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Monograph of the Genus Nesoluma (Sapotaceae)*

A Primitive Polynesian Endemic of Supposed Antarctic Origin

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RIJKSHERBARIUM, LEYDEN, NETHERLANDS

CONTENTS

MATERIAL

In 1935, the Director of Bernice P. Bishop Museum kindly put at our disposal the sapotaceous plants collected by the Mangarevan Expedition. Among them[1] we found several representatives of a peculiar genus which were studied in detail by Mr. Meeuse. At first we could not identify the genus and we considered it a new one until I paid a short visit to the Paris Herbarium (Muséum National d'Histoire Naturelle, Phanérogamie). During my investigations there I was fortunate enough to come upon some specimens of *Chrysophyllum polynesicum* Hillebr. (*Nesoluma polynesicum* H. Baill.) which I recognized as belonging to the same genus. The Director

* Mangarevan Expedition Publication 25.

[1] With some other interesting or critical Sapotaceae from the Pacific islands, Mr. Meeuse and I intend to deal shortly in a separate paper.

of the Paris Herbarium, Professor H. Humbert, kindly put those specimens at my disposal for closer examination. Likewise I received for study the collections from the herbarium of the Royal Botanical Gardens at Kew, Hillebrand's original material preserved in the herbarium of the Botanischer Garten und Museum at Berlin, and all *Nesoluma* material available in the herbarium of Bernice P. Bishop Museum. In addition to this, material from the Gray Herbarium at Cambridge (Mass.), from the herbarium of the New York Botanical Garden, from the U. S. National Herbarium at Washington, D. C., from Dr. Vladimir Krajina at Prague, and from Mr. Otto Degener at Waialua, Oahu, was kindly sent on loan for study. I wish to extend my thanks to the directors of the institutions mentioned and to Dr. Krajina and Mr. Degener for their valuable assistance.

The Paris material (P) contains two species of the genus *Nesoluma* H. Baill., *N. polynesicum,* the type species, and *N. Nadeaudi.* The Berlin collection (B) contains only some fine sheets of *N. polynesicum* among which is the type specimen, a small fragment of which is also preserved at Paris. The Kew Herbarium (K) was found to possess a fragment of *N. polynesicum* attached to a sheet of *"Sapota sandwicensis"* from the Hillebrand collection. The New York Botanical Garden (NY) possesses eight sheets of *N. polynesicum,* including specimens collected by A. F. Judd, J. F. Rock, C. N. Forbes, and O. Degener. The Gray Herbarium (G) has material of *N. polynesicum* from the collections of J. F. Rock (eight sheets) and also one sheet from the Hillebrand collection, apparently from the same specimen that has been quoted as the "second specimen in the Berlin Herbarium". The U. S. National Herbarium (US) possesses five duplicate specimens of *N. polynesicum* and, in addition, a sixth specimen, attached to the same sheet as a duplicate from Hillebrand's collection but belonging to another variety. Dr. Krajina's material (Kr) contains one specimen of *N. polynesicum.* Mr. Degener's herbarium contains five fine specimens of *N. polynesicum.* The Bishop Museum material (H), both from the Mangarevan Expedition and from older collectors, is by far the richest and enabled me to gain an insight into the complicated systematic structure of this remarkable genus. It appeared to contain a third species, *N. St.-Johnianum,* provisionally considered as new. Its type is preserved at Honolulu, while fragments of this type and of several other specimens were given to the Rijksherbarium at Leyden (L).

NESOLUMA

Description

Nesoluma H. Baill., Soc. Linn. Paris, Bull. **2** (121) : 964, 1891, nomen tantum; Hist. d. Pl., **11** : 279, 1892, descr. latina.—Brown, B. P. Bishop Mus., Bull. **130** : 223, 1935.

Chrysophyllum L., sect. *Pleio-Chrysophyllum* Engler, in Engler's Bot. Jahrb. **12** : 520, 1890; Engler und Prantl, Nat. Pflanzenfam., Teil IV, abt. 1 : 149, 1897; Nachträge I : 278, 1897.

Descriptio aucta et emendata:

Arbores parvae laticiferae. Folia alterna exstipulata coriacea petiolata rigida, basi acuta rarius subrotundata, marginibus integra, apice rotundata vel obtusa, nervis tenuibus, reticulatione perminuta saepe areolata. Inflorescentiae in foliorum vel eorum cicatricium axillis fasciculatae. Flores pedicellati, heteromeri, hermaphroditi vel abortione unisexuales (♀). Sepala plerumque 4 inaequalia, nonnunquam 5, rarissime 3 vel 6, aestivatione aperta vel imbricata. Corollae hypogynae vix exsertae variabilis tubus brevissimus, petala valde imbricata (4-)8-10(-12), saepe nonnulla minora petaloidea vel staminodioidea, in floribus femineis androeceo nullo valde reducta. Stamina uniserialia antheris extrorsis (6-)8-10(-12), filamenta saepe extrorso-reflexa corollae ima basi inserta, interdum nonnulla minora vel sterilia, petaloidea vel staminodioidea. Staminodia alternipetalia, si adsunt, petalis et staminibus reductis similia. Pistillum disco distincto privatum basi saepe glabrum, ovario (2-)3-5(-6)-loculato et -ovulato pilosum, stylo subulato vel conico glabrum. Ovula adscendentia, apotropa, ½-totaliter anatropa, loculorum axis basi affixa. Fructus baccati monospermi. Semina testa ossea, cicatrice basilaterali vel fere basali magna suborbiculata, micropyle hylo haud valde approximata. Albumen copiosum cotyledones plano tangentiali et obliquo positas includens. Radicula infera haud exserta.

Small or moderate-sized trees with latex; branches slender, the ultimate innovations rusty or reddish pubescent, adult parts usually glabrous or nearly so or the leaves remaining somewhat pubescent below; stipules none or at least very caducous and inconspicuous. Leaves petiolate, rigid, coriaceous, more or less shining above, more dull underneath, often light greenish or yellowish, or brownish when dry, elliptic or ovate to oblong, rarely oblanceolate, base acute, rarely subrotundate, margins entire, apex obtuse, rounded or more rarely somewhat emarginate; midrib prominent below, secondary nerves

very slender, not prominent, straight, near the margin more or less irregularly high-arched and joined, often with one or two still more slender ones between; reticulation very minute underneath, areoles usually circular, less conspicuous only in some specimens of *N. polynesicum*. Inflorescences fasciculate in the axils of the leaves or their scars, 1- to many-flowered, sometimes on tuberculate dwarf shoots, the bracts very small, semi-ovate or sublanceolate, tomentose or subglabrous. Flowers pedicellate, glabrous except rarely the pedicels, the outer sepals (or the tips of all sepals) and the anthers, more or less heteromerous, hermaphroditic, or unisexual (♀) by abortion. Sepals usually 4, the outer ones smaller, thicker, and deltoid, the inner ones larger, thinner, imbricate, and ovate to ovate-deltoid, the sepals of each pair often not strictly opposite and usually unequal in size; or 5 sepals extant, very rarely 6 or 3 sepals extant, transition forms between sepals and petals extremely rare. Corolla hypogynous, in hermaphroditic flowers with a very short tube and (4-)8-10(-12) imbricate, ovate or obovate petals, sometimes some of these smaller, outside or inside the others and more or less epipetalous, if inside then often differently shaped, namely either with narrowed tip or ± tridentate; in female flowers the corolla usually reduced either to 1-8 free or slightly connate, subulate petaloid small petals (or even abortive?), or to a whorl of irregularly dentate staminodioid petals. Stamens wanting in female flowers, in hermaphroditic ones inserted in the very base of the corolla tube, uniseriate, extrorse, (6-)8-10(-12), not strictly epipetalous, often two or more before a petal and some of them smaller or more or less sterile, in the latter case either staminoid or petaloid (same shape as the acuminate petals but occupying the place of a stamen); filaments subulate and mostly outwardly reflexed at apex; anthers extrorse, dorsifix, oblong, the sacs sometimes with small apical protrusions, more or less laterally dehiscent, alternipetalous staminodes as found in *Sideroxylon*, etc., if any, not distinguishable from sterile petaloid stamens or from reduced petals or stamens except by their position. Pistil oblong, the base often but not always glabrous (gynophore), without a disc, or with a slight indication of an adnate disc, ovary hispidly adpressedly pilose, (2-)3-5(-6)-celled, apex gradually tapering into the short and stout, glabrous truncate style, which is not or hardly exserted from the flower; cells uni-ovulate[2], ovules attached at the base of the central

[2] An apparently anomalous specimen with bi-ovulate cells is mentioned under *N. polynesicum* (p. 146).

axis, half to more or less fully anatropous and apotropous. Fruits small, baccate, pointed at apex, the more or less spreading calyx not or scarcely enlarged, pericarp thin, surrounding the solitary seed[3], which is narrower or at least flattened in the basal part, and has a thick and hard, shining, crustaceous testa, with a large, broad, basal to basilateral scar including a small basilateral hilum and veined inside; upper limit of scar sinuous or round, the scar, if basilateral, abruptly receding below this line; embryo with the foliaceous cotyledons almost completely surrounded by an abundant albumen, plane tangential and oblique toward the flower axis; radicle inferior, cylindrical, not exserted.

The embryo was examined in all of the species. The plane of the cotyledons proved to be oblique to tangential (not radial), as in *Lucuma occidentalis* H. J. Lam (13, p. 229, fig. 62, *i*[4]) and in *Palaquium pseudorostratum* H. J. Lam (14, pp. 393-394, fig. 3, *l, m*); in addition, its main axis is not vertical but makes an angle of about 45 degrees toward the flower axis (cf. *Calvaria,* where it is horizontal).

Discussion

This remarkable genus, the restoration of which is responsible for a new realignment of the whole order, is a fine example of the complexity of the floral features in the Sapotaceae. This complexity has already been pointed out in a most eloquent way by Dubard in the first issue of his series of elaborate papers (4, p. 292). Recently Eyma (9, pp. 156-159, 192-193) has given more examples of complications in the Sapotaceae: in the genus *Achrouteria,* for example, with fruits like those of *Achras* and flowers like those of *Pouteria.* It seemed, therefore, at first sight, no easy task to give the genus *Nesoluma* its proper place in the system of the order as previously published (13, pp. 10-12; 14, pp. 382-385; 15, pp. 549-551).

As is illustrated by the generic synonyms *Palaquium* (*P. Nadeaudi*) and *Chrysophyllum* (*C. polynesicum*), the choice was mainly between the groups with whorled sepals (Palaquieae, Madhuceae) on the one hand, and those with spirally arranged sepals (Chrysophyllinae, Sideroxylinae) on the other.

Moreover, the genus shows a considerable variability in almost every character, which further complicates the classification. How-

[3] A single example of a 2-seeded fruit is mentioned by Hillebrand (12).

[4] Numbers in parentheses refer to Literature Cited, p. 157.

ever, anyone acquainted with the natural order of the Sapotaceae will not be led astray by the calyx being frequently *Madhuca*-like and the number of petals being often more or less twice that of the sepals. He will intuitively know, as did L. Pierre, whose numerous annotations on the Paris sheets it was my fortune to use and to admire, that *Nesoluma* is undoubtedly a member of one of the groups with spirally arranged sepals.

In attempting to place *Nesoluma* in the system of the Sapotaceae, I will now discuss its more prominent features. In comparing *Nesoluma* with other genera and species, I used not only the material extant in the National Herbarium, Leyden, and the literature mentioned at the end of this paper, but also the splendid and valuable set of drawings of Sapotaceae made for L. Pierre by E. Delpy in 1891-1904, and preserved in the Paris Herbarium. Most, or possibly all, of these are unpublished and I am very much indebted to Professor Humbert, Director of the Paris Herbarium, for permission to study these drawings which were most valuable to me in gaining an insight into the systematic relations of *Nesoluma*.

VEGETATIVE PARTS

(Figs. 1-8, 10, 80, 81, 103)

Usually the vegetative parts do not provide generically important features. In the Sapotaceae, however, the nervation of the leaves may be an important generic character (Madhuceae) and the same may be true, although to a lesser degree, for *Nesoluma*. Its reticulation is very characteristic, being mostly extremely minute and areolate (figs. 81, 103) and though in some specimens of *N. polynesicum* (fig. 10) the areoles are more longitudinally stretched (both types may be seen in the same specimen and even in the same leaf), it may be called characteristic for the whole genus. The same type of reticulation is found in several species of *Sideroxylon* (*Calvaria*) and *Lucuma* (*Pouteria*). Particularly the resemblance both in shape and in reticulation with the leaves of *Calvaria inermis* (*Sideroxylon inerme*) (south and southeast Africa) is striking (5; 8, Taf. 7).

INFLORESCENCES

These show no special features that are not inherent to the natural order as a whole.

CALYX

There are usually 4 sepals, but 5 sepals are not rare. When there are 5 sepals the arrangement is spiral and of the ordinary Sideroxylinae type. As the 4-merous calyx is almost always more or less irregular (figs. 11, 14, 42-45, 59, 82)—the outer sepals are usually smaller than the inner ones, unequal in size, and not strictly opposite (cf. *Leptostylis*)—I consider the 5-merous calyx as the basic or at least the original type, of which those with 4, 6, or 3

sepals (given in the order of frequency observed) are variations or derivations. Out of 30 flowers of all species, only one calyx was 3-merous, 20 were 4-merous, 7 were 5-merous, and 2 were 6-merous. In this variability, as in that of other whorls, both a serial and a collateral contraction or duplication seem to play a certain part; in some specimens two sepals are inserted opposite each other (figs. 15, 44, 87), in others two smaller and much imbricate ones seem to take the place of one large sepal (figs. 12, 13, 70). This phenomenon is still more obvious in the corolla. Only one specimen examined had part of an inner sepal petaloid (*N. polynesicum*, St. John 10124, ♀ flower).

