and overlapping several younger nodes, the blades linear, attenuate, plane, erect, the immature somewhat sericeous, the mature glabrous except for the densely sericeous margins, 15-40 cm long, 5-10 mm wide, light green. Thyrses of 10-20 nodes, verticillate, to 5 dm in diameter at base, often bearing to 300 heads, internodes to 5 cm long, longitudinally ridged with peduncular traces, very resinous and beset with numerous stipitate yellow glands; bracts abruptly differing from foliaceous leaves, verticillate, about 10-12 at a node, connate-perfoliate, forming a cup about 1 cm deep, free portion broadly lanceolate, the lowermost 5-8 cm long and 15-20 mm wide, the uppermost shorter and usually broader, glabrous except for the sericeous margins, each bract subtending a peduncle; peduncles simple or, more often, dichotomously forked to bear 2 (sometimes 3-5 on lowermost) heads on pedicels  $\frac{1}{3}$  as long, widely divaricate, slender, densely glutinous and stipitate-glandular, ebracteate or pedicel sometimes subtended by one or more linear bractlets. Involucre urceolate-campanulate, 9-14 mm high and as broad; bracts firmly united for most of their length to form a smooth but viscid cup, the 20 or so free tips 1-3 mm long, very unequal, lanceolate, strongly villous-ciliate, at anthesis erect, at fruiting spreading. Disk-flowers 100-225; corolla yellowish, pubescent only on lobes, 6-7 mm long; anthers exserted. Akenes 6.5-7.6 mm long, dark brown, hispidulous with yellowish ascending hairs. Pappus 1-2.5 mm long; paleae unequal, 9-12, stramineous, fimbriate.

Endemic on the island of Kauai. Type locality: "In montibus Kauai." Wilkes Expedition (US, type; isotype GH); Waimea Canyon on way to Kokee, Swezey 8009 (Deg, SU); at outlook over Waimea Canyon, Kokee, Bush 8010 (Deg); Waimea drainage basin, west side, Forbes 1699.K (Bish, NY, US); Waimea, Mann and Brigham 535 (Bish, F, GH, NY, US); Waimea, Hillebrand (GH); Kaholuamanu, behind Waimea; Forbes 425.K (Bish, C, F, NY, US); Hitchcock 15297 (US); September 1909, Rock (Bish, NY); Rock 5264 (Bish, GH); Halemanu: February 1909, Rock (NY); Rock 225 (Bish); July 1911, Rock (GH); August 10, 1908, Reed (Bish). Sandwich Islands, Knutsen? (GH, M); without definite locality, 1838-42, Sandwich Islands, Wilkes Expedition (US).

Degener states that this plant occurs also at Milolii, Nualolo, and Olokele, on the barren mountain slopes of leeward Kauai. According

to Fosberg, the species has been multiplying rapidly on the island since the cattle have been removed from the forested areas.

The bare stem of this plant thrusts its leafy crown well above the surrounding grasses and herbaceous vegetation. The large inflorescence commences to bloom in June and the fruit may ripen until September or October. The native name of this species is said to be *iliau*.

#### FURTHER NOTES ON DUBAUTIA AND RAILLIARDIA

In order to determine the true affinities of *Argyroxiphium*, it has been necessary to take something more than a superficial glance at the genera *Dubautia* and *Railliardia*. Gaudichaud proposed both of the latter genera on successive pages of his account of the flowering plants collected by him on Freycinet's voyage around the world. He proposed two species, *Dubautia plantaginea* and *Railliardia linearis*. A. P. De Candolle added three species to *Railliardia*, and Asa Gray (7b) published five others in an account in which he proposed three sections for the genus and gave a brief account of its phylogenetic connections. Gray stated that *Railliardia* "differs from *Dubautia* chiefly in the slender and truly plumose setae of the pappus, the absence of chaff to the receptacle (which is convex or obtusely conical and pubescent) and in the nearly valvately uniserial involucre, the scales of which connive or lightly cohere into a cylindrical cup." Hillebrand maintained *Dubautia* and *Railliardia* as distinct genera, but in proposing additional species he found that the characters used to distinguish the genera were increasingly fallible. His observations under *Dubautia* are of interest (9, p. 221):

