THE RELATIONSHIP BETWEEN SPHENOSTEMON OF NEW CALEDONIA AND NOUHUYSIA OF NEW GUINEA

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IN REDUCING THE GENUS *Nouhuysia* to *Sphenostemon* — as a basis for emphasizing a closer relationship between the floras of New Guinea and New Caledonia — Van Steenis (7) concluded his brief paper with the statement, "it is still desirable that the wood anatomy be examined." Having published with Dr. Swamy (1) a detailed study of the endomorphic structures of *Nouhuysia* and of the congeneric *Idenburgia* I proceeded to assemble material of the three known species of *Sphenostemon* for a comparative investigation. In so doing, I was unaware of the fact that Dr. Metcalfe had undertaken, at the suggestion of Professor Erdtman, a study of the anatomy of the stems and leaves of *Sphenostemon*. Doctor Metcalfe has kindly sent me an advance copy of his manuscript. Since I am in complete agreement with his descriptions and conclusions, I shall not attempt to record in detail my own observations upon the anatomy of the vegetative organs of *Sphenostemon*, but shall confine my attention primarily to the reproductive ones.

A totality of available evidence from leaves and small stems of herbarium specimens is clearly indicative of close relationship between *Sphenostemon* and *Nouhuysia*. Particularly significant are similarities in the occurrence and distribution of styloids, in nodal anatomy (trilacunar), in vasculature of the leaf (characteristic more or less triangular stele in the petiole and midrib of the lamina), and in the primitive structure of the first-formed secondary xylem. However, as concluded by Metcalfe (6) available anatomical evidence is insufficient for determining whether the genera are congeneric. In this connection, it is desirable to obtain material from the outer parts of large stems as such material frequently exhibits a wider range of structural differences than do the first-formed secondary tissues of small twigs.

MATERIAL

My investigation of the reproductive structures of *Sphenostemon* is based upon material obtained from the following herbarium specimens: *Sphenostemon balansae* Baill. (*Balansa 1330*), flowers, pollen. *Sphenostemon comptonii* Baker (*Compton 1693*), flowers, pollen. *Sphenostemon pachycladum* Baill. (*Buchholz 1297*), flowers, pollen, fruits; (*Franc* in Herb. Arnold Arb.), flowers, pollen.

The extensive collections of *Idenburgia* and *Nouhuysia* utilized for comparative purposes are listed in the paper by Bailey and Swamy (1).

POLLEN

In commenting upon *Sphenostemon* at the VIII[th] International Botanical Congress, Erdtman (4) suggested that "it might be worth while to investigate whether or not the similarity between the strange pollen grains in this genus and those in *Idenburgia* (or *Nouhuysia*), another genus of uncertain taxonomic position from New Guinea, is taxonomically significant." His suggestion appears to have been based upon a comparison between the pollen of *Sphenostemon balansae* Baill. (*Balansa 1330*) and that of *Nouhuysia papuana* Laut. (*Kostermans 2198*).

When examined in water or lactic acid, the pollen grains of the three species of *Sphenostemon* are closely similar in size ($\pm$ 10 $\times$ 13 μ), in form (oblate) and in structure (3-porate and conspicuously reticulate at magnifications of 600–1500). The pores or apertures in the nexine are relatively large for grains of such comparatively small size and are circular or oval, the orientation of the latter varying from lolongate to lalongate. The polar sexine, as noted by Erdtman (5), is at times thinner with faint or absent reticulation. Each pore is subtended by a plug of colorless, transparent, hygroscopic material which expands when moistened, bulging the tenuous sexinous covering outward. This hyaline substance removes ruthenium red very rapidly from dilute solutions in advance of the gradual deeper staining of the protoplast. In this respect, it resembles the papillae which project from moistened pollen of the New World species of *Drimys*, Bailey and Nast (2).