COROLLA AND ANDROECEUM

More than in any other genus of the Sapotaceae with which I am familiar, there is a strong correlation between the corolla and the androeceum. With the abortion of the male organs in unisexual (female) flowers [cf. *Planchonella obovata* (13, p. 213, fig. 58), *firma*, and *petaloides* (13, p. 196, fig. 53), certain *Sideroxylon* and *Pouteria* species, *Ecclinusa*, *Omphalocarpum* (8, Taf. 1, 4, 5), etc.], which seems to be a feature of certain individual trees, there is generally also reduction of the corolla to leave only a number of small scales at the foot of the ovary. In addition, the flower may often contain peculiar structures that have been called "staminodes", with obvious and justified doubt (by L. Pierre in his unpublished notes). These organs (figs. 22, 23, 33, 36, 39, 40, 47, 48, 52-57, 104, 107) may be inserted either between and inside two petals (figs. 19, 39, 70) where they may be compared with true staminodes, such as are known in *Sideroxylon*, *Planchonella*, *Pouteria*, etc., or they may be inserted opposite a petal, evidently taking the place of a stamen, where they show transitions toward what undoubtedly are sterile stamens (figs. 47, 54-56, 90, 91, 107). On the other hand, they may represent a petal, as appears from their shape as well as from their position and their bearing a stamen (figs. 35, 36, 40, 52, 53). The same phenomena of contraction and, here especially, of duplication[5], mentioned for the calyx, are strikingly apparent in the corolla and the androeceum; and *Nesoluma* shows all transitional organs in the series shown in figure 33. In this connection it is important to note that the petaloid "staminodes" and the scaly petals (fig. 33, *d*, *f*) are often more or less conspicuously 3-dentate (staminodes: figs. 23, 47, 52-57, 104; petals: figs. 63, 65, 66, 73, 74, 102), as are the staminodes of such species as *Planchonella obovata* (13, p. 213, fig. 58), *Krausella Schlechteri* (15, tab. 128), many species of *Omphalocarpum* (8, Taf. 2-6), etc. I mention this point because the so-called "staminodes" of the Sideroxylinae have heretofore usually been interpreted as representing a whorl of sterile stamens, apparently on account of the continuous alternation of the consecutive whorls in the flower. Now that we know *Nesoluma* better, however, they may as well be considered as a whorl of reduced petals.

This problem is worth studying more thoroughly, as there is still another question connected with it. Eichler (6, p. 333) and, probably on his authority, also Hartog (13, p. 8) consider the smaller "staminodes" of *Bumelia*, *Dipholis*, etc. (with a whorl of larger alternipetalous staminodes, and two smaller structures next to each petal), and also of the Mimusopeae, as "Nebenblättchen an den Kronenlappen." This interpretation seems to be supported indeed by the more or less lateral position of the staminodes (ventral in *Bumelia* and *Dipholis*, dorsal in *Mimusops* and *Manilkara*). However, these corollary "stipules" may

[5] Duplication may be merely an atavistic form and thus a primitive phase of the tendency of contraction in the flower.

in *Dipholis* (7, p. 145, fig. 78 B) be tridentate as well and this makes, in my opinion, their stipular nature doubtful. The lateral teeth could as well be considered as the remnants of the pollen sacs [cf. the sterile stamens of *Planchonella petaloides* (13, p. 196, fig. 53 e); also the illustrations of *Calvaria* (8, Taf. 7; 11)]. On account of the staminodes in *Nesoluma*, in other genera mentioned above, in *Achradotypus* with 2, in *Omphalocarpum* with 4, and in *Pycnandra* with 5 or more staminal structures opposite each petal, and in *Cryptogyne* (7, p. 150, fig. 81 B), where the stamens are borne on a petaloid scale (cf. figs. 40, 53), I would suggest provisional interpretation of all structures in the corolla-androeceum region as potential petals as well as potential stamens on the basis of a general tendency of contraction or of duplication. This problem is fundamental for the interpretation of the obdiplostemony (cf. 16, pp. 97-115).

The tendency to pleiomery and duplication in certain whorls (and especially in the corolla and the androeceum) is particularly striking in *Madhuca* (or the Madhuceae in general; cf. 17, p. 102), as already remarked by Eichler (6, p. 334, for *Bassia*=*Madhuca*). In the Sideroxylinae, pleiomery is occasionally noticed in *Planchonella* (*P. kaniensis*, 15, tab. 124, 6-merous flowers) and generally in *Krausella*, with 6-8-merous flowers with gynophores (15, tab. 127-128).

In *Nesoluma* both collateral and serial duplication or contraction are frequent, as has been stated above; I am inclined to accept also for the corolla and for the androeceum the number 5 as the basic one; it can be found in many of the flowers, if the duplication is taken into account (figs. 35, 86). Such a duplication is stated:

Collateral: *a*, in that frequently two small and much imbricate petals or sepals take the place of a single large one (sepals: figs. 12, 13, 70; petals: figs. 18, 19, 70, 86); *b*, in the frequent connations among petals (figs. 35-38, 41), as well as between petals and "staminodes" (figs. 23, 48, 70) and among filaments of stamens (figs. 34, 87, 89).

Serial: in the occurrence of two or three staminal structures, petals or sepals opposite each other (figs. 34, 35, 38, 40, 44, 53, 70).

Considered from this point of view I am inclined to interpret the conditions of *Cryptogyne* as such a fixed serial duplication.

In addition there may exist a certain sectorial correlation between corolla and androeceum (figs. 35-37) with regard to these phenomena (cf. 16, pp. 41-53).

It is a well known fact that pleiomery or meiomery may independently affect certain whorls in a flower. Meiomery is stated in the perianth in *Pouteria*, in the corolla in *Leptostylis* and in the gynaeceum in *Madhuca* and *Burckella*; pleiomery (collateral duplication) in the calyx in *Isonandra* (14, p. 419, fig. 7 f, and p. 420, fig. 8 h, k, m), in the androeceum in *Leptostylis* and *Pycnandra*, in the corolla, androeceum, and the gynaeceum in *Pycnandra*, and in many numbers of the Madhuceae (17, p. 102). Generally, however, pleiomery seems to be more frequent in the corolla and the androeceum, meiomery in the gynaeceum, the reduction of the number of carpels being stated in numerous natural orders. This is also true for *Nesoluma*.

GYNAECEUM

As usual the androeceum and the gynaeceum are strictly separate. However, I found one specimen of *N. polynesicum* which had the connective of a stamen adnate to the pistillum (figs. 24, 25); Pierre mentions the same for the type specimen.

The number of cells is rather variable; of the ovaries of 16 flowers of *N. polynesicum* one was 2-celled, six were 3-celled, five were 4-celled, three were 5-celled, and one was 6-celled. In a few specimens one or more than one cell was sterile, but usually all cells were 1-ovulated. In one specimen of *N. polynesicum* (McEldowney and Skottsberg 369) I found two ovula in a cell, in two cases (figs. 75, 76). One of them was apparently a connation of two complete ovaries, as shown by the flattened style and the 9-celled and quite symmetrical cross section (figs. 77, 78).

Generally the basal part of the ovary is glabrous, suggesting the nature of a gynophore [cf. *Krausella*, 15, tab. 127-128; and *Sideroxylon* (*Calvaria*) *diospyroides*, 8, Taf. 7], and the cells are then situated in the upper hairy part of the ovary (figs. 24, 26, 58, 61, 62, 65, 68, 92, 97). Though no actual disc has been found, a longitudinal section (figs. 71, 97) in some few cases shows the disc adnate to the ovary, as in some *Planchonella* and *Lucuma* species (cf. 15, tab. 129).

The degree of anatropy of the ovula seems to be also fairly variable. In some specimens I found the ovula almost fully or fully anatropous, in others the micropylar part was protruding below the insertion of the funiculus. Accordingly, the position of the seed in the fruit may vary from that in which the scar is practically horizontal (*N. Nadeaudi*, *N. polynesicum*, figs. 111-113, 31) to that in which it is almost lateral (*N. polynesicum*, figs. 30, 32; *N. St.-Johnianum*, figs. 99, 100). As a consequence of this variation the fruit may be more ovoid or subglobose (basal scar) or narrower at the base (lateral scar). The apex may be more or less protracted.

UNISEXUAL FLOWERS

(See also under Corolla and Androeceum)

As has been said above, flowers with abortive stamens and corolla seem to be a feature of individual trees rather than of species, varieties, or forms. However this must be checked in the field. Female flowers may usually be recognized at first sight by their narrower and more pointed buds and by their sometimes exserted styles (figs. 59, 64, 67, 72). In one specimen of *N. St.-Johnianum* (St. John and Fosberg 15105) a single bisexual flower was found among pistillate ones; it possesses only 4 petals and 8 stamens.

It seems also that the pistillate flowers are fewer-flowered than the bisexual ones.

FRUIT

As in many sapotaceous genera the fruit of *Nesoluma* is of almost decisive value in determining the position of the genus in the system of the order. *Nesoluma* shows a certain variability in the fruit, as far as the anatropy of the ovules and, consequently, the more lateral or more basal position of the seed scar are concerned. In *Nesoluma polynesicum* all intermediate forms between a fully basal and an obliquely basilateral seed scar may be found (figs. 28-32), in *N. St.-Johnianum* only the basilateral, in *N. Nadeaudi* only the basal form is known. Although the basilateral form (figs. 99, 100) strongly recalls the seed of *Northia fasciculata* (13, p. 243, fig. 63 m, n), a comparison with the basal form and with the seeds of certain *Sideroxylon* (*Calvaria*) species (8, Taf. 7; 11) indicates that the *Nesoluma* seed shows actually the type, known in the last-named genus. An accurate comparison of the *Nesoluma* fruit and seed with those of certain species of *Sideroxylon* (*Calvaria*) from south and

southeast Africa, Madagascar, and the Mascarenes has convinced me that the two genera are very closely related. The resemblance is based upon such points as:

1. One-seeded fruit
2. Pericarp with abundant and viscid milky juice
3. More or less globular seed
4. Faint ribs on testa [*Nesoluma Nadeaudi, Sideroxylon* (*Calvaria*) *inerme*]
5. Basal seed scar
6. Thick and bony testa
7. Testa veined inside
8. Abundant albumen
9. Tangential and oblique or horizontal position of the embryo

The size of the seed scar of *Nesoluma* is intermediate between the large basal scar of some *Calvaria* species from Madagascar and Réunion (11), and the scar of such species as *Sideroxylon inerme* L. [*Calvaria inermis* (L.) Dub.; see 5] and *S. diospyroides* from south and southeast Africa (8, Taf. 7).

FLORAL FORMULAE

In order to illustrate the above conditions I give here a statement of the structures found in some of the flowers examined. (See also the diagrams in figs. 12-16, 18-20, 34-35, 44-45, 60, 70, 84-87, 95-96, 108.)

RELATIONSHIP

Summarizing and completing our survey, we may say that *Nesoluma* combines features of the following groups and genera:

Leaf type and reticulation: *Sideroxylon* (*Calvaria*) *inerme* and *diospyroides, Sebertia, Lucuma Lecomtei* Guill., and *L. neocaledonica* Engl.

Unisexual flowers: *Ecclinusa*, certain *Planchonella* species (*P. obovata, P. firma, P. petaloides*), certain *Sideroxylon* and *Pouteria* species, *Omphalocarpum*, etc.

Calyx: *Leptostylis*, certain *Pouteria* species.

Pleiomery of androeceum: *Pycnandra, Achradotypus, Omphalocarpum*, many Madhuceae.

Pleiomery of corolla and androeceum: *Ochrothallus, Leptostylis, Krausella*, certain *Planchonella* and *Pouteria* species.

Reflexed filaments: *Calvaria* sensu lat. (in the sense of Dubard, 5), *Leptostylis, Ochrothallus, Pycnandra, Pouteria ptychandra, Pouteria* sect. *Pradosia, Aulandra*, certain *Palaquium* species.

Staminodial structures: no staminodes in *Leptostylis, Pycnandra, Chrysophyllum*, staminodes sometimes reduced in certain species of *Planchonella* and *Pouteria*; shape or position: *Cryptogyne, Calvaria* sensu lat.

Gynophore: *Calvaria* sensu lat. (glabrous basal part of pistillum often extant), *Krausella* (in *Nesoluma*, if any, without a distinct disc).

Gynaeceum: *Sideroxylon, Planchonella*, and *Pouteria*, but often meiomerous as in some *Pouteria* species, *Burckella*, etc.

Ovule: *Leptostylis, Sideroxylon, Pycnandra, Mimusops, Northia.*

Fruit: *Calvaria* sensu lat.

Seed (testa): *Calvaria* sensu lat., *Northia fasciculata* (Warb.) H. J. Lam.

Embryo—plane of cotyledons: *Calvaria*, certain *Pouteria* and *Palaquium* species.

