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Santalum ellipticum, a Restatement of Gaudichaud's Species

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Santalum ellipticum Gaudichaud, the *iliahi aloe* or lowland sandalwood of the Hawaiian islands, is redefined as a single species, exhibiting phenotypic epharmosis and normal variation in flower length, which occurs on Laysan, Oahu, Molokai, Lanai, Maui, Kahoolawe, and Hawaii. *S. ellipticum* var. *littorale, S. cuneatum, S. cuneatum* f. *gracilius,* and *S. cuneatum* var. *laysanicum* are reduced to synonyms of *S. ellipticum.*

During botanical investigations in the arid lowlands of Oahu, carried on for nine months, considerable difficulty was encountered in separating the species, forms, and varieties of the *iliahi aloe* or lowland sandalwood of the Hawaiian islands. Such separation as could be effected was forced and unnatural in the light of actual occurrence, and did not take into account the influence of local site factors on the form and appearance of the plant.

Hawaiian species of the genus *Santalum* have been studied and revised by Skottsberg (Bishop Mus., Bull. **43,** 1927). In this excellent revision two species-groups are established: (1) the *freycinetianum*-group with four species, one each on Kauai, Oahu, Maui, and Lanai; and (2) the *ellipticum*-group with four species, of which *Santalum ellipticum* Gaudichaud is restricted to Oahu, two are restricted to Hawaii, and *Santalum cuneatum* (Hillebrand) Rock occurs on Oahu, Molokai, Lanai, Maui, Kahoolawe, Hawaii, and Laysan. Skottsberg recognizes the close relationship between *Santalum ellipti-*

cum and *S. cuneatum,* and the difficulty of separating them by leaf form. His segregation is based entirely on the length of flower and style, though he states that he has not seen the flowers of Gaudichaud's type specimen. He describes *S. ellipticum* as having flowers 4-5 mm. long; *S. cuneatum,* as having flowers 5-7 mm. long.

The revision of *Santalum ellipticum* Gaudichaud presented in this paper is based on the acceptance of the following taxonomic concepts. 1, Geographical isolation in the islands by itself is not considered sufficient cause for the establishment of a segregate. 2, If a segregate has been described as having certain characters and differences, and these characteristics are proved to be invalid or nonexistent, and no additional characteristics can be determined, the segregate is reduced to synonomy. 3, When morphological variations occur within a restricted geographical range and appear to be correlated with the local existing site factors, and when the variations are related to each other by all degrees of intergradations and distribute themselves so as to form a normal distribution curve, the actual naming of such variations is considered scientifically superfluous. 4, When forms are striking and aberrant, when they apparently are not induced by existing ecological factors, and when they are not related by gradations with the general type, they are considered worthy of taxonomic recognition.

The present investigation within the *ellipticum*-group of Hawaiian *Santalum* is concerned in the first place with the validity of *S. cuneatum* as a distinct species, and in the second place with the status of the varieties and forms of both *S. ellipticum* and *S. cuneatum* as maintained by Skottsberg.

The validity of *S. cuneatum* as a species distinct from *S. ellipticum* is dependent on a consistent difference in the length of the flowers. Field investigation revealed that variation in flower length in each of two colonies of lowland sandalwood was such as to overlap the ranges of both species. Considering the relative rarity of the plant, it must be assumed that each colony was nevertheless a single interbreeding group, within which this character was variable. Furthermore, a study of herbarium material showed that minimum and maximum flower lengths from any one collection exhibit a remarkably small variation, exceeding one millimeter in only ten percent of the specimens. When these data are graphed, the resulting curve is the normal bell-shaped type, with a single peak near the mean of five millimeters,

a condition indicating normal variation of the character concerned. Such evidence eliminates any second species of *Santalum* based on flower length. Further study of herbarium material revealed no characteristics which could be used to segregate an additional species.

