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Santalum in Eastern Polynesia

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RÉSUMÉ

FOSBERG, F. R. & M.-H. SACHET (1985). *Santalum* en Polynésie orientale. *Candollea* 40: 459-470. En anglais, résumé français.

La découverte au sommet du Mt Aorai (Tahiti) d'un *Santalum* apparemment nouveau a amené les auteurs à un examen critique des représentants de ce genre en Polynésie orientale. Il en résulte que les sections *Polynesica* et *Hawaiensis* sont réunies sous ce dernier nom, un lectotype est désigné pour l'espèce *Santalum insulare* A. DC., et deux nouvelles variétés de cette espèce sont décrites, var. *alticola* de Tahiti, et var. *deckeri* des îles Marquises. Tous les taxa connus jusqu'à présent en Polynésie orientale sont considérés comme des variétés de *Santalum insulare*: var. *raiateense*, *raivavense*, *margaretae*, *marchionense*, *mitiaro* et *hendersonense*. Ces variétés sont décrites avec une clé pour les séparer.

ABSTRACT

FOSBERG, F. R. & M.-H. SACHET (1985). *Santalum* in Eastern Polynesia. *Candollea* 40: 459-470. In English, French abstract.

The discovery of an apparently undescribed *Santalum* on the summit of Mt. Aorai (Tahiti) led to a critical examination of the Eastern Polynesian members of the genus. This resulted in merging sections *Polynesica* and *Hawaiensis* under the latter name. *Santalum insulare* A. DC. is lectotypified and a new variety *alticola* from Tahiti and one from the Marquesas, *deckeri*, are described in *S. insulare*. All of the previously recognized taxa from eastern Polynesia are placed in *S. insulare* as varieties *raiateense*, *raivavense*, *margaretae*, *marchionense*, *mitiaro*, and *hendersonense*. Descriptions are provided and a key to separate the varieties.

The Santalaceae are a small family of semi-parasitic flowering plants, almost world-wide in distribution, but seldom a conspicuous element in the vegetation. Two genera, *Santalum* and *Exocarpos*, occur in Polynesia. *Santalum* extends from India, throughout the Indo-Pacific and Australia, east to the Juan Fernandez Islands, and north to Hawaii, where a number of species are found. The heartwood of this genus is the highly prized very fragrant sandalwood, used for carved objects and as the source of a scent used in incense and perfumery.

Briefly characterized, the genus *Santalum* L. contains small trees and shrubs with opposite, usually dull or olive-green simple leaves, no stipules, mostly terminal thyrsoid usually paniculate inflorescences with scale-like (or seta-like) bractlets subtending the ramifications and the flowers; flowers with a single whorl of 4 or rarely 5 perianth segments or tepals, hypanthium obconic, campanulate, or cup-shaped; disk concave or cup-shaped with lobes alternating with the tepals and stamens; stamens with large anthers on short filaments inserted on and opposite the bases of the tepals, ovary inferior or nearly so, unilocular with a single basal ovule, a short simple style and usually a 3- or 4-lobed small fleshy stigma; fruit a drupe with thin flesh and a hard endocarp containing a single large seed.

Carl Skottsberg, the botanist who has studied the Polynesian species of *Santalum* most critically, recognized three sections, *Santalum* in the western Pacific and Hawaii, *Hawaiensis* endemic in Hawaii, and *Polynesica* in eastern Polynesia and Juan Fernandez. They are said to be distinguished by certain minor floral differences. Sect. *Santalum* has the apical portion of the ovary free from the calyx tube or hypanthium, the free part of the hypanthium as long as or longer than

wide, and flowers odorless. In Sect. *Hawaiiensia*, the ovary is completely immersed in the receptacle (inferior) with a very short, obconical or turbinate hypanthium, and the small greenish flowers are fragrant. Sect. *Polynesica* is similar to *Hawaiiensia* but has the apical part of the ovary extending above the disk, attenuating into the style, thus appearing to be merely a swollen lower part of the style, but hollow.

Skottsberg did not typify either of his new sections in any of his publications, nor has anyone since, to the best of our knowledge. We therefore designate as lectotype species of *Santalum* sect. *Hawaiiensia* Skottsberg (Proc. 4th Pacific Sci. Congr. 3: 436, 1930) *Santalum ellipticum* Gaudichaud, as it is the first species described and has generally been included in the section. The type specimen of this species is a Gaudichaud collection in P. For *Santalum* sect. *Polynesica* Skottsberg (op. cit., p. 437), we designate *Santalum insulare* Bertero ex A. DC. as lectotype: it is the earliest described and we refer all the other southeastern Polynesian species to it, either as varieties or synonyms.

Taxa placed by SKOTTSBERG (1938) in his sect. *Polynesica* are found in the principal archipelagoes of high islands in southeastern Polynesia, on Henderson Island, and on Juan Fernandez, off the coast of Chile. Of these, he distinguished five taxa of *Santalum* from southeastern Polynesia, all but *S. hendersonense* varieties of *S. insulare*. Skottsberg did not make clear why *S. hendersonense* was maintained as a species, but the far larger fruit, along with minor or more obscure characters, provided some justification. Our new variety from the Marquesas also has a very large fruit, and a very ample panicle with flowers subsessile in umbellules terminating the racemously arranged inflorescence branches. Except for these characters, it is hard to separate from *S. insulare* var. *marchionense*. This group, Skottsberg's sect. *Polynesica*, seems not to differ much from his sect. *Hawaiiensia*, where F. Brown had placed his *S. hendersonense*. The difference between an inferior ovary and an almost inferior one is not very convincing. We regard to the two as one section, the older name being *Santalum* sect. *Hawaiiensia* Skottsb.