Flower Structure in Nesoluma Species

Species	Specimens	Number of Sepals	Number of Petals				Number of Stamens			Number of Carpels
			Large	Small	"Staminodes"	Total	Normal	Small	Total	
N. polynesicum var. α, forma a	type sp. (P)	5	8	2	1	11	8	..	8	4
	" " "	5	6 (2 with adnate "staminodes")	....	4	10	8	2 (adnate to ovary)	10	?
	" " "	4	5	4	..	9	9 (2 connate and 1 adnate to ovary)	3	11	?
	" " (B)	4	8	..	1	9	9	..	9	4
	" " "	3	8	..	1	9	8	..	8	3
	" " "	4	6	3	..	9	9	..	9	4
	Munro 955 ♀	4	..	3	..	3	..	..	..	5
	Forbes 503	5	?	?	?	?	10	..	10	3
	" " (fig. 35)	6	3+2×2	..	1	8	6	5	11	3
	Forbes 503	4	4	4	..	8	7	..	7	3
	Munro 111	4	5	..	..	5	6	..	6	5
	" " (fig. 38)	4	4+ (2)	..	2	8	7	..	7	6
	Munro 111	4	6	..	1	7	6	1	7	4
N. polynesicum var. β forma a subf. 2	Forbes 11596 ♀	4	..	7	..	7	..	..	..	4
	" " ♀	4	..	8	..	8	..	..	..	4
N. polynesicum var. β forma b	St. John 10124 ♀	4 (1 half petaloid)	..	7	..	7	..	..	..	3
	" " " ♀	4	..	x (irregularly dentate)	..	x	..	..	..	4 (3 sterile)
	Brown and Judd 1307 (fig. 70)	6	6	4	2 (1 adnate to large petal)	12	9	..	9	2
	" " McEld. and Skottsb.	5	4	5	1	10	11	..	11	4
	369 ♀	4	..	x (irregularly dentate)	..	x	..	..	..	5 (2 sterile)
N. St.-Johnianum	St. John and Fosb. 15105 ♀	4	..	3	..	3	..	..	..	4
	" " ♀	4	..	4	..	4	..	..	..	4
	" " ♀	4	..	5	..	5	..	..	..	4
	" " ♀	4	..	8	..	8	..	..	..	5
	" " ♀	4	..	8	..	8	..	..	..	4
	" " ♀	4	4	..	..	4	8	..	8	4
	St. John and Fosb. 15137	5	8	..	..	8	8	..	8	4
	" "	4	3	5	..	8	9	1	10	5
	" "	5	4	4	1	9	8	..	..	3?
N. Nadeaudi	from MS. notes by L. Pierre	5	5-6	5-6	see under stamens	10-12	8 (2 connate) 9-12 (staminodes incl.)			4-6

Systematic Position of the Genus Nesoluma

As far as I know, only two authors have expressed their opinion on the systematic position of *Nesoluma*; Engler considered it, probably on account of the absence of staminodes, as a section of *Chrysophyllum* (see p. 129), which genus has always been a sort of repository for species of doubtful position in the Sapotaceae; Baillon (1, p. 279) inserted it in his Buméliées (= Sideroxylinae Engl.) between *Sarcosperma* (which I consider to represent a separate order; see Blumea, vol. 3, p. 183, 1938) and *Sersalisia*. Although he does not mention it definitely, and staminodes are not quoted in his over-simplified description, he apparently means to include *Nesoluma* in the subtribe Eubuméliées, characterized by alternipetalous staminodes and subbasal seed scar (1, p. 271).

Most of the more recent authors have maintained *Nesoluma* as an insertion in *Chrysophyllum*. This all concerns *"Chrysophyllum" polynesicum*, the only species known up to the present, and known only from the Hawaiian islands. A second species discovered by Nadeaud in Tahiti, was described with doubt as a *Palaquium* (*P. Nadeaudi*=*Nesoluma Nadeaudi*). Its generic identity with *Nesoluma* was stated afterward by Pierre but never published. Now that we know the genus far better and its morphology almost completely, we have to reconsider the systematic position of the genus.

Referring to my earlier publication on the Sapotaceae (13, pp. 8-12), it must be stated, in the light of modern knowledge and particularly in view of the primitive characters revealed in *Nesoluma*, (1) that Baillon's order of succession of the tribes should be preferred to that of other authors, insofar as he puts the tribe with spiral arrangement in the flower first; and (2) that the Chrysophylleae—as a tribe or as a subtribe—must be dropped, since *Nesoluma* may or may not possess the alternipetalous staminodes, which is the criterion of this group.

Consequently I would here propose a tentative alteration of my earlier system of the family; in this scheme the Sideroxylinae are put first, since they must be considered as the tribe with apparently the greatest number of primitive features (spiral arrangement of sepals). Only the Achradidae among this tribe have attained a cyclical arrangement of their sepals.

From the Sideroxylinae may be derived on one hand the Mimusopinae, and on the other (through *Diploknema* and *Aesandra*) the Palaquiinae. The Mimusopinae is a new tribe; it seemed preferable to give the former Mimusopeae that rank, although the definite distinction of this group by the dorsal appendages at the petals is recently blurred by the discovery of *Northia* species in which these appendages are much reduced or even wanting. Although each of the three tribes has its primitive and its secondary characters, the Palaquieae and the Mimusopeae seem to represent slightly younger groups, as the cyclic arrangement in the calyx is generally attained in them. In order to show the connection with the Sideroxylinae as regards the "stipular" appendanges to the petals, the Mimusopinae are put in the second place and therefore the Palaquiinae last.

The subdivision of the tribes Mimusopinae and Palaquiinae involved no special difficulties. The usual subdivision of the Sideroxylinae, however, is based upon the position of the hilum of the seed. When the hilum is basal (Sideroxyleae Dub.) the scar is small and circular and the hilum is situated quite close to the micropyle. When the hilum is lateral to apical (Lucumeae Baill.) the scar is long and narrow or occupies a large part of the testa. In both groups the embryo takes a vertical position. There are some intermediate cases relative to the scar character, which may be a valuable one as it plays also an important part in the subdivision of the Mimusopinae. *Nesoluma* and *Calvaria* (1, p. 258, figs. 274-275; 8, Taf. 7; 11) from south and southeast Africa, Madagascar, and the Mascarenes, take an intermediate position in this respect, insofar as they possess either a large, circular, basal or subbasal scar in which the hilum is not situated very near the micropyle, or a small, circular, basal scar; in both cases the embryo is oblique or horizontal. I agree with Dubard (5, pp. 84-88) that the genus *Calvaria* Commers. must be kept separate from *Sideroxylon*, as it is not only characterized by its basal seed scar but particularly by the horizontal position of the embryo, and also by the characteristic reticulation of the leaves, the petaloid "staminodes" and the albuminous seed. I am inclined, therefore, to accept Dubard's inclusion of such species as *Sideroxylon inerme* L. and *S. diospyroides* Bak. in *Calvaria*, in which the embryo takes a horizontal position, although the seed scar is small, as in the true Sideroxylons. I am not able to check all other species mentioned

under *Calvaria* by Dubard, but I am inclined to accept provisionally his delimitation of the genus. The species from the Mascarenes, Madagascar, and south Africa are of the greatest importance in connection with my ideas on the Antarctic origin of the Calvarieae, a new subtribe comprising the genera *Nesoluma* and *Calvaria* (see below).

New Subdivision of the Sapotaceae

My new tentative scheme is as follows:

Tribe I. Sideroxylinae Engl. (including Chrysophyllinae Engl.).

Sepals spirally arranged and calyx 5-8(-12)-merous or with two whorls of 2, 3 or 4 sepals (if 2, then the sepals sometimes unequal and not strictly opposite); corolla isomerous or rarely pleiomerous (*Nesoluma, Chrysophyllum*); stamens epipetalous and often insomerous with petals, sometimes more (*Nesoluma,* Achradotypeae), in one whorl; alternipetalous staminodes often extant, more rarely none; carpels usually isomerous with the calyx, rarely less, even more rarely more (*Pycnandra*); petals sometimes with ventral or lateral appendages (*Bumelia, Dipholis*) but never with dorsal appendages. Circumtropic.

Subtribe A. Calvarieae, nov. subtr.

Seminis albuminosi subglobosi cicatrix (magna vel parva) orbiculata vel suborbiculata, basalis vel sublateralis. Testa ossea. Embryo tangentialiobliquum vel plus minusve horizontale. Foliorum reticulatione perminute areolata. Staminodia, si adsunt, plerumque magna vel petaloidea.

Key to the Calvarieae

a. Calyx usually 4-5-merous, petals and stamens 8-12, carpels usually 3-5; no regular alternipetalous staminodes extant (Polynesia) ..... **Nesoluma** H. Baill.

aa. Flowers 5-merous in all whorls; alternipetalous staminodes extant (south and southeast Africa, Madagascar, Mascarenes) ..... **Calvaria** Commers.

Subtribe B. Sideroxyleae Dub. sensu stricto (= Eusideroxyleae Dub.).

Hilum basal, close to the micropyle; scar of the testa small and circular, basal. Not in Malaysia or Polynesia. (*Bumelia* Sw., *Dipholis* A.DC., *Sideroxylon* L., *Argania* Roem. and Schult.)

Subtribe C. Pouterieae (9, pp. 159-163), nov. nom. (Lucumeae Baill.).

Hilum lateral or apical, distant from the micropyle; scar of the testa long and narrow or occupying a considerable part of it.

Section 1. Eupouterieae, nov. nom. (= Eulucumeae H. J. Lam).

Stamens as many as petals or at most less than twice their number.

Subsection a. Planchonellidae, nov. subsect.

Sepala spiraliter inserta, interdum biserialia vel subbiserialia (2+2). Circumtropic.

Key to the Planchonellidae of the Pacific

a. Calyx 4-5-, corolla 4-6-merous; gynophore none; disc often extant,
  b. Alternipetalous staminodes extant (in *Pouteria* rarely none); disc often extant,
    c. Albumen usually abundant, cotyledons foliaceous; fruit relatively small, often pointed, pericarp thin, rarely larger, globose and fleshy; sepals always 5, petals 5, exceptionally 6; carpels 5 (tropical Asia to Polynesia).....**Planchonella** Pierre.
    cc. Albumen usually none, rarely somewhat extant, cotyledons fleshy; fruit often large, usually globular, pericarp fleshy; sepals 4-5, petals 4-6, carpels 1-12 (tropical America, Polynesia, Australia, Malaysia, Malay Peninsula, and India).....**Pouteria** Aubl.[6]
  bb. Staminodes and disc none.
    d. Corolla tube shorter than the lobes; sepals usually 5, sometimes 6-7-11; ovary 5-10-11-celled (tropics).....**Chrysophyllum** L.[7]
    dd. Corolla tube much longer than the lobes, sepals 4; ovary 4-celled (New Caledonia).....**Leptostylis** Benth.
aa. Calyx and corolla 6-8-merous; gynophore and disc extant (New Guinea).....**Krausella** H. J. Lam

In this subsection (Planchonellidae) are probably also *Sebertia* (New Caledonia, insufficiently known to me), *Micropholis* Griseb. (tropical America and Angola), *Achrouteria* Eyma (Guiana), *Calocarpum* Pierre (tropical America), and *Bakeriella* Dub. (tropical Africa), etc.

Subsection b. Achradidae, nov. subsect.

Sepala biserialia (3+3: *Achras* L., tropical America; 4+4: *Butyrospermum* Kotschy, tropical Africa); staminodia staminaque sepalis isomera (tropical America and Africa).

Section 2. Achradotypeae H. J. Lam.

Stamens 2 or more opposite each petal. (*Achradotypus* Baill., New Caledonia and New Guinea; *Omphalocarpum*, tropical Africa; *Pycnandra*, New Caledonia.)

Tribe II. Mimusopinae, nom. nov. (= Mimusopeae Hartog).

Petals with dorsal or dorso-lateral appendages (rarely abortive); calyx, corolla, stamens, and staminodes isomerous. Circumtropic.

Subtribe A. Mimusopeae, nom. nov. (= Eumimusopeae Dub.).

Hilum basal, close to the micropyle; scar of the testa small, circular, basal; flowers 8-merous (*Mimusops* L., etc.).

Subtribe B. Manilkareae Dub.

Hilum apical or lateral, distant from the micropyle; scar of the testa linear and narrow [*Manilkara* (Rheede) Adanson, appendages and staminodes large] or broad and large (*Northia* Hooker f., appendages and staminodes small, rarely abortive); flowers 6-merous.

Tribe III. Palaquiinae Dub.

Calyx with two fully cyclical whorls of 3 or 2 sepals, rarely 5 spirally arranged sepals (*Diploknema*); stamens twice as many as petals or more,

[6] Including *Lucuma* Molina (9, p. 159, descr. emend.). There is no sharp distinction between *Pouteria* and *Planchonella*. Both are large genera and *Pouteria* is probably the more primitive.

[7] Apparently a heterogeneous genus, urgently wanting revision; including *Ochrothallus* (which is probably better considered as a separate genus) and *Trouettia*.

rarely less, in two or more whorls; staminodes none (sterile stamens exceptionally extant); petals without dorsal appendages. South and eastern Asia to Australia and Polynesia.

Subtribe A. Madhuceae H. J. Lam.

Petals and carpels more numerous than sepals, usually twice as many, the carpels rarely less (*Burckella*); sepals cyclically or spirally arranged.

Section 1. Diploknemeae H. J. Lam.

Sepals (4-)5, spirally arranged, petals (8-)12, stamens 10-40 in 2-4 whorls, carpels 5-12 (*Diploknema* Pierre, *Aesandra* Pierre).

Section 2. Eumadhuceae H. J. Lam.

Sepals in two dimerous whorls (*Burckella* Pierre, *Ganua* Pierre, *Payena* DC., *Madhuca* Gmel.).

Subtribe B. Palaquieae Engl.