Its distinguishing characters consist in the free involucre bracts, the paleate receptacle and the broader rays of the pappus, which are only shortly ciliate, not plumose. *Dubautia raillardioides* has, however, a connate involucre, while in *Raillardia Menziesii* and *arborea* the union of the bracts is very loose; in the few-flowered *D. plantaginea* and *raillardioides* the receptacle is mostly naked, while in the large heads of *R. Menziesii* several paleae are always found to be present; and again, the long-ciliate rays of the pappus in *D. plantaginea* approach closely in structure to those of a *Raillardia*.

Does it not seem rather strange that an author would be able to point out so clearly exceptions to every character used to maintain a pair of relatively small genera and still feel able to call the genera distinct? Of his new species *Dubautia raillardioides* Hillebrand says: "A remarkable species which connects closely the present with the following genus [*Raillardia*]. . . . The plant has entirely the

habit of *Dubautia*, the leaves not differing from those of *D. plantaginea*; the pappus also, although somewhat peculiar, bears the character of the genus, but as to the involucre it is altogether railliardioid."

A recent extended account of the two genera by E. E. Sherff (16) throws additional light upon their similarities. His generic diagnoses fail to disclose a single pertinent difference that may be applied to distinguish between them. It is clear that the width and pubescence of the pappus, the chaff on the receptacle and the union of the involucral bracts have lost their value here as diagnostic generic characters because each occurs in both groups. From the material I have seen, and from a study of Sherff's account, I am impressed with the fact that there do not seem to be two natural assemblages involved, distinguished by rather intangible but nevertheless real characters such as aspect, which the systematist frequently finds in nature but has trouble in defining. Rather, *Dubautia* and *Railliardia* appear to form a continuous series or network. This calls for their inclusion within one genus and the line between them seems too indistinct to warrant their retention even as subgenera. In addition to the evident morphological similarity between these groups, their various species cohabit in the montane areas in the Archipelago, from the rain forests to the alpine region above timber line. Sherff gives an admirable systematic account of the species, but evades the question of how the two genera are to be distinguished by failing to raise it.

Last, but not of least importance, is Sherff's announcement that two separate interspecific hybrids are known between species of *Dubautia* and *Railliardia*. These are  $\times$  *Railliantia fucosa* Sherff (supposedly *Dubautia plantaginea*  $\times$  *Railliardia scabra* variety *leiophylla*) and  $\times$  *Railliantia fallax* Sherff (supposedly *Dubautia plantaginea* variety  $\times$  *Railliardia demissifolia* or *R. thyrsoiflora*). Sherff has pointed out several other hybrids within *Dubautia* and *Railliardia*. Their occurrence indicates that the species of this group are still able to intercross to some extent at least, and this intermixture of genic materials accounts for the various recombinations of the morphologic characters found here. Such free intercrossing does not characterize the species of two or more genera but rather the species of a single genus by most present day taxonomic concepts.

It is desirable to go beyond the mere statement of fact that *Dubautia* and *Railliardia* should be regarded as one and the same genus, and make the necessary transfer in order that the new combinations



may be put on record and made available. The International Rules of Botanical Nomenclature (1930) state in Art. 56 that when two groups of the same rank are united, if the names are of the same date, the author who unites the groups has the right of choosing one of them. The choice may be made, therefore, between the names *Dubautia* and *Railliardia*, and for the following reasons I choose *Dubautia*: (1) it is the shorter and an equally euphonious name; (2) it was published with page priority; (3) there has been much confusion regarding the spelling of *Railliardia*; (4) there is a species *Dubautia raillardoides* Hillebrand whose specific name would be inappropriate within *Railliardia*. These advantages outweigh the consideration that a greater number of transfers is required by using *Dubautia*.