Table 1. Minimum and maximum lengths of flowers of Santalum ellipticum Gaudichaud[1]

Collection	Length of flowers in mm.	
	Minimum	Maximum
Hawaiian islands:		
Forbes	5.0	6.0
Hillebrand and Lydgate, ex Lydgate	4.0	5.0
U. S. Exploring Expedition*	6.0	6.0
Laysan:		
Bryan	4.5	5.5
Bryan 1903*	5.0	5.0
Bryan 1903 (S. cuneatum var. laysanicum)	5.0	5.0
Fullaway 1912 (S. cuneatum var. laysanicum)	5.5	6.5
Schauinsland 1896-97, type	4.5	5.5
Snyder May 1902*	4.0	6.0
Oahu:		
Bryan 1903	5.0	6.0
Christophersen, Wilder, and Hume 1504	5.0	6.5
Christophersen, Wilder, and Hume 1710	6.0	7.0
Christophersen, Wilder, and Hume 1439	4.5	6.0
Degener 3701*	4.0	4.0
Degener 5301*	4.0	5.0
Degener 5313B*	5.0	6.0
Degener 5321*	5.0	6.0
Degener 5324*	3.0	4.0
Degener 5327*	3.0	3.0
Degener 5328*	5.5	6.5
Degener 5330*	4.0	4.0
Degener 5331*	4.0	5.0
Degener 11323*	3.0	4.0
Degener 11324*	5.0	5.0
Egler 37-101	4.5	6.0
Egler 37-115	4.0	5.0
Egler 37-116	5.0	7.0
Egler 37-418	4.0	5.0
Egler 37-420	4.0	5.0
Forbes 1078 (S. cuneatum)	6.0	7.0

[1] Data were obtained from not less than six measurements from each herbarium sheet. The Latin names in parentheses are those of the collections cited and named by Skottsberg (Bishop Mus., Bull. 43, 1927, and elsewhere). Collections marked with an asterisk are on file in the herbarium of the New York Botanical Garden; all others are in the herbarium of Bishop Museum.

Collection	Length of flowers in mm.	
	Minimum	Maximum
Forbes 1078*	6.0	6.5
Forbes 1445 (S. ellipticum)	3.5	4.5
Forbes 1653 (S. ellipticum)	4.0	5.5
Forbes 1755 (S. cuneatum)	5.0	6.0
Forbes 2276 (S. ellipticum var. littorale)	4.0	5.0
Forbes 2343 (S. cuneatum)	4.0	5.0
Forbes 2442 (S. cuneatum f. gracilius)	5.5	6.0
Forbes 2442*	5.0	5.5
Hillebrand, Kaneohe	4.5	5.0
Hume 160	3.0	4.0
Judd 36 (S. cuneatum) ?	6.0	7.0
Judd 57	5.0	6.0
Judd 59 (S. ellipticum)	3.0	4.0
Judd and Hosaka 2/28/32	4.0	4.5
Neal 7/12/34	5.0	6.0
Rock 12513 (S. cuneatum)	3.0	4.0
Rock 12514	5.0	6.0
Rock 17028	4.0	5.0
Shaw 5920	3.5	5.0
Shaw 8119	4.0	5.5
Shaw 8301	5.0	5.5
Shaw 8348	4.5	5.5
Shaw 8864	4.5	5.5
Shaw 8864	4.5	5.5
Shaw 10091	4.0	5.0
Shaw ex Rock 12514 (S. cuneatum)	5.5	6.0
Skottsberg 118 (S. cuneatum f. gracilius)	6.0	7.0
Stokes 5/2/20	5.0	7.0
Molokai:		
Brigham	5.5	6.0
Degener 5310*	4.0	5.0
Forbes 178	3.5	4.5
Forbes 178 (S. cuneatum)	4.0	5.0
Forbes 353	5.0	6.0
St. John et al. 12693	4.0	5.0
Lanai:		
Forbes 163	6.0	7.0
Forbes 293 (S. cuneatum)	3.5	4.5
Forbes 293	4.0	5.0
Forbes 293*	4.0	4.5
Hillebrand, ex. Mus. Bot. Berol.	3.5	4.5
Mann and Brigham 353 (S. cuneatum)	4.0	5.0
Munro 23 (S. cuneatum)	4.5	5.5
Munro 33	5.0	6.0
Munro 82	5.0	6.0
Munro 98	5.5	6.5