Calyx, corolla, and gynaeceum normally isomerous; calyx whorls fully cyclical (trimerous in *Palaquium* Blanco and *Aulandra* H. J. Lam, usually dimerous in *Isonandra* Wight).

Phylogeny

The survey of the relationship of *Nesoluma* (p. 136) indicates that the more important connections and relationships seem to be particularly with genera from:

1. South and southeast Africa, Madagascar and the Mascarenes (*Calvaria* sensu lat.: leaves, androeceum, testa of seed, embryo!; including *Cryptogyne*: stamens!).
2. New Caledonia (*Sebertia*: leaves; *Lucuma*: leaves; *Leptostylis*: calyx, filaments; *Achradotypus* and *Pycnandra*: androeceum; *Ochrothallus*: pleiomery of corolla and androeceum).
3. New Guinea (*Northia fasciculata*: testa of seed; *Achradotypus*: androeceum; *Krausella*: gynophore).

One of the most striking facts of this statement, it seems to me, is the closeness of relation with south and southeast Africa, Madagascar, the Mascarenes, and to a certain degree also with New Caledonia. Other relationships seem much less significant.

I have already stated (p. 138) the striking resemblance of *Nesoluma* particularly with such species as *Calvaria inermis* (L.) Dub., etc., and I do not think it is too speculative to suggest that the ancestors of the Calvarieae have lived in the Antarctic continent. Among them *Nesoluma* has certainly preserved the greatest number of primitive features such as the instability in the number of whorl parts, concerning which *Calvaria* is already fixed (5-merous throughout). While *Nesoluma* is therefore to be considered as the most primitive genus of its tribe and, consequently, of the whole order, I would suggest that from these extinct Procalvarieae in the Tertiary Ant-

arctic continent, two lines of evolution have survived. One of them has developed into the group with small basilateral seed scar (Sideroxyleae), first with albumen (*Sideroxylon, Argania, Dipholis*), afterward exalbuminous (*Bumelia*); the other has developed into the groups with long and narrow or with very large seed scar (Pouterieae). During this evolutionary process migrations took place along various lines of dispersal. *Nesoluma* maintained itself as a relic in the central part of the Pacific and has, apparently on the basis of a rather rich potential polymorphy, developed a number of closely related forms in various parts of its vast relic area. *Calvaria*, younger and more specialized than *Nesoluma*, has its center in south Africa and the Mascarenes. Such habitats as Cape Verde, Madeira, and Socotra have to be checked; perhaps they are outposts, but more probably they are relics from a formerly larger generic area. This is the more probable as *Sideroxylon*, representing a further phase, has also a disjunct area [according to Dubard(5) : Antilles, Hong Kong, Tonkin, Abyssinia] which can be best explained as a relic area, with which the areas of *Argania* (Morocco) and of *Dipholis* (Antilles) closely agree. The areas of the younger groups need not be mentioned here. Suffice it to state that I consider *Nesoluma* as an Antarctic relic.

Similar conditions are found in other genera, such as *Astelia* (22, p. 3323), that are generally considered as Antarctic relics. The source must be sought in the Tertiary Antarctic continent, which has repeatedly been claimed by such investigators as Setchell (19,20) and Skottsberg (21,22,23) as the rich reservoir of floral elements from which the floras of the Southern Hemisphere have been fed. Skottsberg's maps of the area of *Astelia* (22, pp. 3318, 3323; 23, p. 295) and its sections are particularly interesting in studying the area of the Calvarieae, because the Mascarenes, New Caledonia, Tahiti, and Hawaii are included in the generic area of *Astelia*. The concordance between *Astelia* and *Nesoluma*, however, is not far-reaching, both because the area of *Nesoluma* is much smaller and because *Astelia* is a plant of the high mountains, *Nesoluma* a native of tropical or subtropical foothills (from near the seashore up to about 800 m., as far as my data go). Also *Astelia* consists of a number of species that are not closely related, while *Nesoluma* seems to form one large intercrossing population. Both, however, show no particular adaptations to dispersal; I suppose, at least, that the very thin pericarp of the *Neso-*

luma fruits forms no alluring food for birds; winds and sea currents are still less probable means of dispersal.

There are several other indications of connections between the Mascarenes and Polynesia. Skottsberg mentions several species which are important in this light. One of them is an *Acacia* species close to *A. Koa* (21, p. 15); others are *Sophora,* sect. *Edwardsia* (23, pp. 297-298), *Vincentia* (23, p. 298), and *Weinmannia* (23, pp. 298-299). All these species are taken from what Skottsberg (23, p. 292) calls the tricentric group, which comprises systematic units represented in Africa, America, and Australasia. Thus far we have mentioned examples in which the African sector was represented only by Madagascar and the Mascarenes. When the continent is also taken into account, such genera as *Gunnera* and *Acaena* become important in comparison with *Nesoluma.* We must, however, remember that we lack in *Nesoluma* the knowledge of actual habitats outside the central Pacific and that we have to rely upon supposed, though close, relations instead of actual habitats. The phylogeny of *Nesoluma* is therefore more speculative and more uncertain than that of the other genera mentioned.

Subdivision and Geographic Distribution of the Genus Nesoluma

The specimens of the genus available for investigation show strong variability in many of the characters, a peculiarity of a young group in active evolution. This is strange as the group seems very well circumscript as a genus. Its generic characters—in spite of their instability (which is a generic character itself)—preclude any confusion with other genera; the specific and still smaller features show the same entangling network of always repeated combinations which is so characteristic for the whole order. Most striking generic features are: the flower-characters (particularly their instability), the one-seeded fruit and the quite peculiar seed (large basilateral to basal scar, bony testa, tangential and oblique position of embryo), and to a certain degree also the reticulation of the lower side of the leaves. Features of lesser rank are the drying color (light yellowish green to dark brown); the shape and the dimensions of the leaves; the pubescence of branchlets, leaves, and flowers; the dimensions of the pedicels and the flowers; the number of flowers in the inflorescences; the

unisexuality of the flowers; the extant or non-extant gynophore; the shape and the dimensions of the fruit; and the more or less fully anatropous ovules and the therefore more or less basal position of the seed scar. Several of these features could not be checked in many of the specimens, and therefore they were less appropriate as the basis of a subdivision; many other features supplied no taxonomic constancy and only a slight geographic correlation (see p. 148).

I applied various methods in arranging the various features (cf. 18, pp. 180-184) but none gave a satisfactory result and I was forced to conclude that intercrossing must be as frequent in this genus as it is supposed to be in *Gouldia* (Rubiaceae) (10, pp. 10-12), which occupies a much smaller area than *Nesoluma*. The geographic area of *Nesoluma* is entirely situated in the central Pacific, extending over almost 50 degrees of latitude (or more than 6,500 km.) from Hawaii to Henderson Island and Rapa. Exactly the same form (*N. polynesicum,* var. β, forma a, subf. 1) has been collected both in Hawaii and in the Austral Islands (Raivavae and Rapa). The distinguishing of three different species, then, is to be considered as a provisional scheme; I expect that the study of more material will lead to the combination of these species into one large "linneon."

The main species, *N. polynesicum,* occupies by far the largest area and contains numerous forms. It occurs abundantly in the Hawaiian islands (Oahu, Lanai, Molokai, Maui) and has also been collected (variety β only) in the Austral Islands, a remarkable disjunction that may perhaps be filled in by future collections. Maybe, however, the disjunction in the area of *Nesoluma* really exists. I would, incidentally, suggest that a solution of this problem could then be sought in the geologic history of the Pacific as suggested by Chubb [cited in 24, p. 511 (Geol. Mag. **71**: 300, 1934)].

The two species which I provisionally separate from the main species, partly on geographic grounds, are *Nesoluma St.-Johnianum* from Henderson Island and *N. Nadeaudi* from Tahiti. These two species agree in that they are large-leaved, while the typical *N. polynesicum* is small-leaved (the large-leaved forms of the latter species are in other features discordant to *N. St.-Johnianum* and *N. Nadeaudi*). *N. Nadeaudi* is insufficiently known. It seems to be distinguished also by a relatively large fruit. None of the species can be said to represent a more primitive form than either of the other two.

SPECIES OF NESOLUMA

Key to the Species of Nesoluma

1. a. Leaves generally small and elliptic or ovate or slightly obovate with more or less broadly cuneate or subrotundate base and rounded apex, pubescent or not when young, brown or more rarely somewhat greenish yellow when dry; shape, size, and pubescence of leaves extremely variable, from oblanceolate to ovate and broadly elliptic, generally about 4-8 cm. long and 2-4.5 cm. broad, if up to 12 cm. long then 4-6.5 cm. broad, and with rounded apex; reticulation variable, minutely areolate to more irregularly reticulate; fruit 1-1.5 cm. long, about 1 cm. in diameter (Hawaii and Austral Islands).....1. **N. polynesicum**
   b. Leaves larger, oblong-ovate to oblong, narrowing toward the apex, which is blunt, generally 6-13(-16) cm. long, 3-5.5 cm. broad; reticulation minutely areolate, areoles circular; fruit 1.5-2.5 cm. long (Henderson Island, Tahiti).....2
2. a. Leaves oblong-ovate to oblong, light yellowish green when dry (always?), petioles 1.5-2.5 cm. long; fruit 1.5-1.9 cm. long, 0.7-1 cm. in diameter (Henderson Island).....2. **N. St.-Johnianum**
   b. Leaves ovate to elliptic-ovate, dark brown when dry (always?), petioles 2-4 cm. long; fruit 2.5 cm. long, 1.7 cm. in diameter (Tahiti).....3. **N. Nadeaudi**

1. Nesoluma polynesicum (Hillebr.) H. Baill., Soc. Linn. Paris, Bull. **2**: 964, 1891; Hist. d. Pl. **11**: 279, 1892 (nomen in annot.). Type species (pls. 1-3, figs. 1-79).

Chrysophyllum polynesicum Hillebr.: Flora Hawaiian Is., 277, 1888.

A small tree or large shrub, up to 7 m. high and 20 cm. in diameter, with milky juice, bark rough, brown or gray, sapwood creamy. Branchlets round, up to 0.5 cm. thick, often slender and rather smooth, or wrinkled when dry, the ultimate tips ferruginously tomentose. Leaves variable in size, shape, and pubescence, generally elliptic or ovate, sometimes somewhat obovate, rarely oblanceolate, base usually broadly acute to subrotundate, rarely cuneate, apex broadly rounded, more rarely gradually narrowing and obtuse, margins entire. Blade and petiole mostly dark brown when dry, sometimes lighter brown or greenish brown, more rarely light greenish yellow. Leaves usually thin coriaceous and rather rigid, ferruginously pubescent on either side when very young, this pubescence remaining a longer or shorter time with age especially on the lower side. Midrib prominent below; secondary nerves 7-10-15, very faint and almost inconspicuous below, almost straight, ascending from the midrib at an angle of about 60-70 degrees, united near the margin in an irregular, thin, intramarginal nerve; tertiary nerves of variable type (even in the same leaf), minutely reticulate with a general parallelism to the secondary nerves, with subsequent grades to regularly areolate with circular and very conspicuous areoles. Dimensions of the adult leaves: (1-)4-8(-12.5) cm. long, (0.6-)2-4.5(-6.5) cm. wide, the petioles (1-)2-3(-5) cm. long. Inflorescences 1-5-flowered, with minute bracts which are ferruginously tomentose, fascicled in the axils of the leaves or of their scars, in the latter case in some forms borne upon mammillose dwarf shoots on the older parts of the branchlets. Pedicels

ferruginously pubescent or glabrate, (0.15-)0.4-0.6(-0.8) cm. long. Flower buds ovoid or globose in bisexual flowers, narrower and pointed in pistillate flowers with the style often slightly exserted. Open flowers with spreading corolla, apparently ephemerous, whitish or greenish white, with heavy, sweet odor. Calyx pubescent, glabrate or glabrous, except the very tips of the (outer) sepals, glabrous inside, 0.3-0.5 cm. long; sepals (3-)4-5(-6), spirally arranged and imbricate, if 4 then sometimes seemingly forming two dimerous whorls but usually the sepals of one whorl not strictly opposite and (especially the outer ones) unequal in size, the larger ones 0.3-0.4 cm. long and ovate, the smaller ones deltoid. In ♂ flowers corolla glabrous except sometimes at the insertion of the stamens, with thin veined lobes and thicker, very short tube, the lobes somewhat exserted from the calyx but spreading just before falling off, about 0.3-0.4 cm. long. Petals or petaloid structures ("staminodes" inclusive) imbricate, variable in number and in shape, (5-)7-9(-12), usually the corolla consisting of 6-8 larger ovate and rounded petals and some smaller ones; smaller petals may be inserted either outside the larger sepals and are then usually smaller than these but of the same shape, or inside, and are then either long but narrow (particularly the blunt upper half) or small and then more or less dentate, 3-lobed or fimbriate and with an acute apex. The smaller petals have no definite position and show transition forms to the stamens, in shape as well as in position, and may therefore often recall the alternipetalous "staminodes" of other genera of the Sideroxylinae. Insertion of the petals rather variable on account of the apparently frequent collateral or serial duplication, which is also found in the androeceum. Connations among petals (bifid or bilobed petals) and between petals and "staminodes" are rather frequent. Tube very short, thick because of the adnation of the filaments. In ♀ flowers corolla much reduced to a variable number of tiny scales (1-8) being either free at base or connate into a very short tube, these scales either entire and subulate (petaloid) or irregularly dentate (staminodioid), inserted at or around the base of the ovary. Androeceum closely correlated with the corolla in such processes as duplication and insertion; fertile stamens (6-)8-10(-11), often unequal in maturity, some of them already with opened sacs, others still very young, sometimes some of them sterile, with transitions to the "staminodioid" petals; insertion more or less irregular, sometimes equally distributed, sometimes sectorially somewhat crowded, 1-3 opposite a petal. Normal stamens glabrous or the filaments slightly woolly, filaments stout, subulate and usually flattened and broader at base, adnate to the corolla tube at their base and outwardly reflexed even when ripe, stretched and then exserted and about 0.2-0.3 cm. long in fully open flowers, anthers oblong ovoid, the apex sometimes minutely bifid, 0.15-0.2 cm. long. Pistillum with appressed stiff hairs covering the ovary which is or is not borne upon a glabrous sterile part (gynophore) in which sometimes (on longitudinal sections) an adnate disc can be traced; fertile part slightly furrowed (2-)3-5(-6)-celled, the cells 1-ovuled (bi-ovulate cells are rarely found and are abnormal), ovules half to almost fully anatropous; ovary gradually narrowed into a stout glabrous style, the truncate stigma of which is usually not, sometimes slightly, exserted from the calyx, especially in pistillate flowers. Fruits on hardly or not elongate pedicels and on a persistent and spreading calyx about 0.5-0.7 cm. in diameter, usually solitary, sometimes 2 or 3 in the axils of the leaves or of their scars, glabrous, green when young, afterward turning brownish red and dark purple, black when dry, obovoid, sometimes short and almost globular with small abrupt beak (scar of the seed basal), sometimes narrower and elongate, with long and acutely pointed beak