**Dubautia** Gaudichaud, Freycinet Voy., Bot., p. 468, pl. 84, 1830.  
*Railliardia* Gaudichaud, Freycinet Voy., Bot., p. 469, pl. 83, 1830.

**Dubautia latifolia** (A. Gray) Keck, new combination (*Railliardia latifolia* A. Gray, Am. Acad., Proc., vol. 5, p. 132, 1861.)

**Dubautia scabra** (De Candolle) Keck, new combination. (*Railliardia scabra* De Candolle, Prodr., vol. 6, p. 441, 1837. *R. scabra* variety *hispidula* A. Gray, Am. Acad., Proc., vol. 5, p. 133, 1861.)

**Dubautia scabra** variety **leiophylla** (A. Gray) Keck, new combination. (*Railliardia scabra* variety *leiophylla* A. Gray, Am. Acad., Proc., vol. 5, p. 133, 1861.)

**Dubautia scabra** variety **Munroi** (Sherff) Keck, new combination. (*Railliardia scabra* variety *Munroi* Sherff, Am. Jour. Botany, vol. 20, p. 619, 1933.)

**Dubautia ciliolata** (De Candolle) Keck, new combination. (*Railliardia ciliolata* De Candolle, Prodr., vol. 6, p. 441, 1837. *R. ciliolata* variety *laxifolia* A. Gray, Am. Acad. Proc., vol. 5, p. 133, 1861.)

**Dubautia ciliolata** variety **trinervia** (Hillebrand) Keck, new combination. (*Railliardia ciliolata* variety *trinervia* Hillebrand, Fl. Haw. Isls., p. 226, 1888.)

**Dubautia ciliolata** variety **juniperoides** (A. Gray) Keck, new combination. (*Railliardia ciliolata* variety *juniperoides* A. Gray, Am. Acad., Proc., vol. 5, p. 133, 1861.)

- Dubautia ciliolata** variety **laxiflora** (De Candolle) Keck, new combination. (*Railliardia laxiflora* De Candolle, Prodr., vol. 6, p. 441, 1837. *R. Fauriei* Lévillé, Fedde Repert., Spec. Nov. Regn. Veg., vol. 10, p. 122, 1911. *R. ciliolata* variety *laxiflora* Sherff, Am. Jour. Botany, vol. 20, p. 619, 1933.)
- Dubautia demissifolia** (Sherff) Keck, new combination. (*Railliardia demissifolia* Sherff, Bot. Gaz., vol. 95, p. 78, 1933.)
- Dubautia demissifolia** variety **verticillata** (Sherff) Keck, new combination. (*Railliardia demissifolia* variety *verticillata* Sherff, Am. Jour. Botany, vol. 20, p. 619, 1933.)
- Dubautia molokaiensis** (Hillebrand) Keck, new combination. (*Railliardia molokaiensis* Hillebrand, Fl. Haw. Isls., p. 226, 1888.)
- Dubautia molokaiensis** variety **oppositifolia** (Sherff) Keck, new combination. (*Railliardia molokaiensis* variety *oppositifolia* Sherff, Am. Jour. Botany, vol. 20, p. 619, 1933.)
- Dubautia molokaiensis** variety **stipitata** (Sherff) Keck, new combination. (*Railliardia molokaiensis* variety *stipitata* Sherff, Am. Jour. Botany, vol. 20, p. 619, 1933.)
- Dubautia ternifolia** (Sherff) Keck, new combination. (*Railliardia ternifolia* Sherff, Am. Jour. Botany, vol. 20, p. 618, 1933.)
- Dubautia thyrsoflora** (Sherff) Keck, new combination. (*Railliardia thyrsoflora* Sherff, Am. Jour. Botany, vol. 20, p. 618, 1933.)
- Dubautia thyrsoflora** variety **cernua** (Sherff) Keck, new combination. (*Railliardia thyrsoflora* variety *cernua* Sherff, Am. Jour. Botany, vol. 20, p. 618, 1933.)
- Dubautia lonchophylla** (Sherff) Keck, new combination. (*Railliardia lonchophylla* Sherff, Am. Jour. Botany, vol. 20, p. 619, 1933.)
- Dubautia coriacea** (Sherff) Keck, new combination. (*Railliardia coriacea* Sherff, Bot. Gaz., vol. 95, p. 80, 1933.)
- Dubautia linearis** (Gaudichaud) Keck, new combination. (*Railliardia linearis* Gaudichaud, in Freycinet Voy., Bot., p. 469, pl. 83, 1830.)