Collection	Length of flowers in mm.	
	minimum	maximum
Munro 119	6.0	7.0
Munro 11/6/13	5.0	6.0
Munro 10/19	5.0	6.0
Munro 10/19*	6.0	6.0
Rock 8004 (S. cuneatum)	4.0	5.0
Rock 8004*	3.0	4.0
Rock 8013 (S. cuneatum)	5.0	7.0
Rock 8013*	6.0	7.0
Rock 8048 (S. cuneatum)	4.0	5.0
Maui:		
Degener 5303*	4.0	5.0
Forbes 84 (S. cuneatum)	6.0	7.0
Forbes 1928	5.0	6.0
Forbes 2478	5.0	5.0
Rock 8683 (S. cuneatum)	5.0	6.0
Rock 8683*	5.0	6.0
Hawaii:		
Neal 345	4.0	5.0

The status of the described varieties and forms of *Santalum ellipticum* and *S. cuneatum* cannot rest on an evaluation of morphological differences alone. In general, it may be said that botanists have not always appreciated the effects of the extraordinary extremes in soil moisture, insolation, wind action, and other ecological factors that often exist in close proximity in tropical arid lowlands. These factors are correlated with the protection offered by the topography, with the depth of the soil, and with the development of a closed mature vegetation. These conditions are correlated with striking differences in the form and manner of growth of both indigenous and established alien plants. In some Hawaiian species, variations in the size, shape, and succulence of the leaf, and in the height of the plant correspond closely with local site factors, and are such that when interpreted from herbarium material, in the light of the taxonomy of the plants of temperate regions, they may be given a more important taxonomic significance than they deserve.

Santalum ellipticum var. *littorale* was investigated at the ruins of the Hawaiian village near the sea at Waimanalo where there is a colony of over 100 individuals. Flower sizes on individual plants fit the concepts of both *S. cuneatum* and *S. ellipticum*. No characteristics of flower or fruit were discovered which might differentiate these

plants in any way from other collections of sandalwood from the dry lowlands of Oahu. In habit and growth form the plants are low, wind-clipped, and bear relatively thick leaves, thus conforming to the adjacent, severely clipped plants of the introduced hau, *kiawe, klu,* lantana, and *koa haole.* The characteristics of this sandalwood segregate are apparently induced by the peculiar local environmental conditions. There is nothing to indicate that their genetic constitutions are distinct.

Santalum cuneatum f. *gracilius* was established by Skottsberg in 1926, being based on Skottsberg 118, Ewa coral plain, Oahu. It is characterized as a small tree with slender pendulous branches, with relatively thin leaves and long petioles; the flowers are 6.0-7.0 mm. long. I investigated this form in the type locality, and found that it cannot be interpreted properly without reference to the habitat. The Ewa plain is a raised reef lying 3-15 meters above sea level and covered by a dry open forest of *kiawe.* The soil is thin or absent and conditions are very unfavorable for plant growth. The topography is characterized locally by pits in the fossil reef, often as much as 10 feet in diameter and 15 feet deep. In these depressions, the favorable edaphic and atmospheric conditions permit the growth and development of species of the moist montane flora. Furthermore, there is a striking difference between the habit and form of dry-land plants growing in these moist depressions and those growing on the dry reef surface and on the near-by strand. This is true both for introduced herbs and shrubs and for native plants, including *Capparis sandwichiana* DC. and *S. cuneatum* f. *gracilius.* Variations in height and in foliage of individual specimens of *Santalum* are beyond the limitations of *S. cuneatum* f. *gracilius,* and intergrade with those of *S. cuneatum.* The differences are directly correlated with the favorableness of the site on which the plant grows. Until other differences are discovered, independent of local habitat factors, this *Santalum* must be considered as typical *S. ellipticum.*