As previously shown by Bailey and Swamy (1), the pollen of *Nouhuysia* varies markedly in size, form, and structure. The large ($\pm$ 35 μ), spherical, nonaperturate grains of *Brass 12661* and *Clemens 5499b* have a conspicuously thickened nexine. The tenuous sexine has a faintly detectable pitted or granular appearance at high magnification. The pollen of other collections of *Nouhuysia* differs in being smaller, oblate and provided with conspicuous pores of varying size, number and orientation. The grains of *Clemens 2422* are 4-porate with an admixture of 5-porate ones, those of *Rutten 2240* are 4-porate with an admixture of 3-porate grains and those of *Kostermans 2217*, *Kostermans 2198*, and *Gibbs 5654* are 3-porate with an admixture of 4-porate ones. The transparent material, which subtends the pores, varies in amount and in the case of the relatively small apertures of more or less circular form in *Kostermans 2217*, *Clemens 2422* and *Rutten 2240* is only slightly protuberant when the pollen is moistened, in contrast to the conspicuous protrusions that occur through the larger, oval, usually lolongate pores of *Kostermans 2198* and *Gibbs 5654*. The pollen from *Kostermans 2217* and *Clemens 2422* have a clearly visible reticulate sexine, but of finer texture than that of *Sphenostemon*. This is in contrast to the sexine of *Clemens 3828*, *Kostermans 2198*, *Gibbs 5654* and *Rutten 2240* which has a faintly visible sculpture at high magnification, thus resembling that of the nonaperturate pollen of *Brass 12661* and *Clemens 5499b*.

Although the pollen from each collection of *Nouhuysia* differs from that

of *Sphenostemon* in one or more of its morphological characters, there is a combination of diagnostic criteria in the genus as a whole which, as noted by Erdtman (4), is strongly suggestive of relationship between *Nouhuysia* and *Sphenostemon*. However, evidence from pollen *by itself* is at present inadequate for determining whether the two categories of plants are congeneric.

STAMENS

The stamens of the three species of *Sphenostemon*, as in the case of the stamens of *Degeneria*, *Himantandra* and a number of other ranalian (sensu lato) genera, cannot be described adequately in conventional terms of filament, anther and connective. They are relatively broad,[1] fleshy micro-