- Dubautia linearis** variety **opposita** (Sherff) Keck, new combination. (*Railliardia linearis* variety *opposita* Sherff, Am. Jour. Botany, vol. 20, p. 619, 1933.)
- Dubautia Hillebrandii** (H. Mann) Keck, new combination. (*Railliardia Hillebrandii* H. Mann, Enum. Haw. Pl., no. 238, Am. Acad. Proc., vol. 7, p. 175, 1867.)
- Dubautia montana** (H. Mann) Keck, new combination. (*Railliardia montana* H. Mann, Enum. Haw. Pl., no. 243, Am. Acad., Proc., vol. 7, p. 176, 1867.)
- Dubautia montana** variety **longifolia** (Sherff) Keck, new combination. (*Railliardia montana* variety *longifolia* Sherff, Am. Jour. Botany, vol. 20, p. 618, 1933.)
- Dubautia montana** variety **robustior** (Sherff) Keck, new combination. (*Railliardia montana* variety *robustior* Sherff, Am. Jour. Botany, vol. 20, p. 619, 1933.)
- Dubautia reticulata** (Sherff) Keck, new combination. (*Railliardia reticulata* Sherff, Bot. Gaz., vol. 95, p. 78, 1933.)
- Dubautia struthioloides** (A. Gray) Keck, new combination. (*Railliardia struthioloides* A. Gray, Am. Acad., Proc., vol. 5, p. 134, 1861.)
- Dubautia Rockii** (Sherff) Keck, new combination. (*Railliardia Rockii* Sherff, Bot. Gaz., vol. 95, p. 79, 1933.)
- Dubautia Menziesii** (A. Gray) Keck, new combination. (*Railliardia Menziesii* A. Gray, Am. Acad., Proc., vol. 5, p. 133, 1861.)
- Dubautia Menziesii** variety **angustifolia** (Sherff) Keck, new combination. (*Railliardia Menziesii* variety *angustifolia* Sherff, Am. Jour. Botany, vol. 20, p. 618, 1933.)
- Dubautia arborea** (A. Gray) Keck, new combination. (*Railliardia arborea* A. Gray, Am. Acad., Proc., vol. 5, p. 134, 1861.)
- Dubautia platyphylla** (A. Gray) Keck, new combination. (*Railliardia platyphylla* A. Gray, Am. Acad., Proc., vol. 5, p. 134, 1861.)
- Dubautia platyphylla** variety **leptophylla** (Sherff) Keck, new combination. (*Railliardia platyphylla* variety *leptophylla* Sherff, Am. Jour. Botany, vol. 20, p. 619, 1933.)