Santalum cuneatum var. *laysanicum* Rock was based on Schauinsland 1896-97, Laysan Island. A study of the type collection and other collections in Bishop Museum revealed no characteristics which could be satisfactorily used to separate the Laysan plants from those of the *ellipticum*-group of other Hawaiian islands. Flower length varies normally. Leaf shape varies from suborbicular to elliptical, paralleling the variations on other islands. Leaves are generally but not always

succulent, and are similar to those on plants growing near the sea on Oahu. A photograph of the type locality on Laysan, taken by E. L. Caum, amply shows the very severe conditions and exposure under which these plants grow. The form of the shrub and the succulence of leaf are obviously related to these local site conditions. Geographical isolation is its only claim to taxonomic status.

In accordance with the evidence given in the preceding paragraphs, *Santalum ellipticum* Gaudichaud may now be restated and its synonomy and history revised.

Santalum ellipticum Gaudichaud

Santalum ellipticum Gaudichaud, in Freycinet, L., Voyage autour du monde, Bot., 442, 1826-30 (non vide).

Santalum freycinetianum var. *latifolium* A. Gray, Diagnoses of the species of sandalwood (Santalum) of the Sandwich Islands: Am. Acad. Proc., **4**: 327, 1860 (Maui specimens, not Hawaii specimens).

Santalum "freyienetianum" var. *ellipticum* Mann, Enumeration of Hawaiian plants: Am. Acad. Proc., **7**; 198, 1867 (spelled correctly *freycinetianum* in the index).

Santalum freycinetianum γ var. *cuneatum* Hillebrand, Flora of the Hawaiian islands, 389, Heidelberg, 1888.

Santalum freycinetianum ε var. *littorale* Hillebrand, op. cit., 390.

Santalum cuneatum Rock, The sandalwoods of Hawaii: Bd. Agric. and Forestry, Terr. Hawaii, Bot. Bull., **3**: 37, pl. 11, 1916.

Santalum cuneatum var. *laysanicum* Rock, op. cit., 39, pl. 12.

Santalum littorale Rock, op. cit., 41, pl. 13.

Santalum cuneatum f. *gracilius* Skottsberg, Acta Horti Gothoburgensis, **2**: 222, 1926 (published with description in Bishop Mus., Bull. **43**: 59, 1927).

Santalum ellipticum var. *littorale* Skottsberg, Artemisia, Scaevola, Santalum, and Vaccinium of Hawaii: Bishop Mus., Bull. **43**: 55, 1927.

Santalum ellipticum Gaudichaud, as presented above, has been variously treated by Hawaiian botanists. This species, originally described from Oahu material by Gaudichaud, was further described by A. de Candolle (Santalaceae, Prod., **14**: 682, Paris, 1857). Concerning this species, Gray wrote: "Foliis chartaceis ellipticis oblongis seu ovali-obovatis, petioli gracili; cymis paniculisve saepius axillaribus; perigonii tubo brevi, lobis ovatis; fructu *S. freycinetiani.*" It is ap-

