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A Quarterly Journal containing Scientific Contributions from the Missouri Botanical Garden and the Henry Shaw School of Botany of Washington University in affiliation with the Missouri Botanical Garden.

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Errata in Vol. XLIII:—

Page 299, line 8—Insert "T:" before *Stork*.

Page 309, caption of fig. 11—Castaneda's number should be 900.

Page 316, line 8—After "RB," insert "S,".

Page 347, line 1—For *rhombofae*, read *rbonbofae*.

Page 354, last line, "illustration" should read "specimen".

Page 382, 14 lines from bottom, *beroeensis* should read *bereroensis*.

Page 385, line 28, "mm." should read "cm."

Page 394, line 5, "annulatus" should read "annulata".

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FEBRUARY, 1956

**A Revision of the Genus *Erechtites* (Compositae),
with Inquiries into *Senecio* and *Arrhenechthites* . . .**

Robert O. Belcher 1-85

**PUBLISHED QUARTERLY AT GALESBURG, ILLINOIS
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Vol. 43

FEBRUARY, 1956

No. 1

A REVISION OF THE GENUS *ERECHTITES* (COMPOSITAE), WITH INQUIRIES INTO *SENECIO* AND *ARRHENECHTHITES* *

ROBERT O. BELCHER

INTRODUCTION

This paper is an outgrowth of a study of the botanical collection of the United States of America Typhus Commission, India-Burma Field Party, which collection is now part of the U. S. National Herbarium. It was made by the author and others from June to November, 1945, in the vicinity of Ledo, Assam, and Myitkyina, Burma, mostly from the immediate environs of military camp-sites as part of an investigation of the epidemiology of severe outbreaks of scrub typhus in those areas.

Although a preliminary report of the botanical studies was made to the Commission in 1946, it was never published and the final evaluation of the role of plants in these epidemics has been deferred pending more accurate identification of the species involved. This has been much more difficult than anticipated, because there is no adequate modern floristic treatment of the area from which the plants came.

A further complication has been the unsatisfactory nomenclatural status of many of the species which fall into the category of so-called pantropical weeds and are regarded by many botanists as too well known and widespread to be worthy of serious consideration. Detailed examination of several such "species" has led to the conviction that such weedy genera are quite generally in need of critical review.

* This paper is part of a dissertation presented to the Rackham School of Graduate Studies, University of Michigan, in partial fulfillment of the requirements for the degree of doctor of science. The able guidance of Prof. H. H. Bartlett, Dr. Rogers McVaugh, and others of the doctoral committee is gratefully acknowledged.

Much of the examination of herbarium material was carried out during the academic year 1951-52, when the author was a Fulbright scholar at Bedford College, London, and the Royal Botanic Gardens, Kew. An account of the rich experiences of that year was published in 1953 (*Asa Gray Bull. n.s.* 2:13-16).

The present paper deals with a complex of genera centered around the genus *Erechtites* Raf. in the subtribe SENECTIONINAE of the Compositae.

The Compositae are represented in the weedy flora of the tropics by numerous species, among them *Erechtites hieracifolia* Raf. ex DC. The fact that numerous specimens of the African *Crassocephalum crepidioides* (Benth.) S. Moore in the U. S. A. T. C. collection were originally determined as *Erechtites hieracifolia* led to the discovery that most Asiatic specimens were in fact wrongly determined as the latter species in the major herbaria studied. An effort to clarify the status of these two species in the weed flora led to a critical study of the genus *Erechtites* in the New and Old World. An attempt was made to locate and compare type material for every binominal published in the genus, and to collate the major treatments of the genus. This revision has also necessitated inquiries into related genera, notably *Senecio* L., *Arrhenechthites* Mattf., *Crassocephalum* Moench and *Gynura* Cass. The status of the latter two genera was discussed by me in a recent paper¹.

ERECHTITES

HISTORY OF THE GENUS

Erechtites was originally published by Rafinesque² in 1817, based on an unnamed plant described by C. C. Robin,³ and it contained one species, *E. praealta* Raf. Sprengel⁴ in 1826 in effect reduced the genus to *Senecio* by reducing the species to *S. hieracifolius* L. Cassini⁵ in 1827 placed *Erechtites* Raf. in section OTHONNÉES of the SENECTIONEAE, with "péricline uniserie, tres-simple, nu à la base", because of Rafinesque's description: "Perianthus . . . denudatus . . . perianthe neither caliculate nor sphacelate". Cassini had earlier (in 1820 and 1825) based the well-defined genus *Neoceis* on *Senecio hieracifolius* L.

In 1831 Lessing⁶ identified a Schiede and Deppe specimen as "*Erechtites praealta*", and cited "*Senecio hieracifolius* L." and "*Sonchus agrestis* Sw. fl. ind. occ.!" as synonyms. In 1832 he published⁷ a thoroughly revised diagnosis for "*Erechtites* Raf.", in which the distinctive characters, including the appendaged style-arm apex, are clearly brought out, and reduced *Neoceis* Cass. to synonymy. He recognized two species, *E. praealta* Raf. and *E. cacalioides* (Fisch.) Less.

De Candolle⁸ in 1838 published "*Erechtites* Raf. fl. ludov. (excl. car.)", with a diagnosis much more resembling Lessing's and Cassini's than that by Rafinesque. *Neoceis* became a section of *Erechtites* containing six species from the Americas. Three new sections were added by de Candolle to receive a total of thir-

¹ Kew Bull. 1955:455-465.

² Florula Ludoviciana. p. 65.

³ Voyages dans l'intérieur de la Louisiane et de la Floride occidentale, et dans les isles de la Martinique et de Saint Dominique pendant les années 1802, 1803, 1804, 1805, et 1806. Vol. III. Flore Louisiane. p. 435. 1807.

⁴ Caroli Linnaei Syst. Veg. ed 16, 3:565. 1826.

⁵ Dict. Sci. Nat. 48:446-466. 1827.

⁶ Linnaea 6:411. 1831.

⁷ Syn. Gen. Comp. 395. 1832.

⁸ Prodr. 6:295. 1838.

teen species from Australasia, including two treated by Cassini under *Neoceis* and a number previously published as *Senecio*.

It is significant that although botanists in general, other than Schultz Bipontinus and Mueller, have not openly questioned de Candolle's treatment of *Erechtites*, de Candolle himself included in the diagnosis of each of the three Australasian sections a query as to the propriety of including it in *Erechtites*! Those doubts were fully justified. The indigenous Australasian and Indonesian species must be excluded from the genus *Erechtites* as here defined.

Comparison of the types and other material of the American species with those of the Old World has led to the conviction that they are not really congeneric, just as de Candolle suspected. The American species, with the exception of two which clearly are discoid species of *Senecio*, agree in having the style-arm apex prolonged into a tuft of fused papillose hairs, which is quite similar to the somewhat longer appendage that helps to characterize *Crassocephalum*. The native Old World species, with the exceptions noted below, all agree in having the style-arm apex bluntly truncated or rounded, and nude or with a marginal fringe of diverging papillae; that is, indistinguishable from the style-arm apex characterizing the genus *Senecio*. The American material is heterogamous. Within the Australasian material occurs every degree of transition from the outer two rows of florets pistillate and filiform to all florets perfect and infundibuliform, or to outer florets ligulate and pistillate; in other words, there is intergradation without a break into both the discoid and the radiate groups of *Senecio*.

The name *Erechtites* was first applied to and must be typified by American material. Therefore the non-congeneric Old World species must receive another name. In the absence of any clear-cut distinction between the majority of these species and other Australasian species which have universally been referred to *Senecio*, I have transferred them, except for six species, to that genus, to which, indeed, most of them were originally ascribed. The only alternative to broadening somewhat the limits of *Senecio* is to set up a new and ill-defined segregate, necessarily impossible of separation except on minute, arbitrary, and unreliable features, a course which I reject.

The return of *all* species of *Erechtites* to *Senecio* has twice been briefly advocated. Schultz Bipontinus⁹ found in a specimen of his *Senecio flavus* (*S. Decaisnei* DC.) from the Canary Islands some slender non-ligulate pistillate marginal florets. On the mistaken assumption that the sole difference between *Erechtites* and *Senecio* was in the filiform pistillate marginal florets of the former, he swept all the species of *Erechtites* and of certain other related genera back into *Senecio*. Yet his figure of *S. flavus* in Barker-Webb and Berthelot's Flora of the Canary Islands¹⁰ clearly shows the style arm bluntly truncated with a corona of divergent hairs, indicating that it is a *Senecio* and not an *Erechtites*! Furthermore, two of the three otherwise identical specimens of *S. Decaisnei* in the Prodrum Herbarium,

⁹ Flora 28:497-498. 1845.

¹⁰ Hist. Nat. Iles Canaries 2:319. t. 107. 1836-50.

duplicates of those cited by Schultz, have *ligulate* marginal florets whereas the third does not, and all have senecionoid style arms.

A somewhat similar position was taken independently by Baron Ferdinand von Mueller¹¹ at one time for the Australasian species of *Erechtites*. He listed nineteen species of *Senecio* under cultivation in the Melbourne Botanic Garden, of which two, *S. hispidulus* A. Rich. and *S. quadridentatus* Labill., were revived names for species which both earlier and later he treated in *Erechtites*. His argument was presented by Bentham¹²: "F. Mueller proposes to unite the two genera *Erechtites* and *Senecio* on account of those supposed intermediate species forming de Candolle's section *Plagiotome*". Bentham rejected this view, and Mueller resumed use of the name *Erechtites*. But later¹³, in describing *Senecio haplogynus* from New Guinea, he stated:

"Bentham and J. Hooker observed already (Gen. Plant. II. 208), that occasionally some thin solely pistillate flowers occur in species of *Senecio*; hence the only characteristic which separates *Erechtites* from that genus is unreliable, and therefore the present plant may be placed in either genus."

This applied to the Australasian material, but overlooked the nature of the style-arm apex which further distinguishes the American species.

Exceptions to this reduction of Old World species to *Senecio* are the six species to be referred, one for the first time, to *Arrhenechthites* Mattf. These species, including *Senecio haplogynus*, are well distinguished from *Senecio*, *Erechtites*, *Crassocephalum*, and *Gynura* by their functionally staminate center florets with short style arms which are densely papillose on their outer faces and are not appendaged. The range of *Arrhenechthites*, formerly known only from the mountains of New Guinea, now includes the Blue Mountains of southeastern Australia.

All this leads to the problem in the Candollean treatment of *Erechtites* posed by Merrill:¹⁴

"This generic name has been accepted by all authors, and yet it is rather curious to note that Candolle, Prodr. 6: 294. 1838, in his full description of the genus, states '*Erechtites* Rafin. fl. ludov. (1817 p. 65 (excl. char.)'. This probably should be interpreted to mean char. emend., as, *ex descr.*, the type *E. prealta* Raf. is now placed as a variety of *E. hieracifolia* (Linn.) Raf. *ex DC.*"

In undertaking the compilation of the 'Prodromus', de Candolle had solicited specimens from all and sundry, promising to give full credit for either specimens or names. The scrupulousness with which he carried out this promise is a challenge to his successors and a reproach to more than one. But in this case it led him into difficulties. There is clear evidence in the Prodromus Herbarium that de Candolle originally considered the American species which he finally placed in *Erechtites* to belong to *Neoceis* Cass. This name in his writing appears repeatedly

¹¹ Catalogue of plants under cultivation in the Melbourne Botanical Garden, October, 1858, in General Report of the Government Botanist for 1858. p. 26. 1859—This is the Cat. Hort. Melb. cited by Bentham (Fl. Austral. 3:659) for *Senecio Lessonii* F. Muell.

¹² Fl. Austral. 3:659. 1866.

¹³ Trans. Roy. Soc. Victoria 1²:14-15. 1889.

¹⁴ Index Rafinesquianus, p. 235. 1949.

on the sheets of the first six species. In some instances there is no other generic designation except on the outside label of the cover, which of course was collated to agree with the published text of the 'Prodromus.' He probably also accepted Casini's relegation of the faultily drawn *Erechtites* Raf. to section OTHONNÉES.

This nicely settled state of affairs was rudely upset in 1830 by a letter from Rafinesque, in which he placed *S. hieracifolius* in a new subgenus. This note, of crucial importance in evaluating both Rafinesque's and de Candolle's interpretations of *Erechtites*, is reproduced here for the first time. It is found in a lengthy folio letter entitled: "Serie de Lettres Botaniques adressées au Prof. Decandolle de Genève, par le Prof. Rafinesque de Philadelphie. N. 5. Octobre 1830 philadelphie," and preserved in the library of the Conservatoire de Botanique, Genève. The writing has faded somewhat, so that some words were only doubtfully deciphered. These are identified by bracketed queries or reconstructions. I am greatly indebted to Dr. Charles Baehni, Director of the Conservatoire, for locating the letter for me, to him and Dr. C. E. B. Bonner for help in transcribing the passage in question, and to Prof. H. H. Bartlett for suggestions on deciphering it. It appears to read as follows:

"13. *Senecio* L. Il faut restituer le G. [genus] *Jacobea* T. pour less S. radiés, nos Esp. [species] ont les rayons 3 dentiformi[bu]s [?, dentiformes?] *S. balsamita* rayons 3 fids, S. G.??—Les vrais *Senecio* flosc. nos 3 Esp. *hieracifolius*, *praealtus* Raf. fl. lud. & *elongatus* P. formant mon S. G. [subgenus] *Erechtites* (fait Gen. fl. lud) Per. fol. ovalitis [?, ovatis? ovalibus?] vix calic.-flosc. fem. vix radiis [?, radiatis ?] filiformi[bu]s vix 5 dentatis."

The intention here seems clear enough. The radiate species of *Senecio* are to be returned to *Jacobea* Tourn. (this is an old and recurrent argument), with *S. balsamitae* perhaps the type of a subgenus on account of its trifid rays. The true (i.e., discoid) species of *Senecio* in the United States are sufficiently distinct from the Old World species (as exemplified by *S. vulgaris*) to be placed in a separate subgenus containing three species. This subgenus *Erechtites* of the genus *Senecio* as here redefined is so changed from the 1817 version as to be scarcely recognizable. Formerly it was ecalyculate, with florets hermaphroditic; now it is scarcely calyculate, with feminine florets filiform. That it is still applied to the same material as was the original genus *Erechtites* is supported not only by his explicit reference to its former status but also by the change of gender of the original specific epithet to agree with the new generic name.

This letter, in my opinion, is the one referred to by de Candolle¹⁵ in a footnote: "Cl. Rafinesque in litt. 1832 [i. e., 1830] forte non immerito distinguit *Erechtites* sp. 3, nempe *hieracifolia*, *praealta* fl. lud. et *elongata*, sed descriptiones nullas edidit." The letter would seem to be the authority for the new combination, "*Erechtites hieracifolia* (Raf. in litt.)". That Rafinesque distinguished three species of *Erechtites*; namely, *hieracifolia*, *praealta*, and *elongata*, at least in the 1830 letter, is scarcely accurate. What he actually did was to designate three discoid species which he regarded as together forming a subgenus of *Senecio*. That he

¹⁵ Prodr. 6:294. 1838.

wrote nothing of their descriptions was but natural, since all three had been described previously, by Linnaeus, by Rafinesque (as *Erechtites prealta*), and by Pursh, respectively.

Now that Rafinesque had identified his genus with *S. hieracifolius* as a subgenus of *Senecio*, the revised diagnosis, while still leaving much to be desired, was recognizable as applying to the Linnaean species. I believe that de Candolle wished: (a) to maintain *Erechtites* (*Neoceis*) as a genus, rather than a subgenus; (b) to accept *Erechtites in sensu* 1830 rather than 1817; and (c) to credit the name to the original author. But the *Erechtites* of 1830 was unpublished. De Candolle's solution was to adopt the earlier and validly published name but to exclude the faulty diagnosis, substituting for it a new one based on that of the now superfluous *Neoceis* Cass., which he demoted to a section. I believe de Candolle meant "*Erechtites* Rafin . . . (excl. car.)" literally, and with justification. About the only feature in common between his diagnosis and the one published by Rafinesque is that in both the heads are described as multiflorous!

Early references to *Erechtites* in floristic works for North America were erratic. W. J. Hooker in 1834 and Darlington in 1837 both cited "*Erechtites* [sic!] *praealta* Raf.—Less." as a synonym of *S. hieracifolius*, which Darlington, however, correctly described as having "heads discoid, branches of the style conic at the apex". Torrey and Gray in 1845 took up the Candollean treatment of *Erechtites*, with "*E. hieracifolia* (Raf.)" the only species. Darlington in 1853 gave "*Erechtites* Rafin.", but followed his own and other previous treatments in describing the capitula as discoid but the "florets all fertile".

Grisebach, who, in 1861, was first to bring both the temperate and the tropical forms of *E. hieracifolia* together under one specific epithet, gave in his generic diagnosis an accurate characterization of the two types of florets in the capitulum. His description of the style branches as conical at the summit would restrict the coverage to the American species only, and indeed he did not mention the many Australasian species added by de Candolle and others.

Baker in the 'Flora Brasiliensis', in 1884, gave a generic description in many respects excellent, but unfortunately maintained the genus in the extended sense, with "styli rami elongati apice truncati vel obtusissimi". He adduced several new synonyms for *E. hieracifolia*, maintained Grisebach's varieties, but with new diagnoses, and described a new species, *E. ignobilis*, as well as treating *E. valerianae-folia*. Gardner had earlier (in 1845 and 1848) described new species of *Erechtites* and of *Senecio* from his Brazilian collections without defining the generic limits explicitly. His two species of *Erechtites* were later reduced, one to a variety, the other to synonymy.

Fernald in 1917 described *E. megalocarpa* from Cape Cod, and at the same time revised *Erechtites* in temperate North America, establishing three varieties of *E. hieracifolia*. Cronquist in 1946 reduced *E. megalocarpa* to a variety of *E. hieracifolia*, a change not recognized by Fernald. Standley and Steyermark in 1947

published without comment *E. agrestis* (Sw.) as a new combination for *E. cacalioides* Less.

In the southern hemisphere, meanwhile, Malme in 1899 described *E. missionum* from northern Argentina, to which Chodat and Hassler soon added a var. *lanceolata*. Cabrera recently transferred *Senecio leptanthus* Phil., *S. goyazensis* Gardn., and *S. valerianaefolius* Gardn. to *Erechtites*.

Thus, since 1838 numerous new species have been described as *Erechtites*, but without critical review of the whole genus. During this time considerable confusion has developed in the application of names, circumscription of species, and delimitation of the genus. As a further complication, there is evidence of introgression among certain of the supposed species, the extent of which can only be determined by field and laboratory studies yet to be made.

The search for typifying material was mostly successful, although a few critical specimens are apparently lost. The lack of a type for *E. prealta* Raf. posed a major problem. The many Australasian sheets in Kew Herbarium which were annotated by Hooker, or Bentham, or both, in the preparation of their treatments of this group, were gone over carefully, and every effort was made to collate them with the types, particularly of A. Richard and de Candolle. Several misapplications of names and erroneous circumscriptions which have passed from the works of Hooker and of Bentham very generally into the taxonomic literature of Australasia have thus been detected and corrected. Numerous other adjustments in the nomenclature of this long-neglected group have had to be made.

The proper spelling of the generic name has long been debated. Rafinesque states that the name "*Erechtites*" was "one of those given by Dioscorides to the *Senecio*". But the spelling used by Dioscorides in the 'Materia Medica' was "ερεχθίτις" and the arguments by Bentham¹⁶ and Hegi¹⁷ for using "*Erechtites*" are perfectly valid. Under the International Rules a case could be made for correcting Rafinesque's spelling as an unintentional orthographic error. If the genus were to be maintained in the extended Candollean sense, then the Benthamian spelling, widely adopted in works on Australasian botany, might well be retained. But since the genus should be restricted to the American species, it seems better to retain the original spelling of Rafinesque, used by most American authors, the 'Index Kewensis' and the Gray Herbarium Index, and Dalla Torre and Harms.

CONDENSED KEY TO THE SENECTIONINAE

The tribe SENECTIONEAE may be characterized as having no latex, corollas of the disc florets actinomorphic, anthers ecaudate, pappus capillary (or rarely setaceous), and style arms usually with a crown of diverging pollen-presentation hairs near the truncated, obtuse, or papillose-appendaged apex (but not in *Ligularia*,

¹⁶ Fl. Austral. 3:657. 1866.

¹⁷ Ill. Fl. Mittel Europa 6²:701. 1929.

Homogyne, Gynura, Cacalia (Adenostyles), Psacalium).

The subtribe SENECTIONINAE O. Hoffm. is further distinguished by having the phyllaries free or very nearly so, and the involucre uni- or biseriate, or if pluriseriate then with the style arms of the perfect florets truncated and penicillate or with a distinct crown of longer hairs.

The following key is based on that given by Hoffman,¹⁸ but has been somewhat condensed and extensively modified to accommodate the following groups: *Arrhenechthites* Mattf.; *Crassocephalum* Moench confused with *Gynura* by Hoffman; certain erechthitoid species of *Senecio*, considered by him as included in *Erechtites*; and four genera revived by Rydberg¹⁹ for the North American species commonly referred to *Cacalia*: *Psacalium* Cass., *Pericalia* Cass., *Mesadenia* Raf., and *Odontotrichum* Zucc. emend. Rydb.

KEY TO THE SENECTIONINAE

- A. Receptacle with paleae *Schistocarpa, Neurolaena*
(cf. *Dubautia* spp.)
- AA. Receptacle without paleae..... B
- B. Disc florets sterile..... C
- C. Capitula not all alike in floral composition, plants being more or less dioecious or polygamous *Petasites, Robinsonia, Rbetinodendron*
- CC. Capitula all alike in floral composition, plants being neither dioecious nor polygamous..... D
- D. Herbs with leaves radical or decurrent..... E
- E. Perennial sticky-haired herbs with decurrent leaves..... *Nannoglottis*
- EE. Herbs with leaves radical; scapose stems beset with scale-like leaves..... *Tussilago*
- DD. Undershrubs or perennial herbs with cauline leaves well developed, not decurrent..... F
- F. Glabrous undershrubs; leaves somewhat fleshy..... *Hertia*
- FF. Pubescent perennials; shoots herbaceous or suffruticose; leaves not fleshy
..... **ARRHENECHTHITES**
- BB. Disc florets fertile..... G
- G. Capitula with disc florets perfect; marginal florets pistillate, with corolla tubular, filiform, or irregularly split, not ligulate H
- H. Leaves radical, cauline leaves scale-like *Homogyne, Stilpnogyne*
- HH. Leaves cauline, not scale-like I
- I. Leaves entire, thickly crowded; branches leafy to base of capitulum..... *Erothrix Melaleuca*
- II. Leaves more or less toothed or divided, scattered, reduced to bracts in the inflorescence J
- J. Pistillate florets tubular, 4-fid; shrubs *Faujasia*
- JJ. Pistillate florets filiform K
- K. Style arm with crown of divergent hairs surrounding appendage of fused papillose hairs **ERECHTTITES**
- KK. Style arm with crown of divergent hairs but truncated or bluntly rounded, not appendaged erechthitoid species of **SENECIO**
- GG. Capitula discoid with all florets perfect and nonligulate; or radiate, with marginal florets pistillate and ligulate or (rarely) bilabiate L
- L. Pappus setaceous *Raillardella*
(cf. *Dubautia* and *Raillardia*)
- LL. Pappus capillary M
- M. Phyllaries 3- to many-seriate *Alciope, Culcitium, Lepidospartum*
- MM. Phyllaries 1- or 2-, rarely 3-seriate, often 1-seriate, with shorter calyculus
..... N

¹⁸ Hoffman, O., in Engl. & Prantl's Die Nat. Pflanzenfam IV⁵:286-289. 1894.

¹⁹ Bull. Torr. Bot. Club 51: 369-378, 409-420. 1924.

- N. Leaves opposite, or only the uppermost alternate
 *Mallotopus, Haploesthes, Arnica, Gynoxys*
- NN. Leaves alternate or radicalO
- O. Receptacle hemispherical, conical, strongly arched, or flat with the center produced in a conical prolongationP
- P. Capitula radiate, receptacle various but not flat and without central cone*Crocidium, Bartlettia, Doronicum*
- PP. Capitula discoid, receptacle flat, with center produced in a conical prolongation; corolla white or whitish, with distinct campanulate throat and long lobes; achene terete, oblong
 *Mesadenia (Cacalia § Conophora DC.)*
- OO. Receptacle flatQ
- Q. Phyllaries with leaf-like appendage along midrib*Lopholaema*
- QQ. Phyllaries without leaf-like appendagesR
- R. Capitula radiateS
- S. Marginal florets bilabiate, inner lip short, outer strap-like.....
 *Brachyglottis*
- SS. Marginal florets ligulate, without inner lip, ligule entire or 2- to 3-dentateT
- T. Achene dorsally compressed*Cineraria*
- TT. Achene not compressed but prismatic or cylindrical, 4- or 5-angled or 5- to 10-ribbedU
- U. Style arms virtually glabrous or at most minutely papillose below the truncated or obtuse apex, with crown of divergent hairs but without appendageradiate species of *Senecio*
- UU. Style arms thickly hairy on most or all of the outer face.....V
- V. Capitula in racemes or racemose-paniculate inflorescences
 *Ligularia*
- VV. Capitula solitary, nodding (in one species discoid)
 *Cremanthodium*
- RR. Capitula discoid (marginal florets sometimes with anthers variably abortive)W
- W. Style-arm apices with greatly prolonged, non-stigmatic, frequently recurved appendageX
- X. Appendage vascularized, densely hairy on outer face; leaves somewhat crowded basally and subpetiolate or sessile; stem subscapose *Gynura*
- XX. Appendage not vascularized; basal leaves peltate*Psacalium*
- WW. Style-arm apices with appendage not exceeding arm in length, or not appendagedY
- Y. Style-arm apex obtuse, unappendaged, lacking crown of divergent hairs Z
- Z. Style arm not hairy, but oblong and revolute
 *Cacalia L. (Adenostyles)*
- ZZ. Style arm uniformly beset with hairs
 *Cacaliopsis, Luina, Peucephyllum*
- YY. Style-arm apex penicillate with crown of divergent papillose hairs which is sometimes indistinct in immature floretsa
- a. Achene inverted-pyramidal or obovoid.....b
- b. Achene inverted-pyramidal*Psathyrotes*
- bb. Achene obovoid, elliptic in cross-section, 10- to 15-ribbed; corolla white or whitish with tube long and slender, throat obsolete, lobes long-linear and extending to throat; basal leaves long-petiolate*Odontotrichum*
- aa. Achene prismatic or cylindricalc
- c. Capitula axillary or in axillary panicles*Bedfordia*
- cc. Capitula terminal or in terminal and axillary inflorescencesd

10 ANNALS OF THE MISSOURI BOTANICAL GARDEN

- d. Style arms thickly hairy on all of outer surface; capitulum solitary, nodding
.....*Cremanthodium* sp.
- dd. Style arms glabrous or at most minutely papillose on outer surfacee
- e. Style-arm apex truncated or low-domed, not appendaged, crown of divergent
hairs usually well developedf
- f. Corolla white or whitish, throat elongate and narrowly funnelform, lobes
conspicuously revolute after anthesis, pappus barbellate, slightly clavate.....*Pericalia*
- ff. Corolla yellowish, infundibuliform, lobes usually erect, pappus not clavate
.....discoid species of *Senecio*
- ee. Style arm acute with more or less prominent non-vascularized appendage of
fused papillose hairs, crown of diverging papillae sometimes imperfectly formed
or nearly wantingg
- g. Capitulum ecalyculateh
- h. Apex tufted with a multiseriate crown, the conical apex slightly pro-
longed in appendage of 3 to 6 short fused papillae; corolla deeply lobed;
low canescent shrubs*Tetradymia*
- hh. Style apex with essentially uniseriate crown, conical apex prolonged in
appendage up to half as long as the style arm proper; corolla not deeply
lobed; herbs*Emilia*
- gg. Capitulum calyculatei
- i. Style-arm appendage about as long as or longer than the style arm
.....*Crassocephalum*
- ii. Style-arm appendage not more than half as long as the style armj
- j. Appendage short, conical*Kleinia*
- jj. Appendage ovoid, capitula large*Notonia*

SYSTEMATIC TREATMENT OF *ERECHTITES*

ERECHTITES Raf. Fl. Ludovic. 65. 1817. Type: *E. prealta* Raf.