Our studies suggest also that *Santalum hendersonense* F. Brown must be considered another variety of *S. insulare* rather than a separate species. An amplified description of *S. insulare* var. *insulare* and more adequate understanding of the Marquesan plants of this affinity show that no convincing breaks occur between the populations found in the southeastern Pacific islands, and that all *Santalum* in the region east of Samoa and south of Hawaii belong to a single variable species. This may be separated into at least nine ill-distinguished varieties.

H. U. Stauffer annotated many of the older sheets cited here, placing them all in *S. insulare* without indicating any subdivisions. He did not live to complete this work, so what his final conclusions might have been is unknown.

Santalum fernandezianum F. PHILIPPI (1892) of Juan Fernandez is very similar to *S. insulare*, but differs, judging by the description and illustration published by F. JOHOW (1896), in its perianth being pubescent within, the anthers notably broader than long, and the bilobed stigma sessile on the apex of the conical upper part of the ovary (described by Johow as a conical style). If Johow's description is correct, the Juan Fernandez plant should probably be maintained as a separate, but closely related species placed, along with *S. insulare*, in sect. *Hawaiiensia* as expanded above.

Since our remarks on *Santalum fernandezianum* were written, we have been able, through the courtesy of Professor Tod F. Steussy, to examine several photos of herbarium specimens including one of the type, and of drawings of the plant, from the herbarium at Concepción. The photo of the type shows little more than the leaf-shape. The photos of the herbarium sheet and the drawings indicate, though not clearly, a rather different pattern of inflorescence branching from that in *S. insulare*. Though we can scarcely make a clear description from these, this inflorescence seems to provide sufficient reason for maintaining *Santalum fernandezianum* as a separate species, rather than considering it as merely another variety of *S. insulare*.

A description of the species, *Santalum insulare* in a broad sense, is offered, followed by a discussion of its typification.

***Santalum insulare* Bert. ex A. DC., in DC. Prodr. 14(2): 685-686. 1857.**

General description — Shrubs and small trees, glabrous, smallest branchlets tending to be slightly decussately compressed; leaves simple, ovate to elliptic to oval or almost orbicular, firm

chartaceous to coriaceous, lateral veins (5-)6-12, uneven in strength and spacing, tending to anastomose at least distally, petioles slender, 5 to rarely 15 mm long; stipules none; inflorescence may be interpreted as a terminal or pseudo-axillary thyrsoid panicle, variously ramified, usually with a pair of reduced leaves at the first ramification or as 1-3(-5) thyrses at terminal node (rarely with small axillary thyrses at second and third nodes), a scale-like bractlet subtending each ramification, flowers subsessile or shortly pedicellate in triads or few-flowered glomerules or unbellules at ends of ultimate branches; flowers 4-(rarely 5-)parted, hypanthium obconic to somewhat campanulate, lobes ovate to triangular, up to 3 mm long, somewhat fleshy, valvate, inner edges papillate or papillate-ciliolate, apices slightly cucullate, a fascicle of long hairs at base of inner face of each lobe, behind the stamen; disk cup-shaped, with 4 lobes opposite the sinuses between the calyx lobes, stamens 4, with very short thick filaments attached to inner bases of calyx lobes, below the tufts of hairs, anthers almost or quite as wide as long, partly exserted when calyx lobes are spreading, oblong to oval; ovary mostly inferior but with a hollow beak protruding above the bottom of the cup-shaped disk, narrowed to a short style subequal with stamens or very slightly exceeding them, stigma 3 or 4 lobed, lobes very short, ovary unilocular with one basal ovule; fruit a globose or subglobose to broadly ellipsoidal drupe with a small calyx ring and subpersistent calyx lobes, flesh thin, base sometimes somewhat stipitate, stone strongly rugose, the rugosity evident externally when fruit is dry.

The flower color is variously described as white, greenish white, orange or red. This is probably because it is observed in flowers of different ages. Perhaps it may be described as inner face of lobes white or greenish-white when first opened, gradually becoming reddish and finally dark red. The hypanthium and outer surface of the lobes are pale greenish to reddish green.

The odor, likewise, is variously described as from a strong sweet fragrance to faint, or even foetid. We have only observed it as strongly fragrant.

Typification — A. de Candolle, l.c., included in *S. insulare* specimens collected in the Marquesas by "Navarch. du Petit-Th.!" and in "Taiti" by "Moerenhout! Bert.!", with no indication as to which of these was the principal basis for the species. There are indeed in the Prodromus Herbarium (G-DC) 3 sheets of *Santalum insulare*, one from Tahiti and two from the Marquesas, one collected by Dupetit-Thouars, and one by "Lapère envoyé par M. Lesson" n° 21 (specimen 2 in Skottsberg 1930a: 139). SKOTTSBERG (1930a: 135) states that the material used by A. DC. in drawing up his description included "Tahiti, Bertero 1830, Herb. Paris" [which we have not located in Paris] and "Bertero O Taiti rec. par M. Moerenhout 1835" (G-DC), both sterile. In addition, he says that a Paris sheet also bears "the name" in A. de Candolle's handwriting. There are actually two such sheets annotated *Santalum insulare* by A. DC., both collected by Dupetit-Thouars in the Marquesas and probably duplicates of the G-DC one. These, with the three G-DC specimens, constitute the authentic syntypes of *S. insulare*.