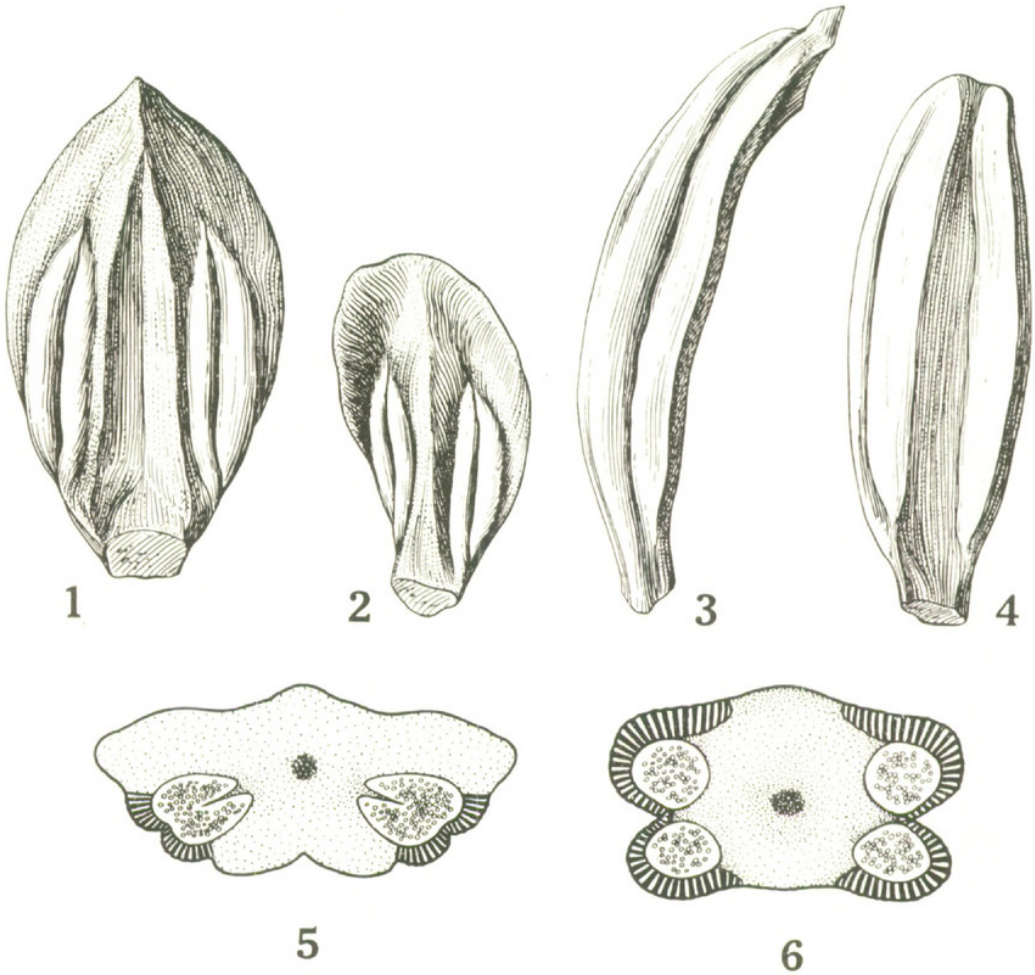


FIG. 1. Stamen of *Sphenostemon pachycladum* Baill. (*Buchholz 1297*), × 15. FIG. 2. Stamen of *S. comptonii* Baker (*Compton 1693*), × 15. FIGS. 3 & 4. Stamens of *Nouhuysia* (*Kostermans 2198*), × 15. FIG. 5. Transverse section of stamen in FIG. 1, × 25. FIG. 6. Transverse section of stamen in FIG. 4. × 25.

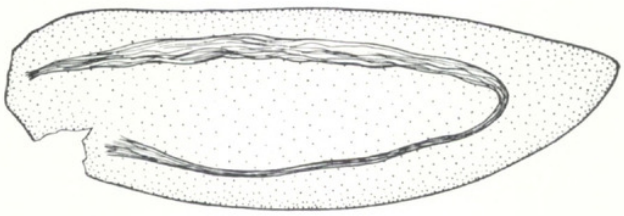
[1] It should be noted in this connection that the normal form of the stamens, i. e. where they are able to expand symmetrically, is frequently modified by excessive lateral pressures of expanding, closely congested organs in the flower buds.

sporophylls, *Figs. 1 & 2*, having deeply embedded sporangia, *Fig. 5*. As in the case of *Degeneria* and *Himantandra*, the fibrous parts of the hypodermis ("endothecium") are restricted to limited areas confronting the sporangia, *Fig. 5*.

In contrast, the stamens of *Nouhuysia* resemble sessile conventional anthers with extensive, markedly protuberant sporangia, *Figs. 3, 4 & 6*. The fibrous parts of the hypodermis are more extensive, *Fig. 6*, in certain collections, e. g. *Clemens 2422*, jacketing the exposed surfaces of the "connective" as well as confronting the protuberant parts of the sporangia.

SEEDS

The seeds of all investigated collections of *Nouhuysia*, and of the congeneric *Idenburgia*, are characterized by a centripetally, deeply lobed stony layer with a corresponding conspicuously ruminate nutritive layer, *Fig. 9*. The vascular system consists of a number of strands, or branches from the supply at the base of the seed. In *Fig. 9*, there are seven such strands, each corresponding with one of the major ruminations of the nutritive layer. The embryo is rudimentary and minute.



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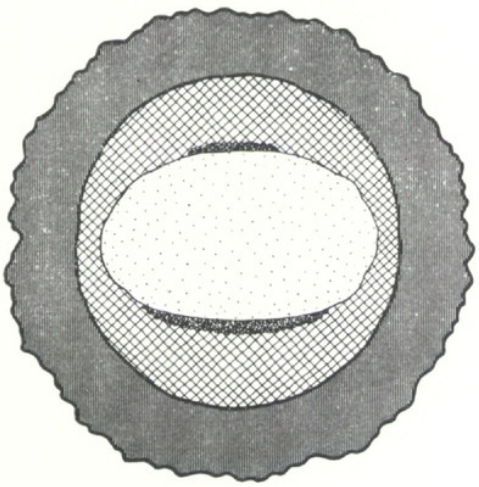

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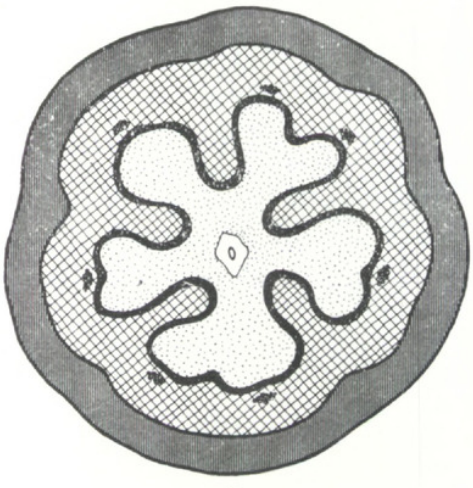