Erechtites Raf. *emend.* Less. Syn. Gen. Comp. 395. 1832.

Erechtites Raf. *sensu extenso* DC. Prodr. 6: 295. 1838; Endl. Gen. Pl. 455. 1836-40; Dalla
Torre & Harms, Gen. Siphon. 561. 1906.

Erechtites Raf. *sensu extenso* Benth. & Hook. Gen. Pl. 2:443. 1873; Hoffm. in Engl. &
Prantl, Nat. Pflanzenfam. IV⁵: 291. 1894.

Neoceis Cass. Bull. Sci. Soc. Philomat. 1820:90. 1820; Dict. Sci. Nat. 34: 386, 1825 (*pro
majore parte*).

Senecio spp. L. *et auct.*

Ptileris Raf. Am. Month. Mag. 268. 1818, *nom nud.*; *ex* Jacks. Ind. Kew. 4:657. 1895,
nom. nud.

Annual or with perennial rootstock; roots fibrous; aerial shoots herbaceous or
slightly woody at base, erect, sulcate, leafy, glabrous or variously pubescent. Leaves
alternate, subpetiolate, decurrent, or semiamplexicaul, rarely petiolate, subentire,
serrate, variously incised or lobed, or pinnatifid, acute, glabrous or variously pubes-
cent. Capitula calyculate, heterogamous. Involucre uniseriate, more or less flask-
shaped; phyllaries linear or lanceolate, equal, plurinervate with margins scarious,
connivent in aestivation and anthesis, more or less divergent in fruit, finally diver-
gent and strongly deflexed. Receptacle always without paleae, inconstantly plane,
alveolate, or fimbriate. Marginal florets filiform, 4- or 5-fid, pistillate or some-
times with rudimentary stamens in some, style-arm apices without marginal fringe

of pollen-presentation hairs but with apex conic-appendaged; central florets slenderly infundibuliform, 5-fid, perfect with functional ovary, style-arm apices divergent with a semi-circular crown of pollen-presentation hairs surmounted by a terminal appendage of fused papillose hairs more or less prominently developed, sometimes nearly wanting in section GOYAZENSES. Achene subcylindric to subfusiform, base inconspicuously callose-annulate, apex conspicuously callose-annulate, slightly constricted below the annulus but not attenuate-rostrate, about 10-ribbed, ribs prominent, cartilaginous, light brown, glabrous, intercostal planes dark brown, sparsely puberulous. Pappus pluriseriate, subequal, capillary.

Distinguished from *Crassocephalum*, *Gynura*, *Cacalia* (*sensu strictiore*), and discoid species of *Senecio* by the heterogamous rather than homogamous capitula, from radiate species of *Senecio* also by the corollas of the filiform marginal florets more or less regularly 4- or 5-fid rather than ligulate, and from erechthitoid (and all) species of *Senecio* by the style arm appendaged with fused papillose hairs rather than truncated or bluntly rounded; and from *Arrhenechthites* by the disc florets being numerous and developing viable embryos, rather than few or solitary and abortive.

Includes five species: one highly polymorphic and widespread in the less-elevated or more humid parts of both Americas and adventive in central Europe, Hawaii, Indonesia, and southeastern Asia; one widespread in continental tropical and subtropical America and adventive through many of the tropical Pacific Islands to northern Australia, Sumatra, the Malay States, and southeastern China; and three restricted to South America; not known from Africa. Formerly considered to include several species with filiform pistillate marginal florets, indigenous to Australasia, but these, without exception, lack the terminal appendage of fused papillose hairs on the style-arm apex and are accordingly here excluded from *Erechthites*, and treated as belonging in *Senecio* or (in one instance) in *Arrhenechthites*.

SECTIONS AND SPECIES OF ERECHTITES

Erechthites may be divided into two sections:

ERECHTITES sectio Hieraciifoliae Belcher, *sect. nov.*

Annuae, herbaceae; foliis caulinis non ultra octies longioribus quam latioribus; corolla lobata, non profunde fissa.

Type: *Erechthites hieracifolia* (L.) Raf. ex DC.

ERECHTITES sectio Goyazenses Belcher, *sect. nov.*

Perennes, suffruticosae; foliis caulinis decies longioribus quam latioribus vel angustioribus; appendicibus styli florum marginalium non obviis; corolla lobata, profunde fissa.

Type: *Erechthites goyazensis* (Gardn.) Cabr.

KEY TO SPECIES OF *ERECHTITES*

- A. Annual, herbaceous; length of cauline leaves usually not over eight times their width; marginal florets with style-arm appendages well developed; corolla shallowly cleft
§ HIERACIFOLIAE
- B. Leaf sessile, or if briefly petiolate then petiole conspicuously alate; diameter of capitulum about $\frac{1}{2}$ its length; marginal florets bi- or pluriserial; pappus white 1. *E. hieracifolia*
- BB. Leaf petiolate or inconspicuously alate at base.
- C. Diameter of capitulum less than $\frac{1}{3}$ its length; marginal pistillate florets uniserial or sub-biserial; style-arm appendages long; corolla and pappus usually more or less reddish.....2. *E. valerianaefolia*
- CC. Diameter of capitulum $\frac{1}{2}$ its length or more; marginal pistillate florets bi- or pluriserial; style-arm appendage short; corolla and pappus whitish.....3 *E. missionum*
- AA. Perennial, suffruticose; length of cauline leaves at least ten times their width; marginal florets with style-arm appendages poorly developed, sometimes wanting; corolla deeply cleft.....§ GOYAZENSES
- D. Capitulum slender, scarcely exceeding 1 cm. long and 0.4 cm. wide; corolla lobes linear-lanceolate.....4 *E. goyazensis*
- DD. Capitulum thick, 2 cm. long, 1 cm. wide, or larger; corolla lobes deltoid
5. *E. ignobilis*

§ HIERACIFOLIAE

1. *ERECHTITES HIERACIFOLIA* (L.) Raf. ex DC. Prodr. 6: 294. 1838.

Annual herb, 4 cm. to 2 m. tall, simple or much branched above; stem glabrous, setose, or pilose. Leaves alate and attenuate at base or semiamplexicaul, acute, with 8 to 25 indistinct pinnate veins on either side, each diverging from the midrib at about 45° , running irregularly forward and terminating in an acute callose tooth; oblanceolate, oblong-lanceolate, lanceolate, or linear-lanceolate; margins subentire, irregularly serrate, incised-serrate, sinuate-dentate, irregularly and coarsely lobate-dentate, or subpinnatifid; glabrous or minutely pubescent on nerves beneath or sparsely to densely clothed with fine unicellular or coarse multicellular hairs up to 5 mm. long in pilose states of var. *cacalioides*; membranous to subcoriaceous; lower ones from 1 to 10 to 30 cm. long, 0.5 to 2 to 7 cm. wide, gradually or abruptly reduced upwards. Inflorescence varying from a single terminal capitulum in depauperate specimens to decomposed terminal and axillary corymbose panicles of 50 or more capitula; branches glabrous to pilose, bracts ranging from broadly amplexicaul to attenuate. Capitula with bracteoles of the calyculus linear, variable in number and length, and glabrous or ciliolate with unicellular or multicellular hairs and either with or without multicellular hairs on their outer faces. Phyllaries 8 to 11 (to 13 to 15) mm. long, 0.5 to 1.0 (to 2.0) mm. wide, broadly linear or oblong, entirely glabrous to sparsely setulose; apices bluntly acute to subobtuse, often darkened but not sphacelate, usually minutely papillose-ciliolate. Florets numerous, varying from 20 to 25 (to 150 or more); corolla of marginal florets in var. *hieracifolia* and var. *cacalioides* 7.5 to 11 mm. long with throat 0.5 to 1 mm. long and only slightly dilated to diameter of 0.5 to 0.75 mm., 4- or sometimes 5-fid, lobes 0.4 to 0.5 mm. long, in var. *megalocarpha* similar, 10 to 12 mm. long; corolla of disc florets in above varieties 8 to 12 mm. long, throat 1.5 to 2 mm. long, slenderly campanulate, with circumference of 1.5 to 2.0 mm., 5-fid, 10-nerved, lobes 0.5 to 0.7 mm. long; corolla lobes in disc florets of var. *megalocarpha*

11 to 13 mm. long, very slenderly campanulate, throat 1 mm. long, 5-fid, lobes 0.75 mm. long, 0.4 to 0.5 mm. wide. Achenes strongly costate.

Species highly polymorphic, but divisible into three varieties. Widely distributed from southern Canada to northern Argentina, but absent from the prairie, high montane, and Pacific coastal regions. Unknown from Africa, the Near East and Australasia. Its reputation as a pantropical weed rests largely on confusion with *Crassocephalum crepidioides* (Benth.) S. Moore.

Several departures of the foliage from the narrowly defined type have been given varietal or even specific rank. In fact, *Erechtites* itself was founded on one such variant. After examining a large suite of specimens, both dried and living, I have concluded that foliar characters do not offer a reliable basis for separation of varieties (nor for the establishment of *formae*) within this species. I have seen every degree of variation in the leaf from the subpetiolate oblanceolate to the broadly amplexicaul lanceolate state without finding at any point an obvious and usable discontinuity. Furthermore, I have been able to duplicate much of the spectrum of variation in greenhouse culture by manipulation of the environment. The same series of foliar variation is clearly discernible in plants both of tropical and of temperate habitat.

I have based the two main varieties maintained here on features which do appear to be discontinuous and to show a geographical pattern. The most accessible of these features are the length of the calycular bracteoles and the type of pubescence. That it has been necessary to use so slender a distinction will perhaps in itself be sufficient answer to those who, without extensive examination of the full range of variation, would establish separate species for the extremes of the temperate and the tropical zones.

KEY TO VARIETIES OF *ERECHTITES HIERACIFOLIA*

- A. Bracteoles of the calyculus extending less than $\frac{1}{4}$ the length of the involucre; bracteoles of the peduncle much shorter than the involucre; all bracteoles glabrous or beset with unicellular hairs only.
- B. Capitula with denuded receptacles less than 1 cm. in diameter; achene 2.5 to 3 m. long, 10-costate.....1 a. var. *hieracifolia*
- BB. Capitula with denuded receptacles more than 1 cm. in diameter; achene 4 to 4.5mm. long, 16- to 20- costate1 b. var. *megalocarpa*
- AA. Bracteoles of the calyculus extending more than $\frac{1}{4}$ the length of the involucre; bracteoles of the peduncle approximately as long as the involucre; all bracteoles ciliolate with multicellular hairs.....1 c. var. *cacalioides*

1a. *ERECHTITES HIERACIFOLIA* var. *HIERACIFOLIA*

Senecio hieracifolius L. Sp. Pl., ed. 1. 866. 1753; ed. 2. 1215. 1762; ed. 3. 1215. 1764; non L. Mant. 469. 1771, which is var. *cacalioides*; non Forssk. Fl. Aegypt. 73. 1775; non Walt. Fl. Carol. 208. 1788, a radiate species; non Herb. Labill., which is *Senecio minimus* Desf. ex Poir.!

Sonchus laevis Sloane, Cat. Pl. Jam. 122. 1697; Nat. Hist. Jam. 255. 1707 (vol. 5, p. 1 Sloane Herb. BM!, first record of temperate var. *hieracifolia* in the Caribbean, surely not in Madeira).

Anonyme Robin, Voy. Louisiane 3:435. 1807, basis of *E. prealta* Raf.

Erechtites praealta Raf. Fl. Ludovic. 65. 1817.

Senecio seminudus Bory, Ann. Gén. Soc. Phys. 1: 303-307. pl. 12. 1819; figure clearly depicting non-amplexicaul reduced upper leaves described by Fernald for var. *intermedia*.

Neoceis hieracifolia (L.) Cass. Bull. Sci. Soc. Philom. 1820: 91. 1820; Dict. Sci. Nat. 34: 387. 1825; type of *Neoceis* Cass.

Neoceis rigidula Cass. 1. c.; by descr. also equivalent to var. *intermedia* Fern.

Senecio hieracifolius L. var. *gigantea* Raf. Med. Fl. 2:262. 1830; by descr. a very robust specimen, to 8 ft. tall, of the typical variety.

Senecio Vukotinovici Schloss. Oesterr. Bot. Zeit. 31: 5. 1881; Schloss. ex Vukot. Rad. Jugoslav. Akad. 58: 85, 145. 1881.

Senecio sonchoides Vukot. Fl. Exsicc. Austro-Hungr. n. 658. 1881 [?], based on Schlosser's species, superfluous; *non* Kunth in HBK. Nov. Gen. & Sp. 4: 178. 1820.

Erechtites hieracifolia (L.) DC. var. *glabrescens* O. Ktze. Rev. Gen. Pl. 1:335. 1891, *nom. nud.*

Erechtites hieracifolia Raf. forma *minor* Waisb. Oesterr. Bot. Zeit. 45:109. 1895; said to be united to the typical state by "Uebergangsformen"; *Waisbecker* (US!) agrees exactly with authentic material of var. *praealta* Fern.

Ptileris hieracifolia Raf. ex Jacks. Ind. Kew. 2:657. 1895; *nom. nud.*

Erechtites hieracifolia (L.) Raf. in DC. var. *typica*, var. *intermedia* Fern., and var. *praealta* (Raf.) Fern. Rhodora 19:27. 1917; Gray's Man., ed. 8. 1528. 1950.

Cytology: Cooper, Bot. Gaz. 98:348-355, 1936.

Seedling Morphology: Kummer, Weed Seedlings, 381-382, 1951.

Common names: Fireweed; Butterweed (Kentucky Mountains).

Lectotype: "*Senecio hieracifolius*," 996-1 (LINN!)²⁰

Habit, stem, and foliage as in the species. Bracts subtending the peduncles and peduncular bracteoles usually not as long as the capitulum, often not half as long; calycular bracteoles linear, very short, glabrous or sometimes minutely ciliolate with unicellular hairs, never having coarse multicellular hairs; phyllaries (7 to) 11 to 16 (to 21), linear, glabrous or minutely glandulose-papillose. Denuded receptacles (3 to) 5 to 8 (to 9) mm. in diameter. Achenes 2.5 to 3 mm. long, 0.5 mm. in diameter, 10-costate.

Prince Edward Island to southeastern Saskatchewan to Minnesota, south to southeastern Texas, to Florida; of scattered occurrence in the West Indies from Cuba to Puerto Rico and possibly through the Lesser Antilles to Venezuela and the Guianas; an introduced weed in the Hawaiian Islands and Central Europe; primarily an occupant of recently disturbed areas in forest zones.

CANADA. PRINCE EDWARD ISLAND: Bunbury, Aug. 1912, *Fernald, Long & St. John* 8242 (K). QUEBEC: St. Lawrence Estuary, Portneuf, Aug. 1928, *Marie-Victorin* 28309 (K, S); Île Perrott, Oct. 1928, *Marie Victorin* 28657 (K, S); Gatineau Park Skyline Trail, July 1941, *Senn* 2078 (S). ONTARIO: Battersea, Aug. 1898, *Fowler* (F); Galt, bogs, Aug. 1899, *Umbach* (F); Algonquin Park, Aug. 1900, *Macoun* 21827 (F) SASKATCHEWAN: Alameda, *Drummond* (K).

UNITED STATES. MAINE: Mt. Megunticook, Camden, Aug. 1930, *Steyermark* 2181 (F); Megunticook Lake near Tsuga Lodge, Sept. 1946, *Friesner* 20982 (S). MASSACHUSETTS: Cambridge, waste ground, Aug. 22, 1928, *Smith & Steward* in *Pl. Exsicc. Gray* 899 (as var. *intermedia* Fern., F, K, MICH, S); Cape Cod near Nine Mile Pond, Sept. 1898, *Greenman* 399 (K); Wakefield, Tyler's Woods, Sept. 1915, *Ripley* 15816 (S); S. Dartmouth,

²⁰ Herbaria in which cited specimens are located are indicated by abbreviations recommended by Lanjouw (International Code of Botanical Nomenclature adopted by the Seventh International Botanical Congress, Stockholm, 1950).

Salter's Point, Sept. 1917, *King 146* (F); Dracut, sandy field, Aug. 1930, *Beattie* (K, det. as var. *praealta* Fern., very depauperate). CONNECTICUT: New Haven, 1858, *Eaton*, (S); Groton, dry woods, Sept. 1927, *Janssen* (S). NEW YORK: mint woods near North Che-mung, July 1896, *Lucy 5216* (S); Binghamton, Ely Hill, recent clearing, Aug. 1886, *Millspaugh* (F); Long Island, Cold Spring Harbor, Aug. 1903, *Whitford 75* (F). NEW JERSEY: Milltown, July 1891, *Halstead's Amer. Weeds No. 40* (MICH); Pleasantville, in marsh, Oct. 1916, *Tidestrom 7999* (F). PENNSYLVANIA: Bethlehem, Aug. 1832, *Moser* (K, FI); Philadelphia, Sept. 1849, *Prior* (K); West Chester, *Darlington* (K, FI); Dauphin, Sept. 1887, *Small* (F); Lancaster Co., near Smithville, Sept. 1892, *Heller & Halbach* (F); Strattonville, Oct. 1928, *Eggleston 22838* (US). OHIO: Elyria, shale banks of Black R., Oct. 1891, *Strong* (MICH); Albion, July 1897, *Ashcroft* (F); Sandusky, Sept. 1908, *Mosely* (F); Lawrence Co., clay pit south of Blackfork, Sept. 1952, *Belcher 1115, 1116, 1117*; same location, Oct. 1952, *Belcher 1122 to 1140* inclusive (series to show range of variation, with achenes for planting). INDIANA: Dune Park, Aug. 1890, *Hill 116* (F); Wells Co., near Bluffton, Aug. 1898, *Deam* (F); Miller, base of dune, Sept. 1900, *Lansing 1198* (F, 2); west of Metamora, Sept. 1935, *Friesner 9187* (F). ILLINOIS: Lake View (Chicago), Sept. 1884, *Oblendorf* (F). MICHIGAN: New Richmond, Aug. 1910, *Kauffman* (MICH); Benton Harbor, near St. Joseph Riv., Sept. 1910, *Lansing 2877* (F); Clinton, Sept. 1838, *Houghton* (MICH); Prairie Rhonde, edge of rich maple woods, Sept. 1903, *Burgess 287* (F); Mackinac Co., Prentis Bay, Sept. 1916, *Eblers 272* (MICH); Menominee Co., between Cedar River and Stephenson, Aug. 1933, *Grassl 3005* (MICH); Drayton Plains, Aug. 1922, *Farwell 6354* (MICH); St. Clair Co., near Port Huron, Aug. 1892, *Dodge*, (MICH); Flowerfield, *Burgess 424* (F); Ann Arbor, Aug. 1862, *Almendinger* (MICH). WISCONSIN: Raukana, Aug. 1879, *Schuette* (F, upper leaves broadly amplexi-caul, most westerly station noted for this variant); Dane Co., N. of Cross Plains, Sept. 1916, *Heddle 2667* (F); Trempealeau, Aug. 1927, *Fassett 4496* (MICH). MINNESOTA: Center City, Aug. 1892, *Taylor* (S). IOWA: Decatur Co., Aug. 1898, *Fitzpatrick* (F). MISSOURI: St. Louis, 1832, *Drummond* (K, 2); Davis Spring, Aug. 1937, *Moore* (F); Shelby Co., N. W. of Emdem, Sept. 1948, *Steyermark 66595* (F); N. W. of Chillicothe, Aug. 1951, *Sparling 1325B.* (F). DELAWARE: dune region between Cape Henlopen and Rehoboth Beach, *Snow 72, 192* (F). MARYLAND: Relay, Aug. 1910, *Jones* (F). DIST. OF COLUMBIA: near Georgetown, Oct. 1858, *Schott* (F); Washington, Sept. 1897, *Pieters* (MICH, complete plant 8.5 cm. tall, one capitulum). WEST VIRGINIA: Smyth Co., Pine Glade Mtn., Aug. 1892, *Small* (F). NORTH CAROLINA: Statesville, *Hyams* (MICH); Hot Springs, Aug. 1924, *Wehmeyer 694* (MICH, 2). KENTUCKY: Bell Co., near Wasioto, Sept. 1893, *Kearney 502* (F); Meade Co., Otter Creek, Sept. 1950, *Een* (S); about 2 mi. west of Ashland, on weathered shale in highway cut, Sept. 1952, *Belcher 1118, 1118A*; roadside mark 7 mi. E. of Vanceburg, by edge of woods, Sept. 1952, *Belcher 1119* (shade form, leaves petiolate). ARKANSAS: Bradley Co., Jersey, "bottom thickets, 8 ft. high", Sept. 1938, *Demaree 18313* (F); Warren, banks of Saline River, Sept. 1938, *Demaree 18388* (F). TEXAS: Harrisburg, Sept. 1875, *Joor* (MICH); Hocklev, 1890, *Thurow* (F). FLORIDA: Miami, *Hitchcock* (F); S. of Florida City, March 1930, *Moldenke 744* (K, S); Duval Co., waste places., *Curtiss 1556* (K, S); vicinity of Eustis, March 1894, *Nash 111* (K, MICH); Ft. Myers, 1900, *Hitchcock 142* (F); Clarcona, Nov. 1899, *Meislabn 126* (US); Palm Beach, 1896, *Hitchcock 925* (F).

WEST INDIES. CUBA: Havana, Guanabacoa, May 1914, *Ekman 618* (S); Oriente, Bayate. Nov. 1914, *Ekman 3403* (S); Sierra Maestra, above Daiquiri, Oct. 1916, *Ekman 8063* (S). JAMAICA: St. Louis, roadsides, 1850, *Prior* (K); Glasgow, near Troy, Oct. 1917, *Harris 12637* (F). HAITI: Dept. du Nord, cultivated field north of St. Michel, Dec. 1925, *Leonard 7741* (F); Massif du Nord, May 1927, *Ekman H8305* (S). DOMINICAN REPUBLIC: Santo Domingo City, at Rio Ozama, Jan. 1929, *Ekman H-11375* (S). PUERTO RICO: waste ground, Martin Pena, March 1924, *Dale* (MICH); Cayey, in Monte Llano, Sept. 1885, *Sintenis 2412* (F, left and center specimens only, right is *Sonchus* sp.).

EUROPE. CZECHOSLOVAKIA: Moravia, prope urbem Pferov, Aug. 1928, *Ortuba, Fl. Exsic. Reipub. Bohem. Slov. 951* (S, US); Olmüvzl, Pferov, Sept. 1938, *Laus* (K). AUSTRIA: prope Purkersdorf, Sept. 1909, *Keller 5102* (S); Söchau, Waldblössen, Aug.

1909, *Sabransky* (S), Waldrodungen, *Sabransky* (US); Wurmberg prope Pettau, Sept. 1915, *Maly* (K, 2). HUNGARY: Comit. Arad. in silvis caeduis montis Piliske, Aug. 1916, *Kümmerle & Jávorka*, *Fl. Hung. Exsic.* 588 (F, K, S, US); Reposmere, Sept. 1922, *Jávorka* (K); Waldschläge bei Güns, Aug. 1897, *Waisbecker* (US, as "*E. hieracif.* Raf. v. *minor* Waisb."); Croatia, in silvis caeduis Maximir, July 1883, *Vukotinovič* (K), in silvis caediis ad Zagrabam, *Wormastiny*, *Fl. Exsic. Austro-Hung.* 658 (K). RUMANIA: Transylvania, ad Görzcuysrentinirc, Sept. 1913, *Heuzyel* (S).

HAWAIIAN ISLANDS. KAUAI: near Hanalei, Sept. 1922, *Degener 1521* (NY). OAHU: Honolulu, "introduced weed", June 1916, *Hitchcock 13716* (US); Honolulu, Tantalus Mountain, June 1923, *Degener 1520* (NY). MOLOKAI: Tukoo, Oct. 1916, *Hitchcock 15034* (US). WEST MOLOKAI: Hauakea, Pali, arid plain, April 1928, *Degener 18134* (NY). HAWAII: Flow of 1840, Puwa [?], July 1915, *Forbes 1055-H* (NY).

Fernald concluded that "*Erechtites hieracifolia* is a very polymorphous plant and that much tropical American material referred to it belongs clearly to some other species. In the eastern United States and Canada the plant, although apparently all of one species, is very variable." He defined *Senecio hieracifolius* L. as having auriculate-based clasping leaves, on the basis of Hermann's figure and the diagnosis in the 'Species Plantarum'; and *Erechtites praealta* Raf. as having all leaves basally narrowed, on the basis of Rafinesque's description. He then stated that these two plants are "in their involucre and achenes clearly extremes of one species, but so different in foliage that they should be designated as forms or varieties". Fernald next stated that the most common variation appeared to be neither of the above, but one "with the upper leaves sessile and broad at the base but very rapidly decreasing to small bracts below the inflorescence", which he described as a new variety, *intermedia*. From an examination of herbarium material he concluded that "the three plants seem to have somewhat different ranges and they are therefore here treated as geographic varieties"; namely, var. *typica*, var. *intermedia* Fern., and var. *praealta* (Raf.) Fern. This treatment he maintained without modification in the 8th edition of 'Gray's Manual.'

Fernald's paper afforded an excellent starting point for my investigations, but I have to disagree with his conclusions. The tropical material is not specifically distinct from that of the temperate zone. His new variety *intermedia* has previously been described as a species. The three states he named do not in fact have clearly distinct geographical ranges, but may exist side by side in the field and may occur in the progeny of a single plant during greenhouse culture. Finally, he formed a very inadequate concept of *E. praealta*.