The "buds of a Marquesan specimen" mentioned by SKOTTSBERG (1930a) as probably used in his description by A. DC. doubtless came from the Dupetit-Thouars sheet in the Prodromus herbarium, which is said to have four very young flowers, fide Prof. G. Bocquet, who kindly had it examined for us. One of the Paris sheets of Dupetit-Thouars has a few buds in a pocket, but Lapère 21 (G-DC) is said to be sterile.

Skottsberg did not actually designate a lectotype from the material available to A. de Candolle, but essentially narrowed the choice down to the Tahiti plants when he said: "It is evident that Bertero's name applies primarily to a species found by him in Tahiti, so that, if the Marquesas species is different, the name "insulare" should be reserved for the Tahitian sandalwood". He then proceeded to describe the Marquesan element as a separate species, *S. marchionense*. Of the two Tahitian syntypes, that in G-DC, "Bertero rec. par M. Moerenhout 1835" is the logical candidate for lectotype, having been without question in de Candolle's hands, and is so designated here by us.

As a historical footnote, it may be noted that Bertero visited Tahiti at the urging and as a guest of J.-A. Moerenhout from Nov. 1830 to April 1831, when he left for Chile on a ship which was lost with all hands. His Tahiti plants remained with Moerenhout, who later shipped them or took them with him back to Europe. The two men may have collected together, but Bertero was probably alone most of the time.

In 1977, Betsy Gagné sent us for identification collections from southeastern Polynesia which included a dwarfish specimen of *Santalum* from the top of Mt. Aorai, Tahiti, accompanied by

an excellent color photo. It appeared to be different from most of the taxa we knew from the area and we undertook to name it. This led us to realize how poorly circumscribed *S. insulare* is, and to reexamine it and its relatives.

Key to varieties of *Santalum insulare*

1. Inflorescences mostly about 2 × 1.5 cm var. **alticola**
- 1a. Inflorescences notably larger 2
2. Inflorescences of 1 (or 3) simple pedunculate thyrses, their lowest branches not branched, ending in triads or glomerules of flowers 3
- 2a. Inflorescences trichotomous, their lowest branches again branched 4
3. Leaf blades elliptic, apices bluntly acute var. **margaretae**
- 3a. Leaf blades broadly elliptic to oval, apices mostly obtuse or rounded var. **raiavense**
4. Inflorescences usually 6-11 cm long, main axis usually over 4 internodes, branches appearing racemoid, secondary branches short, bearing triads or glomerules of flowers, fruit exceeding 20 mm diameter var. **deckeri**
- 4a. Inflorescences usually not over 6-7 cm long, main axis commonly of 3-4 internodes 5
5. Leaf veins usually 5-6 on a side, inner edges of tepal margins papillate-ciliolate, disk lobes slightly emarginate var. **mitiaro**
- 5a. Leaf veins usually 6 or more on a side, inner edges of tepal margins merely papillate, disk-lobes not emarginate 6
6. Leaves mostly less than twice as long as broad, fruit 20 or more mm long, subglobose var. **hendersonense**
- 6a. Leaves usually at least twice as long as broad, fruit less than 20 mm long, ellipsoid to globose 7
7. Leaves mostly ovate, apical portion triangular with straight sides, flowers in glomerules or umbellules var. **raiateense**
- 7a. Leaves elliptic to broadly ovate, sides of apical portion convex, flowers in triads 8
8. Panicle usually 3-5 cm long, tips of anthers included when tepals are spreading or reflexed, stigma 4-lobed var. **marchionense**
- 8a. Panicle usually over 5 cm long, anther tips sub-exserted when tepals are spreading or reflexed, stigmas 3-lobed var. **insulare**

All characters used in this key are variable and only when most of the examples correspond will the key work reliably. For many users' purpose it may serve to consider the whole species as a variable complex and disregard the varieties.

Santalum insulare Bertero ex A. DC. var. **insulare**

Small tree or shrub (the stature of sandalwood plants cannot be reliably stated as most of the specimens are from regrowth or stump sprouts), glabrous, branchlets slender; leaves opposite, elliptic to broadly ovate or broadly elliptic, apex bluntly acute to obtuse or rounded, base contracted, acute or cuneate to obtuse and slightly decurrent, venation not prominent, 6-8 veins on a side, arching upward distally, angle of divergence varying with width of leaf, petiole 1 cm or less (leaf width varies on different collections, narrowly elliptic, or broadly ovate and small, or broadly ovate and large, maximum length about 12 cm, maximum width 8 cm, mostly smaller) (4 sheets of Bertero or Moerenhout (syntype?) material all sterile, leaves 6-8 × 2.5-3(-4) cm, elliptic to slightly ovate); inflorescence terminal, thyrsoid, 5-10 cm long, 1 or 3 at terminal node, subtended by a pair of somewhat reduced leaves, main axis of 3 or usually 4 internodes, branching decussate, tending to be at right angles (divaricate), lowest branches with 2 or 3 internodes, next pair with

1 or 2 internodes, the same branching habit on branches, ultimate branches ending in triads of shortly pedicellate to subsessile buds or flowers, each branch of thyrses subtended by a caducous ovate to oblong scale-like bract, each flower likewise, flowers with 4 ovate calyx lobes and a broadly campanulate or turbinate hypanthium the whole about 3 mm long, lobes slightly cucullate, inner edges of margins minutely papillate; disk lobes bluntly obtuse; upper ends of stamens somewhat lobed, barely subexserted when calyx lobes are reflexed, stigma very slightly more exserted than stamens, slightly trilobed (see SKOTTSBERG, 1930a: figs. 16-23); SKOTTSBERG (1930a: 139, figs. 18 & 23) shows hairs behind stamens; fruit globose to subglobose, about 20 × 17 or 17 × 17 mm, the dried surface bumpy from rugosities of stone within, calyx ring about 5 mm wide, neither of the 2 fruits available are at all stipitate.