(scar of the seed basilateral), (0.9-)1.2-1.4(-1.7) cm. long, (0.7-)0.9-1.1(-1.3) cm. in diameter, 1-seeded; seed somewhat shorter but with hardly smaller diameter than the fruit, namely 1-1.2 by 0.75-0.85 by 0.7-0.75 cm., the testa thick and bony, veined inside, shining brown without, except the scar which is roundish or elliptic and from almost fully basal to obliquely lateral; when obliquely lateral the seed is much narrower in its basal part. Embryo with copious albumen, plane tangential and oblique toward the flower axis; radicle inferior, not exserted.

A small tree in valleys, dry foothills, open slopes and dry forests from near the seacoast to about 1,500 ft. altitude, said to be good firewood (Rapa). Flowers and fruits have been collected in all months of the year. Native names: *Keahi* (Oahu, Lanai); *Kalaka* (Rapa).

Distribution: Hawaiian islands (Oahu, Molokai, Lanai, Maui), Austral Islands (Raivavae), and Rapa.

Subdivision of Nesoluma Polynesicum into Varieties and Forms

The subdivision of this polymorphous species must be provisional. Much more material than is available at the present is needed to get a satisfactory insight into the taxonomic and genetic structure of this "linneon", the constituents of which are probably interbreeding. Therefore, some or many of the forms described below may be only ephemerous and not taxonomically fixed. This is the reason why I did not add Latin descriptions to the forms and subforms. If, in spite of this instability, I have accepted two varieties, it does not mean that these varieties are undoubtedly geographically distinguished, though a certain geographical correlation of some of the groups cannot be denied (p. 148). The main subdivision has been based upon the pubescence of the leaves and the number of secondary nerves. I am aware of the fact that this is far from being a firm basis; neither is it a character which allows a positive identification of all specimens (cf. Forbes 112). All features, however, show a more or less continuous scale and I have the impression that there is a certain tendency to produce entirely glabrous forms in the southern area and pubescent forms in the northern area. The next feature to serve as a criterion would be the length of the petiole, but the pubescence of the leaves seems to be more in accordance with natural tendencies. Inflorescences, flowers, and fruits were absent in too many specimens to be used as a basis for subdivision; moreover they would probably not prove sufficiently stable.

CONSPECTUS OF THE SUBDIVISION OF N. POLYNESICUM

(For full particulars see pp. 148-153)

Plate 1, figures 1-9

Var. α typicum: adult leaves more or less pubescent, except the older ones; secondary nerves 7-10.
Hawaii (Oahu, Lanai, Molokai, Maui).
Forma a. genuinum: leaves small and broad (about 7 by 3.5 cm.), with short petioles (1.5-2.5 cm.).
Lanai, Molokai, Oahu.
Forma b. longipetiolatum: leaves small, with long petioles (2.5-4.5 cm.).
Lanai, Maui.
Subforma 1. originarium: leaves broad or narrow, pubescent, rigid.
Lanai, Maui.
Subforma 2. laurinum: leaves narrower, sooner glabrate, thinner, habit more slender.
Maui.
Forma c. microphyllum: leaves very small (up to 5 by 2 cm.), oblanceolate and crowded.
Maui.
Forma d. macrophyllum: leaves broadly elliptic to oblong, larger (up to 12.5 by 6.5 cm.).
Molokai, Lanai.
Var. β glabrum: adult leaves very soon glabrate; secondary nerves 9-15.
Hawaii, Austral Islands, and Rapa.
Forma a. genuinum: leaves shaped as in var. α, forma a.
Hawaii, Austral Islands, and Rapa.
Subforma 1. originarium: leaves larger, habit stouter, petioles up to 3 cm long.
Hawaii (Kauai, Oahu, Molokai), Austral Islands (Raivavae), and Rapa.
Subforma 2. gracilis: leaves smaller, habit more slender, petioles up to 2.3 cm. long.
Rapa.
Forma b. longipetiolatum: leaves larger, petioles longer (2-5 cm. long).
Hawaii (Oahu, Molokai).

ENUMERATION OF THE MATERIAL

Nesoluma polynesicum var. α **typicum** H. J. Lam, nov. var. (pl. 1, figs. 1-5; pl. 2).

Folia adulta praecipue subtus pubescentia, ultimatim vetustiora glabrata; nervi secundarii 7-10.

Adult leaves ferruginously pubescent, especially at lower side, the older ones ultimately glabrate; secondary nerves 7-10.

Forma **a. genuinum** (fig. 1).

Leaves small, ovate, elliptic or obovate with broadly rounded apex, dark brown when dry, with short petioles; blade (2.5-)6-8 cm. long, (1.2-)3-4(-6) cm. broad, petioles 1.5-2.5(-2.8) cm. long; inflorescences in the axils of the leaves, rarely more or less prominent, dwarf shoots extant.

Hawaiian islands: Lanai, July 1870, *Hillebrand* without number (B, P, L, US), type in Berlin Herb., with fruit and flowers; native name, *keahi*; "Lanai, *Keahi* in convallibus Makaleha", [4 sepals, in one specimen 3 (out of 21)], small fragment with extensive annotations and figures by L. Pierre (P, *Pierre 6067*).

Molokai, Lanai, and Oahu, *Hillebrand* (B, G), fruit and flowers, [5 sepals, in two specimens 6 (out of 15)]. "Makaleha u. Wailupe auf Oahu," *Hillebrand* (B, K); another label in Berlin Herb. mentions Makaleha Valley, *Keahi,* with a Latin description, some fruits; probably Kew fragment is from this. "Mauna Loa auf Molokai," June 1870, *Hillebrand* (B), with fruit.

Hawaiian islands, Lanai: 1851-1855, *J. Remy 474* (P, L), 2 specimens with fruit in Paris Herb.; west end, dry forests, June 1913, *C. N. Forbes 153 L* (H, L, NY, US), with fruits and flower buds (seed scar very much lateral, fruit oblong and pointed); Paomai, dry forest, Aug. 1913, *G. C. Munro 31* (H, L), with fruits and some buds (probably ♀ tree; reticulation of leaves almost inconspicuous); Kaa desert, July 1910, *J. F. Rock 8671 a* (G), with fruits (fruits oblong and pointed; the number of the label was 8671, which had to be changed as 8671 is var. *α* forma b, subf. 1, from Maui); Kamao, alt. 1,500 feet, June 17, 1929, *G. C. Munro 955* (H), with fruits and flower buds (seed scar almost basal, fruit obovoid to globular, the only flower examined ♀, reticulation of leaves circular-areolate); Koele-Maunalei, July 1910, *J. F. Rock 8040?* (sic) (H), with fruits (fruit oblong and pointed, up to 1.7 cm. long, seed scar basilateral; leaves long remaining pubescent); another identical specimen, July 26, 1910, from windward open slopes of Lanai, bears the number *J. F. Rock 8040* (H, G, NY, US), with flowers.

Hawaiian islands, Molokai: Kaluakoi, Mauna Loa, on Puu Nana, alt. 200-400 m., March 10, 1930, *Krajina 126* (Kr, L), with fruits (pedicels exceptionally short, 0.15 cm. in flower, 0.3 cm. in fruit; fruit small and pointed, scar of the seed basilateral); Mauna Loa, June 1912, *C. N. Forbes 112 Mo.* (H, L), with fruits (transition form to var. *β*, forma a, subf. 1, inasmuch the leaves on some of the branchlets are very soon glabrous); no locality given, *H. Mann and W. T. Brigham 363* (H).

Forma **b. longipetiolatum.**

Leaves brown or somewhat greenish when dry, shape as in forma a or more obovate (the apex more narrowed), but petioles long and slender, 2.5-4.5 cm. long.

Subforma **1. originarium** (fig. 2).

Leaves as in forma a, rigid, with rounded and relatively broad apex, sometimes narrower but with the venation, pubescence and general habit of forma a; inflorescences often on the older wood, on more or less prominent dwarf shoots in the axils of leaf scars.

Hawaiian islands, Lanai: Mahana, near Maunalei road, Sept. 22, 1913, *G. C. Munro 111* (H), with flowers and fruits; a second specimen without number but with identical label and with the addition, "Keahi", probably belongs here; west end, Sept. 1917, *C. N. Forbes 503 L.* (H), with flowers and 1 fruit (fruit oblong and pointed; flowers globular and relatively large, 0.5 cm. long, calyx 0.35 cm., flower parts very unstable; reticulation of the leaves very coarse).

Hawaiian islands, Maui: lava fields Auwahi, Nov. 1910, *J. F. Rock 8671* (H, G), with fruits (fruits obovoid, about 1.2-1.5 by 1-1.1 cm., seed scar almost basal; leaves narrower and more pointed and somewhat crowded toward the tips of the branchlets (cf. forma c; transition form to subf. 2).

Hawaiian islands: no locality given, 1913, *Wilder* (H), sterile.

Subforma *2.* **laurinum** (fig. 3).

Leaves thinner and sooner glabrate, narrower with cuneate base and gradually narrowed apex with slender branchlets; inflorescences in the axils of leaves.

Hawaiian islands, Maui: Kamana, S. slope of Haleakala, March 23, 1920, *C. N. Forbes 2074 M.* (H, L), with young fruits (leaves light brown, soon glabrate; fruits obovoid).

Forma **c. microphyllum** (fig. 4).

Leaves oblanceolate, crowded at the tips of the branchlets, brown when dry, very small, 4-5 by 1.8-2.2 cm., petioles 1-1.5 cm. long; inflorescences not on prominent dwarf shoots.

Hawaiian islands, Maui: Olowalu Valley, May 9, 1920, *C. N. Forbes 2277 M.* (H, NY), with fruits (fruits obovoid, seed scar almost basal; leaves long remaining pubescent).

Forma **d. macrophyllum** (fig. 5).

Leaves large, elliptic or ovate to oblong, 8-12.5 by 4-6.5 cm., petioles 2-4 cm. long, blade yellowish brown when dry; inflorescences on prominent dwarf shoots.

Hawaiian islands, Molokai: Mauna Loa, April 1910, *J. F. Rock 7052* (H, G, NY), with young fruits (fruits obovoid); Mahana, April 1918, *J. F. Rock 14068* (H, US), with young fruits; same

locality, April 1909, *J. F. Rock* without number (G), with young fruits; same locality, March 1910, *J. F. Rock* without number (NY), with young fruits; Waiahewahewa Gulch, last relic of dry forest, April 18, 1928, *Otto Degener 10642* (NY), with young fruits.

Hawaiian islands, Lanai: *Hillebrand* without number (US), small specimen attached to a sheet of var. α, forma a.

Var. β **glabrum** H. J. Lam, nov. var. (pl. 1, figs. 6-9; pl. 3).

Folia adulta mox glaberrima; nervi secundarii (9-)10-15.
Adult leaves very soon entirely glabrous; secondary nerves (9-)10-15.

Forma **a. genuinum.**

Leaves shaped as in var. α forma a—small, ovate, elliptic or obovate with broadly rounded apex, about (1-)3-7(-9.5) by (0.6-)1-3.5(-5.3) cm., petioles 1-2.5(-3) cm. long, blade sometimes brown but often greenish when dry; inflorescences in the axils of the leaves or at least not on prominent dwarf shoots.

Subforma **1. originarium** (fig. 6).

Leaves brownish or greenish when dry, up to 9.5 cm. long and 5.3 cm. wide, petioles up to 3 cm. long.

Hawaiian islands, Oahu: Wailupe Valley, right hand branch, April 14, 1918, *J. F. Rock 17125* (H), with fruits (fruits obovoid to oblong ellipsoid); Honouliuli, Kaloi, in dry foothills, open country, alt. 300 m., May 10, 1937, *C. S. Judd 57* (H), with young fruits (small tree, 3.5 m.; fruits pointed); Waianae Mountains, southeast of Palehua, Nov. 23, 1935, *Otto Degener, Kwan Park and M. Takamoto 10108* (NY), with flower bud.