The earliest name applied to the "intermediate" state is *Erechtites praealta* Raf.! As there is no specimen surviving, it must be typified by Robin's description. This is of a discoid Composite some 6 or 7 feet tall; with sessile leaves 1 foot long and 4 inches wide, oblong, attenuated toward the base, irregularly toothed, acute, glabrous with the nerves underneath covered with down; the involucre "monophyllous" 7 to 8 lines long, 3 to 4 lines in diameter, fleshy, "glanduleuse", striate, terminated by a score of little teeth; florets white, 5-toothed; growing in the open near woods and flowering in September.

This description undoubtedly applies to an *Erechtites*, despite omission of several details. It also obviously refers to a very robust specimen. The description of the

leaf is hardly definitive. The measurements of size certainly do not apply to all of the leaves indiscriminately, but surely only to the lower ones. It then is reasonable to assume that the phrases which immediately follow these measurements; namely, "oblongues, plus rétrécies à la partie inférieure", also apply to these same large lower leaves and therefore *not necessarily* to those higher up which are of course smaller. It is a general feature of every complete dried plant of *Erechtites* which I have seen, and of all those which I have grown from seed or seen in the field, that the lowest leaves are basally narrowed, even to the extent of being briefly petiolate.

This intimate association of the description of the size and of the base of the leaves was, however, severed by Rafinesque, who also modified the description in other unfortunate ways. Thus Fernald, apparently without referring to Robin's original description, construed Rafinesque's "foliis . . . basi attenuatis" as applying to *all* the leaves and particularly to the upper ones. He therefore placed the taxon *praealta* in varietal status, containing the plants which do have all the leaves attenuated; that is, those depauperate specimens called f. *minor* by Waisbecker. Although Fernald cited no specimens for his var. *praealta*, all of the sheets distributed from the Gray Herbarium under this name which I have seen are of this depauperate state, scarcely one foot tall, so much at variance with Robin's description and so contradictory of the epithet.

In several hundred sheets of *E. hieracifolia* var. *hieracifolia* from a dozen major herbaria, I have seen virtually every conceivable degree of intergradation among the extremes recognized by Fernald. And, like Deam,²¹ I have seen and collected not two but all three of these extremes plus other intermediate states in the same location, growing virtually side by side, with the variation in leaf form correlated with over-all size and that apparently directly related to soil fertility and moisture supply.

This field experience has been substantiated by four years of growing these plants in the greenhouse under varying conditions of moisture, fertility, and photoperiod. These studies, still incomplete, seem to indicate that the lower nodes always produce leaves with attenuate, even subpetiolate, bases; that expansion of the basal region of the leaf begins rather abruptly about the 30th to 35th node, and reaches the broadly amplexicaul condition only if the sudden bolting which marks the transition from the vegetative to the reproductive phase is delayed beyond the maturation of this region. If vegetative growth is retarded by limiting either water or nutrients, or terminated by the onset of short days, floral initiation appears before leaf-base expansion can occur. By varying the degree of stress applied, sister plants grown from achenes taken from a single capitulum of a plant with broadly amplexicaul bracts have been made to yield a spectrum of variants ranging from minute specimens only 6 cm. high and bearing four or five subpetiolate leaves and a single tiny capitulum to specimens over 2 m. tall and bearing hundreds of

²¹ Fl. Indiana, p. 994. 1940.

large capitula, the lower ones on extensively ramified branches subtended by large broadly amplexicaul bracts.

The "intermedia" condition arises readily in summer plants restricted in access to soil nutrients by being retained in 3-inch pots without additional fertilizer but well supplied with water. Such plants commonly show signs of nitrogen starvation in the lowest leaves, and fail in various degrees to develop complete tops. Their growth is usually good at first but later it slows down so that the critical day length is reached, and bolting, sharply marked by a maximal internodal length, occurs just after leaf-base expansion has begun. Once bolting starts, the expansion of leaves at the superior nodes is severely and progressively retarded, resulting in the familiar series of bracts and bracteoles. Furthermore, in plants undernourished at and after bolting, the development of floriferous axillary branches is greatly inhibited and may not descend below the 40th node, whereas in well-nourished plants such branching may extend to or even below the 20th node. This results in the condition described by Fernald, of the "upper leaves sessile and broad at the base but very rapidly decreasing to small bracts below the inflorescence". A more accurate statement would be that the lower part of the inflorescence fails to develop properly, for minute capitula can usually be discerned in the axils of these supposedly reduced leaves, which are indeed bracts.

The common name of var. *hieracifolia* is well explained by Pursh²²: "This is one of the plants which spring up in the most remote western counties when the land is cleared of timber, particularly when the brushwood is burnt on the ground; from which circumstance it is generally known by the name of fireweed." The logic of the name "butterweed", by which this plant was well known to me as a boy in the hills of Kentucky, has eluded me.

1b. *ERECHTITES HIERACIFOLIA* var. *MEGALOCARPA* (Fern.) Cronq. *Rhodora* 48: 122. 1946.

Erechtites megalocarpa Fern. *Rhodora* 19:24. 1917.

Leaves large, 10 to 15 cm. long, 3 to 7 cm. wide, fleshy; capitula 1 cm. or more in diameter (pressed) and to 2 cm. long including pappus; phyllaries 16 to 21 or more, lanceolate, 13 to 15 mm. long; florets 100 or more, corolla lobes with brown margins and nerves; achenes (3.5 to) 4 to 5 mm. long, up to 1 mm. in diameter (i. e., twice the diameter of the achene of var. *hieracifolia*), subturbinate, 16- to 20-costate.

TYPE: Upper and middle regions of sandy sea-beach, West Yarmouth, Mass., Oct. 8, 1916, *Fernald, Butters & St. John 15468* (G).

Coast of southern New England, where it occurs along the beaches and in salt marshes.

CONNECTICUT: Groton, seashore, Sept. 1927, *Janssen* (S); Oct. 1927, *Janssen* (S).

MASSACHUSETTS: Yarmouth, sandy beach of Nantucket Sound, Oct. 14, 1916, *Fernald & Butters, Pl. Exsic. Gray 299* (F, K, MICH, S, W; paratypes); salt marsh northeast of Bass River Light, Dennis, Sept. 1918, *Fernald & Long 17636* (F, K, MICH, 2); Bourne, inner edge of Monument Beach, Sept. 1929, *Blake 10975* (F, K, S); Wareham, *Blake 10962* (K).

²² Fl. Amer. Sept. 2:529. 1814.

In reducing Fernald's species to varietal rank, Cronquist stated that he was unable to see any real specific discontinuity, with which I agree, and that he regarded it as a "saline marsh ecotype". Fernald apparently was not convinced, since he continued to treat it as a species. It may well be that this large-headed state is a polyploid, perhaps a simple tetraploid, of var. *hieracifolia*.

Most of the specimens of var. *megalocarpha* which I have seen strongly resemble the broad-bracted state of var. *hieracifolia* but have the bracts or uppermost leaves just below the inflorescence very broad at the base, up to as much as 5 cm. wide. It is therefore of particular interest that one of the specimens examined from Connecticut, *Janssen*, Oct. 3, 1927, shows a distinct departure from this pattern, even as represented by *Janssen*, Sept. 3, 1927. In the former, the leaves immediately below the inflorescence, instead of being very broadly semiamplexicaul and large, are much reduced in all dimensions, with the semiamplexicaul base only 1 cm. wide, and the medial leaves are basally attenuated instead of being broadly clasping. Although the specimen lacks the basal portion, it seems probable from the reduction in the degree of branching and in the size of the branches that this October gathering was from a plant less robust than the others. This would accord well with the thesis that foliar form is largely under environmental control, not only in var. *hieracifolia* but in var. *megalocarpha* as well. It also reinforces the interpretation of this taxon as being of varietal rather than of specific rank.

1c. *ERECHTITES HIERACIFOLIA* var. *CACALIOIDES* (Fisch. ex Spreng.) Griseb. *emend.* Belcher.

- Erechtites hieracifolia* (L.) DC. var. *cacalioides* (Fisch. ex Spreng.) Griseb. Fl. Brit. W. Ind. 381. 1861 (species incorrectly attributed to Raf. and var. to Less.), and var. *carduifolia* (Cass.) Griseb. *l. c.* (incorrectly attributed to DC.).
- Senecio hieracifolius* L. Mant. Pl. 469. 1771, Type: *P. Browne* (LINN 996-2), *non* Sp. Pl. 886. 1753; Willd. Sp. Pl. ed. 4. 3:1974. 1800, *pro parte*.
- Senecio cacalioides* Fisch. ex Spreng. Nov. Prov. 37. 1819; Syst. Veg. 3:565. 1826; Link, Enum. Pl. Hort. Berol. 2:325. 1822.
- Sonchus agrestis* Sw. Prodr. 110. 1788, *excl. syn.*; Fl. Ind. Occ. 3:1289. 1806, *excl. syn.*; Willd. Sp. Pl. ed. 4. 3:1513. 1800; Spreng. Syst. Veg. 3:648. 1826.
- Neoceis carduifolia* Cass. Bull. Sci. Soc. Philom. Paris 1820:91. 1820; Dict. Sci. Nat. 34:386. 1825.
- Sonchus occidentalis* Spreng. Neue Entdeck. 2:143. 1821; Syst. Veg. 3:648. 1826. Type: Sprgl. Herb. n. 1985 (P!).
- Senecio carduifolius* (Cass.) Desf. Cat. Hort. Paris. ed. 3. 177. 1829 (not 1819, as cited by de Candolle).
- Erechtites cacalioides* (Fisch. ex Spreng.) Less. Syn. Gen. Comp. 395. 1832; DC. Prodr. 6:295. 1838 (as *Erechtites*), as to descr., not specimen.
- Erechtites carduifolia* (Cass.) DC. Prodr. 6:294. 1838; Benth. Vidensk. Meddel. Naturhist. Forening Kjoben. 106. 1852; Walp. Ann. Bot. Syst. 5:290. 1858.
- Erechtites hieracifolia* Walp. Rep. Bot. Syst. 2:651. 1843; Cabr. Rev. Mus. La Plata 4:286, f. 90. 1941; *non* DC.
- Sonchus brasiliensis* Meyen & Walp. Nov. Act. Acad. Caes. Leop. Carol. Nat. Cur. 19, Suppl. 1:293. 1843.
- Senecio Fischeri* Sch. Bip. Flora 28:498. 1845.
- Erechtites sulcata* Gardn. Lond. Jour. Bot. 7:419. 1848. Type: Goias, *Gardner* 3868 (K!).
- Erechtites hieracifolia* (L.) DC. var. *cacalioides* Less. f. *pubescens* O. Ktze. Rev. Gen. Pl. 1:335. 1891, *nom. nud.* Of 4 collections cited, one at least, "Java, Sindanglaja, *Kuntze* 4488 (NY!)", is typical var. *cacalioides*.

- Erechtites carduiifolia* DC. var. *latifolia* Klatt, Bull. Soc. Roy. Bot. Belg. 36:291. 1896, *nom. nud.* Type: Costa Rica, San Rafaël, *Pitt.* 6968, not seen.
- Gynura zeylanica* Trim. var. *malasica* Ridl. Jour. Str. Br. Roy. Asiat. Soc. 61:24. 1912.
- Gynura malasica* (Ridl.) Ridl. Fl. Malay Penins. 2:190. 1923, *excl.* Griffith's specimens from Malacca, which are true *Gynura*.
- Gynura aspera* Ridl. Jour. Malay Br. Roy. Asiat. Soc. 1:74. 1923. Type: Sumatra, Beras-tagi, Feb. 8 ("dwarf form"), Feb. 10, 1921, *Ridley* (K!).
- Erechtites agrestis* (Sw.) Standl. & Steyerl. Field Mus. Publ. Bot. 23:265. 1947; *Rydberg*, *in herb.*

Bracteoles of the calyculus long, extending to one-third to one-half the length of the involucre, typically ciliolate with coarse multicellular hairs; phyllaries 12 to 14 (to 21), glabrous or sparsely and irregularly beset with multicellular hairs.

Holotype (?): "Senecio cacalioides, Fischer, 1818, Sprgl., *herb. n.* 1687, Syst. III, 565, n. 176." (P!).

Very variable in habit and leaf form, showing much the same series of variations as in var. *hieracifolia*, with the variations intergrading in every degree. A characteristic state in Florida is intermediate between var. *cacalioides* and var. *hieracifolia* in that the bracteoles are long but lack multicellular hairs. Especially variable in Brazil, one particularly interesting state from Paraná having a distinct basal rosette of leaves.

MEXICO. TAMAULIPAS: Tampico de Tamaulipas, Feb. 1827, *Berlandier* (FI, 2); vicinity of Tampico, Jan. 1910, *Palmer* 107 (F, K). VERA CRUZ: "Savannes de Mirador", 1838, *Linden* 1180 (K, P); damp places near Jalapa, 1840, *Galeotti* 2240 (K); near Jalapa, May 1899, *Pringle* 8187 (BM, F, K, S); Sanborn, April 1910, *Orcutt* 3018 (F); vicinity of Vera Cruz, *Wawra* (W). JALISCO: "Jalisco, 1886", *Palmer* 248 (BM); Quimixto, Nov. 1926, *Ynes Mexia* 1193 (BM, F, MICH). CHIAPAS: Mt. Ovando, Escuintla, Nov. 1945, *Matuda* 16169 (F); Mandolopez, June 1947, *Matuda* 16647 (F). TABASCO: Boca Cerro, Tenosique, July 1939, *Matuda* 3581 (MICH). CAMPECHE: Palizada, July 1939, *Matuda* 3858 (F, K, MICH). YUCATAN: Buena Vista, Xbac, *Gaumer* 1438 (F, S); Pocobach, *Gaumer* 2394 (BM, F).

GUATEMALA. EL PETEN: La Libertad & vicinity, 1933, *Aguilar* 207 (MICH); Lake Zotz, May 1933, *Lundell* 3294 (MICH). ALTA VERAPAZ: Cobán, Jan. 1908, *von Türckheim* II 1319 (BM, F, MICH, S); Finca Socuyó, N. E. of Carchá, April 1939, *Standley* 70260 (F). GUATEMALA: near Amatitlán, Dec. 1938, *Standley* 61433 (F). IZABAL: Livingston, sandy beach, Feb. 1905, *Deam* 244 (MICH). SACATEPÉQUEZ: along Rio Guacalate, N. of Antigua, Feb. 1939, *Standley* 64698 (F). SUCHITEPÉQUEZ: Mazatenango, March 1928, *Morales* 1039 (F). ESCUINTLA: S. of Rio Burrios, March 1941, *Standley* 89624 (F). SANTA ROSA: Volcan Jumaytepeque, 8000 ft., Jan. 1893, *Heyde & Lux* 4227 (F), 6000 ft., Dec. 1892, *ibid* 4247 (K, 2). JALAPA: between Jalapa and La Laguna, Nov. 1940, *Standley* 76933 (F). ZACAPA: Sierra de las Minas, Oct. 1939, *Steyermark* 29638, 29719 (F). JUTIAPA: Lago Retana, between Ovejero and Progreso, Nov. 1939, *Steyermark* 32027 (F).

BRITISH HONDURAS: Belize River, Sunnyland bank, March 1933, *Lundell* 4028 (K, MICH); Prospecto, northern river, *Gentle* 918 (K, MICH, S). HONDURAS: Morazán: Zamorano, Feb. 1945, *Rodriguez* 2302 (F); Santa Clara Creek, Rio Yeguaré valley, Aug. 1946, *Williams & Molina* 10338 (F); lower slopes of Cerro de Uyuca, *Standley & Molina* 4181 (F); moist valley near Las Mesas, Feb. 1947, *Williams & Molina* 12053 (F); hills above Jicarito, Nov. 1950, *Williams* 17293 (F). El Cayo: Mountain Pine ridge, March 1931, *Bartlett* 11917 (MICH). Atlántida: Lancetilla Valley, near Tela, *Standley* 53644 (F). Santa Barbara: Los Dragos, on Rio Chamelecón, April 1947, *Standley & Linderlie* 7426 (F). NICARAGUA. Grenada: Volcan Mombacho, Feb. 1904, *Baker* 2346 (K). Managua: Sierra de Managua, *Gaumer* (F). Chontales, 1867-8, *Tate* 183 (221) (BM, 2; K). Without data: *Lévy* 274 (K); 1867, *Seemann* 96 (BM). COSTA RICA: Cartago, Dec.

1887, *Cooper* 5802 (K, F); Ferme de Guacimo, July 1901, *Tonduz* 14744 (BM); Galieros, cultivas, Aug. 1919, *Lankester* K-154 (K); La Palma de San Ramón, Nov. 1927, *Brener* 5806 (F); Tablazo, Jan. 1935, *Valerio* 1090 (F); Prov. San José, vicinity El Général, July 1936, *Skutch* 2706 (K, MICH, S); Guadeloupe de Zarcero, 4500 ft., Oct. 20, 1937, "herb . . . with erect branches to 16 [sic!] feet . . . in rich loam in sun in land recently cleared of forest", *Austin Smith* A-557 (F). PANAMA: Empire station, Nov. 1861, *Hayes* 587 (BM, K); "in ruderalis prope urb. Panama", *Seemann* 444 (BM, K, P); Canal Zone, Barro Colorado Island, July 1931, *Starry* 283 (F).

WEST INDIES. BAHAMAS: Red Bays, Andros, April 1890, *Northrup* (F). CUBA: Heradura, March 1906, *Hitchcock* (F); Camaguey, Tiffin, March 1909, *Schaffer* 1090 (F); Havana, Puentes Grandes, April 1914, *Ekman* 483 (S); Oriente, Bayate ad Rio Jagua, May 1919, *Ekman* 9610 (F, S), Sierra Maestra supra Daiquiré, Oct. 1916, *Ekman* 8177 (F, S). ISLE OF PINES: Pedernales Point, Feb. 1889, *Millspaugh* 1418 (F). JAMAICA: *P. Browne* (LINN 996-2); "*Sonchus agrestis*", *Swartz* (S); Castleton Hill, July 1900, *Fawcett* 8024 (F); Castleton, April 1910, *Harris* 10890 (F, K). HAITI: Dept. du Sud, prope Civette, June 1917, *Ekman* H-221 (S); Massif de la Selle, Croix des Bouquets, Terrelonge, March 1927, *Ekman* H-7810 (S). DOMINICAN REPUBLIC: Sto. Domingo City, ad Rio Ozama, Jan. 1929, *Ekman* 11374 (S, very large leaves with broad amplexicaul bracts); vicinity of Santiago, near La Cumbre, Jan. 1946, *Allard* 14587 (S); *Voiteau* (FI). PUERTO RICO: Wydla, 1825,—(FI); Mayagüez, Oct. 1881, *Sintenis* 164 (K); Cayey, in monte Llano, Sept. 1885, *Sintenis* 2412 (F); prope Bayamon, Feb. 1888, *Stahl* 865 (S). ST. THOMAS: *Riedle* (FI); St. Peter, Jan. 1881, *Eggers* 209 (K). ST. CROIX: "Spray garden", July 1896, *Rickseckler* 474 (F). GUADELOUPE: "*E. hieracifolia* Rafin. Guadeloupe" (K). GRENADA: Vendome, St. George's, May 1905, *Broadway* (F). TOBAGO: April 1913, *Broadway* 4463 (S); Mason Hill near the river, May 1913, *Broadway* 4507 (F); Caroni swamp, July 1931, *Williams* 12579 (K).

SOUTH AMERICA. FRENCH GUIANA: Acarouany, 1854, *Lagotz* (S). DUTCH GUIANA [SURINAM]: Upper Sipoliwini R., March 1936, *Rambouts* 544 (K, 2). BRITISH GUIANA: Hyde Park, Demerara, May 1922, "Wild cotton for cooling the blood of children as well as of adults", *Warren* (F); Pomeroun, Jan. 1923, *De la Cruz* 2947 (F); Kabakaburi, Feb. 1923, *ibid.* 3293 (F); Northwest district, Waini River, April 1923, *ibid.* 3756 (F); *Jenman* 1496 (K). VENEZUELA: Montevideo, Caracas, March 1937, *Legrand* 1061 (F); Bolivar, Gran Sabana, Oct. 1944, *Steyermark* 59280 (F). COLOMBIA: Magdalena, near Lake Zapatoza, Aug. 1924, *Allen* 277 (K); Santa Marta, *Smith* 666 (F, S). Chocó: Playa de Togoromá, June 1944, *Killip & Cuatrecasas* 39075 (F). Valle: Rio Colima, La Trogita, 1944, *Cuatrecasas* 16502 (F). Cauca: la Paila, 1853, *Helton* 384 (K); Popayán, *Lehmann* 5224 (K), *Lehmann* 7598 (F, K), *Lehmann* 7985 (F); ad pag. El Tambo, June 1938, *von Sneidern* 1535 (S). Tolima: Ibagué *André* K 262 (K). Meta: Villavicencio, Dec. 1928, *Apolinar-Maria* 427 (F). Vaupés: Bocas del Carurú en Casa Alvarez, Sept. 1939, *Cuatrecasas* 7009 (F). PERU. Loreto: Lower Rio Nanay, May 1929, *Williams* 282 (F); Caballo-Cocha on Amazon River, Aug. 1929, *Williams* 2489 (F). Ambo, 7000 ft., April 1923, *Macbride* 3158 (F). Amazonas: Chacapayas, *Matthews* (K). Piedra Grande: estación near Rio Santo Domingo, *Macbride* 3673 (F). Junin: Satipo, Aug. 1945, *Soukup* 2841 (F). BOLIVIA. Reyes: Rurrenabaque am Rio Beni, 1930, *Fleischmann* 147 (S). La Paz: Apolo, April 1902, *Williams* 182 (K). "Nord-Yungas", Milliguaya, Dec. 1917, *Buchtien* 4072 (F). "Sud-Yungas: Sireapaya bis Yoinacachi", Dec. 1906, *Buchtien* (W). Santa Cruz: Buena Vista, July 1924, *Steinbach* 6208 (K). Larecipa: "viciniis Sorata, Canale Challapampa riv.", 1860, *Mandon* 117 (K, det. as *E. ambigua* DC.; S). Casana im Tipuani-Tal, Sept. 1922, *Buchtien* 7589 (S). BRAZIL. Amazonas: Taperinha bei Santarem, July 1927, *Ginzberger* 412 (F). Para: Boa Vista on Tapajós River, 1929, *Dahlgren & Sella* 137 (F); Belém, Instituto Agronomica do Norte, Oct. 1942, *Blake* 7755 (K). Pernambuco: Tapera, Sept. 1931, *Pickel* (F, MICH). Bahia: "Bahia in convallibus humidis" (W). Goias: near Villa de Arrayas, *Gardner* 3868 (K, 2, syntypes of *E. sulcata* Gardn.). Minas Gerais: Caldas, 1845, *Widgren* 211 (S, 2); Lagoa Santa, Nov. 1864, *Warming* (S, 2). Rio de Janeiro: in locis humidis, Dec. 1831, *Riedel* 230 (P); road between Alto de Serra and Meio de Serra, Dec. 1928, *Smith* 1551 (S). São Paulo: Campinas, March 1900, *Novaes* 134 (US). Paraná: Curityba, Feb. 1904, *Dusén* (S); Ponta

Grossa, March 1904, *Dusén* (S); Iacarehý, Sept. 1908, *Dusén* 6583 (S); Jaguariahya, June 1914, *Dusén* 15110 (S). Rio Grande do Sul: pr. São Martinho, Apr. 1893, *Malme* 826 G (S); Ijuhy, April 1893, *Malme* 746 (S); São Leopoldo, 1941, *Eugenio* 63 (F). PARAGUAY: Chaco-y pr. Concepción, *Hassler* 7267 (S); in viciniis Caaguazú, Feb. 1905, *Hassler* 8886 (K, S); "Villa River," *Jørgensen* 3512 (F, S); *Hassler* 1405 (K); "in Paraguay legit *Fleischer*" (P). ARGENTINA. Jujuy: Quinta, prope Laguna de la Brea, June 1901, *Fries* 100 (S); Rio Grande, Feb. 1924, *Venturi* 3418 (US). Tucuman: April 1928, *Venturi* 6095 (F). Sierra de Cordoba: March 1876, *Hieronimus* 499 (F). Misiones: Posadas, prope "La Granja", Nov. 1907, *Ekman* 1106 (F, S); Apostales, San Jose, Feb. 1946, *Bertoni* 2722 (F). URUGUAY: Dept. de Colonia, Riachuelo, Charca, April 1935, *Cabrera* 3319 (S, several plants; most southerly specimens seen).

ASIA. CHINA: Kwangsi, Shang-sze Dist., Shap Man Taai Shan, May 1933, *Tsang* 22219 (BM, GH, S). SIAM (all det. as *Gynura malasica* Ridl.); Surat, Panam, March 1927, *Kerr* 12413 (K); Kurabi, Kao Sataw, *Kerr* 12424 (K); Pattoni, Kao Kalakino, March 1928, *Kerr* 14868 (K); Takinapa, Kapang, Feb. 1929, *Kerr* 17551 (K); Kurabi, Tambur Kao Panom, April 1930, *Kerr* 18830 (K). MALAYAN FEDERATION (all det. as *G. malasica*): Selangor, Kuala Lumpur, Damansara Road, Dec. 1920, *Ridley* (K); Negri-Sembilan, Bukit Tanga Pass, *Ridley* (K); Johore, Sungai Tukong, July 1930, *Spare* F802 (K). BRITISH NORTH BORNEO: Myburg Prov., Sandakan, 1921, *Elmer* 20159 (K, det. as *Sonchus arvensis*); Elphinstone, Prov. Tawau, *Elmer* 20977 (S, K, det. as *Sonchus oleraceus*); Mt. Kinabalu, Marai Parai, 5500 ft., Sept. 1933, *Clemens* 30243 (BM, GH). SARAWAK: Kuching, Jan. 1915, *Ridley* (BM, K); Rajang Rubber Estate, May 1929, *Clemens* 5090A (K). SUMATRA: Berastagi, Feb. 8, 1921, *Ridley* (K, det. by Ridley as "*Gynura aspera*, dwarf form"); Berastagi, open country, Feb. 10, 1921, *Ridley* (K, det. by Ridley as *Gynura aspera*; holotype?); East Coast, Loendoet Concession, Koealoe, May 1927, *Bartlett* 7661 (NY, US); East Coast, vicinity of Loemban Ria, Asahan, 1935, *Rahmat Si Boeea* 7395 (GH, US); Island of Siberoet, Sept. 1924, *Boden-Kloss* 14556 (K). JAVA: Sindanglaja, May 1875; *Kuntze* 4488 (NY); Sumbing Vulcan, Aug. 1875, *Kuntze* 5578 (K; NY, 2); Gedeh, Tjibodas, Feb. 1897, *Möller* (S, right-hand specimen only; left is *E. valerianaefolia*).

Grisebach was apparently the first to propose combining all of the Caribbean material under *E. hieracifolia*, and to use differences in bracteole length to distinguish varieties. By considering length and width of phyllaries, length and number of calycular bracteoles, and general pubescence, he established three varieties, including the typical one. Unfortunately, the number of bracteoles, upon which he based the tropical varieties, is not consistent, even from capitulum to capitulum on the same inflorescence, even on the very specimens he cited. The description of var. *carduifolia* as glabrescent is not generally applicable, the description as pubescent or as setaceous, given by Cassini, Desfontaines, and de Candolle, being much more appropriate.