The specimens of var. *insulare* have almost no locality data and very little on habitat or characteristics of the plants, so not much can be said about occurrence or pattern of variation. The material can be roughly sorted into three groups on leaf characters. We attach no taxonomic significance to these but mention them for future workers. One series including the lectotype has leaves more narrowly elliptic than the others. Another has leaves larger and broadly elliptic or ovate, often somewhat falcate. The third has them smaller and tending to be rather broadly ovate to elliptic and flat rather than falcate. Confused with the series in this third group collected by Savatier were two sheets of *Amylotheca (Decaisnina) forsteriana*, labelled *Santalum*, which may have contributed to the apparent variation described by previous workers, since the leaves are somewhat similar. This Loranthaceae may have been parasitic on the *Santalum* and mistaken for a part of it by the collector.

The specimens of the three groups mentioned above are cited separately. All are from Tahiti, probably from elevations lower than 1000 m, thus altitudinally well separated from var. *alticola*, found on the top of Mt. Aorai (2066 m). All are in P unless otherwise noted. The labels are quoted in some detail, so as to permit (as did Skottsberg) easy recognition of individual sheets.

Specimens examined

Narrowly elliptic-leaved group: "Bertero O Taiti rec. par M. Moerenhout 1835" (G-DC, lectotype). [Tahiti] "Eai," s. coll. (sterile branch and piece of wood). Taiti, M. Moerenhout in 1834, "Eai" (incol.); Taiti, Moerenhout, dedit D. Guillemin in 1836; Taiti, Bertero & Moerenhout in 1831 (Herb. Richard); Taiti, M. l'Amiral Dupetit-Thouars.

Large-leaved group: Tahiti, Vieillard?; Taiti, Coll. Vieillard "in Collibus Insula Taiti..." MM. Vieillard & Pancker in 1855, Lenormand 1856 (Herb. Roussel); Taiti, M. Vesco in 1847; Tahiti, coteaux abruptes peu ombragés, leg. Pancker; Tahiti, Santal rouge des crêtes au delà de Heiaa [?], 860 m, Nadeaud, 27 sept. 1898 (leaves very broad, to 3 cm, not falcate). Leg. Lépine 194 "Santal "ai," montagnes 800-1000 m, fleurs verdâtres, arbre de 10-16 mètres". Tahiti, Jules Lépine 194 (US, P) "montagnes de Tairabu (800-1000 m), arbre de 10-16 m, fleurs verdâtres; "ai".

Smaller ovate to elliptic-leaved: crêtes de Pirae à 900 m, 11 Mars 1898, s. coll. [Nadeaud?]. Ile de Tahiti, Nadeaud 328 (species no., not coll. no.) (3 sheets, 1 with a fruit). Tahiti, Nadeaud. "Ahi des indigènes, leg. Nadeaud" (herb. Drake) (has a fruit). Nadeaud: Tahiti (Ahi) Environs du Pinai, près de Tipae-arui, Punauia-Haapape, octobre 1856. (Ahi) Nov. 1856, Pinai, Nadeaud: Tahiti. Taiti, le 29 sept. 1877, L. Savatier 919 "Ahi" (Expéd. Magicienne). Tahiti, 29 sept. 1877, leg. Savatier (herb. Drake). s.l. Savatier (Expéd. Magicienne, 3 sheets).

Santalum insulare var. *alticola* Fosberg & Sachet, var. nov.

Frutex, foliis parvis ellipticis obtusis coriaceis, inflorescentia reducta 2 × 1.5 cm, pauciflora, floribus sessilibus, fructus ruber late ovatus, 11 × 8-9 mm, putamine rugoso.

Shrub, stems nodose, blackish, bark of twigs finely checked, possibly somewhat fleshy when living, internodes mostly shorter than 1 cm, compressed, with 4 low blunt keels, alternate pairs stronger, decussate, branching appearing dichotomous; leaves elliptic 3-4(-5) × 1.5-2, obtuse to rounded at apex, cuneate contracted at base, texture firm to stiff coriaceous, veins 5-6(-7), finer network obscure, petiole about 5 mm long; inflorescence terminal, becoming axillary by development of a branchlet from terminal node, at anthesis about 2 cm long and 1.5 cm wide, compact, 3 branches very short, each with (1-)3(-5?) sessile flowers, these including contracted base about 6 mm long, lobes 2-2.5 mm, ovate, firm, rather fleshy, greenish outside, pink within, apex with an inward-directed hook, margins internally papillose; fruit red, substipitate, broadly ovoid, total