parent that Gray was referring to Gaudichaud's species. Gray's *Santalum freycinetianum* var. *latifolium* is based on Maui specimens of *S. ellipticum* and on Hawaii specimens of *S. paniculatum* Hooker and Arnott. Mann (1867) reduced Gaudichaud's *S. ellipticum* of Oahu to a variety of *S. "freyienetianum"* and accepted Gray's *S. freycinetianum* var. *latifolium,* adding Lanai specimens of *S. ellipticum.* Wawra (Flora, **58**: 172, 1875), while preserving *S. freycinetianum* var. *latifolium* for Maui specimens of *S. ellipticum,* did not separate any other sandalwoods of the *ellipticum*-group from *S. freycinetianum.* Sinclair (Indigenous flowers of the Hawaiian islands, 34, pl. 34, 1885) misused the name *S. ellipticum* for *S. pyrularium* A. Gray. Hillebrand (1888) distributed *S. ellipticum* among four varieties of the unrelated *S. freycinetianum*: (1) var. *latifolium,* including *S. paniculatum* from Hawaii, and the Maui, Kahoolawe, and Molokai specimens; (2) var. *cuneatum,* for Lanai specimens; (3) var. *ellipticum,* including an unrelated Kauai *Santalum* and the Oahu specimens; and (4) var. *littorale,* for the Oahu plants growing near the sea. The sandalwood called *S. ellipticum* by Heller (Minn. Bot. Stud., **1**: 818, 1897) was collected on Kauai, where *S. ellipticum* in the present sense does not occur. According to Skottsberg it is *S. pyrularium* A. Gray. Bitter (Abh. Nat. Ver. Bremen, **14**: 433, 1900, non vide) considered the Laysan plant as *S. freycinetianum.* Rock misinterpreted the two species in his first treatment of *Santalum* (Indigenous trees of the Hawaiian islands, p. 126, Honolulu, 1913). In his second treatment (1916) he misapplied *S. ellipticum* and distributed the true *S. ellipticum* among four segregates: (1) *S. paniculatum,* which was extended from Hawaii to embrace Maui, Molokai, and Kahoolawe specimens; (2) Hillebrand's var. *cuneatum,* which was raised to specific rank and comprised Lanai and Maui plants; (3) *S. cuneatum* var. *laysanicum,* which was established for the sandalwood on Laysan; and (4) Hillebrand's var. *littorale,* which was raised to specific rank and comprised Oahu and Hawaii specimens. Skottsberg (1927) recognized five segregates: (1) *S. ellipticum,* for the small-flowered forms of Gaudichaud's species; (2) *S. ellipticum* var. *littorale,* a reduction of Rock's species, for the Oahu specimens growing near the sea; (3) *S. cuneatum,* embracing the large-flowered forms of Gaudichaud's species; (4) *S. cuneatum* f. *gracilius,* established for a sandalwood growing under favorable conditions on the Ewa plain, Oahu; and (5) *S. cuneatum* var. *laysanicum* of Rock, maintained for the

plants on the relatively isolated island of Laysan. In this paper I have reduced the last four of Skottsberg's segregates named above to the status of synonyms of *Santalum ellipticum* Gaudichaud, a single normally variable taxonomic unit, known to occur on Laysan, Oahu, Molokai, Lanai, Maui, Kahoolawe, and Hawaii.

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Since this manuscript was prepared, Skottsberg has stated in correspondence that he shares my opinion concerning the invalidity of *S. cuneatum.* Furthermore, Otto Degener has published a revision of Skottsberg's *ellipticum*-group (Flora Hawaiiensis, Oct. 4, 1937). Degener combines Skottsberg's *S. ellipticum* and *S. cuneatum* as *S. ellipticum* Gaudichaud. He reduces *S. ellipticum* var. *littorale* and *S. cuneatum* var. *laysanicum* to synonyms of *S. ellipticum,* an interpretation with which I agree. *S. cuneatum* forma *gracilius* of Skottsberg (which I do not maintain) becomes *S. ellipticum* var. *gracilius,* about which Degener remarks, "Some of my specimens are difficult to separate from the species proper." Degener establishes three additional segregates: (1) *S. ellipticum* forma *physophora,* abundant near the Hawaiian village at Waimanalo, previously identified by Skottsberg as *S. ellipticum* var. *littorale* which I have reduced to *Santalum ellipticum*; (2) *S. ellipticum* forma *annectens* from Kaalualu, Hawaii; and (3) *S. ellipticum* var. *luteum,* a segregate from *S. paniculatum* in Hawaii. Until more complete material is available it is impossible to evaluate these three new segregates.