Despite the artificiality of his varietal limits, the epithets which Grisebach used for his varieties have clear priority in that rank, and at least one must be maintained. Since I could not locate any authenticated material of *Neoceis carduifolia*, I have taken up *cacalioides*. The epithet *agrestis*, although clearly the first unpreoccupied name to be applied to the tropical material, was used only in specific rank, where it has priority for those that might wish to continue to separate the temperate and the tropical states into different species.

Swartz described *Sonchus agrestis* from Jamaica. There is no type in the strict sense, for Dr. Asplund informs me that there are two specimens of *E. hieracifolia* at Stockholm which were collected by Swartz in the West Indies but that the prin-

cipal annotations are by J. E. Wikström. I have examined both of these sheets, together with a third Swartz specimen labelled by Banks as *Sonchus agrestis* and now in the herbarium of the British Museum (Natural History). I at first believed that Swartz applied *Sonchus agrestis* to the smaller of the two specimens said to have been collected by him. This specimen, closely resembled by the one in London, has the phyllaries glabrous but only 7 or 8 in number, the bracteoles of the calyx only 2 mm. long, and the leaves attenuate and non-amplexicaul at the base. These lesser specimens, however, do not have tomentose, or even sub-tomentose, branches, nor incised-serrate leaves, nor many capitula, as described by Swartz. Particularly because of their glabrous phyllaries and short bracteoles these lesser specimens must be the typical variety, with the more depauperate specimens of which they agree well. Although Swartz may have included some features of these lesser specimens in the amplified description in his later work, the name should be interpreted by the earlier diagnosis, which applies better to the larger specimen with the multicellular hairs and other features of var *cacalioides*.

Fischer in 1818 at Halle raised from Jamaican seed some plants to which he evidently gave the name of *Senecio cacalioides*. He appears to have sent a named specimen to Sprengel at Berlin, who gave it an excellent description in his account of the new introductions at Berlin and at Halle for that year. Although it is not clear if the specimen of "*Senecio cacalioides* Fischer, 1818" in Sprengel's herbarium is the one actually grown by Fischer, it agrees in every respect with Sprengel's description, particularly in being distinctly pubescent with multicellular hairs.

The fact that the Compositae of Sprengel's herbarium are in the Paris Herbarium seems not generally known, but is of considerable importance to the synantherologist, particularly in the interpretation of the "hort. berol." synonyms used by de Candolle now that the Compositae in the general herbarium at Berlin are destroyed. When Sprengel's collection was sold, the Compositae were bought by Schultz Bipontinus, whose collection of this family alone was said by Alphonse de Candolle²³ to have numbered 50,000 specimens. His collection, containing much type material, was in turn acquired by Cosson, and this eventually (after publication of "La Phytographie") by the Muséum d'Histoire Naturelle. Sprengel's sheets are identified by uniform tickets reading: "Sprgl.! herb. n. _____, Syst. III, [page n. _____], n. _____". I believe that these tickets are in the writing of Schultz, rather than that of Sprengel. This reduces their claim to authenticity, and I hesitate to cite these specimens as holotypes for names that originated with Sprengel, particularly those from publications which preceded the "Systema Vegetabilum". But for those specimens which I have examined the collation to page number, species number, and description in the "Systema Vegetabilum" is excellent. Link also attributed *Senecio cacalioides* to Fischer, but based his own description on a similar plant from Brazil. De Candolle later reduced Link's name to *Erechtites ambigua*, but wrongly, the latter actually being the petiolate form of *E. valerianaefolia*.

²³ La Phytographie. p. 450. 1880.

Sprengel first described *Sonchus occidentalis* as similar to *S. agrestis* Sw., but with glabrous peduncles and leaves. In the "Systema Vegetabilum" this was revised to very glabrous, in greater contrast with *S. agrestis*. Some authors have assumed that these descriptions therefore apply to those virtually glabrous specimens of var. *hieracifolia* which occur scattered throughout the West Indies. But the confusion surrounding this epithet has been removed by discovery of Sprengel's type, or at least an authentic specimen, in the Paris Herbarium. This specimen is not as glabrous as the descriptions indicate. With magnification the scattered stumps of multicellular hairs can be seen on the lower surfaces of the leaves and on the stem. The capitula have long calycular bracteoles which are ciliolate with multicellular hairs. This material of *S. occidentalis* thus belongs to the tropical variety. Rydberg apparently made a new combination in *Erechtites* for this species, for Degener has used this name on tickets on certain of his collections of *Erechtites* from Hawaii, attributing the combination to "Rydberg in herb". On comparing these and other Hawaiian sheets with Sprengel's specimen, I find that the Hawaiian material uniformly has glabrous phyllaries, very short calycular bracteoles, peduncular bracteoles less than one-half the length of the involucre, and no multicellular pubescence on either type of bracteole. These characters exclude it from *E. hieracifolia* var. *cacalioides*, and place it in var. *hieracifolia* instead.

Erechtites hieracifolia is represented in the Orient, however, by var. *cacalioides* only, and appears to be neither widely distributed nor abundant there. Most of the specimens from this region which are so determined have proved actually to be the African *Crassocephalum crepidioides* (Benth.) S. Moore. The two are readily distinguishable, the latter by the longer style-arm appendages, small dark-red achene, lyrate pinnatifid and petiolate lower leaf, and usually lacking pistillate marginal florets. Merrill²⁴ fell victim to this confusion when he wrote: "Two species of the American *Erechtites*, both with pink flowers, may be dominant wherever they have been introduced, *E. hieracifolia*, fig. 185A, and *E. valerianaefolia*, fig. 185B." True *E. hieracifolia* never has pink florets, whereas *C. crepidioides* does, as numerous specimens of it incorrectly determined by Merrill as *E. hieracifolia* testify. As for the figures cited, fig. 185A is certainly *E. valerianaefolia* (instead of *E. hieracifolia* as stated), with its characteristic pinnatisect leaf, whereas fig. 185B is *C. crepidioides* but shows only the subentire foliar leaves. Merrill is of course by no means alone in this misapprehension, as it is evident in nearly all of the herbaria which I have studied.

Grisebach reported *E. hieracifolia* var. *hieracifolia* from Mauritius, based, I believe, on two specimens at Kew. One is ticketed: "Senecio? fl. roseo. Growing in high mountains, Mauritius. *Senecio cacalioides* Bojer. H. M. 188, *Erechtites hieracifolia* Raf.". This proved to be *Crassocephalum rubens* (Jacq.) S. Moore. The other specimen, simply labeled "Telferin. Mauritius", and determined as *E. hieracifolia*, was immature and poorly pressed, but appeared to be *Crassocephalum sarco-*

²⁴ Plant Life Pacific World, p. 143. 1945.

basis (Bojer) S. Moore, *vel aff.* I have yet to see *Erechtites* from Mauritius, Madagascar, or vicinity.

These two major varieties of *Erechtites hieracifolia* are not absolutely distinct; quite possibly they intergrade where their ranges overlap in the Caribbean basin. Occasional specimens of tropical material have the calycular bracteoles rather shorter than usual or have longer calycular bracteoles which are on first inspection apparently devoid of multicellular pubescence. Occasional temperate-zone specimens occur in which calycular bracteoles approach the length which characterizes the tropical variety. Nature continues to defy our pigeon-holes.

Several subsidiary considerations, in my experience, may help establish or confirm the varietal determination in such cases. The width of the calycular bracteoles is usually greater in var. *cacalioides* than in var. *hieracifolia*, to as much as twice as wide, even in bracteoles of the same length. In determining the length of the bracteoles the most reliable measurements can be obtained on capitula which have fully elongated but have not yet begun to expand the floret buds, as during anthesis the bracteoles begin to flex. By fructescence they are quite often both strongly flexed (and thus apparently shorter) and appreciably withered. The lateral expansion of the receptacle which normally occurs during maturation of the achenes also tends to distort the ratio between calyculus and involucre.

Care should be taken in examining younger parts of the inflorescence, to distinguish between members of the calyculus proper, whose insertions are always upon the expanded torus, and the bracteoles of the peduncle and the bracts subtending the peduncles. Either of the last two may, before the peduncle is fully elongated, overlap the calyculus and appear to be a part of it. It is also true, though, that both of these structures tend to be longer in var. *cacalioides* than in var. *hieracifolia*. Indeed, length of these parts may be a helpful secondary characteristic if the peduncles are fully elongated, although a less reliable one than length of the calyculus.

Short multicellular hairs may occur occasionally on the stems and leaves of var. *hieracifolia*, and indeed do so on the Linnaean lectotype, and often occur abundantly on the stem and leaves of var. *megalocarpa*. But I have not yet observed any occurring on the inflorescence of any truly temperate-zone specimen, not even on those Gulf Coast specimens which have the long bracteoles of the Caribbean variety. I therefore conclude that any specimen with even remnants of multicellular hairs in the inflorescence is var. *cacalioides*.

2. ERECHTITES VALERIANAEOFOLIA (Wolf) DC. Prodr. 6: 294. 1838.

Senecio valerianaefolius Wolf, Ind. Sem. Hort. Berol. 1825, *teste* Reichenb. Icon. Bot. Exot. 59, *tab.* 85. 1827.

Annual; stem herbaceous, subsimple to much branched above, glabrous or occasionally sparsely hispidulous, striate, 0.5 to 1.0 (to 2.0 or more) m. high. Lowest leaves petiolate, ovate-lanceolate to lanceolate, entire or serrate to irregularly dentate; medial leaves petiolate with narrowly decurrent wings, very deeply pinnately lobed, the lobes lanceolate and serrate to irregularly incised-dentate, or pinnatisect with linear segments entire or minutely serrulate, or entire or subentire

like the lower leaves; upper leaves similar to the medial leaves but slightly reduced in size upward, or sometimes abruptly reduced several nodes below the inflorescence. Inflorescences terminal and axillary, forming a rather congested cymose panicle. Capitula slender, at anthesis about 10 mm. long, 3 mm. wide, scarcely ventricose, with linear calycular bracteoles extending to one-fourth or one-third the height of the involucre; involucre of 12 to 14 (to 16) phyllaries; phyllaries 7 to 8 mm. long, 0.5 to 0.75 mm. wide, linear and acute to acuminate, with keel flat and 4- or 5-nerved, glabrous or rarely minutely hairy; marginal florets uniseriate or sub-biseriate, corolla 5-fid, with lobes 0.5 mm. long and 0.2 mm. wide, apices glandulose-thickened and incurved; style-arm apices shortly conic-appendaged. Disc florets more numerous than the marginal, the outer ones transitional in size and shape, with corolla 7 to 8 mm. long, only slightly longer and more dilated than the pistillate florets, the inner ones with corolla slightly longer and larger, slender, infundibuliform, 5-fid, with lobes 0.5 mm. long and 0.2 to 0.35 mm. wide, their apices glandulose-thickened; style-arm apices with conical appendage approximately 0.05 to 0.1 mm. long. Achene cylindrical, 2.5 to 3.5 mm. long, with about 10 heavy, pale brown ribs, dark brown and entirely glabrous to minutely villous or hispidulous in the grooves. Pappus multiseriate, slender, rose-lilac to very pale reddish, rarely nearly or quite faded to white, subequalling the florets, exceeding the phyllaries.

Widespread in tropical America, where it sometimes hybridizes with *E. hieracifolia* var. *cacalioides*; adventive as an aggressive weed into tropical Asia, many of the Pacific islands, and northern Australia.

Separable on the basis of differences in the foliage into four fairly well-marked forms.

KEY TO THE FORMS

- A. Medial and upper cauline leaves pinnatisect or subpinnateB
 B. Leaves only slightly reduced in size upward below the inflorescenceC
 C. Segments of the strongly pinnatisect leaves lanceolate, broad, serrate to incised-dentate2a. f. *valerianaefolia*
 CC. Segments of the pinnatisect leaves linear, entire or minutely serrulate.....2b. f. *organensis*
 BB. Leaves abruptly and markedly reduced in size several nodes below the inflorescence2c. f. *reducta*
 AA. Medial and upper cauline leaves entire or subentire2d. f. *preanthoides*

2a. ERECHTITES VALERIANAEOFOLIA f. VALERIANAEOFOLIA

Senecio valerianaefolius Wolf, Ind. Sem. Hort. Berol. 1825, teste Reichenb. Icon. Bot. Exot. 59, tab. 85. 1827; Link ex Spreng. Syst. Veg. 3:565. 1826.

Senecio valerianaefolius Desf. Cat. Hort. Paris. ed. 3. 178, 403. 1829; by descr. florets all perfect, a discoid *Senecio*, but type (FI ex Hb. Desf. !) has marginal florets pistillate.

Crassocephalum valerianaefolium (Wolf) Less. Linnaea 5:163. 1830; Syn. Gen. Comp. 395. 1832.

Sonchus erythropappus Meyen & Walp. ex Walp. Nov. Act. Acad. Caes. Leop. Nat. Cur. 19, Suppl. 1: 293. 1843.

Senecio valerianaefolius Gardn. Lond. Jour. Bot. 4: 127. 1845.

Gynura rosea Ridl. Jour. Str. Br. Roy. Asiat. Soc. 61: 25. 1912.

Erechtites Gardneriana Cabr. Brittonia 7: 54. 1950.

Neotype: "*Senecio valerianaefolius* ex. h. Raffeliano, 1825" (W, "collectio Reichenbach fil., aqu. 1889, no. 16256").

Medial cauline leaves 5 to 20 (to 30) cm. long, 2 to 8 (to 15) cm. wide, strongly pinnatisect or subpinnate with narrowly winged rachis; segments 3 to 7 on either side, broadly lanceolate, coarsely and irregularly serrate to incised-dentate, sometimes basally sublobulate.

Widely distributed from Central Mexico to Brazil and Argentina, rare in the Lesser Antilles; adventive in Southeastern Asia, the East Indies, Philippine Islands, New Guinea, Queensland, Fiji Islands, Samoan Islands, Hawaiian Islands, and elsewhere in the Pacific as an aggressive weed.

CENTRAL AMERICA. MEXICO: Vera Cruz, recent clearings near Jalapa, *Pringle* 8334 (BM, F, S, W); Chiapas, Pinales, Siltepec, 1938, *Matuda* 1971 (MICH); Mt. Tacana, Aug. 1938, *Matuda* 2451 (MICH); *MacDaniels* 861 (F). GUATEMALA: Alta Verapaz, Cobán, Nov. 1907, *von Türckheim* II 1396 (F, S). EL SALVADOR: Ahuachapán, vicinity Apaneca, Jan. 1947, *Standley & Padilla* 2928 (F); *Carlson* 969, 3939 (F). HONDURAS: Morazan, *Standley & Molina* 4138 (F). NICARAGUA: Summit of Mt. Mombacho, near Grenada, *Grant* 829 (F); Jinotega, *Grant* 7303 (F); *Tate* 181 (485) (BM); *Standley* 10619 (F). COSTA RICA: San José, vicinity of El General, July 1936, *Skutch* 2751 (MICH, S); San Loié, 1853, *Scherzer* (W). PANAMA: *Allen* 1367 (F); *Davidson* 528 (F).

WEST INDIES. PUERTO RICO: headwaters, Inabón River, Jan. 1941, *Otero* M-111 (MICH). LEEWARD ISLANDS: Montserrat: Fergus Mtn., Jan. 1907, *Schafer* 333 (F). WINDWARD ISLANDS: Dominica: *Hodge* 777 (BM).

SOUTH AMERICA. VENEZUELA: *Vogl* 475 (F); *Moritz* 340 (BM). COLOMBIA: Santa Marta, *Smith* 508, 664 (BM, F, S). ECUADOR: *Rimbach* 277 (F). PERU: Aug. 1854, *Lechler* 2461 (W, 2). BOLIVIA: Hacienda Simaco sobre el camino a Tipuani, Feb. 1920, *Buchtien* 825 (BM, F, S); Mapiri, April 1886, *Rusby* 1671 (BM, MICH); *Bang* 2068 (F, MICH, W; not BM, which is f. *organensis*). BRAZIL: Bahia, *Blanchet* (W); Bahia in humidis, *Salzman* (G Prodr., FI); Bahia, 1842, *Glocker* 17 (US, S). Minas Gerais: Caldas, March 1875, *Regnell* I 272 (S, 3; a fourth sheet dated 1866-67 is f. *prenantoides*); Viçosa, Agricultural College lands, March 1930, *Ynes Mexia* 4415 (BM, F, MICH, S). Rio de Janeiro: "in montosis," 1832, *Lund* (G Prodr.); ad aquas circa Rio de Janeiro, *Pohl* 646 (W); Organ Mts., open bushy places, 3000 ft., *Gardner* 522 (K, diseased, type of *S. valerianaefolius* Gardn.). São Paulo: Campinas, Oct. 1904, *Heimer* 228 (S). Paraná: Passo, March 1904, *Dusén* (S); Iacarechý, Aug. 1914, *Dusén* 15351 (F, S). Santa Catarina: *Mueller* 454 (K). Rio Grande do Sul: Canôas pr. Pôrto Alegre, Nov. 1892, *Malme* 298 (S, 5) Ijuhy, April 1893, *Malme* 750 (S, 4); São Leopoldo, Oct. 1936, *Dutra* 1401 (S). PARAGUAY: Villarrica, *Jørgensen* 7489 (F, S); San Bernardino, *Hassler* 3625 (BM, W); "ad ripas Paraguay", Jan. 1873, *Gilbert* 1066 (K, stem flexuous); *Hassler* 11815 (BM); *Fiebrig* 634 (F). ARGENTINA: Misiones, Posadas, Nov. 1907, *Ekman* 1103 (F, S); S. José dos campos, Aug. 1909, *Löfgren* 299 (S).

ORIENT. JAPAN: Hachijoo Island, Mitsume-mura, Dec. 1948, *Shigetake Suzuki, Plantae Japonicae* 391088 (GH), Jan. 1949, *ibid.* (US). CHINA: Hainan, Sha po Shan, Taai Shui ravine, Aug. 1927, *Tsang* 682 (NY, US); Yaichow, 1933, *How* 70622 (GH, NY, US); S. W. Seven Fingers Mtn., April 1932, *Liang* 61669 (F, GH, NY); near Tau Ti P'o, April 1922, *McClure* 9128 (NY); Tam dist., S. of Fan Ta, May 1929 *Tsang & Fung* 223 (NY); Taam-Chau dist., Nodoo, July 1927, *Tsang* 110 (NY, US). MALAYAN FEDERATION: Pahang, Cameron Highlands, April 1937, *Henderson* 32659 (GH). (Numerous other specimens from the Malay States, many collected by Ridley and determined as *Gynura rosea* Ridl., observed at Kew and the British Museum, by oversight were not listed). SUMATRA: Karo Highlands, Berastagi, June 1928, *Hamel* 428 (GH, NY); vicinity of Rantau Parapat, Bila, 1932, *Rabmat Si Toroes* 1716 (NY, US); Adian Rindang, Asahan, 1935, *Rabmat Si Boeea* 8842 (GH). JAVA: "Java (iter javanum secundum)", *Zollinger* 2658 (G Deles., P); "ad rivulos pr. Gadok, 1600 ft., 12 Nov., 18—," *Zollinger* I 3655 (W, 2); Magamendon, May 1875, *Kuntze* 4407 (NY); Gedé, May 1875, *Kuntze* 4807 (NY); Preanger Prov., Tjiboeroem, forested middle slopes of Mt. Gedé, April 1909,

Palmer & Bryant 197 (US). SARAWAK: without locality, *native collector* 727 (US). BRITISH NORTH BORNEO: Mt. Kinabalu, Penataran River, July 1923, *Clemens* 34047 (GH). REPUBLIC OF THE PHILIPPINES: Luzon: Sorsogon, Irosin, Mt. Bulusan, Dec. 1915, *Elmer* 15364 (F, GH, NY, S, US, W). Catanduanes: 1917, *Ramos* 30251 (US). Samar: Catubig River, 1916, *Ramos* 24422 (US). Negros: Negros Oriental, Sibulan, Malangco So., Sept. 1948, *Edaño* 6799 (GH). Balut Island, Oct. 1906, *Merrill* 5412 (NY, US). Mindanao: Todaya (Mt. Apo), Davao, May 1909, *Elmer* 10463 (F, NY, US); Agusan, Cabadbaran (Mt. Urdaneta), Aug. 1912, *Elmer* 13580 (F, GH, K, NY, US); Bukidnon, vicinity of Tanculan, July 1916, *Fenix* 24936 (US); Cotabato, Nutol, 1932, *Ramos & Edaño* 84871 (GH). CELEBES: "P. Boeton: Kaboengka", Feb. 1929, *Kjellberg* 238 (S). NEW GUINEA: (N. E., Morobe, bei Salamaua, Malalo Mission, Nov. 1936, *Clemens*, cited by *Mattfeld*, *Engl. Bot. Jahrb.* 38:288). AMBOINA: Soja, Aug. 1913, *Robinson* 1836 (NY, US).

OCEANIA. AUSTRALIA. Queensland: Beaudesert, April 1907, *Boorman* (NSW); Eumundi, March 1915, *White* (NSW); base of Mt. Gravatt near Brisbane, Nov. 1930, *White* 6856 (NY). New South Wales: Billinudgel, May 1911, *Stephenson* 3 (NSW); Hat Head, Jan. 1953, *Constable* (NSW); Durimbal to Berkeley Vale, Oct. 1953, *Salasoo* (NSW). SOLOMON ISLANDS: Guadalcanal, east fork of Tenam Riv., Aug. 1945, *Riley* 16 (US). FIJI ISLANDS: Vanua Levu, Thakaundrove, hills south of Nakula Valley, Nov. 1933, *Smith* 333, Viti Levu, Mba, summit of Mt. Koroyanitu, May 1947, *Smith* 4194 (US). SAMOAN ISLANDS: Upolu, Vailima, Aug. 1905, *Rechinger* 769 (NY, W); Upolu, Launtoo, Aug. 1905, *Rechinger* 1844 (W, 3). HAWAIIAN ISLANDS: Hawaii, Kilauea region, July 1929, *Degener* (NY); Oahu, Tantalus Mt., Honolulu, June 1923, *Degener* 1519 (NY); Lanai, Kalulu, March 1916, *Munro* 534 (NY); West Molokai, Hauakea Pali, April 1928, *Degener* 18133 (NY); Maui, east of Plinda, Oct. 1916, *Hitchcock* 14924 (US).

CULTIVATED: "*Senecio valerianaefolius* Link, Hort. Berol." (W); "*Senecio valerianaefolius* h. p." (FI, ex Hb. Webb. ex Hb. Desf., type of *S. valerianaefolius* Desf., marginal florets 4-fid, pistillate).

There is some question as to who actually authored the 1825 seed list, whether Wolf or Link, and this I have been unable to establish. Every effort to locate a copy of this list has so far been unsuccessful. I have been unable to learn even whether the first appearance of the name was accompanied by a description or not. If not, then the first description is the brief but sufficient paragraph by Sprengel, and the citation would be "Link *ex* Sprengel." But Reichenbach and Lessing, who cite Sprengel, both credit the name to Wolf. Therefore I accept Wolf as the original author pending finding of the 1825 seed list. The sheet, "*Senecio valerianaefolius* ex h. Raffeliano, 1825," is in very excellent detailed agreement with Reichenbach's description, and appears to be the original from which his pl. 85 was prepared. In view of the reported destruction of any type material there may have been of this species in the Berlin Herbarium, I designate this sheet as neotype.

Gardner gave his *S. valerianaefolius* the number 252 in the 'London Journal,' but the corresponding specimen at Kew is *Gardner* 522, Organ Mts., Brazil. It is a monstrous specimen with the capitula mostly much distorted as if by an infection. (The symptoms are very similar to, if not identical with, those produced by the aster yellows virus.) A few capitula at the apex of the inflorescence are fairly normal, however, and show the typical structure of *E. valerianaefolia*, including pistillate marginal florets and a faintly colored pappus. The leaves are quite typical of f. *valerianaefolia*. Gardner's proposed species, which is really not valid anyway since it is based on a monstrosity, thus reduces to *E. valerianaefolia* f. *valerianaefolia*.

Erechtites Gardneriana Cabrera, based on it, is therefore superfluous.

Lessing transferred *S. valerianaefolius* Wolf to *Crassocephalum*, as emended and greatly extended by himself. It is true that the appendage of fused papillose hairs which terminates the style arm of *E. valerianaefolia* is somewhat longer than that of *E. hieracifolia*, and might be taken to indicate intermediacy between the latter species and the widespread *Crassocephalum crepidioides*. The heavily ribbed brown achene of *E. valerianaefolia*, however, is scarcely or not distinguishable from that of *E. hieracifolia*, whereas the characteristic achene of *Crassocephalum* is shorter, more uniformly cylindrical, weakly ribbed and short-haired on the ribs, and reddish in color. The florets of *Crassocephalum* are tubulous, rather than filiform, and are more coarsely lobed.

2b. ERECHTITES VALERIANAEOFOLIA f. *organensis* (Gardn.) Belcher, comb. nov.

Erechtites organensis Gardn. Lond. Jour. Bot. 7: 420. 1848.

Erechtites valerianaefolia var. *organensis* (Gardn.) Baker, Mart. Fl. Bras. 6³: 300. 1884.

Differing from the typical form in having the leaves very finely divided, the segments entire or only minutely serrulate; plants usually of small stature.

Holotype: Brazil, Rio de Janeiro, "open bushy places on the Organ Mountains, 3000 ft., March 1841", *Gardner 5790* (BM!).

Known only from subtropical Brazil and Bolivia.

BRAZIL: Paraná: Ypiraugá Feb. 1904, *Dusén* (S); São João, March 1910, *Dusén 9349a* (BM, K, S). Minas Gerais: Marianne, 1833, *Vauthier 306* (G Prodr.); Caldas, 1845, *Widgren 210* (S, 2); Caldas, Feb. 1875, *Regnell III 794* (S, 3). BOLIVIA: *Bridges* (BM); *Bang 2068* (BM; not F, K, which are f. *valerianaefolia*).

In addition to the finely divided leaves, Gardner's species was characterized by its hairy stem, smaller capitula, and shorter achenes, hispid instead of villous. The hairy stem is frequently found in f. *prenanthoides* and not uncommonly in f. *valerianaefolia* from widely scattered parts of its range. As for the smaller capitula, those of *Gardner 5790* have the phyllaries 7.5 mm. long, not 9 mm. as given by Gardner, but other specimens of f. *organensis* exceed this while numerous specimens of f. *valerianaefolia* closely approach it, so that there seems to be no useful discontinuity. Moreover, I have yet to see a truly villous achene, such as Gardner ascribed to *E. valerianaefolia*, anywhere in the genus *Erechtites* proper.