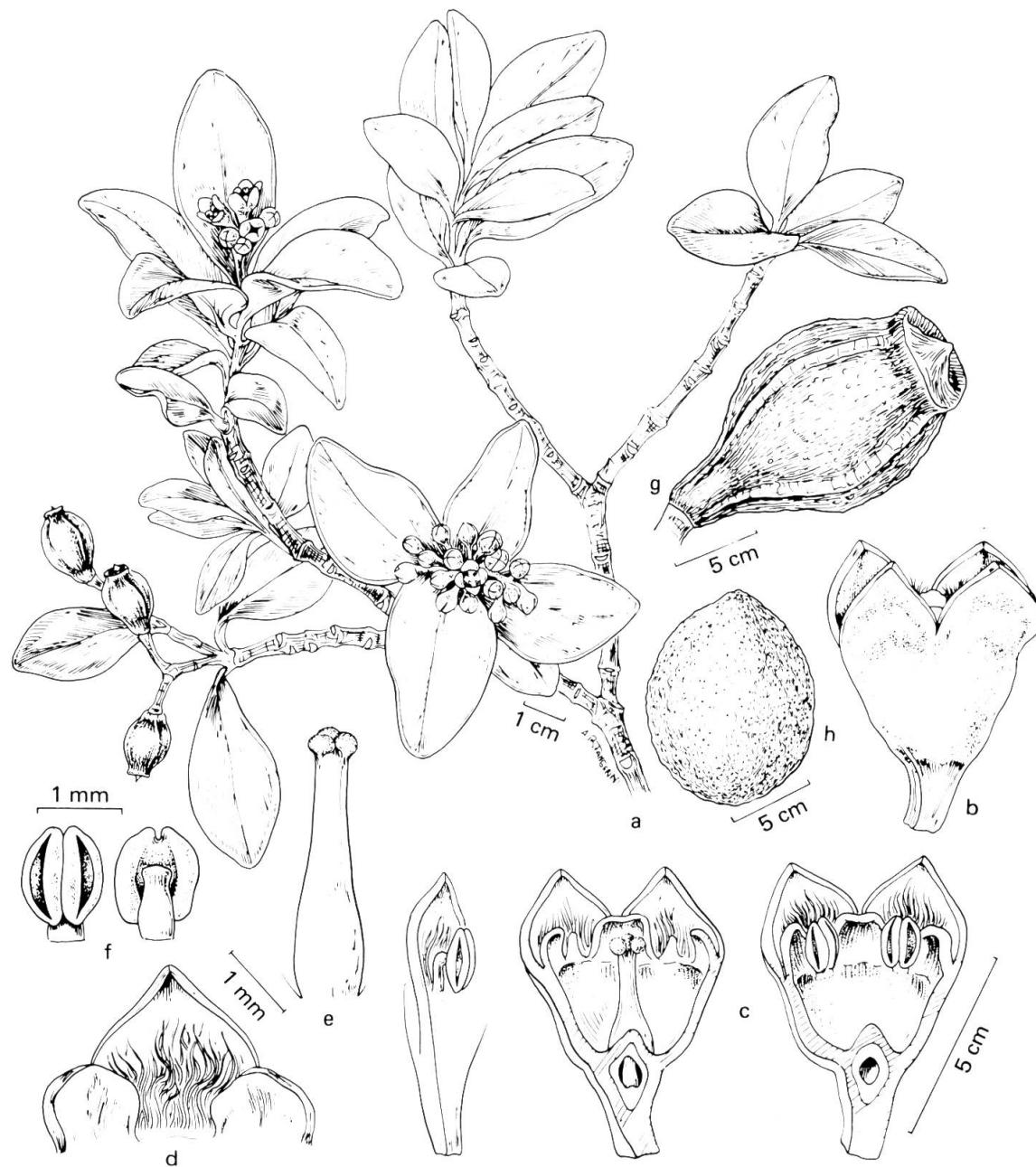


Fig. 1. — *Santalum insulare* var. *alticola* var. nov.

a, habit (from Gagné 1552); **b-h**, flowers and fruit (from Balgooy 1825): **b**, flower; **c**, longitudinal sections; **d**, inner face of perianth part with hairs and disc lobes; **e**, pistil; **f**, stamen; **g**, fruit; **h**, stony endocarps.

length up to about 15 mm, body 11 × 8-9 mm, flesh apparently thin, "stipe" 4 mm, conic, persistent base of calyx truncate, persistent style-base conic, endocarp rugose, rugosities showing through dried flesh.

Society Is.: Tahiti, Mt. Aorai: scattered along ridge top just below summit (2000 m) and up to summit (2066 m), *Gagné* 1552 (US, holotype, BISH, isotype); (2000 m) *van Balgooy* 1825 (L); (6420 ft) *Grant* 3785 (BISH), (6770 ft) *Grant* 3890 (BISH).

***Santalum insulare* var. *raiateense* (J. W. Moore) Fosberg & Sachet, comb. nov.**

- = *Santalum raiateense* J. W. Moore, Bish. Mus. Bull. 102: 27. 1933.
- = *Santalum multiflorum* J. W. Moore, l.c.

Leaves ovate, widest below middle to 7-8 × 3.5-4 cm, apex narrowly triangular, sides straight, point bluntly acute, blade subcoriaceous, venation obscure above, petiole 8-10 mm; inflorescence open, thyrsoid, peduncle 2 cm, secondary peduncles to longer than peduncle, ultimate ramifications subglomerate, outline of entire thyrsse from rounded to flattish (corymbiform); fruit subglobose 18 × 15 mm, on a 1.5-2 mm pseudo-pedicel or stipe.

Moore's two species from Raiatea were considered inseparable from the Tahiti plant by SKOTTSBERG (1934). We cannot see that they are separable from each other, but there seems enough difference between the Raiatea population from that of Tahiti to warrant maintaining the combined Raiatea taxa, with the two Moorea collections, as a single variety, on a par with the 8 other varieties that we admit for *S. insulare*. Hence the varietal combination is made here, selecting the epithet *raiateense* as the more appropriate one of the two.