Hawaiian islands, Molokai: west Molokai, Mahana, March 1910, *J. F. Rock 12505* (H, NY), with fruits (fruits ovoid); same locality, April 1909, *J. F. Rock* without number (G), with fruits (fruits obovoid, up to 1.5 by 1 cm.).

Hawaiian islands, Kauai: Halemanu, near bottom of Waimea Canyon, Feb. 1907, *J. F. Rock 2336* (H), sterile.

Austral Islands, Raivavae: Pic Rouge, southwest ridge, patch of woods, alt. 170 m., Aug. 5, 1934, *H. St. John and F. R. Fosberg 15935* (H, L), (tree 6 m. high, 20 cm. in diameter; fruit green, sap milky); same locality, upper edge of forest, base of cliff, same date, *H. St. John and F. R. Fosberg 15936* (H, L), (tree 5 m. high, 20 cm. in diameter; flower whitish, perianth divergent, odor heavy, sweet; sap milky, bark rough, brown; sapwood creamy, streaked).

Rapa: Pake, mountain side, alt. 700 feet, Oct. 31, 1921, *A. M.*

Stokes 391 (H), with fruits (tree 14 ft., diameter 2 in., fruits turning brownish red, good firewood, native name *kalaka*; all fruits sterile, possibly an unfertilized ♀ tree?); same locality, Oct. 24, 1921, *A. M. Stokes 406* (H) (same annotations and remarks).

Subforma **2. gracile** (fig. 7).

All parts more slender, leaves light green when dry, up to 7.2 cm. long and 3.3 cm. broad, petioles up to 2.3 cm. long.

Rapa: Hiri Valley, south slope of Morongota, alt. 175 m., dense forest, July 20, 1934, *F. R. Fosberg 11596* (H, L), with flowers (small tree 6 m. high; ♀ flowers only).

Forma **b. longipetiolatum** (figs. 8, 9).

Leaves brown or yellowish green when dry, larger and with longer petioles, 6.5-11.5 cm. long, 2.8-5.2 cm. broad, petioles 2-5 cm. long. Leaf shape rather variable, from broadly elliptic to oblong. Inflorescences often on prominent dwarf shoots.

Hawaiian islands, Oahu: Maunalua, Hahaione Valley, edge of pali, alt. 600 ft., Dec. 14, 1929, *H. St. John 10124* (H), with flowers (♀ only; in one of the flowers half of a sepal was petaloid); Hahaione Valley, March 19, 1932, *A. F. Judd* without number (H, NY, wood specimen Bishop Mus. no. 2491), with fruits (fruits ovoid); Kuapa Cliffs, on steep dry slope, alt. 200 m., Aug. 23, 1924, *F. B. H. Brown and A. F. Judd 1307* (H), with flowers and fruits (tree, about 7 m., diam. 20 cm., flowers greenish white [not reddish], fruits dark purple, bark gray, rough, native name: *keahi*; buds almost globular, 0.4 by 0.35 cm., opened flower 0.7-0.8 cm. in diameter, leaves rather small, up to 9 cm. long, fruits obovoid); Mokuleia, slopes of Kaala, April 26-May 16, 1912, *C. N. Forbes* without number (H, US), with fruits (fruits obovoid); right fork Wailupe Valley, Jan. 12, 1920, *D. Wesley Garber and C. N. Forbes 148* (H, L), with fruits (fruits almost globular, up to 1.1 cm. long); Wailupe Valley, April 11, 1917, *C. N. Forbes 2471 O.* (H), with fruits (leaves large, fruits globular, 1 cm.); Kaala, Makaleha, Aug. 30, 1922, *G. McEldowney and C. Skottsberg 369* (H, Göteborg), with flowers (leaves large, ♀ flowers only, some ovary cells bi-ovulate, others sterile); middle Palawai Ridge, on grassy rocky slope, decadent dry forest, May 12, 1936, *O. Degener and M. Takamoto 10666* (H), with fruits (fruits beaked, 1.3 cm. long, leaves oblong, petioles 2-2.5 cm. long); ridge with Hadden Trail, Kuliouou Valley, single tree on lantana-

covered slope, June 23, 1935, *O. Degener* and *D. Toppina 10098* (Herb. Deg.), with fruits (fruits globular to ovoid, 1.2 cm. long); talus slope southwest of Waimanalo landing, single tree, remnant of decadent dry forest, April 10, 1936, *Degener, Takamoto,* and *Martinez 11277* (Herb. Deg.), with young fruits.

Hawaiian islands, Molokai, Mauna Loa, June 1912, *C. N. Forbes 1 Mo.* (H), with fruits (fruits obovoid).

2. **Nesoluma St.-Johnianum** H. J. Lam and B. J. D. Meeuse, nov. spec. (pl. 4, figs. 80-102).

Arbor parva; folia glabra dispersa, oblonga vel elliptica vel elongato-ovata, basi acuta, apice obtusa vel paulo emarginata; nervi secundarii (8-)10-14 angulo 60°-70° de costa adscendentes, reticulatione perminuta distincta, areolis circularibus; inflorescentiae in foliorum axillis fasciculatae, ♂ 5-12, ♀ 1-6-florae; pedicelli cum alabastris ♂ ovoideis, ♀ oblongo-acutis glabri; corolla glabra, petala in floribus ♀ vix exserta, (5-)7-9 ovata imbricata, saepe nonnulla minora petaloidea vel staminodioidea, in floribus ♀ valde reducta, 8-0, ligulata (petaloidea) vel (sub)tridentata (staminodioidea), libera vel basi paulo connata; stamina in floribus ♀ nulla, in floribus ♂ 8-11 glabra, interdum nonnulla minora, sterilia, staminoidea vel petaloidea; filamenta apice reflexa antheris oblongo-ovatis apice minute bifidis aequilonga vel paulo longiora; pistillum valde laticiferum, basi glabrum, ovarium 5-4(-3)-loculatum, hispido-pilosum, in stylum glabrum haud exsertum truncatum contractum; ovula fere tota anatropa; fructus monosperma obovoidei, apice plus minusve abrupte acuminati; semina characteribus generis.

A tree, up to 10 m. high and 30 cm. in diameter, the bark greenish brown, the sapwood white. Youngest parts reddish brown tomentose. Branchlets about 0.3-0.5 cm. thick, round and smooth, the older ones somewhat rugose. Leaves entirely glabrous, greenish when dry (always?), elliptic or oblong or slightly oblong-ovate, with obtuse or rounded or somewhat emarginate apex and acute base, (2.2-)4.5-15.8 cm. long, (1.6-)2.6-5.7 cm. wide, petioles rather slender, 0.9-2.5 cm. long, secondary nerves (8-)10-14 diverging at an angle of about 60-70 degrees, reticulation very minute and distinct, areoles circular. Inflorescences crowded in ♂ flowers and 5-12-flowered, not crowded and 1-6-flowered in ♀ flowers. Pedicels glabrous or nearly so, in flower 0.4-0.7, in fruit 0.8-0.9 cm. long. Buds of hermaphroditic flowers ovoid and 0.4-0.5 cm. long, of female flowers oblong and acute, and 0.25-0.3 cm. long, 0.15 cm. in diameter. Sepals usually 4, more rarely 5, glabrous except at the tips. In ♂ flowers corolla glabrous, hardly exserted. Petals ovate and much imbricate, (5-)7-9, often some of them smaller and then either petaloid or staminodioid. In ♀ flowers corolla much reduced, petals 8-0, if any, either ligulate (petaloid) or more or less tridentate (staminodioid), free at base or slightly connate. Stamens in ♀ flowers none, in ♂ flowers 8-11, glabrous, the subulate filaments outwardly reflexed, as long as or somewhat longer than the oblong-ovate anthers, some of the stamens sometimes smaller and then sometimes sterile and either staminoid or petaloid. Pistil with glabrous base (with sometimes an indication of an adnate disc) and much milky juice, 0.3-0.5 cm. long, ovary hispidly pilose, usually 4-, sometimes 5- or 3-celled, style glabrous, truncate, not exserted; ovules almost fully anatropous. Fruit 1-seeded, ovoid with more

or less abruptly narrowed, acute beak, green when young, black when ripe, 1.5-1.9 cm. long, 0.7-1.0 cm. in diameter, the beak 0.3-0.4 cm. long. Seed showing generic characters, the scar (in accordance with the shape of the fruit) basilateral.

Henderson Island: north end, jungle on elevated, dissected coral, alt. 33 m., June 18, 1934, *H. St. John and F. R. Fosberg 15137,* type (H, L), with flowers and fruits (tree 8 m. high, 15 cm. in diameter; flowers whitish; some branches fasciated); same locality, June 17, 1934, *St. John and Fosberg 15105* (H, L), with flowers and fruits (tree 10 m. high, 30 cm. in diameter; flowers, ♀ only, and fruits green; bark greenish brown, sapwood white); same locality, June 18, 1934, *St. John and Fosberg 15146* (H, L), with flowers and fruits (tree 5 m. high, diameter 15 cm., flowers green, fruit black, tasting somewhat like olives, with milky juice).

Nesoluma St.-Johnianum is characterized by its large, oblong, glabrous leaves which are, as far as known, greenish yellow when dry. The areoles of the reticulation of the leaves are circular.

3. **Nesoluma Nadeaudi** (Drake) Pierre (nomen in schedula, Paris Herb.)[8] (pl. 5, figs. 103-114)[9].

Palaquium? Nadeaudi Drake: in Nadeaud, Morot's Jour. de Bot. **11**: 110, 1897.

A tree about 10 m. high, bark red inside, wood reddish and very hard (e descr.). Branchlets erect, round, tuberculate by the old inflorescences, about 0.5-0.7 cm. thick, glabrous except the very tips. Leaves glabrous, dark brown when dry (always?), elliptic or rather ovate, bluntly acute at apex, the margins entire, acute and slightly decurrent at base, 6.5-13 by (3-)3.7-5.7 cm., petioles 1.8-3(-4) cm. long, the blade rigid, midrib prominent below, secondary nerves 12-14(-16) not prominent, very slender, straight, ascending at an angle of 50 degrees in the apex and 70 degrees in the base of the leaf; reticulation very minutely and regularly areolate below, areoles circular, inconspicuous above. Inflorescences axillary, fasciculate, 2-4-flowered. Pedicels glabrous, 0.8 cm. in flower, 1.2 cm. in fruit. Flowers (not seen by me, description mostly after Pierre's annotations which in some respects disagree with Drake's description and also with Delpy's pencil drawing) in bud ± 0.4 cm. long, when open 1.2 cm. in diameter and greenish white. Calyx with 5 sepals, 2 larger outside, 3 smaller within, ovate and acute, minutely pubescent outside. Corolla with a very short tube and (5-)6 ovate petals, apparently with some additional smaller and 3-lobed ones which conform to the petaloid stamens; therefore petals and

[8] The label mentions in Pierre's handwriting: "Bull. Soc. Linn., Par. 1899", but Professor Humbert informed me that no mention of this name was found in that journal and volume (which was not available to me). Therefore it is apparently an unpublished new combination.

[9] Description of vegetative parts after the type specimen; also after the description by Drake (which is in many points wrong) and the pencil drawing by Delpy; description of flower mostly after Pierre's annotations and sketches accompanying one of the specimens.

stamens variable in number. Stamens inserted in the base of the corolla tube (7-)9-10(-12), some of them petaloid. Ovary pubescent, apparently without a glabrous basal part, 4(-5?)-celled, contracted into a glabrous conical style, the ovules ascendant with inferior micropyle. Fruit acuminate, 2.5 cm. long and 1.7 cm. in diameter, the pericarp with an abundant and very viscid latex, surrounding a single seed, attached at the very base, 1.5 cm. long and 1 cm. broad, testa hard and thick, dark brown, shining except the large, almost circular and basal scar, faintly trigonous in cross section, the embryo tangential and oblique, with abundant albumen surrounding the thin cotyledons.

Society Islands: Tahiti, "In convallibus Pinai, ad altitudinem 800 m., in (24) aprilo floret et in (12) junio (1896) fructifert", *Nadeaud 402,* type, (P); Moorea, Mount Raai'ri, near Temae, *Nadeaud* without number, Aug. 1897 (P, L).

There is one sheet of the type specimen with a branchlet and a few flower buds, bearing the number Nadeaud 402, and one sheet from Pierre's herbarium with some detached leaves, two dissected flowers and a part of a fruit. This last sheet bears a label with the name *Mimusops dissecta* (non R. Br.) Nadeaud (which is probably a *nomen nudum*) in addition to the name *Palaquium (?) Nadeaudi* Drake. There are several small sheets with annotations by Pierre together with a pencil drawing by Delpy, which, however, is wrong in some details (flower diagram, corolla, and biseriate androeceum, too regularly 5-merous throughout, which does not agree with Drake's description as compared to Pierre's annotations). The specimen from Moorea is represented by four sheets and conforms with the type, except that it is sterile. This being apparently all that is left of the material, it is too scanty to allow detailed checking. I therefore had to depend on Drake's and especially on Pierre's authority.

As has been noted by Pierre in his annotations to the specimen, the "staminodes" (= the smaller petals) may turn fertile, so the number of stamens is variable as well as that of the petals. Moreover the "small petals" or "petaloid stamens", figured in Pierre's rough sketches (copied in figs. 104-108), are found in other species of the genus. Other items of Pierre's drawings agree perfectly with those of the other species of *Nesoluma*. I therefore fully agree with Pierre as to the inclusion of the species in the genus *Nesoluma*, although further examination of more material remains highly desirable.