Although of the three non-typical forms of the species this one comes closest to having a distinct geographical range, it does not replace the typical state within that range but occurs with it as a comparatively minor element. Nor is the morphological distinction by which it is recognized a very great one. For these reasons this taxon is better given the status of a form. Hasskarl²⁵ arrived at a similar conclusion more informally: "Misschien is *E. organensis* Grnd. [sic!] (Wlp. Rep. II. 906. 2) niets, dan eene oude of magere vorm." There remains, of course, the possibility that it is ecologically very distinctive, but this can not be decided on the basis of the very meager information which accompanies the material cited.

²⁵ Verh. Meded. Kon. Akad. Wet. 5:100. 1857.

The type was obtained at an elevation of 3000 feet in a brushy opening on the mountain, whereas Dusén collected it in the Paraná Valley in swampy places at unspecified elevations not more than three hundred miles further south (but a greater distance westward). Nothing is stated about the habitat of the specimens from Bolivia.

2c. *ERECHTITES VALERIANAEOFOLIA* f. *reducta* Belcher, forma nova.

Folia 4 vel 5 superiora abrupte reducta, circa 2 cm. longa et 1 cm. lata, sessilia, pinnatifida, segmentis utrimque 4-6, lanceolatis; folia ad caulis mediam 8-10 cm. longa, 3.5-5 cm. lata, subpetiolata, inaequaliter dentata seu lobata, lobis distinctis plerumque 2 vel 3, raro 4.

Specimina typica (syntypi 2) legit Dusén (n. 14156) in Brasilia, Paraná, prope Antonia opp. in locis ruderalis, 29 Aug. 1912 (S!).

Differs from the typical form by the upper leaves being sessile, markedly reduced in size for several nodes below the inflorescence to as little as 2 cm. long and 1 cm. wide, deeply pinnatifid, with 4 to 6 lanceolate lobes on either side, often much more dissected than the median cauline leaves, which seldom have more than 2 or 3 distinct lobes per side but are 8 to 10 cm. long and 3.5 to 5 cm. wide and subpetiolate. The plants are simple below the inflorescence and of somewhat reduced stature, 40 to 70 cm. tall. Capitula are comparatively few. Occurs in southern Brazil; also Mindanao, Philippine Islands, and has been in cultivation.

BRAZIL: Rio de Janeiro [?], *Gardner 5528* (BM); Bahia, *Lockhart* (BM); Ceará, June 1929, *Bolland 39* (K). PHILIPPINES: Mindanao, Camaguin, 1912, *Ramos 14452* (US). CULTIVATED: "*Senecio valerianaefolius* H. P., J. de Paris, 1828" (G Prodr.); "*Erechtites valerianaefolia* DC.", ex hort. bot. Petropolitano (K, US).

This well-marked foliage state has never been described previously, as far as I can discover. From the limited number of specimens of this form among quite numerous specimens of *E. valerianaefolia*, it would seem to be very infrequent in the field. Because of its comparatively small stature, it would seem rather more likely to be collected by the casual collector, who often selects individuals of a size easily pressed, than the somewhat larger and more succulent f. *valerianaefolia*. I am unable to establish any valid pattern of distribution from the limited material seen so far. This interesting form might well be the object of careful attention from collectors, in order to extend the data on distribution and frequency. It should also be brought into cultivation along side the other forms for comparison and genetical analysis.

The very diffuseness of distribution, as indicated by the quite characteristic specimen from Mindanao, suggests that this form may simply be the product of a recurring mutation. That it is fertile is implied by the two plants from the Petrograd garden, which are presumably of the same progeny, and also by the two specimens from Antonina, Paraná. Both sets imply that there might be populations.

2d. *ERECHTITES VALERIANAEOFOLIA* forma *prenanthoides* (Kunth) Cuatr. in herb., comb. nov.

Cacalia prenanthoides Kunth in HBK. Nov. Gen. & Sp. 4:167. 1820, folio ed. 4: 131. 1820; non A. Gray, Proc. Amer. Acad. 19: 53. 1883.

Erechtites ambigua DC. Prodr. 6: 295. 1838, excl. syn.; non Sch. Bip. Bull. Soc. Bot. Fr. 12: 80, 1865.

Erechtites petiolata Benth. Pl. Hartw. 209, 1845. Type: Popayán, Hartweg 1160 (K!).

Senecio albiflorus Sch. Bip. Flora 28: 498. 1845.

Senecio lactuoides Klatt, Leopoldina 24: 125, 1888.

Erechtites prenanthoides (Kunth) Greenm. & Hieron. ex Hieron. Engl. Bot. Jahrb. 29: 63. 1900; *ibid* 28: 628. 1901, Type, Popayán, Lebmann 5665 (K!); non DC. Prodr. 6: 296. 1838.

Differs from the typical form in having all the leaves comparatively smaller, more or less petiolate, undivided, either merely serrate or at most the upper ones pinnately incised on the basal portion only; stem sparsely setaceous-hispid, leaves more or less scurfy-pubescent on the nerves beneath.

Syntypes: "*Cacalia prenanthoides*", Humboldt & Bonpland (P, 2 sheets, in Herb. Humb. & Bonpl.).

Of sporadic occurrence over much of the range of forma *valerianaefolia*.

BRAZIL: Sellow (G Prodr., holotype of *E. ambigua* DC.). Rio Grande do Sul: Cruz Atta, April 1893, Malme 776 (S, 2). Paraná: São João, March 1910, Dusén 9349 (S, 2). Minas Gerais: Lagoa Santa, Warming (S); Caldas, 1866-67, Regnell 1 272 (S, complete plant, this sheet only; others of this number with later date are typical form); Caldas, April 1874, Mosén 1421 (S). COLOMBIA. Cauca: Popayán, Silvio Yepes Agredo 328 (F); ad pagum El Tambo, June 1938, von Sneidern 1531, June 1939, von Sneidern 2770 (S). Valle: Cordillera Occidental, Hoyo del Rio Cali, Pichindé El Abismo, Cuatrecasas 18651 (F, 2). Cundinamarca: Salto de Tequendama, Cuatrecasas 54 (F). Magdalena: Santa Marta, Smith 2165 (K, lacking petioles); around San Andres de la Sierra, Pittier 1711 (F); Santa Marta, Recuerdo, Nov. 1947, Engstedt 84 (S). "Nouvelle Grenada", Triana 2806 (BM). PERU: Pennell 13982 (F). ECUADOR: Pichincha, Tandapi, July 1920, Holmgren 825 (S); Tungurahua, Hacienda San Antonio pr. Baños, Dec. 1937, Sydow 575 (S); Eastern Cordillera, valley of River Pastaza, Rimbach 492 (S); Camp E-4275 (F). MEXICO: Vera Cruz, Galeotti 2242 (K, G Deless.).

CHINA: Kwangtung, Kao-Yao Dist., Ting Woo Shan, beside stream, July 1932, Lau 20160 (NY). HAINAN: Kau-en Dist., Chim Fung Ling, near Sam Mo Watt village, April 1934, Lau 3870 (S, right only, left is typical form). SAMOA: Savaii, Safune, in rain forest along trail, May 1924, Bryan 121 (NY).

MATERIAL EXCLUDED: Of the several numbers of *Elmer* widely distributed as *E. petiolata* all that I have seen are small states of f. *valerianaefolia* with the petiolate entire lower leaves carried upward higher than usual, but with the upper leaves distinctly pinnatifid. Mandon 117 (K) det. as *E. ambigua* is *E. hieracifolia* var. *cacalioides*.

The Humboldt & Bonpland specimens are cited as syntypes because Kunth included both in his description, as indicated by the two measurements given, "sesqui- aut bipedalis". One specimen is 18 inches long, the other totals 22 inches in two pieces. Kunth's careful description of the leaves as petiolate, lanceolate-oblong, pinnatifid-incised toward the base, and decurrent on the petioles, makes clear that this name applies to the taxon with petiolate subentire leaves. The place of collection of the type specimens, usually precisely stated by Kunth, is for this species given dubiously as "Nova Hispania?" There is nothing on either syntype to correct this or to confirm it, unless it be the number "20" which occurs on one of the labels. Since this form has been collected from Mexico by others, in the vicinity of Vera Cruz, it may be that Mexico is the type locality, although it appears to be much more frequently found in Colombia. Kunth called the plant

a perennial, even while confessing "folia radicalia ignota". It actually appears to be a strict annual.

Greenman and Hieronymus apparently were the first to recognize *Cacalia prenanthoides* as an *Erechtites*. They transferred Kunth's specific epithet to this genus, reasoning that since the name *Cacalia prenanthoides* (1820) was older than *Senecio prenanthoides* A. Rich. (1832), the combination *Erechtites prenanthoides* (A. Rich.) DC. must fall and be replaced by *E. Labillardieri* Hieron.! Greenman and Hieronymus appear to have overlooked the appropriately named *E. petiolata* Benth.

Erechtites ambigua DC. was reduced by Baker to *Erechtites hieracifolia*. This error apparently can be traced to a sheet laid in at Kew as the "type" of *E. ambigua*. This is *Mandon 117*, determined by Schultz Bipontinus²⁶ as *Erechtites ambigua* in the list of determinations of Mandon's plants. The sheet at Kew has four specimens on it, all being *E. hieracifolia* var. *cacalioides*. If Baker accepted this sheet as authentic *E. ambigua*, he was fully justified in the reduction, and, indeed, it seemed quite logical in the light of de Candolle's ambiguous description of the leaves, which actually approximate those of some states of *E. hieracifolia*, and the flat statement that the pappus was white, not purpurascens. Although the pappus in the exposed capitula on de Candolle's holotype of *E. ambigua* has faded to an off-white except where concealed by the phyllaries, the capitula in the packet have distinctly pinkish pappus hairs, and de Candolle's statement is inaccurate.

Asa Gray, on unspecified evidence, equated *Cacalia prenanthoides* with *Senecio runcinatus* Less. (*E. ? runcinata* DC.) and maintained Kunth's name as the proper designation for the latter. Lessing's species actually is a discoid homogamous *Senecio* with unappendaged style arms and must be maintained as a *Senecio*. Its corollas are reddish purple and do not agree at all with Gray's definition of *Cacalia* as white-flowered with deeply cleft corollas. *Cacalia prenanthoides* A. Gray is thus a later homonym of *C. prenanthoides* Kunth.

After I had established the above synonymy, I found a specimen in the herbarium of the Chicago Museum of Natural History, collected by Cuatrecasas in Colombia and determined by him as "*E. valerianaefolia* forma *prenanthoides*". Cuatrecasas considers that this petiolate state, which he finds to be characteristic of the paramos, is an ecological response to the peculiar sort of xerophytic environment found there, with intense insolation. I can not wholly agree with him, mainly because of those specimens, probably including Kunth's syntypes, which have been collected at lower elevations from distant and discontinuous points, but I am glad to acknowledge his previous recognition of the identity and subsidiary status of *E. prenanthoides* (Kunth) Greenm. & Hieron. ex Hieron. The possible ecological status of this form needs to be investigated in the experimental garden.

3. *ERECHTITES MISSIONUM* Malme, Kungl. Sv. Vet.-Akad. Handl. 32: 73. 1899, excl. var. *lanceolata* Chod. & Hassl. Bull. Herb. Bois. II, 3: 732. 1903.

Annual herb. Stem strongly sulcate, glabrous, much branched above, to 1 m. high (or taller), leafy. Leaves as much as 20 cm. long and 8 cm. wide, usually somewhat less, approximately three times as long as wide, petiolate with the petioles

²⁶ Bull. Soc. Bot. Fr. 12:80. 1865.

narrowly or not at all winged, ovate to subovate, acute to briefly acuminate, irregularly incised-serrate with acuminately callose teeth, glabrous or minutely hairy beneath, sometimes more or less pinnately lobed toward the base of the blade, with lobes long-triangular and directed forward with their principal veins diverging from the midrib at an angle from 45° to 60° and the sinuses rounded, the lobes numbering from one to four on each side. Inflorescences terminal and axillary cymose panicles, congested in bud, becoming diffuse at anthesis, glabrous or sometimes with minute tightly appressed simple hairs on juvenile parts; peduncles suberect and elongating to 2.5 to 5 cm. at maturity; bracts subtending the primary branches much reduced in size but similar in shape to the cauline leaves, bracts of the secondary branches filiform, bracteoles of the peduncles 2 to 4, linear, 2 to 5 mm. long. Capitula solitary, at anthesis about 15 mm. long including pappus hairs, about 5 mm. in diameter when pressed, ventricose; calycular bracteoles few, linear, much shorter than the involucre, glabrous or with minute simple hairs; involucre of 12 or 13 attenuate-subulate phyllaries 11 to 13 mm. long, 0.7 to 1.0 mm. wide at base, abruptly reduced to a width of 0.5 to 0.8 mm., then linear, acute, finely multinervate with nerves becoming indistinct toward the apex, glabrous or minutely hairy in bud. Pistillate marginal florets in two or three rows, sometimes with rudimentary stamens; corolla filiform, 9 to 10 mm. long, 5-fid, with slender, acute lobes 0.5 to 0.6 mm. long. Disc florets hermaphroditic, more numerous than the marginal; corolla slenderly infundibuliform, 11 to 12 mm. long, 5-fid; lobes 0.5 to 0.6 mm. long, slightly then abruptly tapered to an acute and slightly papillose-thickened apex. Style-arm apex briefly appendaged with a cone of fused papillose hairs which has a fringe of divergent hairs at its base in the hermaphroditic florets. Achene 2 to 2.5 mm. long, subcylindric, dark brown and puberulous between the ribs. Pappus niveous, exceeding phyllaries by about 2 mm. and equalling the florets.

Indigenous to the Paraná River Basin in Argentina, Paraguay, and Brazil; also known from isolated stations in Peru and Venezuela, an extension of the previously reported range.

BRAZIL: Rio Grande do Sul: Colonia Ijuhy, in "roças" nec non juxta vias in silvas, April 1893, *Malme* 744 (BM, isotype; S. holotype, 3). Paraná: Cahnnon, March 1910, *Dusén* 9317 (S, an *E. valerianaefolia*?); Iacarehý, 1914, *Dusén* 15271 (BM, F, S); Jaguariahya, Nov. 1914, *Dusén* 15899 (F, S); Tres Barras, Jan. 1916, *Dusén* 17624 (S, very immature); Nova Galisia, Feb. 1916, *Dusén* 17700 (S). PARAGUAY: Caaguazú, Nov. 1874, *Balansa* 930 (K, a branch with pinnatifid leaves; G Deless., pinnatifid leaves on branches but subtending leaves similar to the type). ARGENTINA: Misiones: Posadas, Bonpland, April 1908, *Ekman* 1104 (S). PERU: 1835, *Matthews* 1739 (K). VENEZUELA: "prope coloniam Tovar", 1856-7, *Fendler* 1972 (K); "Bajo Cotiza, en la sombra al lado de rio", Sept. 1940, *Vogl* 417 (F).

This species is not easily distinguished from glabrous states of *E. hieracifolia*, the most usable characters being the nature of the leaf base and the length-width ratio of the leaf blade. Other characters, such as relative length and width of capitulum, number of florets, size of phyllaries, time of flowering, etc., are of little value because of variation in these features within both species. There is some

ground for suggesting that it is the South American equivalent of *E. hieracifolia* var. *hieracifolia*, and should be treated as no more than a variety. This possibility requires investigation by hybridization experiments and other such analyses, however, before it can be more seriously advanced. Until such studies have been made, the two species should be kept apart, although they are undoubtedly very closely related.

Judging from the rather meager ecological data on the tickets, this species is largely confined to the forest edge in rather moist situations. It is worth noting that altitudinally it ranges from near sea-level (below 200 m.) in the Paraná Valley at the southern end of its range at about 30° S. latitude, to well above 1000 meters in the Sierra Mérida of Venezuela, at about 8° N. latitude. What its altitudinal location in Peru may be is not indicated, but it is perhaps somewhat higher there, nearer the equator. It is very unlikely that the distribution of this species is as disjunct as these scattered records indicate. A search for it along the eastern foothills of the Andes on the edges of the forest openings and along trail-sides at about the 1000-meter contour from Venezuela to Peru and gradually descending southward to Bolivia and Argentina might establish many additional stations.

This species, aside from the original description, and the erroneous assignment to it of var. *lanceolata* by Chodat and Hassler (see below, under *E. goyazensis*), I have seen alluded to only once, by Cabrera²⁷. This was merely a statement that it was one of four well-known species of *Erechtites* in Brazil.

Chodat and Hassler undoubtedly must have assigned Hassler 8362 to *E. missionum* as var. *lanceolata* because of the resemblance of the capitula. But this resemblance does not extend to the florets nor to the leaves, whereas in both of these features there is detailed agreement between the several duplicates of Hassler 8362 and the type of *E. goyazensis*. The variety is to be excluded from *E. missionum*.

§ GOYAZENSES

4. ERECHTITES GOYAZENSIS (Gardn.) Cabr. Brittonia 7: 54. 1950.

Senecio Goyazensis Gardn. Lond. Jour. Bot. 7:421. 1848.

Erechtites missionum Malme var. *lanceolata* Chod. & Hassl. Bull. Herb. Bois. II, 3:732. 1903.

Perennial, suffruticose, 1 to 1.5 m. tall, branching from near the base, branches erect. Stem glabrous, leafy, with internodes only approximately 1 cm. long. Leaves sometimes 20 cm. long and 2 cm. wide, but usually less, with sharply and minutely callose-serrate margins and acuminate apices; midrib inflated beneath; lateral veins numerous, fine, prominent, diverging from midrib at an angle of 30° or less, glabrous; lower leaves narrowly oblanceolate or rarely obovate, subpetiolate, upper leaves lanceolate to linear-lanceolate with semi-amplexicaul bases. Inflorescence of several to many capitula in a paniculate corymb from terminal and axillary branches; capitula at anthesis solitary on elongated peduncles 2 to 3 cm. long, which bear

²⁷ Brittonia 7:54. 1950.

several linear-subulate bracteoles, calyculate with short linear bracteoles; phyllaries of the involucre 12 to 14, glabrous, linear, 9 (to 13) mm. long, acute. Florets rather variable, with corollas coarsely filiform to infundibuliform; the outermost one or two florets in each spiral series pistillate or with more or less well-developed staminodia, their style-arm apices rounded to shortly appendaged; inner florets all hermaphroditic with corolla campanulate, deeply 5-lobed; the lobes linear-lanceolate, 1.0 to 1.25 (to 1.5) mm. long, 0.25 mm. wide, conspicuously papillose-thickened apically; style-arm apices appendaged above a fringe of divergent papillose hairs. Achene 2.5 to 3 mm. long, strongly ribbed, glabrate. Pappus white, slightly exceeding the phyllaries and subequaling the florets.

Upper Paraná River Valley in Brazil, with an outlier in northeastern Paraguay; co-extensive with *E. ignobilis* Bak.

BRAZIL. GOIAS: near Natividade, in shady woods, Dec. 1839 (or bushy places near Ville Natividade, Jan. 1840), *Gardner 3300* (BM, holotype; K, 2; F ex G, fragment; F ex P; F, photograph ex B). MINAS GERAIS: Lagoa Santa, *Warming 102* (S); Caldas, Feb. 1865, *Regnell III 795* (S, 4); 1844, *Weddell 1603* (P ex Hb. Sch. Bip., det. as *S. ignobilis*). SÃO PAULO: "in paludosis ad Mugi", Nov. 1833, *Lund 844* (G. Prodr., det. as *E. hieracifolia*). WITHOUT SPECIFIC DATA: *Pohl 633* (K, 2); *Pohl 2056* (W). PARAGUAY: Bellayista (Apa), Hassler 8362 (S); Flum. Apa, Jan. 1902, Hassler 8362 (G. Deless., 3, presumptive types of *E. missionum* var. *lanceolata*, but redetermined by Chodat as a var. of *E. ignobilis*; BM; K, 2; W). Specimen excluded: Brazil, *Glaziov 16174* (BM, K; det. as *S. Goyazensis* but is homogamous, is *S. Grisebachii* Bak. var. *leptotus* Cabr.).

Cabrera gave the following reason for transferring *Senecio Goyazensis* Gardn. to *Erechtites*: "The marginal florets of this species are tubulous without anthers. The involucre is also typical of *Erechtites*." He did not cite specimens, nor is it clear that he examined the type. The sheets at Kew and the British Museum (Natural History) had not been loaned, but *Gardner 3300* appears to have been a very widely distributed number, and he probably saw an isotype.

Dissection of representative capitula on the type and on other specimens reveals that the trend toward unisexuality of the outer florets is only partially and quite variably developed. Some capitula have all the series-terminating florets with rudimentary stamens or an occasional floret with one or two stamens polliniferous. Other capitula show complete abortion of anthers in the terminating florets, with some reduction in the next one or two florets inward in each spiral. Furthermore, the terminal appendage of the style arm is variable. Occasionally it is merely short-conic with only a few very short papillae at its tip, but with a corona of low pollen-presenting papillae below, while sometimes the apical papillae are more elongated and fused, with a much closer approach to the tuft of fused hairs which characterizes *E. hieracifolia*. Never have I observed a truncated or merely low-domed apex such as is common in *Senecio* and is seen in *S. leptanthus* Phil., which has been also (I believe, wrongly) reduced to *Erechtites* by Cabrera.

I retain Gardner's species in *Erechtites* where Cabrera has placed it because of this conic and sometimes appendaged style-arm apex, and because of the size of the capitulum and the number of florets. In these latter features it is much closer to *E. hieracifolia* and *E. missionum* than it is, for example, to the erchthitoid species

of *Senecio* in Australia, which are characterized by usually much smaller heads and by quite abruptly truncated style arms. Finally, the large and strongly ribbed glabrate achene indicates closer affinity with *Erechtites* than with *Senecio*, it being in fact scarcely distinguishable from that of *E. hieracifolia*.

The type of *E. missionum* var. *lanceolata*, Hassler 8326, has leaves rather narrower than those of Gardner 3300, but is identical with it in floral features, including the very deep lobing of the corolla. The difference in leaf width is bridged by Pobl 633, which is intermediate between these two. The several specimens of Gardner 3300 are not all alike, the holotype (BM) having leaves both shorter and wider than on the other sheets, whence the measurements in Gardner's description. Pobl 2056 (W) is another broad-leaved specimen which is otherwise in good agreement.

Both Gardner 3300 and Hassler 8362 have corolla lobes linear-lanceolate, 1.25 mm. long, 0.25 mm. wide, with the apices glandulose-thickened; whereas Malme 744 (holotype of *E. missionum* Malme) has corolla lobes deltoid, 0.5 mm. long and 0.33 mm. wide, with apices only slightly thickened. Malme 744 has leaves petiolate, broadly lanceolate to ovate, and is irregularly toothed or subincised; whereas both Gardner 3300 and Hassler 8362 have leaves sessile, narrowly lanceolate, and regularly serrate. I am certain that the proper affiliation of Hassler's specimen is with *E. goyazensis* rather than with *E. missionum*, as Chodat at first supposed. The sheets in the Delessert Herbarium reveal that Chodat later determined Hassler 8362 as a small-headed form of *E. ignobilis*, but neither Chodat nor Schultz Bipontinus ever published this name. Actually, there is good reason to suppose that the name *Senecio ignobilis* may have originally been given by Schultz Bipontinus to a specimen of this taxon of Gardner's rather than to the large-headed taxon to which Baker later applied it, judging by specimens in his herbarium (see below, under *E. ignobilis*).

The affinities of *E. goyazensis* are much closer to *E. ignobilis* than to any of the other species of *Erechtites*, but the two species differ not only in the sizes of the several parts of the capitulum but also in corolla lobing and in leaf margin and venation. Were it not for these features, *E. ignobilis* might be simply a polyploid of *E. goyazensis*, and these differences do not exclude the possibility. The relationship of these two co-extensive perennial species might well be the subject of a cytogenetic study.

5. *ERECHTITES IGNOBILIS* Baker, in Mart. Fl. Bras. 6³: 299. 1884.

Senecio ignobilis Sch. Bip. in sched. ex Baker, l. c., in syn. nom. nud.

Perennial from a woody base; shoots subherbaceous, glabrous, 40 to 80 cm. high (or more?), sparsely branched in the inflorescence only. Leaves rather crowded toward the base, margins remotely and sharply dentate, apices acute; lowest leaves obovate to oblanceolate, subpetiolate, 7 to 10 cm. long, 12 to 18 mm. wide, upper leaves lanceolate to linear-lanceolate, sessile, smaller. Inflorescence corymbose, consisting of a few capitula borne singly on long peduncles which terminate the stem and the few axillary branches; capitula 18 to 25 mm. long,

9 to 12 mm. wide when pressed. Involucre oblong, of about 15 linear, glabrous phyllaries 16 to 20 mm. long, with 4- or 5-nerved keel and scarious margins, exceeded by both pappus and florets at full maturity; outermost one or two florets of each spiral-series filiform, functionally pistillate but frequently containing rudimentary stamens; remainder of florets hermaphroditic; style-arm apices shortly appendaged; corollas 16 to 18 mm. long. Achene 4 mm. long, subcylindric, strongly ribbed, glabrate, dark brown; pappus abundant, white, exceeding phyllaries, sub-equalling florets.

Easily distinguished from *E. goyazensis* by the much larger and fewer capitula.

Lectotype: "Brasilia, ex herb. hort. Petropolitani, rec'd. 11/66, *Senecio ignobilis* Sch. Bip. (*teste* Sch. Bip.)", *Riedel* (K!).

Apparently confined to the Paraná River Valley.

BRAZIL. "Brasilia, etc.", *Riedel* (BM); "379 ex hb. hort. Petrop., *S. ignobilis* Sch. Bip. (*teste* Sch. Bip.), Brasilia", *Riedel* (W); "512 . . . in paludosis Yttu, Febr. 1836", *Riedel* (P, ex Hb. Sch. Bip., not det. as *S. ignobilis*!). MINAS GERAIS: Lagoa Santa, *Warming* (K, F; photograph as no. 106 ex Hb. Haun., F); Lagoa Santa, *Lund* (S). SÃO PAULO: Cana [?] verde, Feb. 1849, *Regnell III* 796 (S). PARANÁ: Turma, Jan. 1910, *Dusén* 9061 (S); Jaguarahyva, April 1910, *Dusén* 9698 (S, 22 cm. high, only 2 capitula), *Dusén* 9727 (S), Oct. 1910 *Dusén* 10528 (S), Dec. 1910, *Dusén* 11006, Nov. 1914, *Dusén* 15994 (S), *Dusén* 15998 (F, S). PARAGUAY: Caaguazú, *Hassler* 9255 (K, S, W); in regione fluminis Corrientes, *Hassler* 5864 (K, G Deless., S).

Baker described this species as an annual herb, but several specimens, including *Riedel* 379 (W), *Hassler* 9255 (K, W), and indeed two of the sheets at Kew determined by Baker, including the lectotype, have stems with distinctly woody bases and portions of perennial rootstocks attached.

Five collections are cited by Baker in the original description. Since no one specimen is designated as the nomenclatural type, all must be considered as syntypes. The name-bringing specimen being *Riedel*'s, I have designated it as the lectotype.