Raiatea, E path of Mt. Temehani, 355 m, *J. W. Moore* 87 (BISH, 3 sheets, type of *S. multiflorum* Moore, MINN, isotype). Ridge S. end of island, 200 m, *J. W. Moore* 615 (BISH, 4 sheets, type of *S. raiateense* Moore, MINN, isotype). Moorea, plateau above village of Afarea'tu, *H. M. Smith* 171 (BISH, US); Paopao, Crête de Rotui, 485 m, *Florence* 4956 (US).

***Santalum insulare* var. *marchionense* (Skottsb.) Skottsb., Bishop Mus. Occ. Pap. 14(1): 33. 1938.**

- = *Santalum marchionense* Skottsb., Medd. Göteborgs Bot. Trädg. 5: 142. 1930; F. Brown, Bishop Mus. Bull. 130: 64-65. 1935.
- = *Santalum freycinetianum* sensu auct. plur., non Gaudichaud, Bot. Voy. Uranie 442. 1839.
- = *Santalum insulare* Bertero ex A. DC., Prodr. 14: 685-686. 1857, pro parte.

Small tree; leaves elliptic or somewhat ovate to broadly ovate or oblong-oval, veins 6-7 or more on a side, prominent beneath, apex acute or obtuse, base acute to a short petiole, 1 cm or less; panicle trichotomous and several times branched, not usually exceeding 3-5 cm, subglobose, or somewhat irregular, ultimate branches ending in triads of very shortly pedicellate or subsessile flowers, these 4-5 mm long; 4 calyx lobes triangular-ovate, with a small tuft of hairs at base within; stamens 1.2-1.3 mm long; disk lobes obovate-obtuse, exceeding stamens; stigma 4-lobed; fruit notably stipitate 16 × 9 mm length including stipe, or not as in *Henry* s.n., 15 × 15 mm (see SKOTTSBERG, 1930a: figs. 31-33).

Skottsberg based his species on eight specimens, two collected by du Petit Thouars, without locality (G-DC and P), one by Lapère (Lesson) from Nukuhiva (G-DC), two by F. B. H. Brown from Nukuhiva, and three by Brown from Tahuata. The Brown collections were sent on loan to Skottsberg from the Bishop Museum (1930a: 139) and we have examined sheets of all of them in the Museum. Whether Skottsberg left duplicates is not mentioned. From this syntype material no type was chosen. We here designate as lectotype the Bishop Museum sheet of *Brown* 985, from Tahuata, that was studied by Skottsberg, because it is the only one indicated by him as having a fruit. To distinguish this from the other Marquesan variety, *S. deckeri*, the size and shape of the fruit is the most reliable character. Unfortunately, of the material cited below, all but 2 collections lack fruit.

Specimens examined

Marquesas: s.l., *Dupetit-Thouars* (P 2 sheets, one with label in A. de Candolle's hand, the other, n° 47, with his name across the label, the latter annotated by Skottsberg) "puahi"; "hauts plateaux," *Henry* 44 in 1919 (P). **Nukuhiva Island:** s.l., "plante parasite, kouna", *Le Batard* 53



Fig. 2. — *Santalum insulare* var. *marchionense*

a, habit, with flowers (from Schäfer 5149); **b-g**, habit with very young fruit, and details (from Decker 1246): **c**, flower; **d**, longitudinal section; **e**, inner face of perianth part with hairs and disc lobes; **f**, stamen; **g**, stages in the development of the fruit, including fully developed one.

(P) (the name kouna actually applies to *Amylotheca forsteriana*, Loranthaceae); “puahi,” *E. Jardin* in 1855 (P); 800 m?, *Quayle 1313* (BISH); Tapuaooa?, 3000 ft., *PES 578* (LeB); Mauu, 800 m, *F. Brown 439* (BISH); Tovii, ± 800 m, *F. Brown 523* (BISH); Plateau de Tovii, *F. Hallé 2055* (US; P); Toovii, épaulement au-dessus du réservoir, 880 m, *Florence 4295* (US; P); Tovii Valley, near Tapuaooa shelter, ca. 800 m, *Gillett 2187* (US, UC, BISH); west side of Tunoa-Pahuhiuone Ridge, 3200 ft, *Hambuechen & Decker 309* (US). **Hivaoa Island:** Ridgecrest above Anatuakina, between Hanamenu and cave Anatuakina, 300-600 m, “puahi,” *Decker 1246* (US, BISH, P, POM) (has small fruit and a rather open inflorescence); montagnes NW du Temetiu, crête au sud du campement, N de la haute vallée de Hanamenu, 850 m, *Schäfer 5899* (US, MPU); Tepehi, above Hanamenu, dry region, 465 m, June 1929, perfume extracted from wood grated & mixed with coconut oil, “puahi,” *PES (M & A) 421* (BISH, LeB); Mokovau, dissected plateau, 700-800 m, now rare, few old trees left in isolated region, formerly wood used for bowls, tikis, sticks, etc., still used as perfume, “puahi,” *PES (M & A) 59* (BISH, UC, LeB) (crushed immature fruit 10 mm long on BISH sheet). **Tahuata Island:** Vaitahu, 500 m, *F. Brown 985* (BISH, lectotype) (small fruit); 984 (BISH); 400 m, 931 (BISH).

***Santalum insulare* var. *deckeri* Fosberg & Sachet, var. nov.**

Frutex, usque ad 3 m, glaber, foliis late-ellipticis vel ovatis satis falcatis plicatisque, 8 × 10-11 cm, subcoriaceis; paniculus amplus, usque ad 11 × 11 cm, binternatis terminans ad glomerulos paucifloros; fructus globosus 22-24 × 21-23 cm putamine valde rugoso.