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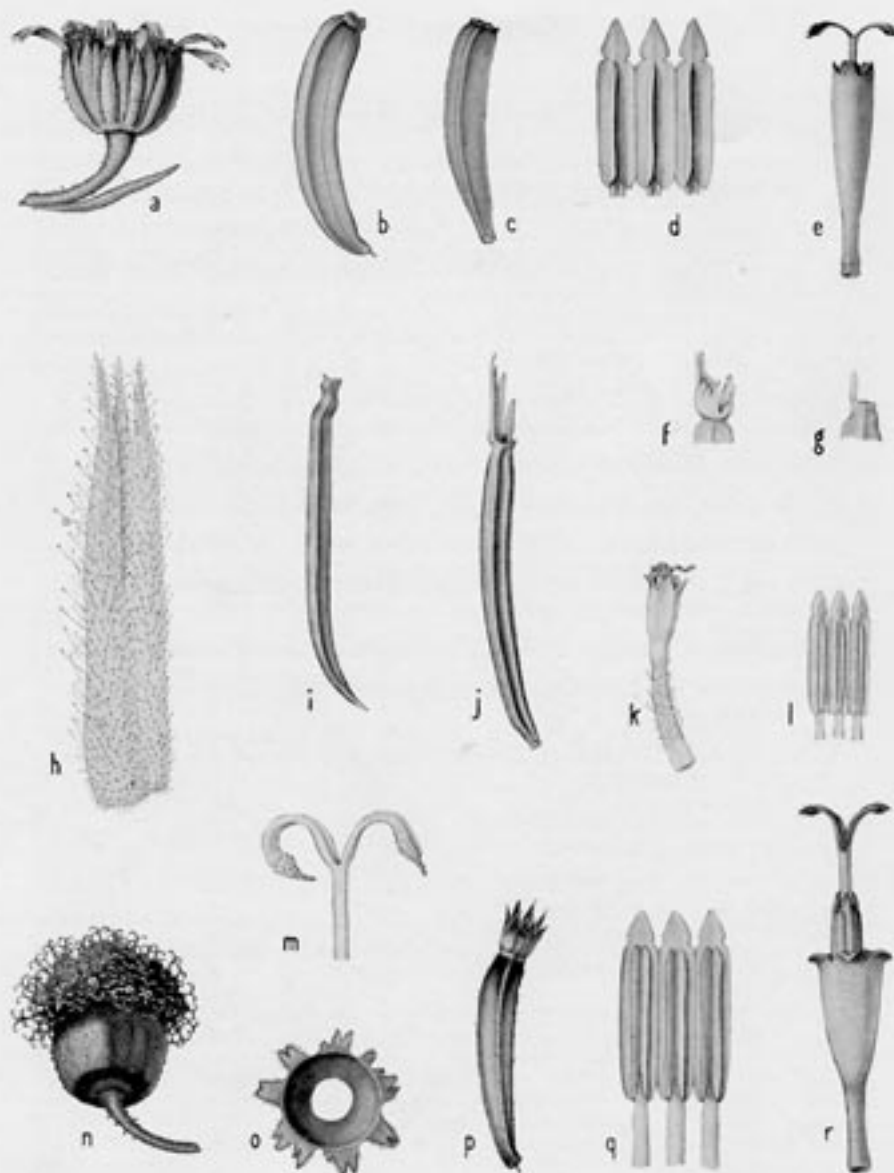


PLATE 1.—*Argyrocephalum sandwicense* De Candolle (a-g): a, head,  $\times 1$ ; b-c, ray- and disk-akene,  $\times 4$ ; d, anthers,  $\times 8$ ; e, disk-flower,  $\times 4$ ; f-g, disk- and ray-pappus,  $\times 4$ ; a-e, Degener No. 3527; f-g, type in De Candolle Herbarium. *Argyrocephalum virescens* Hillebrand (h-l): h, involueral bract adherent to bracts of receptacle,  $\times 4$ ; i-j, ray- and disk-akene,  $\times 4$ ; k, disk-flower,  $\times 4$ ; l, anthers,  $\times 8$ ; h-l, Degener No. 3528. *Argyrocephalum gymnoxiphium* (A. Gray) Keck (m-r): m, style-branches,  $\times 8$ ; n, head,  $\times 1$ ; o, involucre as seen from above,  $\times 1$ ; p, akene,  $\times 4$ ; q, anthers,  $\times 8$ ; r, floret,  $\times 4$ ; m-r, Swezey No. 8009. Drawn by Link Malmquist.



PLATE 2.—*Arggyrotrichum sandwicense* De Candolle. Crater of Haleakala, Maui. (Photograph from B. P. Bishop Museum.)



PLATE 3.—*Argyroxiphium sandwicense* De Candolle, young plant with secondary rosette, crater of Haleakala, Maui. (Photograph by R. J. Baker, Honolulu.)