The inclusion of *Senecio ignobilis* in synonymy by Baker does not constitute valid publication, and its association with *Riedel*'s specimen appears to be the result of a curatorial error, probably at the St. Petersburg herbarium, which Baker, unsuspectingly perpetuated. The specimens in *Schultz*'s herbarium which bear this epithet all belong to other taxa.

ERECHTHITOID SPECIES OF SENECEO IN AUSTRALASIA

SENECEO L. Gen. Pl., ed. 5, 375. 1754, *et auct., in sensu extenso*.

Trees, shrubs, or herbs; the erechthitoid species mostly semi-woody perennials. Capitula with all florets perfect and infundibuliform, or with the marginal florets more slender, pistillate, and either ligulate, subligulate, or irregularly or regularly 2- to 5-fid and sometimes with rudimentary stamens that very rarely may be polliniferous; style-arm apices truncated or low-domed, with crown of divergent papillose hairs at least in the perfect florets, and not prolonged into an appendage of fused papillose hairs.

The erechthitoid species are distinguished from true *Erechtites* by the style-arm apices truncated or low-domed rather than prolonged in an appendage of fused papillose hairs, as well as by smaller and less heavily ribbed achenes and usually smaller capitula. Represented by numerous species in Australasia, with outlying species in New Guinea and one in Java; occasionally met with elsewhere, as *S. leptanthus* Phil. in Chile and forms of *S. flavus* Sch. Bip. (*S. Decaisnei* DC.) from Arabia. Two Australasian species, *S. minimus* and *S. glomeratus*, are adventive on the Pacific Coast of the United States.

De Candolle divided the Australasian species of *Erechtites* into three sections, MICRODERIS, TULODISCUS, and PLAGIOTOME. Subsequent authors have only rarely attempted to classify their new taxa as to section. This probably reflects the fact that the separations made by de Candolle are highly artificial and do not stand examination. In returning these species to *Senecio* I have not retained these sections. Neither is it advisable to create a new section in *Senecio* for these erechthitoid species. Although they can, for the most part, readily be separated from the other Australasian species of *Senecio*, there are within the group some species which clearly intergrade into the discoid group and others which intergrade into the radiate group. Therefore, pending a badly needed revision of Australasian species of *Senecio* proper, I shall refer to the heterogamous material only as erechthitoid *Senecio*.

Our understanding of the relationships between the non-erechthitoid species of *Senecio* in Australasia is poorly developed, since it has not passed beyond the crude separation into discoid versus radiate species. The soundness of this separation has been questioned by virtually every competent syntherologist from the time of Linnaeus to the present. For example, Bory de St. Vincent²⁸, in criticizing Thunberg's confused efforts to restore *Jacobaea* Tourn., claimed that Linnaeus joined (discoid) *Senecio* and (radiate) *Jacobaea* as *Senecio* on the premise that the presence or absence of ligulate florets is not a constant character even in the same individuals of a single species. In support of this, Bory cited his own experience of finding that the late autumnal flowers of several radiate species, notably *Senecio Doria* L. (*Jacobaea pratensis*, *altissima*, *Limonii folio* Tourn.) lacked the ligulate florets ordinarily so conspicuous in earlier flowerings, and so could have been classified into a different genus from the one to which they would have been referred some months earlier, if the radiate and the discoid species were separated as Thunberg proposed.

A related situation is the existence of radiate varieties of discoid species, such as the not uncommon var. *radiatus* of *S. vulgaris*, the standard species of the genus, or the ligulate var. *fallax* (Greenm.) Fern. of *S. pauciflorus* Pursh. This latter species was regarded by W. J. Hooker²⁹ as a "rayless state of *S. aureus*".

Examination of a large number of specimens of *S. glomeratus* (*E. arguta* DC.) has revealed that in this species in particular the boundary between radiate and non-radiate conditions is very imperfect. A single specimen often possesses some pistil-

²⁸ Ann. Gén. Sci. Phys. 1:304-305. 1819.

²⁹ Flora Boreali-Americana 1:332-333. 1834.

late marginal florets so obliquely one-toothed as to be actually briefly ligulate, some that are irregularly bidentate, others that are irregularly 3-fid with one sinus twice or thrice as deep as the others, and still others that are perfectly regularly 3-fid with shallow sinuses. The same situation has been observed, but much less frequently, in other erechthitoid species.

In the folder of *Senecio aureus* var. *subnudus* at Kew there is a specimen (Great Slave Lake, *Gates & Mellenby*) which indicates that the outermost whorl of florets, those terminating each phyllotaxic spiral in the capitulum, is unstable in another direction. This is a discoid specimen which has rare marginal florets with stamens non-polliniferous, although the style-arm apex is clearly truncated. This is a close approach to the condition in *Erechtites*, especially in section *Goyazenses*, where an occasional marginal floret may bear a set of rudimentary stamens. It is a situation found over and over again in the erechthitoid species of Australasia, and is the basis for the statement made above concerning the intergrading of the discoid and the erechthitoid groups.

Another instance of an erechthitoid *Senecio* is the Chilean *S. leptanthus* Phil., recently transferred by Cabrera³⁰ to *Erechtites* because of its rather coarsely filiform pistillate marginal florets. This has a velutinous, weakly ribbed achene and low-domed, non-appendaged style-arm apex and is much better left in *Senecio*. The significant fact is that erechthitoid states of *Senecio* are not confined to Australasia, but are also found elsewhere. This adds weight to the point made by Mueller, that, as conceded by Bentham and Hooker in the 'Genera Plantarum', the genus *Senecio* could have slender pistillate florets. The limits of *Senecio* are not being unduly expanded or strained by the inclusion of heterogamous non-ligulate material from Australasia.

KEY TO ERECHTHITOID SPECIES OF *SENECIO*

- A. Phyllaries 5 to 9, rarely 10 or 11 in some but not all capitulaB
 B. Marginal florets pistillate, subligulate, disc florets androgynomorphic but with ovaries abortive and style arms rounded and densely hairy on outer face...see *Arrbenechthites*
 BB. Marginal florets pistillate or occasionally with incomplete set of stamens, 3- to 5-dentate, disc florets fertile, style arms truncate, not densely hairy on outer face but with crown of divergent hairsC
 C. Leaves distinctly once or twice pinnatisect1. *S. bipinnatisectus*
 CC. Leaves not divided, merely toothed or incisedD
 D. Achenes with short subappressed hairs in grooves between broad low ribs; florets not or scarcely exceeding phyllaries in numberE
 E. Leaves scarcely or not at all auriculate, coarsely and irregularly toothed, teeth varying in size and spacing and often denticulate; florets 5-fid, marginal florets devoid of rudimentary stamens, disc florets infundibuliform2. *S. biserratus*
 EE. Cauline leaves auriculate, coarsely but regularly toothed, teeth almost uniform in size and spacing; all florets 4-fid, subfiliform, and perfect, but with number of stamens varying from 1 to 43 *S. kermadecensis*
 DD. Achenes with fine white subappressed hairs on sharp narrow ribs, glabrous in the grooves; florets twice or more as numerous as the phyllariesF

³⁰ Not. Mus. La Plata 14 (Bot. No. 69):76. 1949.

- F. Leaves minutely and regularly toothed, 5 to 8 per cm., variably arachnoid beneath, glabrate with age, sparsely arachnoid or glabrate above, not lobed, oblong or oblong-lanceolate; stem glabrate or beset with minute unicellular hairs4a. *S. minimus* var. *minimus*
- FF. Leaves less regularly fine-toothed, with prominent hispid pubescence in addition to arachnoid hairs, more or less lobate, especially the lower ones, obovate to oblong; stem beset with hispid multicellular hairs4b. *S. minimus* var. *picridioides*
- AA. Phyllaries 11 to 13 or more, or rarely a minority of capitula with 11 or 10G
- G. Phyllaries 16 or moreH
- H. Achenes short, subcylindric; leaves lanceolate with margin variably and irregularly dentate or lobate, teeth or lobes obtuse, pubescence mixed, hispid and arachnoid; phyllaries glabrous on inner face.....5. *S. squarrosus*
- HH. Achenes long and attenuate; leaves linear-lanceolate, margin sharply denticulate with occasional larger coarse loboid teeth; pubescence arachnoid on stem, leaf, and inflorescence; phyllaries arachnoid on both inner and outer faces6. *S. pyrophilus*
- GG. Phyllaries 11 to 15, usually 12 or 13I
- I. Leaves only about 3 times as long as wide; plants glabrous or nearly soJ
- J. Achenes 1.5 to 2.0 mm. long, short-cylindric, densely and uniformly covered with very short appressed hairs, glabrate, plump, and indistinctly ribbed when mature; leaves up to 8 cm. long and 3.5 cm. wide, ovate-lanceolate or broadly oblanceolate, irregularly coarse-toothed, with sharply denticulate teeth, auriculate and semi-amplexicaul at base, entirely glabrous7. *S. laceratus*
- JJ. Achenes 3 to 3.5 mm. long, slenderly subcylindric, not densely and uniformly pubescent; leaves oblong, subpetiolate and slenderly auriculate, sinuate-dentate with 3 to 5 teeth on either side, glabrous above, minutely short-haired on nerves beneath; lower leaves 4 to 5 cm. long and 1 to 1.5 cm. wide; plant of New Guinea8. *S. papuanus*
- II. Leaves more than 3 times longer than wide; pubescence variousK
- K. Leaves and stems glabrous or sparsely cottony-haired when youngL
- L. Leaves runcinately pinnatifid, the segments long, narrow, and retrorse, apical segments on upper leaves filiform-acuminate; phyllaries 1 cm. long; marginal florets about 40, disc florets about $\frac{1}{3}$ as many; achenes 2.5 to 3 mm. long, subrostrate, with short, suberect papilliform hairs on the ribs..9. *S. runcinifolius*
- LL. Leaves subentire to sinuate-lobate, with lobes broad, not retrorsely pinnatifidM
- M. Achenes 4 mm. long, faintly ribbed, glabrous or sparsely white-haired in the grooves; leaves oblong-linear to broadly oblong, obtuse, sinuate-dentate, sinuate-lobate, or pinnatifid; marginal florets 10 to 15, disc florets about twice as numerous; phyllaries 6 mm. long with short-acute apices10. *S. wairauensis*
- MM. Achenes 3 mm. long, prominently ribbed, hairs suberect on or beside the ribs but not in the bottom of the grooves; phyllaries 5 to 5.5 mm. long with apices abruptly narrowed and then bluntly acuminate; radical leaves oblanceolate, long-attenuate to subpetiolate, 3.5 cm. long and 6 mm. wide; cauline leaves linear-lanceolate to linear-oblong, 6 cm. long, 5 mm. wide, remotely sinuate-dentate to subentire11. *S. dunedinensis*

(Glabrate states of *S. quadridentatus* may be sought here; may be recognized by leaves linear-lanceolate, with margins minutely denticulate and strongly revolute, and phyllaries slenderly acuminate.)

- KK. Leaves and stems conspicuously pubescent, hairs arachnoid or hispid or both combined; sometimes nearly glabrate at maturity
.....N
- N. Leaves entire or denticulate; achenes more or less fusiform, 2.5 mm. long or longerO
- O. Leaves linear to lanceolate, to as long as 9 cm., 0.3 cm. wide; phyllaries 6.5 to 8 mm. long, at first arachnoid then glabrate, except basally, 2-nerved on lower third only, apices acuminate12. *S. quadridentatus*
- OO. Lower leaves oblanceolate or obovate-lanceolate, 8 to 12 cm. long, 1.5 to 1.8 cm. wide; phyllaries 6 mm. long, glabrous or sparsely arachnoid at base, 2-nerved, often purplish, apices acuminate13. *S. gunnii*
- NN. Leaves toothed, incised, or irregularly lobed, achenes short-cylindric, 1.5 to 2.0 mm. longP
- P. Receptacle and base of involucre lanate; leaves densely arachnoid beneath, sparsely arachnoid to glabrate aboveQ
- Q. Achene with 10 low broad ridges; apex of phyllary acute with scarious margin14. *S. glomeratus*
- QQ. Achene with 5 extremely narrow high thin ridges; apex of phyllary long and slenderly acuminate and essentially lacking scarious margin15. *S. laticostatus*
- PP. Receptacle and involucre glabrous; phyllaries strongly 2-ridged; leaves with crisped multicellular hairs beneath and hispid or scabrid above, rarely glabrate; bidentately auriculateR
- R. Leaves callose-denticulate to coarsely dentate or somewhat lobateS
- S. Hairs on upper leaf surface with subtuberculate bases; achenes 1.5 to 1.75 mm. long.....16a. *S. hispidulus* var. *hispidulus*
- SS. Hairs on upper leaf surface without subtuberculate bases; achenes 1.75 to 2 mm. long16b. *S. hispidulus* var. *scaberulus*
- RR. Leaves once-pinnatisect, the segments denticulate.16c. *S. hispidulus* var. *dissectus*
- PPP. Receptacle and involucre glabrous or densely lanate; leaf pubescence both arachnoid and hispid; achenes usually short, various introgradient hybrids*S. glomeratus* × *S. hispidulus*

1. *SENECIO bipinnatisectus* Belcher, nom. nov.

Erechtites Atkinsoniae F. Muell. Frag. Phytogr. Austr. 5: 88. 1865. .

Senecio Atkinsoniae F. Muell. *ibid.* ut synonym, nom. nud.; non *Senecio Atkinsonii* C. B. Clarke, Comp. Ind. 207. 1876.

Stout plant with stem strongly striate, subglabrous or sparsely short-haired, branched above with branches ascending, densely leafy; basal portion not seen. Cauline leaves and bracts pinnatisect or bipinnatisect, with segments irregularly denticulate or subentire, slender, markedly revolute, sessile, with pinnatisect auricles; lower leaves up to 10 cm. long with segments up to 5 cm. long, size gradually reduced upward; older leaves glabrate, younger subarachnoid beneath with a few glandular or tuberculate-hispid hairs above. Inflorescences decomposed, corymbose, varying in expansion from very simple corymbs with 3 or 4 capitula per branch to repeatedly rebranched clusters 25 cm. in diameter with scores of capitula, axes glabrous throughout or sparsely short-haired on peduncles; peduncles with

several simple, subulate, erect, sometimes ciliolate bracteoles. Capitula usually with 8 phyllaries, sometimes as many as 11 on some but not all capitula; phyllaries 6 to 6.5 mm. long, slender, usually 2-nerved and only moderately keeled, glabrous or minutely glandular-pubescent, apices shortly tapered, obtuse or very slightly acute. Florets slightly longer than the phyllaries and equaling pappus, marginal ones pistillate, filiform, 3- or 4-fid, twice or thrice as numerous as the hermaphroditic slenderly infundibuliform 5-fid disc florets. Achene 2 mm. long, short-subcylindric, not attenuate-rostrate, dark red, ribbed, glabrous or sparsely set with very short white hairs especially when immature.

Apparently confined to the Coastal Ranges of New South Wales and southeastern Queensland.³¹

AUSTRALIA. NEW SOUTH WALES: Blue Mountains, *Louise Atkinson* (K, det. by Mueller, syntype duplicate and lectotype); Monkey Creek towards Port Jackson, *Woolfs* (MEL, syntype); Sydney, *Wilkes Exp.* (US); "Senecio, Australasia, N. S. W.", *Hugel* (W); Brushy Mountains near Gloucester, 1881, *Betche* (NSW); Port Macquarie, 1898, *Boorman* (NSW); Port Stacking, Feb. 1899, *Camfield* (NSW); Blackheath, April 1899, *Maiden* (NSW, W); Bulli Pass, 1900, *Hamilton* (NSW); Blackhurst, swamp, Jan. 1903, *Camfield* (NSW); Jervis Bay, 1926, *Rodway* (K, NSW); Beaumont, 1935, *Rodway* 1687 (K); Braidwood, 1936, *Stenfield* (NSW). QUEENSLAND: Blackwall Range, April 1918, *White* (K); Candle Mountain, May 1918, *White* (NSW); Main Range, top of Mt. Mitchell, 3760 ft., *White* 6872 (NY). WITHOUT LOCALITY: "Iter Australiense 1802 to 1805", *R. Brown* 2279 (K); "Nova Hollandia, *Erechtites sonchoides* Cand.", *Ferd. Bauer* (W).

The new epithet refers to the characteristic deep division of the leaf and bract blades. As stated by Mueller, this species differs from all its erechthitoid congeners by the form of its leaves. But in *Senecio* it resembles *S. anethifolius* in its pinnatisect leaves with narrow divisions. Comparison of specimens of *S. bipinnatisectus* with the type of *S. anethifolius* (G!) shows them to be readily distinguishable even in the sterile state. The leaf segments of the former are strongly revolute, irregularly denticulate, minutely tuberculate-hispid above and subarachnoid beneath, whereas those of the latter are slightly revolute, non-denticulate, and glabrous. The floral features are, of course, much more distinct, the former having moderately keeled and minutely glandular-pubescent phyllaries 6 to 6.5 mm. long, and marginal florets pistillate, filiform, and scarcely exceeding the phyllaries; whereas the latter has glabrous phyllaries 5.0 to 5.5 mm. long, and marginal florets hermaphroditic, infundibuliform, and much exceeding the phyllaries. I do not know any other Australasian species with which either of these might be confused, unless it might be *S. hispidulus* var. *dissectus* (Benth.) Belcher. In this variety, however, the leaves are only once or very imperfectly twice dissected, the segments are sharply angulate-lobate rather than denticulate or entire, and the pubescence is coarsely tuberculate-hispid. The inflorescence is, of course, unmistakably distinct from both the above species.

³¹ The description of this and each subsequent erechthitoid species is followed by a list of specimens examined, with the herbaria in which they are found indicated by the symbols proposed by Lanjouw. In the case of the more commonly collected species, the list is a selected one to show the range of distribution and variation. Of less common species, all material examined has been cited. In each case the typifying specimen, if seen, is listed first.

Mueller gave the number of phyllaries as "11 to 13". I have not found any capitulum with more than eleven, and the majority had only eight. The lectotype at Kew does have a few heads with up to eleven. A certain amount of instability in the number of phyllaries seems to be common in those genera of Compositae with essentially uniseriate involucre, and indeed seems rather widespread in the family. For individual plants, however, it is usually possible to find that the modal phyllary number of a majority of the capitula is very close to one of the peaks of the phyllotaxic series: 8, 13, 21, etc. Further, there is generally a correlation with other characters of taxonomic significance, so that the use of the modal number of phyllaries as an easily seen key character is valuable. Because this modal number for *S. bipinnatisectus* is 8, and seems not to reach the value of 13 assigned by Mueller, I have placed this species in the group with eight phyllaries.

The number of florets per capitulum is quite variable, and little dependence should be placed on the exact numbers given in descriptions, as by de Candolle. Richard, who appears to have studied these species more carefully, omitted almost all reference to specific numbers of florets. Approximate numbers, however, are helpful, and the ratio between pistillate and perfect florets may be significant. For this species a representative count is sixteen pistillate to five perfect florets in one capitulum, a ratio of about three to one.

Immature buds of this species closely resemble those of *S. minimus* in size, shape, number of phyllaries, and particularly in a spiraled appearance. This is caused by the unexpanded phyllaries running slantingly rather than lying straight from base to apex. The leaves also agree with those of *S. minimus* in having usually quite large auricles, and these two species are undoubtedly quite closely related.

2. *SENECEO biserratus* Belcher, nom. nov.

Senecio flaccidus A. Rich. Sert. Astrolabe, 110-112. 1834; non Less. Linnaea 5: 161. 1831.

Erechtites sonchoides DC. Prodr. 6: 296. 1838; non *Senecio sonchoides* Kunth, in HBK.

Nov. Gen. & Sp. 4:178. 1820.

Erechtites prenanthoides Benth. Fl. Austral. 3: 658. 1866, *pro parte*, non DC.; Black, Fl.

S. Austral. 4: 609-610, *pl.* 50. 1929, non DC.

Stem erect, to 5 feet tall, glabrous or glabrate, simple or sparingly branched above, leafy. Leaves rather crowded and suberect, membranous, as much as 11 cm. long and 4 cm. wide, gradually and proportionately reduced upward, sessile, the lower ones slightly or much attenuated and not clasping, the upper ones auriculate and semiamplexicaul, all oblong to oblong-lanceolate, serrate, with irregular larger teeth again finely toothed, glabrous or sparsely set with rather long multicellular hairs. Inflorescence a corymbose panicle, open and lax at maturity, the branches, peduncles, calyculi, and involucre essentially glabrous; bracteoles broad, subulate. Involucre of 7 or 8 phyllaries; phyllaries 5 to 6 mm. long, alternately narrower and broader, to 1 mm. wide, keel more or less conspicuously 2-ridged with a broad or narrow shallow groove between, apices alternately moderately long-acute and quite bluntly obtuse (i.e., probably actually 2-seriate), all minutely ciliolate, with a marked tendency to curl after achenes have been shed. Florets scarcely exceeding phyllaries in number. Marginal florets pistillate, filiform, 5-fid, lacking rudi-

mentary stamens; disc florets hermaphroditic, slenderly infundibuliform, 5-fid. Achene 2.5 to 2.75 mm. long, subcylindric, slightly tapered toward base, apex not attenuate-rostrate but slightly contracted below the apical callus, with white hairs in grooves between heavy low flattened ribs. Pappus and florets exceeding involucre by 1 to 2 mm.

AUSTRALIA. TASMANIA: "N. Holl. détr. d'Entrecasteaux", ex itin. *Baudin* (P. holotype); "Nouv^e Hollande cote merid^e, Mus. de Paris, 1821" (G Prodr., isotype?, holotype of *E. sonchoides* DC.); Deloraine, Jan. 1902, *Maiden* (NSW); Mount Field East, ca. 4000 ft., March 1906, *Maiden* (NSW); Eaglehawk Neck, Nov. 1924, *Lucas* (NSW); Hobart, near Myrtle Gully, Cascades, "in open forest burnt out previous summer, ca. 900 ft., stout upright herb 4½ ft. tall", March 1940, *Gordon* (HO, leaves as much as 11 cm. long, 4 cm. wide, coarsely lobed); Florentine Valley, Adamsfield track, 1500 ft., Feb. 1943, *Gordon* (HO); Gordon, Dec. 1952, *Curtis* (HO). VICTORIA: Port Fairy, *Whan* (NSW); Port Fairy, Nov. 1900, *Walker* 7 (NSW). NEW SOUTH WALES: Port Jackson, *R. Brown* 2277 (K). NEW ZEALAND. SOUTH ISLAND: Canterbury, Akaroa, *Raoul* 30 (K); Otago, *Lyall* (K); Otago, Milford Sound, *Lyall* (K ex Hb. Hk. as *E. prenanthoides*, left-hand specimen only; right is *S. wairauensis*). STEWART ISLAND: "In arenosis maritimis", *Thouroude* (P). AUCKLAND ISLANDS: "*Erechtites arguta* var. *glaberrima*", *Wilkes Exped.* (K, US).

Bentham's reduction of this perfectly good species to *Erechtites prenanthoides* DC. (i.e., *S. minimus* Poir.) is unjustified, despite several points of similarity. By direct comparison of the types in the Prodromus Herbarium they may be separated rather easily by differences in achenes and leaf margins. The achene of *S. biserratus* is 2.5 to 2.75 mm. long, flat- and broad-ribbed, with hairs *between* the ribs; that of *S. minimus* ranges from 1.5 to 2.0 (to 2.25) mm. long, is sharply and narrowly ridged, and is hairy *on* the ridges rather than between them. The leaves of the former are coarsely and irregularly doubly serrate, as the new epithet indicates, whereas those of *S. minimus* are uniformly finely denticulate. Again, the former species is virtually glabrous except for the achene and sparse appressed hairs on both sides of the leaf, lacking the arachnoid pubescence on the lower surfaces of the leaves and on the juvenile parts which characterize the latter.

E. prenanthoides Black, by figure and description, is *S. biserratus*. The figure of the cross-section of the achene which shows hairs only in the narrow grooves is critically diagnostic, as is the irregularly toothed leaf. Black gives the distribution simply as "South-East". If this species actually is in southeastern South Australia, then it should also be more generally present in Victoria, to link up with its presence in New South Wales and Tasmania. The specimen from the Auckland Islands, incidentally, is the most southerly specimen of erechthitoid *Senecio* which I have seen.

De Candolle's diagnosis of *E. sonchoides*, based on a specimen at Geneva, was formed independently of Richard's, but agrees fairly well with it. He was uncertain of the identity, and queried Richard's name in the synonymy. He need not have been so cautious. His type and that of Richard are certainly conspecific, and are probably a part of the same gathering, by the expedition of Baudin. From de Candolle's account of the small number of phyllaries and florets, it seemed *E. sonchoides* might be an *Arrhenechthites*. Accordingly, the florets, and particularly the style arms of the central florets, on the type were carefully examined with the aid of detergent solution. The central florets are hermaphroditic, developing nor-

mal rather than abortive achenes; the style arms are long, recurved, and stigmatic; the style-arm apices are squarely truncated and not papillose on either apex or dorsum. It is a good *Senecio* despite the reduced number of parts.

3. *SENECIO kermadecensis* Belcher, sp. nov.

Perennis (?), caule herbaceo, solum versus apicem ramoso, dense foliaceo; foliis sessilibus late auriculatis, amplexicaulibus, vix constrictis super auriculas, ovato-lanceolatis, inaequaliter dentatis, acutis vel subobtusis, nonnihil scabris, subglabris, majoribus (infimis haud visis) 13 cm. longis, 4 cm. latis; inflorescentiis corymbosis; capitulis cylindricis, calyculatis; involucri squamis plerumque 6 (5 - 7), linearibus, glabris, 5 mm. longis; floribus paucis, numero squamis similibus, omnibus tenuiter filiformibus, apice vix dilatatis, 4-dentatis; staminibus 1-4 numero variante in floribus capituli singuli, omnibus polliniferis, ramis styli truncatis, papillis marginalibus divergentibus praeditis; achaeniis subcylindricis, 2 mm. longis, 10-costatis, subappresse puberulis inter costas; pappo niveo, subsetaceo, pluriseriato.

Specimen typicum legit W. R. B. Oliver in insula prope Novam Zeelandicam "Sunday Island" dicta in Archipelagine Kermadecensi. Endemica species. Specimen in herbario Kewensi.

Cheeseman, in 1925, confused this species with *E. prenanthoides* DC., and attributed to W. R. B. Oliver the statement that it was "not uncommon on Sunday Island" of the Kermadec Islands. Oliver's specimen at Kew, the holotype, bears that statement on its label. Erroneously determined as *E. prenanthoides* DC., this specimen superficially resembles that species, but is actually distinct and apparently undescribed.

It is remarkable in the genus for its unusual capitulum, with phyllaries 5 to 7, usually six, and the florets about equal in number. All florets appear to have styles and functional stamens, the number of stamens varying within the same capitulum from 4 to 1. The florets are nearly filiform, very little dilated apically, and 4-fid; the style-arm apices are truncate with a fringe of diverging papillae. Some achenes in the capitula examined were less developed than others in the same capitulum, suggesting partial sterility, but this appeared not to correlate with the position of the achene in the capitulum nor with the number of stamens. The achenes, although similar in size to those of *S. minimus*, resemble those of *S. biserratus* in being hairy *between* the ridges. The leaves, though resembling those of *S. minimus* in general shape, were much more broad and coarse than is typical for that species.