Shrub to 3 m tall, glabrous, youngest internodes decussately slightly compressed, with two strong keels or ridges and two weaker ones, decussately alternating; leaves elliptic to oval or somewhat ovate, tending to be falcate and somewhat folded, to 8 × 10-11 cm, subcoriaceous to firm-chartaceous, 6-9 principal veins on a side, irregularly alternately or oppositely arranged, not equidistant, lower ones closer, anastomosing distally into a network, petiole 6-12 mm long; panicle pedunculate, node at summit of peduncle bearing (1-)3-5 (or more) branches. These tending to elongate thyrsoidally, rarely with 2 strong branches at first node, but tending to have a series of pairs of short branches each bearing an umbellule of 3 or more very shortly pedicellate or subsessile flowers, giving a racemoid appearance. The whole inflorescence usually rather open, up to 10-11 cm high and wide; flowers very fragrant, greenish white to cream, turning maroon within, almost sessile, pedicels 1 mm or less; flowers about 4 mm long, hypanthium narrowly turbinate, about 2 mm long, lobes ovate, bluish, about 2 mm long, sub-fleshy, tips slightly cucullate, margins minutely papillate on inner edges, inner face of lobe minutely granulate-papillate, with a small group of long curly hairs at base above insertion of stamen filament; disk appendage broadly ovate, obtuse, apparently fleshy; anthers about 0.8 mm long and wide, suborbicular in outline dorsally; style about 2 mm long including dilated base (or projection of ovary above disk about 0.5 mm); fruit globose or very slightly longer than wide, 22-24 × 21-23 mm, endocarp notably rugose, the rugosity showing through the dried thin flesh, stipe not or scarcely developed.

Type from the Marquesas, Hivaoa I., *Sachet 2113*. Named for our colleague and friend, Dr. Bryce G. Decker, whose large Marquesan plant collections include several specimens of *Santalum*. Non-fruiting material cannot be placed here with certainty, although more ample panicles with a somewhat racemoid appearance point to var. *deckeri*.

Specimens examined

Marquesa, Nukuhiva Island: s.l., *Mercier no 1*, in 1847 (P); headwaters of Taipi River, on trail from Toovii to Taiohae, 10 km from Takuaoa shelter, 700 m, *Gillett 2216* (US, BISH, UC) (fruit); route Toovii-Terre Déserte, km 4 après le col, 940 m, *Florence 4352* (US) (fruit); Tovii, 800 m, *Brown 523* (BISH); *Thibault 137* (US); Toovii, épaulements du Mt. Oomu, 835 m, *Florence 4215* (US); Taupua’o’oa, 800 m, *Decker 2010* (US, BISH, P, POM, A); Ana’onihi, 800 m, *Decker 2016* (US, BISH, P, UC, CHR, NY, L, G). **Hivaoa Island:** dry crest above Taaoa, 250 m, *Sachet 2113* (US, holotype, L, BISH, POM isotypes) (fruit); hill above Taaoa, 260 m, *Oliver & Schäfer 3258* (US, BISH, L, NY); crest above Taaoa, 250 m, *Sachet 1942* (US, BISH, P, POM, A); ridge above Taaoa, SW of village, 250 m, *Sachet & Decker 1876* (US, BISH, P, POM, MO, K, CHR). These are essentially from the type locality, and are reasonably sure to be this variety. “Lieu sec, au pied de la montagne à Hanamenu, niveau de la mer, août 1922” *Henry* (P) (small fruit). **Tahuata**



Fig. 3. — *Santalum insulare* var. *deckeri* var. nov. (from Sachet 2113, type).

a-b, habit; **c**, flower; **d**, longitudinal sections; **e**, inner face of perianth part showing hairs and disc lobes; **f**, stamen; **g**, fruit; **h**, stony endocarp.

Island: *F. Hallé* 2156(US, P). This has greenish flowers and the large open inflorescence, but since it is from Tahuata, may be an extreme variant of var. *marchionense*. **Fatuhiva Island:** upper Hanauta Valley, 400 m, *Decker* 2610 (US, BISH, P).

Santalum insulare var. **mitiaro** Sykes, Pac. Sci. 34: 79. 1980.

Small tree to 4 m, glabrous; leaves ovate to less commonly ovate-elliptic to elliptic, 3-4(-4.5) \times 1.3-2(-2.25) cm, coriaceous, apex obtuse, often mucronulate, 5-7 veins on a side, petiole 2-5 mm (no information on branching habit), up to 50 flowers in triads terminating the inflorescence branches, flowers 5.5-6.2 mm including 1 mm of pedicel, calyx lobes ovate, slightly cucullate, 2-2.7 mm long; ciliolate-papillate, disk lobes 0.5-0.7 mm long, almost quadrangular, apex incurved, slightly emarginate, anthers almost completely exserted, stigma somewhat more exserted, 3(-4) lobed; ovary with free portion more prominent than in other varieties, about half of it free, fruit not available.

Endemic on Mitiaro Island, Cook Group. We have not seen material of this variety, but have extracted the above description from the paper by W. R. Sykes, who cites a half-dozen collections in (CHR). This variety differs mainly by an accumulation of minor details. We have too little information on the form and branching of the panicle and none on the size and shape of the fruit. It is curious that it is found only on this almost smallest and lowest of the southern Cook Group.

Cook Is., Mitiaro I.: Sykes 1045/CI (CHR, holotype).

Santalum insulare var. **margaretae** (F. Brown) Skottsb., Occ. Pap. Bishop Mus. 14(4): 34-36. 1938.