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FIG. 7. Cleared seed of *S. pachycladum* Baill. (*Buchholz 1297*), showing pattern of vasculature, × 5. FIG. 8. Transverse section of fruit and seed of *S. pachycladum* Baill. (*Buchholz 1297*), × 10. FIG. 9. Transverse section of fruit and seed of *Nouhuysia* (*Clemens 2240*), × 9; carpellary wall dark, stony layer cross-hatched, nutritive layer stippled, vascular strands dark.

The dry fruits of *Sphenostemon pachycladum* Baill., *Buchholz 1257*, are of much elongated form (22 × 6 mm.) in contrast to the more or less globose (12 × 10 mm.) or subglobose (15 × 12 mm.) fruits of *Nouhuysia*. The correspondingly elongated seeds contract markedly in drying, but even when reexpanded the sclerotesta and nutritive layers exhibit no evidence of lobing or rumination, *Fig. 8*. The vascular tissue is in the form of a *single* broad band which extends from the base of the seed toward the apex and back again toward the level of attachment of the seed, *Figs. 7 & 8*. That the absence of rumination is not due to immaturity of the fruit is indicated by the fact that rumination of the undifferentiated tissues of *Nouhuysia* is detectable during early stages of the enlargement of the seeds.

DISCUSSION

Evidence from all organs is clearly indicative of close relationship between *Sphenostemon* and *Nouhuysia*. The most conspicuous differences between the two categories of plants are in the reproductive, rather than in the vegetative, organs. The problem of the congeneric status of the genera resolves itself, accordingly, into a matter of consistency in taxonomic judgments. Does the totality of morphological differences exceed the limits of a single generic boundary?

The most outstanding and consistent differences between available collections from New Caledonia and those from New Guinea are at present in the stamens. However, if the seeds of *S. comptonii* Baker and *S. balansae* Baill. resemble those of *S. pachycladum* Baill., fundamental differences in vasculature and rumination may eventually prove to be equally, if not more, significant taxonomically.

It should be noted in this connection that broad microsporophylls with more or less deeply embedded sporangia occur in various representatives of the Magnoliaceae, as well as in *Degeneria* and *Himantandra*. As demonstrated by Canright (3) the chief specializations in the stamens of the Magnoliaceae (sensu stricto) appear to be (1) elongation of the apices, (2) differentiation of a filament, (3) reduction in the number of veins from three to one, (4) an increase in the relative size of the sporangia and a concomitant increase in their amount of protuberance, (5) transition from a laminal to a marginal position of the sporangia, and (6) development of an enveloping fibrous layer in the "connective." It is evident that the differences between the stamens of *Sphenostemon* and those of *Nouhuysia* involve changes comparable to items 4–6 in the Magnoliaceae. If broad sessile microsporophylls with deeply embedded sporangia, e. g. *Magnolia maingayi* King, are to be retained in the genus *Magnolia*, it might not be inconsistent taxonomically to reduce *Nouhuysia* to *Sphenostemon*. However, it seems that final judgment in such matters should be based upon the totality of evidence from all parts of the plant rather than upon similarities or differences in any single organ or morphological feature.

When the differences in the stamens are considered in connection with differences in the pollen, in the seeds, and in the perianth (*Nouhuysia*, 4

tepals or "sepals"?, *Sphenostemon*, 8 tepals or 4 "sepals"? + 4 "petals"?) it appears premature to reduce *Nouhuysia* to *Sphenostemon* until additional material of the plants has been collected and carefully investigated. Furthermore, striking differences in the pollen from different collections of *Nouhuysia* raises the question whether all of them can be included in *N. papuana* Laut.

It should be emphasized in conclusion that the microsporophylls of *Sphenostemon* and the very primitive structure of the xylem in both *Nouhuysia* and *Sphenostemon* make these genera unusually significant phylogenetically. They clearly do not belong in the Guttiferae or Trimeniaceae and it seems unlikely that they are closely related to the Aquifoliaceae. More comprehensive investigations of adequately preserved material are essential for determining their true relationships.

ACKNOWLEDGMENTS

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