Senecio kermadecensis must be regarded as a discoid *Senecio* of unusual interest, suggesting a transition between the discoid and the erechthitoid kinds, as shown by the partial sterilization and the slenderness of the florets. It also suggests a transition between *Senecio* and *Arrbenechthites*, as shown by reduction in floret number and possible tendency to abortion of some ovaries. Its closest affinity in the erechthitoid group is not with *S. minimus*, as Oliver and Cheeseman thought, but with *S. biserratus*, as shown by the drastic reduction in floret number and by the achenial pubescence. I hesitated to describe it without examining more material. But since it raises the interesting possibility that other peculiar endemics may be masquerading as well-known species, it seemed desirable to call attention to it.

4. *SENECIO MINIMUS* Poir. in Lam. Ency. Méth. Bot. Suppl. 5: 130. 1817.

Inflorescence a corymbose panicle, usually large with very many capitula, diffusely much branched, branches suberect or lax; arachnoid in bud, glabrate when expanded; bracts subtending the branches rapidly and progressively reduced in size upward, two or three bracteoles on each ultimate peduncle, capitulum with calyculus of 5 or 6 short slender inconspicuous bracteoles. Involucre of 8 phyllaries, rarely one or two more or less; phyllaries 6 to 7 mm. long, linear, alternately 2-nerved and broader with broadly obtuse apex, and 1-nerved and narrower with narrowly obtuse apex, glabrous or subglabrous but with apices ciliolate and slightly darkened or not. Florets exceeding involucre, slightly exceeded by pappus; marginal florets filiform, briefly 3-, 4-fid, somewhat more numerous (ca. 12 versus 7) than the disc florets, which are hermaphroditic, slender, slightly expanded into a narrowly infundibuliform 5-fid limb. Achene 1.75 to 2.0 (to 2.25) mm. long, short-cylindric, dark reddish-brown or brown, with fine white subappressed hairs on the narrow ribs, the grooves glabrous, non-attenuate but with apex callose-annulate. Pappus white, filiform.

4a. *SENECIO MINIMUS* var. *minimus*

Erechtites minima (Poir.) DC. Prodr. 6: 437. 1838, in synonymy.

Erechtites pumila DC. Prodr. 6: 297. 1838, said by DC. to be based on "*S. pumilus* Poir.", which is non existent; *non* Armstrong, Trans. N. Z. Inst. 13: 338. 1887.

Erechtites prenanthoides DC. Prodr. 6:296. 1838; *non* A. Rich. (as *Senecio*, based on *Gaudichaud* 4, Pl, which is *S. quadridentatus*); *non* Greenm. & Hieron. Engl. Bot. Jahrb. 29:63. 1900, which is *E. valerianaefolia* f. *prenanthoides*.

Senecio hieracifolius Hb. Labill. ex DC. Prodr. 6:296. 1838, *ut syn.*; *non* Linn. Sp. Pl.

Erechtites prenanthoides Hook. f. Fl. N. Z. 141. 1853, *pro parte*, excl. var. *minor* Hook. f.

Senecio Mülleri Regel, Ind. Sem. Hort. Bot. Imp. Petrop. 31, 1863; *non* Kirk, Trans. N. Z. Inst. 15: 359. 1883; *non Erechtites Mülleri* Lange, Ind. Sem. Hort. Haun. 28. 1861 [not seen]; Bot. Tidskr. II. 4: 5. t. 3. 1874.

Senecio Warscewiczii Hort. Berol. apud Vatke, App. Ind. Sem. Hort. Bot. Berol. 21. 1875; *non* A. Br. & Bouché, Ind. Sem. Hort. Bot. Berol. App. 13. 1851; *Linnaea* 25: 298. 1852 (from Guatemala).

Senecio heterophylla [sic !] Colenso, Trans. N. Z. Inst. 27: 389. 1894.

Erechtites Labillardieri Hieron. Engl. Bot. Jahrb. 29: 63. 1900, superfluous.

Herbaceous plant of somewhat glabrate aspect, robust specimens exceeding 1 m. in height, others as low as 15 cm. Stem erect, sulcate, simple or sparingly branched below the inflorescence or with numerous short axillary branches with much-reduced leaves, glabrous or sparsely set with minute white hairs. Leaves rather variable in size and shape, lower cauline ones on robust specimens reaching or somewhat exceeding a length of 10 cm., 1.5 cm. wide, size rather rapidly reduced upward on stem, width decreasing proportionately more rapidly than length; lower leaves broadly lanceolate, upper linear-lanceolate; lower portion of blade not or only slightly constricted, rarely subpetiolate, the base slightly to conspicuously expanded into clasping lobes or auricles; the reduced leaves of axillary branches sometimes appearing non-auriculate, subpetiolate, oblanceolate; margins evenly denticulate, with 5 to 8 teeth per cm., or slightly irregularly denticulate with some teeth a little coarser but never pinnatifid; youngest leaves densely arachnoid below, sparsely so above, older leaves glabrate.

Generally distributed in temperate Australia, Tasmania, and New Zealand; adventive weed in California and Oregon.

AUSTRALIA. TASMANIA: "Capite Van Dieman", *Labillardière* (FI, "*Senecio hiera-cifolius* Lin., *Billardière*, N. Holl.", with specific epithet deleted and "minima" written beneath in *Poiret's* script, holotype; P, "*Senecio minima* Enc. Sup., *Labill. Nov. Holl.*", fragment of holotype, ex Hb. *Poir.*; BM; K; G Deles.; G Prodr., "*Senecio hyeracifolius e nova hollandia*, m. *Labillardière* 1808", holotype of *E. prenanthoides* DC.); *Gunn* 1175, Georgetown (K, 2), Marlborough (K), St. Patrick's (K, NSW); *Maiden*, Recherche Bay 1908, Swanport to Swansea 1902, Port Arthur 1906, Mount Field East 1906 (all NSW); Russell Falls, March 1910, *Cheel* (NSW); Lilydale, Jan. 1943, *Wardrop* (HO). VICTORIA: *Wendu Vale*, *Robertson* 469 (K, NSW); Dandenong Range, *Mueller* (K); Blacks Spur, Jan. 1900, *Deane* (NSW); Bonang, Jan. 1910, *Forsyth*, (NSW). NEW SOUTH WALES: New Castle Bay, *R. Brown* 2276 (K); Sydney & Newcastle, May-June 1855, *Harvey* (K); New England, *Mueller* (K); Box Point to Kangaroo Island, Oct. 1898, *Maiden* (NSW, W); Mt. Kembla, Nov. 1899, *Fletcher* (NSW); Blackhurst, Jan. 1903, *Camfield* (US, in 2 non-contiguous pieces, the sterile one with leaves to 16 cm. long and 4 cm. wide but otherwise congruent).

NEW ZEALAND: "New Zealand 1769-70", *Banks & Solander* (US); Nelson, Graham River, *Cheeseman* (US); Wairau Valley, *Travers* 16 (K); *Colenso* (K, isotypes (?) of *S. heterophylla*); *Hooker* (W ex Hb. Sch. Bip.); Westland, Parvu, Jan. 1937, *Lothian* (K).

UNITED STATES. CALIFORNIA: Campeche, 6 July 1931, *Jones* 59096 (BM); Humboldt Co., Trinidad, Sept. 1931, *Parks* 01058 (BM, F, MICH, NSW); Marin Co., Almonte, edge of salt marsh, July 1944, *Howell* 19857 (F, S). OREGON: Lane Co., Aug. 1949, *Cronquist* 6107 (S).

CULTIVATED: "809 *Senecio Warscewiczii*" 62 Hort. Berol. (P ex Hb. Sch. Bip.); "*Senecio Muelleri*", Hort. Bot. Petrop., 1863 (K, isotype (?) of *S. Müllerii* Regel).

I designate the piece of *S. minimus* at Paris as a fragment of the holotype, rather than an isotype, because the jagged base exactly matches the stump of a branch on the holotype. *Poiret* evidently obtained this small branch for himself when he described the species. All the other sheets of *Labillardière's* "*Senecio hyeracifolius*" which I cited are authentic isotypes, with the sole exception of the ligulate fragment on the sheet at Florence from *Labillardière's* own herbarium, and there are probably still other sheets in other herbaria.

The isotype of *S. Müllerii* Regel was compared with the holotype fragment of *S. minimus* and found conspecific. It was unquestionably distinct from presumably authentic specimens of *E. Muelleri* Lange which were raised at Vienna from seed from Copenhagen and which appear to be a form in the hybrid swarm, *S. hispidulus* × *S. quadridentatus*. *Vatke's* assumption of identity between *Regel's* species and *Lange's*, made in a note clarifying the status of *S. Warscewiczii* Hort. Berol., was an error.

This is one of the most distinctive of the erechthitoid species of *Senecio*, and shows little affinity with the other species. Its closest resemblance is to *S. biserratus*, as discussed above, although the two are readily separable. *Cheeseman's* statement that this species is "not uncommon on Sunday Island" of the Kermadecs appears to be based on *Oliver's* specimen, the holotype of *S. kermadecensis*. *S. minimus* is not to be included in the flora of the Kermadec Islands on this evidence.

4b. *SENECIO MINIMUS* var. *picridioides* (Turcz.) Belcher, comb. nov.

Erechtites picridioides Turcz. Bull. Soc. Imp. Nat. Mosc. 24: 200. 1851; Black, Fl. S. Austral. 4: 610. 1929; non Sond. & Muell. Linnaea 25: 253. 1852, which is *S. runcinifolius* Willis.

Erechtites prenanthoides DC. var. *picridioides* (Turcz.) Benth. Fl. Austral. 3: 658. 1866.

Differing from var. *minimus* in having the stem more robust and coarse and beset with hispid multicellular hairs; the leaves larger, lobate, and hispid, with acute callose teeth; and the corollas somewhat variable in number of lobes.

WESTERN AUSTRALIA: Swan River, 1845, *Drummond 132* (K, 2; FI; all isotypes).

I have not seen the holotype of this taxon, but the isotypes which I saw agreed well with the description. Dissection of florets, however, revealed much variation in lobing of the corollas. Pistillate florets were 2-fid, 3-fid, or 4-fid; the perfect florets were 3-, 4-, or 5-fid. I have not observed such variability in var. *minimus*. From hispid pubescence and callose-dentate leaves, as well as this variation in lobing, I suspect possible hybridization with *S. hispidulus*. But because of the great similarity in the other floral and the fruit characters between these specimens and the holotype of var. *minimus* I have maintained the varietal status given them by Bentham, pending further study.

Turczaninow stated: "*Species Er. senecioidi et argutae affinis.*" I find no other reference to the former, and it is presumably a *nomen nudum*. The Kew sheets of *Drummond 132* have tickets reading: "Erechtites / *E. sonchoidi* DC. Prodr. / Sw. riv. Drummond". "*E. sonchoidi*" is written hastily, and likely was miscopied by Turczaninow.

Black maintained this taxon as a species, separate from his *E. prenanthoides*. This was fully justified, since the latter is actually *S. biserratus*! He gave for *E. picridioides* a wide distribution in South Australia; namely, Encounter Bay, Kangaroo Island, Murray Lands, Yorke and Eyre Peninsulas, South-East. I have seen none of these specimens.

5. *SENECIO SQUARROSUS* A. Rich. Sert. Astrolabe, 107, *tab. 35*. 1834.

Erechtites Richardiana DC. Prodr. 6: 297. 1838.

Erechtites hispidula Benth. Fl. Austral. 3: 660. 1866, *pro parte*; non (A. Rich.) DC. Prodr. 6: 296. 1838; non Black, Fl. S. Austral. 4: 610. 1929.

Stem erect, simple, leafy, sparsely arachnoid. Leaves lanceolate-linear, 7 to 10 cm. long, 0.8 to 1.0 cm. wide, acute, minutely to coarsely remotely toothed to sublobulate, glabrous or sparsely arachnoid beneath and somewhat scabrid above; lower subpetiolate, upper sessile with more or less coarsely toothed auricles. Inflorescence a terminal cyme of relatively few capitula, sparsely arachnoid on peduncles and bracteoles. Capitula about 10 mm. long, 9 mm. wide, calyculate, bracteoles of the calyculus linear, arachnoid. Involucre of 16 to 20 linear phyllaries 7 to 8.5 mm. long with arachnoid bases, hyaline margins and recurved apices. Marginal florets pistillate, corolla filiform, 7 mm. long, 5-fid, lobes long-acute, 0.4 to 0.5 mm. long, 0.1 mm. wide, apices glandular, sinuses not all always of same depth. Disc florets hermaphroditic, corolla slightly infundibuliform, 5-fid, lobes similar to those of the marginal florets but slightly broader, style arms exerted. Achene 2 mm. long, blackish, thick-cylindric, rather thickly set with short white or tawny hairs.

Pappus white, slightly exceeding phyllaries and florets.

AUSTRALIA. NEW SOUTH WALES: Port Jackson, *Gaudichaud* 5 (P, holotype; frag. G Prodr.). VICTORIA: Wendu River, in forest, Sept. 1842, *Robertson* 289 (K); Wendu Vale, Sept. 1843, *Robertson* 690 (K, on same sheet with 289 and another large-headed *Robertson* specimen, the latter indet.); in meadow between Melbourne and Darbent's Creek, Oct. 1852, *Mueller* (K ex Hb. Hk., immature but appears to be this species); ? Cataract Hills, Oct. 1863, *Mueller* (NSW). TASMANIA: Formosa, 4 Nov. 1844, *Gunn* 508 (K, on same sheet with one specimen of Launceston, *Gunn* 508, which is indet. but definitely not this species); Launceston, 11 Nov. 1844, *Gunn* 508 (K, a separate sheet from the preceding); Van Dieman's Land, *Gunn* 508 (W, rather more pubescent than the Kew sheets); Hobart, Nov. 1923, *Lucas* (NSW); Blackman's Bay near Kingston, Nov. 1935, *Rodway* 2039 (K).

The identity of *S. squarrosus* was completely lost, due to Bentham's inclusion of it in his *E. hispidula*. Yet it is easily one of the most distinctive of the erechthitoid species, readily recognized by its large capitulum, numerous phyllaries, short blackish achene, and coarsely toothed leaves. The holotype agrees well with Richard's plate and description, including the serration of the leaves. The abscission line (?) depicted at the base of each leaf is misleading, however. No such feature can now be seen on the type, and it is likely only an artist's device for marking the leaf base. One of the distinctive features, the number of phyllaries, is not described by Richard, but can be recognized in the drawing of the capitulum.

Erechtites hispidula Benth. is a mixture of at least two separate elements, as shown both by the description and by the specimens at Kew determined by Bentham. Bentham mistook certain specimens of Gunn's distribution number, 508, to be true *E. hispidula*, and to these added other specimens with large capitula which superficially resembled them but which have long attenuate-rostrate achenes, hence his statement, "Achenes slender and striate as in *E. quadridentata* or rather shorter." A comparison of the Launceston specimen of *Gunn* 508, which Bentham determined as *E. hispidula*, with the types of *S. hispidulus* and *S. squarrosus* showed that it was identical with the latter, not the former, and has the short achene as shown in the figure of *S. squarrosus*.

The large-headed specimens with long, attenuate-rostrate achenes are also characterized by somewhat fewer phyllaries, nearly linear subentire leaves, and cottony pubescence with sometimes a few hispid hairs added. It is to this group, rather than to *S. squarrosus*, that *Erechtites hispidula* Black applies, judging from his description of it as "near the preceding, *E. quadridentata*", and "achenes as in *E. quadridentata*". Certainly *S. hispidulus* is excluded by his description, particularly by the dimensions given for the capitulum. The status of this group is still unsettled, but a plausible suggestion is that it may represent a polyploid state of *S. quadridentatus*. It has not yet been given a name of its own by any one, and I have refrained from doing so until its status can be clarified.

6. SENECEO PYROPHILUS Zoll. & Mor. ex Zoll. Nat. - en Geneeskundig Arch. v.

Neerland's - Indië 2: 266. 1845; Syst. Verzeichn. 125. 1854.

Erechtites pyrophila Sch. Bip. ex Miq. Fl. Ind. Bat. 2: 97. 1856; Koorders, Nat. Tijds.

Neder. Indië 60: 250. 1900; Exkursionsfl. von Java 3: 342. 1912 (as *E. pyrophila* (Zoll.) Sch. Bip.).

Erechtites quadridentata O. Kuntze, Rev. Gen. Pl. 1: 325. 1891; non DC.

Perennial, with several to many spreading, then ascending, subherbaceous shoots from a short woody base. Stems sulcate, arachnoid to lanate especially on younger portions, with erect branches, leaves crowded on the basal portion and more distant above. Lower leaves 6 to 9 cm. long, 4 to 6 mm. wide, linear-oblongate, long-attenuate, not auriculate, sharply callose-denticulate with occasionally a few larger coarse lobate teeth, subglabrous to arachnoid above, arachnoid to lanate beneath; upper leaves only slightly shorter, not attenuate, linear-lanceolate, briefly and narrowly auriculate just above the attachment. Inflorescences corymbose, at first compact, then rather lax, with peduncles elongate and distant at maturity; lanate when young, later glabrate; bracteoles few, scattered, linear-subulate. Capitula few, with calyculus and receptacle arachnoid. Phyllaries 16 to 18, long-linear, 7 to 8 mm. long, 0.75 to 1 mm. wide; keel broad, flat, scurfy-arachnoid on entire length, obscurely 2-nerved with nerves narrow and only slightly darkened, scarious margins quite narrow, apices long-acuminate, minutely ciliolate. Marginal florets approximately 40, pistillate, corolla filiform, 3- to 4-fid, about 6 mm. long; disc florets about 20, hermaphroditic, corolla very slenderly infundibuliform, 5 to 6 mm. long, ca. 0.3 mm. in diameter, 5-fid. Achene 4 mm. long, light olive-brown, narrowly subcylindric, very markedly attenuate-rostrate, nerves 5, rounded, low, hairs short, scabrid, subappressed in shallow grooves between the nerves. Pappus copious, slender, exceeding the phyllaries and subequalling the florets, niveous to faintly tawny.

With somewhat the aspect of *S. quadridentatus* Labill. and doubtless related to it, but distinguished from it by denser pubescence, more numerous phyllaries scurfy-arachnoid all over the keel, and longer achenes.

JAVA: Tengger, "Senecio pyrophilus Z. et M. flos lutei. In arenosis volcanicis M. Tenanja-an (Tengger) 6-8000', XI." Zollinger 2564 (P, 4 sheets, including one *ex* Hb. Sch. Bip. and annotated by him, isotypes); Bromo, 7000', 16 Sept. 1875, Kuntze 6026 (NY, det. by him "*Erechtites quadridentata* DC. (Labil.) = *E. pyrophila* Sch. Bip."); "Ost-Java: auf dem Tengger bei und oberhalb Ngadisari von 2000-2400 m. ü. m. an den trockensten Stellen", Koorders 37403, 37404, 37780 (K, det by Koorders as *E. hispidula* [sensu Benthami]); Res. Besoeki, Yang Plateau, 2100 m., 11 Aug. 1916, Koorders & Koorders-Schumacher 43646 (K).

The packet on Schultz's isotype sheet bears a notation: ". . . . anth. ecaud., flores ex. foem., cent. hermaph." The reduction of this species to *Erechtites*, attributed by Miquel to "Schultz Bip. mss.", doubtless was made as a result of this dissection. Schultz appears not to have examined the style-arm apices, which in this material are definitely senecionoid. I do not find where Schultz himself published the combination, and conclude that both citations by Koorders are technically incorrect. In his "Exkursionsflora" he wrote of *E. pyrophila*: ". . . comp. *Erechtites hispidula* DC. Prodr. VI. (1837) 296; Benth., Fl. Austral. III. 660. Ich halte diese australische Art vermutlich für identisch mit der japanischen [sic!] *E. pyrophila*." In this connection he cites Koorders 37402 bis 37404 and 37780, which, however, he publishes as *E. pyrophila*. The sheets at Kew are determined as *E. hispidula* DC., a misidentification which undoubtedly arose as a direct result of

his working at Kew with those Australasian sheets so thoroughly confused by Hooker and Bentham. Some components of *E. hispidula* Benth. do resemble *S. pyrophilus*, but these are misidentified and are not *S. hispidulus* A. Rich. It is to Koorders' credit that he never actually published the reduction implied by his comment.

But Koorders' provisional comment is reflected in the determinations of Compositae in Diel's "Beitrage zur Flora des Sarawaket-Gebirges". In commenting on the determination of *Keysser 40*, Mattfeld³² wrote to the effect: that only a single Indonesian species, *E. pyrophila* from East Java, belonged in the New Zealand and Australian section of *Erechtites*, concerning which Koorders supposed that it was identical with the Australian *E. hispidula*, to which then Keysser's plant might also belong, but that he, alas, lacked authentic material of *E. hispidula*, and so had to determine it as *E. arguta* because of its pubescence and small capitula.

This confusion has prevented accurate identification of *Keysser 40*. I could not locate duplicates, and the specimens at Berlin and Breslau presumably are destroyed. The characters given by Mattfeld could apply to either *S. hispidulus* or *S. glomeratus* (*E. arguta* auct.). At least one can be certain from the small capitula that Keysser's plant was *not* *S. pyrophilus*. It could, of course, be an endemic novelty.

Although this species has somewhat the aspect of *S. quadridentatus* in the narrow elongate leaves, long-attenuate achene, and arachnoid pubescence, it is easily distinguished by its coarser leaves with an occasional exerted tooth on the lower ones, by its 16 to 18 phyllaries, by the very short pubescence which extends over the entire length of the phyllary on both its faces, and by the slightly longer and more slender achene. It differs from *S. squarrosus* by the phyllaries being pubescent and lacking the reflexed apices which give the latter its name; it also has much longer achenes and quite different leaves.

This species is known to me only from eastern Java, and is apparently the only species from Sundaland, west of "Wallace's Line". A careful search eastward along the summits of the Sunda Islands and particularly on Timor might conceivably turn up additional stations or, possibly, even related species. At present *S. pyrophilus* remains an interesting phytogeographical anomaly in the distribution of erechthitoid *Senecio*. It appears to be confined to the higher mountains at and above 2000 meters. From the notes of Zollinger and of Koorders it seems to prefer dry sandy habitats or volcanic ash.

7. *SENECIO laceratus* (F. Muell.) Belcher, comb. nov.

Erechtites lacerata F. Muell. *Linnaea* 25: 417. 1852.

Erechtites arguta Benth. *Fl. Austral.* 3: 659. 1866, *pro parte; non* (A. Rich.) DC. *Prodr.* 6: 296. 1838.

An erect annual with well-developed taproot, virtually glabrous. Stem unbranched below the inflorescence or with a few small branches from the medial

³² Engl. Bot. Jahrb. 62:500. 1929.

axils, to 30 cm. high and disproportionately thick, up to 5 mm. in diameter at the base, striate, densely clothed above with numerous appressed and overlapping leaves. Leaves up to 8 cm. long, 3.5 cm. wide, usually not over three times as long as wide, ovate-lanceolate, the lower sometimes broadly oblanceolate, irregularly coarse-toothed, each tooth usually with several sharply acute denticulations, the upper leaves less irregular, auriculate and semi-amplexical at the base, entirely glabrous. Inflorescence corymbose, rather crowded and compact especially before anthesis, glabrous except for occasional minute simple hairs on peduncles and bracteoles; bracts subtending main axes broadly denticulate-auriculate, rapidly tapering to acuminate triangular; bracteoles on peduncles broadly subulate, appressed; calyculus of a few short slender subulate bracteoles. Involucre of 10 to 13 phyllaries, much exceeded by florets and pappus; phyllaries glabrous, to 4 mm. long, 0.5 to 0.75 mm. wide at base, apices abruptly narrowed to acute or narrowly obtuse points often reflexed at maturity, lower half of phyllary strongly keeled and usually with a very narrow median nerve more or less prominently raised above the keel surface but sometimes submerged in it. Capitulum of 25 to 30 florets, of which about 10 are hermaphroditic. Marginal florets pistillate, corolla 4-, 5-fid, 3 mm. long, filiform, styles slightly exerted, style-arm apices bluntly truncated. Disc florets hermaphroditic, corolla 5-fid, slenderly infundibuliform, 3.5 mm. long, anthers minutely sagittate, style-arm apices truncate. Achenes 1.5 to 2 mm. long, short-cylindric, light brown and angular when immature, becoming plump, dark reddish brown and very indistinctly ribbed when mature, whole achene except the straw-colored annulus covered uniformly and rather densely with very short appressed papillose hairs, glabrate at maturity. Pappus white, capillary, slightly exceeding the florets.

Apparently confined to the interior of Australia.

AUSTRALIA. SOUTH AUSTRALIA: Cudnaka River, Mueller (MEL, paratype, *teste* Willis [isotype?]); Basedow Range, 20 July 1889, Tietkins (MEL, det. by Muell). NORTHERN TERRITORY: Bagot's Creek, Horn Expedition, 1894, Tate (K).

Bentham included Mueller's type of *E. lacerata* in his *E. arguta* complex, presumably because of its rather small capitula and compact inflorescence, plus the resemblance of its phyllaries to the larger glabrous ones of *S. hispidulus*, to which the larger part of his description of *E. arguta* (*S. glomeratus*) applies (see below). Mr. J. H. Willis has kindly informed me by letter that: "Bentham treated this as an inland, coarse and glabrous variety of *E. arguta*; in which he has been followed ever since at the Melbourne Herbarium". Mueller, at least as late as 1889, regarded it as a separate species, as shown by his determination of Tietkin's collection.

This distinctive species is especially noteworthy for the proportionately greater width of the leaf blade, approached among erechthitoid species only by *S. papuanus*, from which it is otherwise distinct. It is also almost entirely glabrous, a feature readily separating it from *S. glomeratus*, from which it can also be distinguished by the entirely regular corolla of the pistillate florets and by the uniformly and densely hairy (immature) achene.

The distribution can scarcely be indicated by the three specimens seen, except as "inland". The Tietkins and the Tate specimens are both of terminal fragments only; they have leaves somewhat smaller than those of the type, and are more mature. The description is based on all three specimens.

8. *SENECIO papuanus* (Lauterb.) Belcher, comb. nov.

Gynura papuana Lauterb. Fedde's Repert. Spec. Nov. 13: 242. 1914.

Erechthites papuana (Lauterb.) Mattf. Engl. Bot. Jahrb. 62: 442. 1929.

Senecio erechthitoides F. Muell. Trans. Roy. Soc. Victoria 12: 15. 1889; *non* Baker, Jour. Bot. 20: 171. 1882.