Nesoluma Nadeaudi is particularly characterized by its ovate, bluntly acute leaves which, as far as known, are dark brown when dry, its relatively large fruits and seeds, and the peculiar, almost basal scar of the seed.

LIST OF COLLECTORS

Brigham, W. T., see under Mann, H.

Brown, F. B. H., and A. F. Judd
1307: N. polynesicum var. β, forma b

Degener, O.
10098 (with Park and Toppina): N. polynesicum, var. β, forma b
10108 (with Park and Takamoto): N. polynesicum var. β, forma a, subf. 1
10642: N. polynesicum var. δ, forma d
10666 (with Takamoto): N. polynesicum, var. β, forma b
11277 (with Takamoto and Martinez): N. polynesicum, var. β, forma b

Forbes, C. N.
1 Mo.: N. polynesicum var. β, forma b
112 Mo.: N. polynesicum var. α, forma a
153 L.: N. polynesicum var. α, forma a
503 L.: N. polynesicum var. α, forma b, subf. 1
2074 M.:N. polynesicum var. α, forma b, subf. 2
2277 M.: N. polynesicum var. α, forma c
2471 O.: N. polynesicum var. β, forma b
no nr. (April-May 1912): N. polynesicum var. β, forma b
See also under Garber, D. W.

Fosberg, F. R.
11596: N. polynesicum var. β, forma a, subf. 2
See also under St. John, H.

Garber, D. W. and C. N. Forbes
148: N. polynesicum var. β, forma b

Hillebrand, W.
no nr. (several specimens in several herbaria): N. polynesicum var. α
no nr. (1 specimen, US): N. polynesicum var. α, forma d

Judd, A. F.
no nr. (March 1932): N. polynesicum var. β, forma b
See also under Brown, F. B. H.

Judd, C. S.
57: N. polynesicum var. β, forma a

Krajina, V.
126: N. polynesicum var. α, forma a

McEldowney, G. and C. Skottsberg
369: N. polynesicum var. β, forma b

Mann, H. and W. T. Brigham
363: N. polynesicum var. α, forma a

Munro, G. C.
31: N. polynesicum var. α, forma a
111: N. polynesicum var. α, forma b, subf. 1
955: N. polynesicum var. α, forma a

Nadeaud, J.
402: N. Nadeaudi
no nr. (1897): N. Nadeaudi

Rémy, J.
474: N. polynesicum var. α, forma a

Rock, J. F.
2336: N. polynesicum var. β, forma a, subf. 1
7052: N. polynesicum var. α, forma d
8040: N. polynesicum var. α, forma a
8040?: N. polynesicum var. α, forma a
8671: N. polynesicum var. α, forma b, subf. 1
8671a: N. polynesicum var. α, forma a
12505: N. polynesicum var. β, forma a, subf. 1
14068: N. polynesicum var. α, forma d
17125: N. polynesicum var. β, forma a, subf. 1
no nr. (April 1928): N. polynesicum var. α, forma d
no nr. (March 1910): N. polynesicum var. α, forma d
no nr. (April 1928): N. polynesicum var. α, forma d

St. John, H.
10124: N. polynesicum var. β, forma b

St. John, H. and F. R. Fosberg
15105: N. St.-Johnianum
15137: N. St.-Johnianum
15146: N. St.-Johnianum
15935: N. polynesicum var. β, forma a, subf. 1
15936: N. polynesicum var. β, forma a, subf. 1

Skottsberg, C.,
See under McEldowney, G.

Stokes, A. M.
391: N. polynesicum var. β, forma a, subf. 1
406: N. polynesicum var. β, forma a, subf. 1

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LEGENDS FOR PLATES

PLATE 1 (figs. 1-9).—*Nesoluma polynesicum*: 1, var. α, forma a (from *Munro 955*); 2, var. α, forma b, subf. 1 (from *Forbes 503 L.*); 3, var. α, forma b, subf. 2 (from *Forbes 2074* M.); 4, var. α, forma c (from *Forbes 2277 M.*); 5, var. α, forma d (from *Rock 7052*); 6, var. β, forma a, subf. 1 (from *Rock 12505*); 7, var. β, forma a, subf. 2 (from *Fosberg 11596*); 8, var. β, forma b (from *McEldowney* and *Skottsberg 369*); 9, var. β, forma b (from *St. John 10124*).

PLATE 2 (figs. 10-41).—*Nesoluma polynesicum*, var. α: 10, branchlet with inflorescences; 11, flower bud; 12-16, diagrams of various calyx types; 17, corolla in bud; 18-20, diagrams of flowers; 21, longitudinal section of flower; 22, part of corolla inside, with two stamens and a "staminode" obliquely attached to one of the petals (cf. diagram below); 23, petal inside with stamen and adnate "staminode"; 24, stamen with additional filament (?), adnate to the pistillum; 25, the stamen of fig. 24 detached; 26, longitudinal section of ovary; 27, fruit; 28, seed, ventral side; 29, the same, lateral view; 30-32, various types of seeds; 33, various corollary structures, a. small outer petal, b. normal petal, c. the two types of inner petals (usually ovate though some have narrowed tip), d. two types of petaloid "staminodes" (petaloid, staminoid), e. two types of staminoid "staminodes", f. two types of scaly petals in ♀ flowers, the ligulate petaloid type (left) and the staminodial one (right, distinguished by its irregular shape, recalling tridentate staminodes); 34, diagram of flower (without calyx) with four large and four small petals and seven stamens, two of which are connate; 35, diagram of flower (without calyx) with fundamentally 5-merous corolla, two of the petals being deeply 2-lobed (see also fig. 86); in addition, there are one deltoid "staminode" and 11 stamens which are smaller (younger) in the part of the corolla in which the petals are not subject to collateral duplication; the three ripe anthers are indicated by an asterisk; 36, inner side and 37, outer side of the corolla of fig. 35; crosses indicate corresponding regions; 38, diagram of a flower with two connate petals, two "staminodes", seven stamens and six carpels; 39-41, various parts of the corolla of fig. 38 as indicated by the arrows, figs. 39 and 40 inside, fig. 41 outside; in fig. 40 the anther of the middlemost stamen has been removed. Figure 10 drawn from type specimen; 11-29 from second specimen in Berlin herbarium; 30 and 32 drawn from *Rock 8040 ?*, 31 from *Munro 955*, 34-37 from *Forbes 503 L.*, 38-41 from *Munro 111*.

PLATE 3 (figs. 42-79).—*Nesoluma polynesicum*, var. β: 42 and 43, two different calyx types; 44 and 45, diagrams of calyces, serial duplication in 44; 46, petals outside; 47, petal inside with one stamen and one "staminode" (cf. "staminode" detached and diagram above); 48, petal with one stamen and obliquely adnate "staminode"; 49, two petals with stamens opposite; 50, petal with filaments and basal hair tuft, the anther has been removed; 51, the same in longitudinal section; 52, petaloid "staminode" with hair tuft like a petal but without bearing a stamen; 53, a similar structure but bearing a stamen; 54-57, various types of staminoid or petaloid "staminodes"; 58, pistillum with longitudinal section and ovule; 59-68, ♀ flowers; 59, type of ♀ flower with exserted style; 60, diagram of same; 61, pistillum of same with longitudinal section, the corolla is scaly and of the petaloid type; 62, pistillum with free petals, one of which is larger; 63, various types of reduced petals in ♀ flowers; 64,

another type of ♀ flower; 65, pistillum of same with scaly corolla of the staminodioid type; 66, corolla of fig. 65; 67, another ♀ flower; 68, pistillum of same, corolla scaly and of petaloid type; 69, flower with petals covering part of an inner sepal, the upper portion somewhat enlarged at left; 70, diagram of this flower with petals of various sizes, two "staminodes", one of which is laterally adnate to a petal, duplication in calyx and corolla, and a bi-merous gynaeceum; 71, longitudinal sections through pistillum of the same flower with indication of an adnate disc; 72-78, ♀ flowers; 72, ♀ flower; 73, ovary and scaly corolla of same; 74, corolla of figs. 72 and 73, staminodioid type; 75 and 76 cross sections of ovaries with sterile cells, in 75 one of the cells biovulate; 77, broadened pistillum with cross section, apparently originating from two connate pistillums; 78, cross section through ovary of same (bilateral symmetry) with two biovulate cells; 79, fruit. (Figures 42-57 drawn from *St. John* and *Fosberg 15936*; 58-63 from *Fosberg 11596*; 64-68 from *St. John 10124*, 69-71 from *Brown* and *Judd 1307*; 72-78 from *McEldowney* and *Skottsberg 369*; 79 from *St. John* and *Fosberg 15935*.)

PLATE 4 (figs. 80-102).—*Nesoluma St.-Johnianum*: 80, branchlet with inflorescences (♂ flowers); 81, portion of lower side of leaf magnified to show the areolate reticulation; 82, flower bud; 83, open flower; 84, diagram of calyx; 85-87, diagrams of three different flowers, in 86 the corolla is fundamentally 5-merous (cf. fig. 35); 88, part of corolla inside, with stamens; 89, two stamens with connate filaments from the flower of fig. 87; 90, two sterile stamens (or staminoid "staminodes"); 91, petal with two sterile stamens; 92, pistillum with longitudinal section; 93, ovula; 94, female flower, the style not exserted; 95 and 96, diagrams of ♀ flowers; 97, pistillum of ♀ flower with some free petals (petaloid type) and longitudinal section with indication of an adnate disc; 98, fruit; 99, seed, lateral view; 100, the same, ventral side; 101, the same, cross section; 102, various types of reduced petals in ♀ flowers. [Figures 80-93 drawn from *St. John* and *Fosberg 15137*; 94, 97-101 and 102 (right-hand figure) from *St. John* and *Fosberg 15105*; 95, 96 and 102 (two left-hand figures) from *St. John* and *Fosberg 15146*.]

PLATE 5 (figs. 103-114).—*Nesoluma Nadeaudi*: 103, branchlet with leaf reticulation magnified; 104, one stamen and some "staminodes"; 105, ovary with longitudinal section; 106, cross section of same; 107, one petal with two fertile stamens and one sterile one; 108, diagram of flower; 109, fruit; 110, longitudinal section of same; 111, seed, lateral view; 112, the same, ventral side; 113, apical view; 114, embryo without albumen. (Figure 103 drawn from type specimen, 104-108 from Pierre's ms. drawings; 109-114 from Delpy's ms. drawings.)