= *Santalum margaretae* F. Brown, Bishop Mus. Bull. 130: 62-64, fig. 12a-k, 1935.

Tree to 7.5 m, glabrous; leaves firm chartaceous or "soft coriaceous", elliptic, 4-8 \times 1.5-3.5 cm, apex very bluntly acute, base acute, veins 5-9, usually about 7, on a side, not prominent, anastomosing irregularly toward margin, petiole short, 5-9 mm; panicle simple, 3-6 cm long, main axis of 4(?) internodes, branches short, bearing triads of sessile flowers, these 5 or even 6 mm long, (Brown says also "floriferous shoots commonly developing from the 2 nodes below the terminal panicle" but we have not observed this and Skottsberg does not mention it either), hypanthium turbinate, calyx lobes ovate, 2.5-3 \times 1.8-2 mm, obtuse; disk lobes rotundate-quadrangular, described by collectors of 15692 as "fimbriate scales"; style 1.2 mm long, stigmas of 15692 mostly 3, described by Brown as 4; fruit 12 \times 10 mm, with a calyx ring about 5 mm across, center of disk slightly raised.

Endemic to Rapa, Austral Group, known from three collections.

Austral Is., Rapa: Tanga, 240 m, Stokes 392 (BISH, holotype); péninsule du Sud entre baie Anatekuri Nako et baie Akao, J. Florence 7698 (P, 2 sheets); saddle west of Mt. Tanga, 250 m, St. John & D. Anderson 15692 (P, US).

Santalum insulare var. **raivavense** F. Brown, Bishop Mus. Bull. 130: 62. 1935; Skottsberg, Occ. Pap. Bishop Mus. 14(4): 33-34. 1938.

Small tree to at least 5 m tall; leaves firm chartaceous to subcoriaceous, broadly elliptic to oval, 5-10 \times 3-6 cm, apex bluntly acutish to obtuse, base obtuse to acutish, abruptly decurrent to the slender, 6-17 mm petiole, veins 5-13, unevenly disposed, anastomosing, beneath; panicle small, 4-6 cm long, main axis 3-4 internodes including peduncle, branches terminating in triads or umbellules of very few subsessile or very short-pedicelled flowers, these 5 mm long (incl. pedicels), lobes triangular-ovate, 3-3.5 mm long; stigma usually 3 lobed; described by Brown as 4; disk lobes about 1 \times 1 mm, orbicular-quadrangular, entire; fruit unavailable. Description largely adapted from those of BROWN (1930) and SKOTTSBERG (1938), both of whom cite specimens which we have seen earlier but not studied critically, only Fosberg 11687(US) and 11683(P) being immediately available to us and contributing details to our description.

The variety is endemic to Raivavae, in the Austral Group. It has the simplest inflorescence of the taxa treated here.

Austral Is., Raivavae: Taniora, 900 m, Stokes 100 (BISH, holotype). Vaianaua Peninsula, W. side, 60 m, Fosberg 11683 (P), 11687 (US).

Santalum insulare var. **hendersonense** (F. Brown) Fosberg & Sachet, **comb. nov.**

= *Santalum hendersonense* F. Brown, Bishop Mus. Bull. 130: 66. 1935; St. John and Philipson, Tr. R. Soc. N. Z. Bot. 1: 180. 1962; Fosberg & al., Atoll Research Bulletin 272: 30. 1983.

Trees to 8 m tall, leaves broadly ovate to elliptic, oval or suborbicular, 5-9 × 3.2-5.7 cm, apex acutish or even acuminate to obtuse or rounded, base obtuse, rarely acutish, to rounded, subtruncate, veins not prominent, 6-9 on a side, subcordate, slightly more prominent below, petiole 4-8 mm; panicles usually 3 at terminal node, 4-6(-8) cm long, subtended by two almost full-sized leaves, main axes 4 internodes long, branches ascending ending in irregular few-flowered glomerules or triads of pedicellate flowers, bractlets subtending branches and flowers lanceolate (to setose fide Brown), smaller thyrses in upper axils of some plants, these with peduncles long in proportion to branching part; flowers about 5 mm long on pedicels of 1.5-2 mm, hypanthium obconic 2-2.5 mm high, calyx lobes ovate 2.5-3 × 2 mm, apices obtuse to rounded, slightly cucullate, pilose within at base, hairs 2 mm long, disk lobes rounded-quadrangular (or ovate-triangular, subacute), stamens 1.5 mm long, style subequal with them or slightly shorter, stigma lobes 3(-4), drupe subglobose, 23 × 17 mm.

Considering the variability of *Santalum insulare* including its varieties, and the now established size of the fruit of var. *insulare* (20 × 17 mm), the status of this taxon seems too dubious to retain as a species. All of its characters seem to fall within the ranges in *S. insulare* sensu lato.

Henderson I.: *Quayle X* in 1922 (BISH, holotype, though Brown failed to cite any specimen). SKOTTSBERG (1938: 37) notes this fact but says the type must be a specimen collected by Mrs. Stokes, who never visited Henderson Island. M. L. Grant, in his card catalogue of Polynesian plants cites *Quayle X* as the specimen representing *S. hendersonense* but does not designate it formally as type. ST. JOHN & PHILIPSON (1962) designated *Quayle X* as lectotype, but since it is known to be the only specimen studied by Brown, we regard it as the holotype.

Other specimens seen: *St. John & Fosberg 15110* (BISH, US, P), *15114* (BISH), *15078* (BISH), and *15079* (BISH). Only the first of these did we examine critically after the present study was well advanced. We have depended on SKOTTSBERG's (1938) treatment for some details.

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