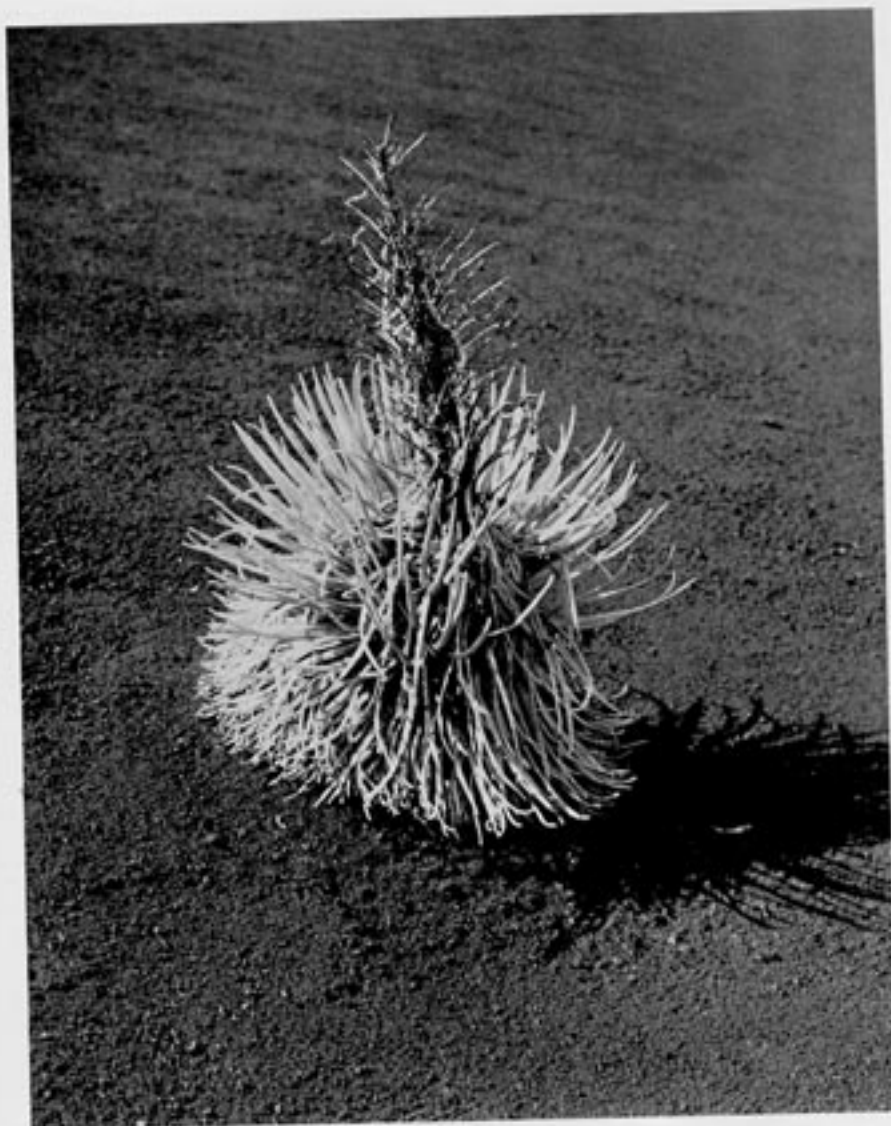


PLATE 4.—*Argyroxiphium sandwicense* De Candolle, showing remains of the inflorescence. (Photograph by R. J. Baker, Honolulu.)





PLATE 5.—*Argyroxiphium sandwicense* De Candolle, 1/2.2 natural size.



PLATE 6.—*Argyroxiphium virescens* Hillebrand, 1/2.4 natural size.



PLATE 7.—*Argyroxiphium caliginum* Forbes. (Photograph from B. P. Bishop Museum.)



PLATE 8.—*Argyroxiphium caliginum* Forbes, young plant with immature rosettes, 1/2 natural size.



PLATE 9.—*X* *Argyroxiphium* Kai (*A. caligini* *X* *Grayanum*), 1/24 natural size.