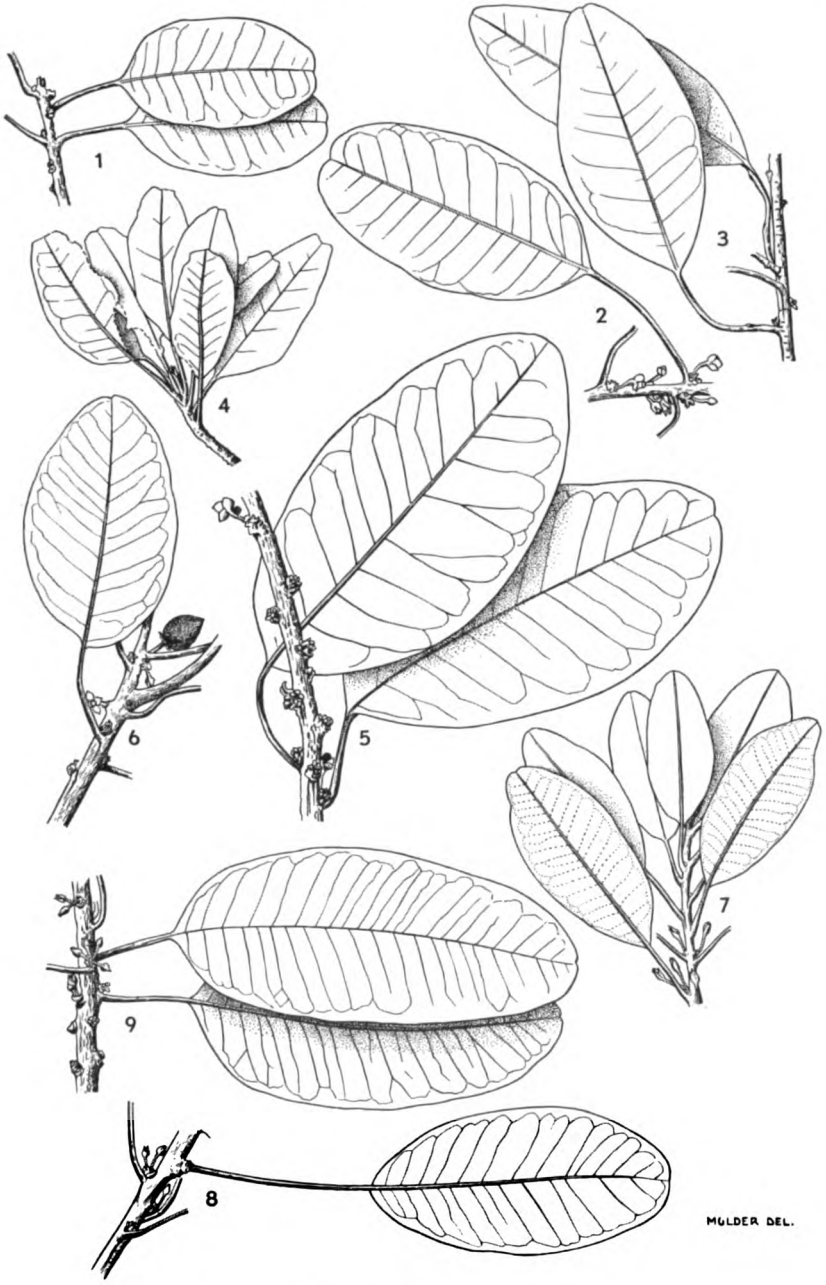

PLATE 1.—*NESOLUMA POLYNESICUM*

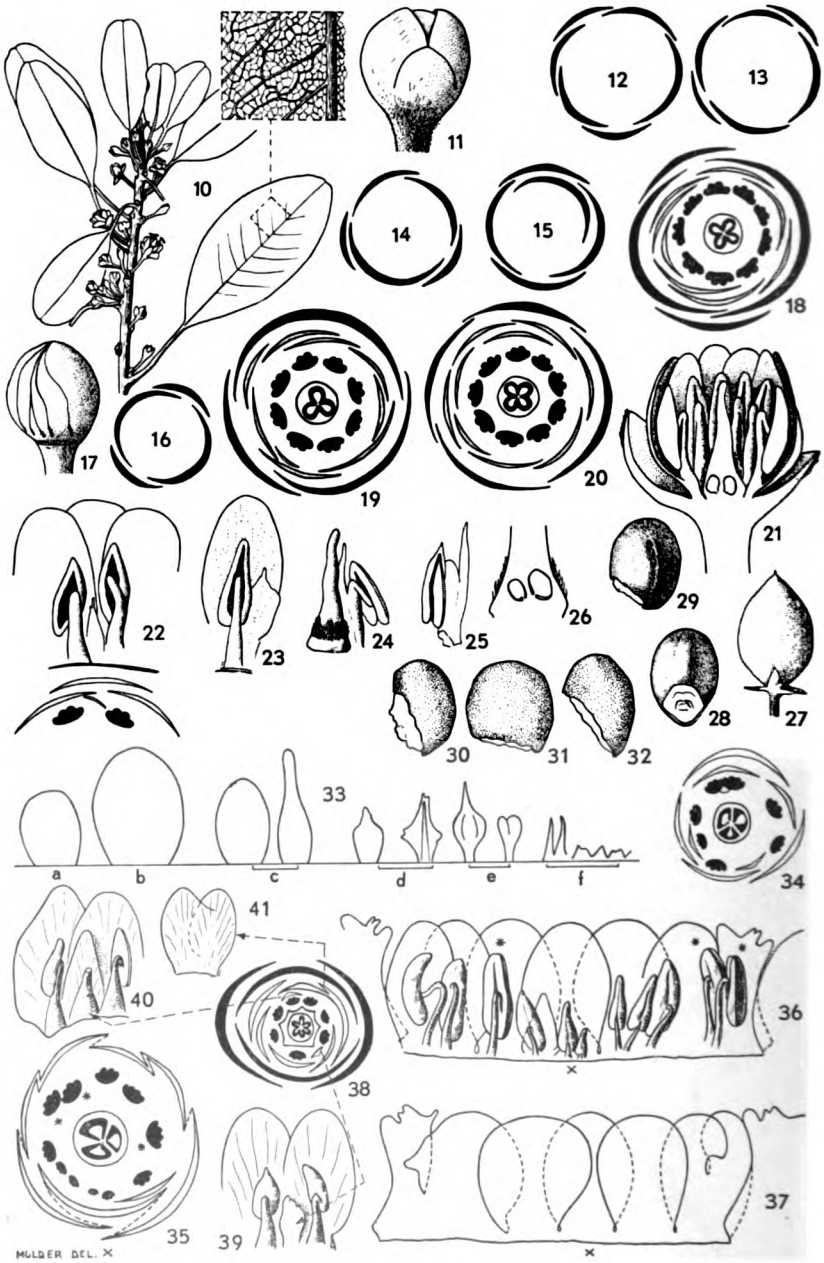

PLATE 2.—*NESOLUMA POLYNESICUM*, VAR. α

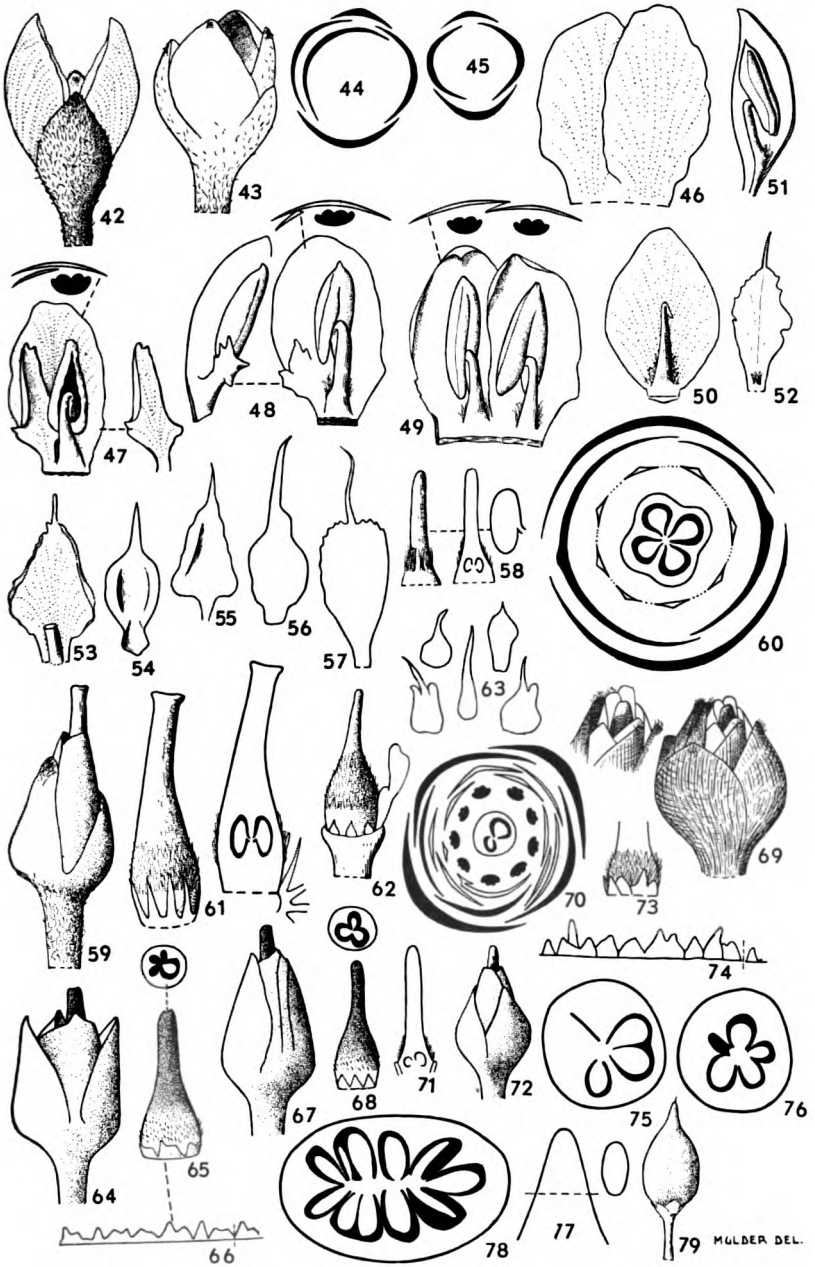

PLATE 3.—*NESOLUMA POLYNESICUM*, VAR. *β*

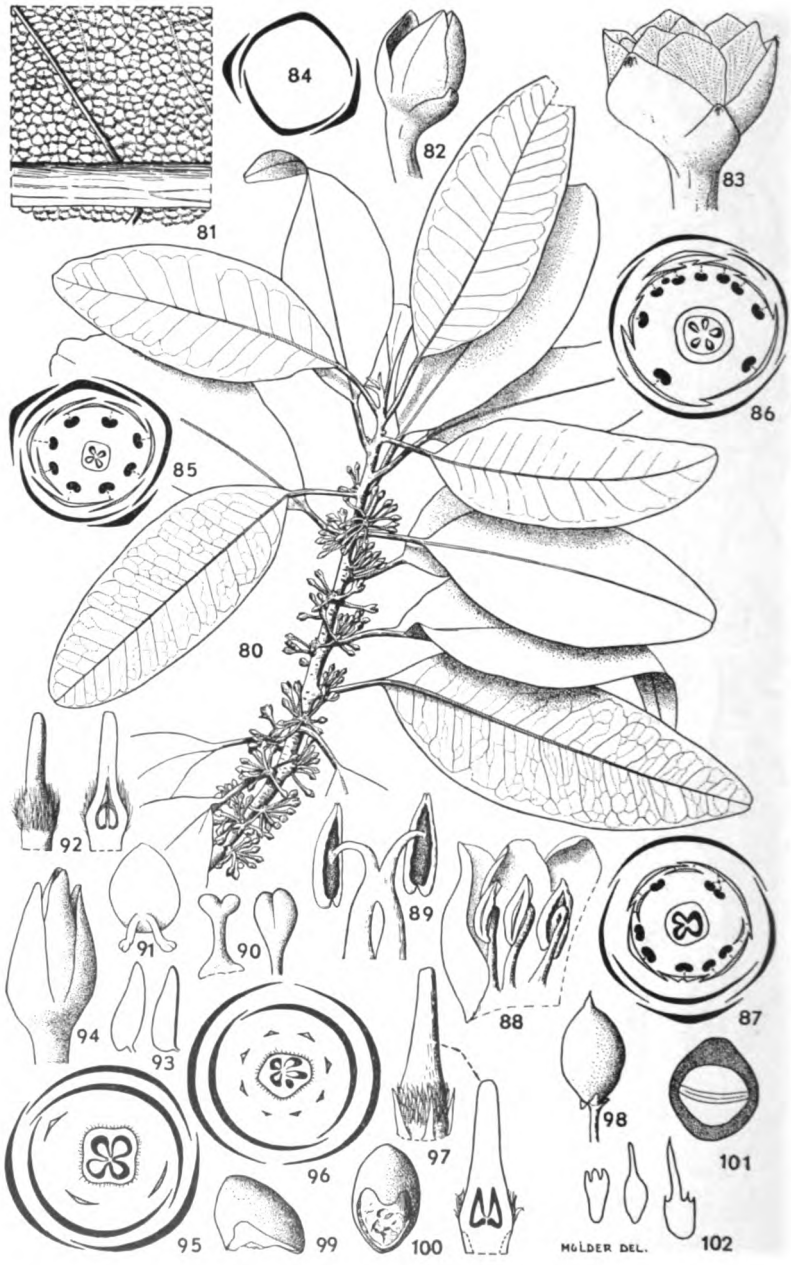

PLATE 4.—*NESOLUMA ST.-JOHNIANUM*

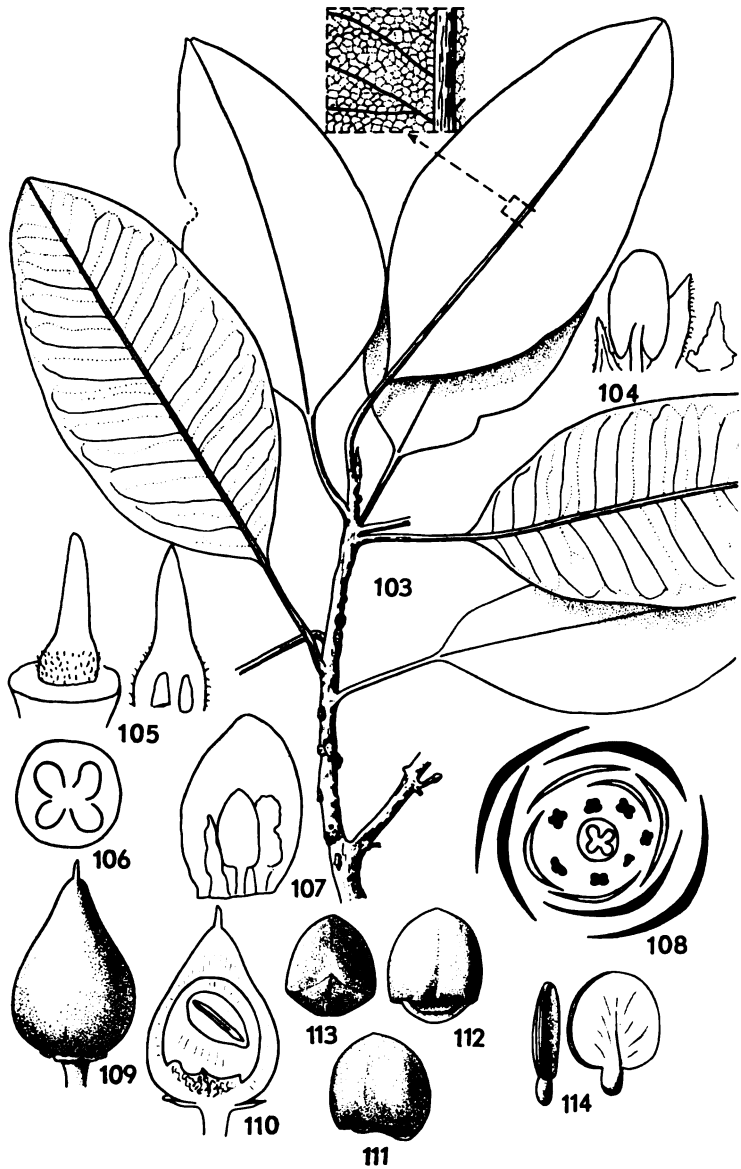

PLATE 5.—*NESOLUMA NADEAUDI*