Erechthites erechthitoides (F. Muell.) Mattf., *l. c.*

Perennial; stem erect, leafy toward apex but lower leaves abscised, very nearly glabrous, terete, striate. Leaves 4 to 5 cm. long, 1 to 1.5 cm. wide (or larger, below?), gradually reduced in size upwards, cuneate, oblong, sinuate-dentate with 3 to 5 teeth on each side, acute, glabrous above, minutely short-haired on nerves beneath, sometimes purplish beneath; lower subpetiolate and slenderly auriculate, upper sessile with coarser auricles. Inflorescences axillary and terminal, corymbose, of two to several capitula borne singly on peduncles 1 to 5 cm. long and bearing a few linear acute bracteoles 3 mm. long. Capitulum 11 mm. long, 4 to 5 mm. wide, with calyculus of 2 to 5 linear bracteoles subapical on the peduncle. Phyllaries 12 to 14, 7 to 8 mm. long, obtuse. Marginal florets pistillate, in two rows; corolla filiform, apex slightly expanded and 5-fid; style-arm apices slightly domed, without corona. Disc florets hermaphroditic; corolla slenderly infundibuliform, regularly 5-fid; style arms short, apices truncate and flat with corona of very short diverging hairs. Achene (immature) 3 to 3.5 mm. long, slenderly subcylindric, not attenuate-rostrate but with expanded apical annulus; pappus multiseriate, white, slightly exceeding phyllaries and equaling florets.

NEW GUINEA: Kaiser-Wilhelmsland, Bolan, 2400 to 3000 m., 1913, *Keysser 317* (cited by Mattfeld as in Hb. Breslau, fragment and photograph in Hb. Berlin, both presumably destroyed. Isotype, BM!); Papua, Albert Edward Mts., central part, 3680 m., "common weed on burnt areas", *Brass 4225* (NY); Mt. Wilhelm, on open places above the tree-line, 11000 to 15000 ft., 5 Aug. 1953, *Semple & Rayner* (MEL). Other specimens reported, but not examined by this author: Southeastern New Guinea, Crest of Owen Stanley Range, 1889, *MacGregor* (MEL, holotype of *Senecio erechthitoides* F. Muell., too fragmentary now to loan); Northeastern New Guinea, Sarawaket Mts., 2 March 1937, *Clemens 5682* (cited by Mattfeld).

As far as is known from these five widely scattered collections, this species is endemic in the mountains of eastern New Guinea at elevations above 2500 meters. Further explorations should clarify the nature and distribution of this distinctive outlier, which bears so little superficial resemblance to most other erechthitoid species of *Senecio*. It is similar to *S. laceratus* in the proportionately very broad leaf, but is readily distinguished from it by the size of the capitulum, almost twice as large as that of *S. laceratus*.

9. *SENECIO RUNCINIFOLIUS* Willis, Proc. Roy. Soc. Queensl. 62: 106, *pl.* 7, *figs.* 34-37. 1952.

Erechtites picridioides Sond. & Muell. Linnaea 25: 523. 1852; *non* Turcz. Bull. Soc. Nat. Mosc. 24: 200. 1851.

Erechtites mixta Benth. Fl. Austral. 3: 659. 1866, *pro majore parte*; Black, Fl. S. Austral. 4: 610. 1929; *non* (A. Rich.) DC. Prodr. 6: 297, 1838.

Herbaceous, pale green, glabrescent, 15 to 80 cm. high, young parts and leaf axils slightly arachnoid-pubescent. Leaves sessile, lanceolate, acuminate, largest 12 cm. long and 4 cm. wide at base, with up to 8 more or less retrorse sinuate-lobed segments on each side, uppermost leaves less toothed, with very long subfiliform apices. Inflorescence corymbose, lax, up to 100 capitula or more, peduncles slender, as much as twice as long as the calyculate capitulum. Involucre minutely arachnoid, glabrous in fruit; phyllaries 12-14, about 10 mm. long, 0.5 to 0.7 mm. wide, narrowly deltoid, with obtuse or subacute non-sphaceolate apex. Marginal florets pistillate, about 40, corolla slenderly filiform, usually 3-fid, often with one or two much deeper sinuses, giving a subligulate aspect, or sometimes unequally 4-fid, lobes papillose, thickened. Disc florets about 13, hermaphroditic; corolla infundibuliform, tube about 0.5 mm. in diameter at base of the 5 papillose-thickened lobes; anthers 5, about 1 mm. long, ecaudate; style arms about 0.33 mm. long, apices enlarged and recurved, without fused terminal papillae. Pappus silky, lustrous, at length exceeding florets by 2 mm. and phyllaries by as much as 5 mm. Achene 2.5 to 3 mm. long, about 0.3 mm. in diameter, subrostrate, 9- or 10-ribbed, with short suberect papilliform hairs on the ribs.

AUSTRALIA. SOUTH AUSTRALIA: Moorundee near Blanchetown, Murray River, Feb. 1851, *Mueller* (MEL *ex* Hb. Sonder, holotype); "towards Spencer's Gulf", *Warburton* (MEL). VICTORIA: "10 mi. west of Cohuna", Aug. 1946, *Vickery* (NSW); Berribee Tank, Murray River flood plain, 31 Aug. 1948, *Willis* (MEL); Cohuna, 8-9-1952 (NSW *ex* MEL, 39" tall, lower leaves to 10" long). NEW SOUTH WALES: "S. W. . . . of Piper's Hill", *Fraser* (K, syntype of *E. mixta* Benth.); ". . . Banks of the Lachlan, 1817", *Fraser* (BM, same gathering as preceding?); Warrego River, Western Plains, Sept. 1885, *Betche* 15 (MEL); Warrego River, 12-8-1885 (*Betche* ?) (NSW); junction of Murray and Darling rivers, 1889, *Mrs. Holding* (NSW *ex* MEL); Zara, Wanganella, Dec. 1905, *Officer* (NSW, US); Brindingabba, Arrara, 1912, *Boorman* (NSW, "eaten by stock voraciously"); Nelia Yari (Menindee Dist.), 20 Nov. 1947, *Constable* (NSW).

This is a comparatively rare plant, apparently confined to riparian habitats mostly in the Murray River system, and to be expected in, but not yet reported from its extensions into extreme southern Queensland. Its scarcity may be explained by the note on *Boorman's* specimen.

As pointed out by Willis, this species was originally described from very depauperate specimens, and under a name already preoccupied. Bentham evidently recognized the relationship between the type and the more robust specimen from Spencer's Gulf. To these he united collections by Robert Brown and by Fraser, and identified the whole group with *E. mixta* DC. His description was entirely original and applies well to the Fraser specimens. Neither the description nor the specimens agree with Richard's type of *S. mixtus*, which belongs to the genus *Arrhenechthites*. The "Memory Cove, R. Brown" specimen cited by Bentham as

E. mixta appears to be "Senecio plebejus β , Memory Cove, R. Brown 2282" (BM!). Too over-mature for accurate identification, it belongs in the vicinity of *S. hispidulus*, with glabrous achenes. It is neither *S. mixtus* nor *S. runcinifolius*, definitely.

There should be no confusion between this species and the similarly named *S. runcinatus* Less., a true discoid *Senecio* from Mexico, which has a large leaf up to 30 cm. long and 12 cm. wide with its margin closely set with callus-tipped teeth and the runcinate lobes at essentially right angles, instead of reflexed. Lessing's species was erroneously placed in *Erechtites* by de Candolle, but must be excluded from that genus.

The material examined includes five of the six collections cited by Willis, through whose kindness I was able to examine them. The 1952 specimen from Cohuna appears to be part of a collection received by Willis after the publication of his paper. In a personal communication he stated that it has: "robust stems twice as tall as the limit fixed in my diagnosis", which was forty centimeters. I have emended the diagnosis accordingly.

10. *SENECIO wairauensis* Belcher, nom. nov.

Erechtites glabrescens T. Kirk, Trans. N. Z. Inst. 9: 550. 1877; Student's Fl. N. Z. 335. 1899; Cheeseman, Man. N. Z. Fl. ed. 1. 366. 1906; ed. 2. 1008. 1925; Illus. N. Z. Fl. 1: tab. 110. 1914; non DC. Prodr. 6: 295. 1838.

Erechtites prenanthoides DC. var. β *minor* Hook. f. Fl. N. Z. 141. 1853.

Stem herbaceous, erect, sulcate, 30 to 80 cm. tall, simple or sparingly branched above, glabrous throughout or with a few minute soft hairs in the grooves of the peduncles; leafy. Leaves suberect, crowded and overlapping, up to 15 cm. long, 5 cm. wide, gradually reduced in size upward usually with little change in proportions, sessile, often auriculate-amplexicaul or even sagittate below an attenuated narrowly winged petiole, or rarely merely sessile without auricles, varying from oblong-linear and obtuse to broadly oblong with a large ovate terminal lobe, sinuate-dentate, sinuate-lobate, or pinnatifid with denticulate lobes, glabrous or with soft hairs scattered on lower surface, especially along nerves, and more sparsely on upper surface, wings of petiole often ciliolate, blade very thin and membranous when dried, often purplish beneath. Inflorescences terminal and axillary, racemose in bud, becoming paniculate or subcorymbose. Capitula borne singly on slender peduncles of irregular length, often 1 to 2 cm. long, 3 to 8 (to 14) per branch, never solitary. Peduncles glabrous or with a few minute hairs in grooves; two or three linear-subulate bracteoles 3 to 5 mm. long on the peduncle proper, and one slightly longer bract subtending each peduncle. Phyllaries of involucre (10 to) 12 to 14, 6 mm. long, 0.5 mm. wide, glabrous, shorter than florets and pappus, keel bearing two broad low nerves with a narrow median fissure between them, margins scarious, apices shortly acute. Pistillate florets 10 to 15, hermaphroditic florets 20 to 25. Marginal florets pistillate or occasionally with some rudimentary stamens also, with style-arm apices truncate and without hairs; corolla 4-fid, filiform, 4 mm. long. Disc florets hermaphroditic, style-arm apices truncate with a marginal fringe of a few short hairs; corolla 5-fid, slenderly infundibu-

liform. Achenes long-tapered, subcylindric, non-rostrate but with slightly expanded annulus, faintly ribbed, glabrous or sparsely white-haired in the grooves, 4 mm. long. Pappus very fine, capillary, white, slightly exceeding florets.

NEW ZEALAND: SOUTH ISLAND: Roto Iti, *Kirk* 824 (K, syntype and lectotype); Wairau Gorge, 3000 ft., *Cheeseman* (K, extreme marginal florets 3-fid, pistillate, next florets 4-fid with rudimentary stamens); Canterbury, Mt. Cook Dist., Hermitage 2500 ft., *Cheeseman* (K); 3000 ft., Jan. 1898, *Cheeseman* (NSW); 1860-61, *Sinclair & Haast* 132, 25 (K, det. Hk. f. as *E. prenanthoides* var. β ; left & center specimen, right specimen is *S. dunedinensis*); Canterbury, Southern Alps, 2000-4000 ft., 1862, *Haast* 527 (K); Otago, *Lyall* (K, very immature); Lake District, *Hector & Buchanan* 2 (K, very immature); Milford Sound, *Lyall* (K ex Hb. Benth., det. as *E. prenanthoides* var. β , leaves very narrow and scarcely lobed; K ex Hb. Hook., right specimen only, left is *S. biserratus*). STEWART ISLAND: "In arenosis maritimis", *Godey* (P, immature, peduncles lanate, det. *E. arguta*). Also reported by Cheeseman from a few localities on North Island.

Kirk's sketchy original description of this endemic New Zealand species was only slightly amplified by him later. Cheeseman gave an improved description and a good figure. This is a well-defined, valid species which, because of its truncated and unappendaged style arm, is certainly a *Senecio*, not an *Erechtites*. The new epithet is based on Kirk's identification of the original locality of Travers.

Hooker's diagnosis of *E. prenanthoides* var. *minor* is simply, "var. β , *minor*; foliis sinuato-lobatis subpinnatifidisve". In the description of the species, further, the leaves are, "all sharply toothed, lobed and pinnatifid throughout their length in var. β ." But the two specimens cited by Hooker for this variety, "Milford Sound and Otago, Lyall", unmistakably are referable to this species and not to *S. minimus* (= *E. prenanthoides* DC.). Furthermore, in Hooker's annotated copy of the 'Flora of New Zealand' in the library at Kew he has written, "Also Haast 132, 25", in the margin beside var. *minor*. This sheet, determined as var. β in Hooker's script, is *S. wairauensis* except for the right-hand specimen.

11. *SENECIO dunedinensis* Belcher, nom. nov.

Erechtites diversifolia D. Petrie, Trans. & Proc. N. Z. Inst. 19: 323-324. 1887; non *Senecio diversifolius* Du Mort., 1827.

A slender erect herb from a perennial rootstock, unbranched or only sparingly branched below the inflorescence, and the inflorescence more or less branched. Stem shallowly sulcate, glabrescent or sparsely cottony, leafy for its entire length, the lower leaves slightly crowded. Radical leaves to 3.5 cm. long, 6 mm. wide, oblanceolate, long-attenuate to subpetiolate; cauline leaves as large as 6 cm. long, 5 mm. wide, linear-lanceolate to linear-oblong, shortly attenuate to sessile but not clasping; margins remotely sinuate-denticulate on lower leaves, becoming subentire on upper leaves; blades glabrescent to sparsely arachnoid beneath, nowhere hispid. Inflorescences terminal and axillary, corymbose, with relatively few capitula, at first moderately congested, becoming very lax at full maturity, peduncles glabrous or sparsely arachnoid, with 2 to 6 subulate purple-tipped bracteoles 2 mm. long or less. Capitula calyculate; involucre of 12 to 14 phyllaries; phyllaries 5 to 5.5 mm. long, shorter than florets and pappus, sparsely and very shortly glandular-

pubescent, apices rather suddenly narrowed and then prolonged in a bluntly acuminate point, shortly ciliolate and darkened, keels basally two-ridged with a median nerve emerging midway and becoming more prominent as the ridges are reduced, margins scarious. Pistillate florets marginal in two rows, corolla 4-fid, lobes thick-tipped; hermaphroditic florets central, 5-fid, lobes thick-tipped. Achenes somewhat fusiform, slightly constricted below the expanded rim, 3 mm. long, nerves prominent, rounded, rather narrow, grooves very narrow, hairs short, white, suberect on or beside the nerves but not in the bottom of the grooves. Pappus very fine, slender, equaling the florets and much exceeding the phyllaries.

NEW ZEALAND. SOUTH ISLAND: Otago, Naseby, 1800 ft., Dec. 1892, *W. Petrie* 858 (K, det. as "*Erechtites diversifolia* D. Petrie, ex Herb. W. Petrie, Dunedin."); interior of Otago, *D. Petrie* (NSW, undated); Prov. Canterbury, 1860-61, *Sinclair & Haast* 132, 25 (K, right-hand specimen only, others being *S. wairauensis*); Canterbury, Godley River bed, *Haast* 617 (K).

Petrie did not designate a type nor cite any specimens for *E. diversifolia*. I do not find that any other author has designated a type, although several gatherings have been listed. I did not, in limited correspondence, locate a collection by Petrie dating from 1887 that might have served as his type. The Petrie specimen at Kew, collected some years later, agrees with the description and could serve as neotype if further search for the holotype should be unsuccessful.

Cheeseman³³ reported this species on North, South, and Stewart Islands, and common in some places. Judging from its scanty representation in the herbaria, it must be rather rarely collected. I have named it *S. dunedinensis* in allusion to the type locality. Although apparently not very close to any other erechthitoid species, its leaf and achene suggest *S. wairauensis*, from which it can be distinguished by its smaller capitula and shorter phyllaries.

12. *SENECIO QUADRIDENTATUS* Labill. Nov. Holl. Pl. Spec. 2: 48, *tab* 194. 1806.

Neoceis tomentosa Cass. Dict. Sci. Nat. 48: 458. 1827, *nom. prov.*

Senecio prenanthoides A. Rich. Sert. Astrolabe, 96. 1834, *non E. prenanthoides* DC.

Prodr. 6: 296, 1838, which is *S. minimus*.

Erechtites quadridentata (Labill.) DC. Prodr. 6: 295. 1838, *et auct.*

Erechtites glabrescens DC. Prodr. 6: 295. 1838; *non* T. Kirk, Trans. N. Z. Inst. 9: 550. 1877.

Erechtites glandulosa DC. Prodr. 6: 295. 1838.

Senecio glandulosus Cunningham. *apud* DC. ex Sch. Bip. Flora 28:498. 1845.

Senecio glabrescens (DC.) Sch. Bip. Flora 28: 498. 1845.

Erechtites incana Turcz. Bull. Soc. Nat. Mosc. 24: 85. 1851.

Erechtites quadridentata var. *glabrescens* (DC.) Benth. Fl. Austral. 3: 660. 1866, *pro parte*.

Erechtites erecta F. Muell. ex Lange, Bot. Tids. 4: 6. 1874.

Perennial; stems erect, striate, densely incanous-arachnoid to lanate when young, more or less glabrate later, nowhere hispid or scabrid, sparingly or much branched below the inflorescence, with branches suberect to erect. Leaves linear to lanceolate and as much as 9 cm. long and 0.3 cm. wide or sometimes the lower

³³ Man. N. Z. Fl. p. 1007. 1925.

ones oblong-lanceolate, sessile, attenuated toward the base, sometimes with minute linear and simple auricles, more or less minutely and distantly callose-denticulate, usually revolute, typically densely arachnoid to lanate especially when young, sometimes becoming subglabrous especially on upper side, acute to subacuminate. Inflorescences terminal and axillary, forming corymbose cymes, slightly congested becoming lax, usually densely arachnoid, sometimes glabrate; capitula calyculate with linear bracteoles about 2 mm. long; phyllaries of the involucre 11 to 13, 6.5 to 8 mm. long, 0.4 to 0.5 mm. wide, at first arachnoid later glabrate towards the apices, 2-nerved with nerves prominent on the lower third only, acuminate, ciliolate. Marginal florets pistillate with filiform (3-) 4-fid corolla 5.5 to 6 mm. long. Disc florets hermaphroditic with slenderly infundibuliform 4- (5-) fid corolla with blunt lobes papillose-thickened apically. Achenes 2.5 to 3 (to 4) mm. long, straight or slightly arcuate, more or less attenuate-rostrate, narrow grooves between broadly flattened ribs beset with short white subappressed hairs, reddish or olive-brown at maturity. Pappus multiseriate, niveous, exceeding the phyllaries by 2 mm., equaling the florets.

AUSTRALIA. TASMANIA: "Nova Hollandia in capite Van-Dieman", *Labillardière* (FI, holotype; BM, K); Port Dalrymple, *R. Brown* 2283 (K, except for center specimen); Gun Carriage Island, 23 Oct. 1844, *Gunn* 1978 (K); Hobart, 1870, *Hannaford* (HO); "Corra Leen", 13 Feb. 1878, *Beccari* (FI); Blackman's Bay, Feb. 1929, *Rodway* H506 (K); "Between Nat'l. Park and Westerway in railway cutting", 30 Nov. 1929, *Comber* 1757 (K). NEW SOUTH WALES: Port Jackson, *Gaudichaud* 4 (P, holotype of *S. prenanthoides* A. Rich.; G. Prodr.); Barham, 13 Oct. 1949, *Vickery* 577 (K, US). VICTORIA: Wendu Vale, 17 Nov. 1843, *Robertson* 691 (K); Werribee, 24 Sept. 1892, *Morrison* (K); 14 Jan. 1924, *Williamson* (F, center and right; left is *S. glomeratus*); Melbourne, Tooroorong, 8 Nov. 1936, *Mauritzon* (S). SOUTH AUSTRALIA: "Austr. felix, Exp. Novara", *Mueller* (W); "Nov. Holl. meridional.", *Mueller* (FI, W); Mt. Lofty ranges, Sept. 1903, *Koch* 837 (K). WESTERN AUSTRALIA: Swan River, *Drummond* 379 (FI; K, 4 sheets; W; isotypes of *E. incana* Turcz.); Freemantle, *Hugel* (W); Toodyay, *Preiss* 73, 126 (S).

NEW ZEALAND. NORTH ISLAND: Wellington (W); Woodhill, Kapara, Oct. 1882, *Cheeseman* (US). SOUTH ISLAND: Canterbury, Waiiau Marble Quarry, limestone cliff, Dec. 1936, *Lothian* (K); Prov. Canterbury, 1860-61, *Sinclair & Haast* 321 (W); Awatere, *Kirk* 17 (US); Central Otago, Alexandra, 15 Nov. 1929, *Sledge* 391 (K).

TIMOR: *Decaisne* (P).

This was the first of the erectitoid species of *Senecio* to be published. The type material, including the holotype sheet which has pinned to it the manuscript draft of the original description plus four specimens, reveals much of the range of variation in habit, leaf shape, and pubescence of this species. Subsequent collections have added to the known variation, and several extremes have received specific rank. There has been apparent introgression with allied species, especially *S. hispidulus*, and some such states have also been described as species. It is doubtful if a really satisfactory disposal of all the names in this complex can be made without intensive experimental investigation.

Richard redescribed *S. quadridentatus* Labill., making the corolla lobes non-glandular. He then described *S. prenanthoides* to contrast sharply with his *S. hispidulus*. But both his specimens of the former two have corolla lobes glandu-

lose-papillose, and are in full agreement except for pubescence. The inflorescence of *Gaudichaud 4*, the holotype of *S. prenanthoides*, is virtually glabrous, although what pubescence there is, particularly on the phyllaries, is arachnoid, as on Labillardière's types. These extremes of pubescence are united by specimens showing all intermediate degrees, and by some which show one extreme on one branch and the other on another. I can not justify retaining *S. prenanthoides* even as a form.

The type of *E. glabrescens* DC., *Cunningham 134* (G!), is quite comparable to *Gaudichaud 4* in pubescence but has less revolute leaves. Broader subpetiolate basal leaves also give this and similar specimens a somewhat different aspect, although such leaves probably develop normally in this species but are usually lost before maturity. They certainly were present on seedlings raised from Tasmanian achenes furnished me by Dr. Curtis. This specimen is identical in floral details with the type of *S. quadridentatus*.

The variety *glabrescens* Benth., defined by specimens determined by him at Kew, included not only the specimens of *Cunningham 61* which accurately represent *E. glabrescens* DC., but also such diverse elements as *Adamson 343* and *Gunn 508* (Circular Head), which appear to be hybrids between *S. quadridentatus* and *S. hispidulus* A. Rich. Bentham regarded *E. glandulosa* DC. as a luxuriant state of *E. quadridentata*. The type, *Cunningham 141* (G!), is definitely related to *S. quadridentatus* by achene, leaf shape, and lanate-arachnoid pubescence, but differs in being less pubescent and in having larger and auriculate leaves. I agree with Bentham, although the auricles may be evidence of hybridity with *S. hispidulus*.

Erechtites erecta Mueller ex Lange has never been indexed as published, probably because the name occurred in a discussion of the affinities of *E. Muelleri*, written in Danish. I am indebted to Mr. W. C. Worsdell at Kew for a translation of Lange's article, from which I quote the passages pertaining to *E. erecta*:

"This second name of Müller's (*E. erecta*) is ascribed to a plant which differs from that here figured [*E. Muelleri*] by denser and longer, very loose felt over the entire plant (also on the upper surface of the leaves), by stiff and erect, nearly adpressed, narrow linear leaves, with strongly reflexed margins and almost devoid of teeth, by more rigid branches, more congested heads, and a distinct beak on the achene. This *E. erecta* F. Müll., sched. pl. exsicc., (not mentioned in Bth. & Müll.) agrees fairly closely with the original *S. quadridentatus* Labill., fl. nov. holl. tab. 194, and with the description of the same in DC. It perhaps answers to the var. *Gunnii* Bth. & Müll., whose description runs thus; 'very woolly white, leaves mostly petiolate, oblong, entire with a few remote teeth'. But it must be noted, that most leaves on the Müller specimens are not stalked, but sessile, and that they are not 'oblong' but just narrowly linear . . ."

I consider this valid publication.

I have not seen Lange's type, but have seen a number of sheets determined as *E. erecta*, some by Mueller himself. These specimens bear out Lange's description, except that the achenes vary some in the attenuation of the neck. The differences between these specimens and typical *S. quadridentatus* are in the direction of greater xeromorphism, and probably are an ecological adaptation to the more arid conditions of South Australia, from which most of the authentic material has come. Lange's tentative identification, with var. *Gunnii* Benth. (= *E. Gunnii* Hk. f.) is of course

not supported by comparison with Hooker's type. I regard this simply as an extreme of *S. quadridentatus*, lacking sufficient discontinuity from the type to be recognized.

13. *SENECIO gunnii* (Hook. f.) Belcher, comb. nov.

Erechtites Gunnii Hook. f. Lond. Jour. Bot. 6: 122. 1847; Fl. Tasm. 1: 220, *tab* 63. 1860.
Erechtites quadridentata var. *Gunnii* (Hk. f.) Benth. Fl. Austral. 3: 660. 1866.

Perennial from rhizome, annual shoots herbaceous or slightly woody at base. Stems erect, arachnoid to lanate but eventually glabrate. Leaves sparsely arachnoid and hispidulous above, moderately lanate and hispid beneath; lower ones obtusely oblanceolate or obovate-lanceolate, 8 (to 12) cm. long, 1.5 (to 1.8) cm. wide, subentire but minutely denticulate, base long-attenuate and subpetiolate, slightly broadened at attachment and sometimes with small auricles 1 to 2 mm. long; upper ones smaller, sessile, not attenuate. Inflorescences a corymbose-panicle, varying from rather compact to lax, branches lanate to arachnoid or eventually glabrate, capitula several to numerous on rather short peduncles, calyculi lanate; phyllaries 11 to 13, 6 mm. long, glabrous, minutely glandular-papillose, or basally sparsely arachnoid, more or less prominently keeled, 2-nerved, often purplish, apices acuminate, ciliolate; marginal florets pistillate, corolla filiform, apices of the 4 lobes thickened-glandulose. Disc florets hermaphroditic, corolla subfiliform, slightly and abruptly dilated above, apices of the 5 lobes thickened-glandulose; anther bases obtusely lobulate. Achenes 3 mm. long, slightly arcuate, light brown, strongly ribbed, with short white hairs in deep grooves between the ribs or lacking, apex definitely attenuate-rostrate. Pappus slightly exceeding phyllaries and florets, white.

AUSTRALIA. TASMANIA: Marlboro, Jan. 1841, *Gunn* 700/1842 (K, syntype; NSW); Arthur's Lakes, 17 Jan. 1843, *Gunn* 700 (K, syntype; NSW); 1844, *Gunn* 700 (K ex Hb. Benth.); Western Mountains, 18 Feb. 1843, *Gunn* 700 (K, 3 on same sheet as next), *Lawrence* 297 (K); Table Mountain, April 1804, *R. Brown* 2284 (BM, 2); *Hugel* (W); Mt. Wellington, 19 Feb. 1878, *Beccari* (FI); Mount Field East, 4000 ft., March 1906, *Maiden* (NSW); Mt. Wellington, 3800', March 1944, *Curtis* (HO); near Great Lake on Bronte Road, 27 Jan. 1949, *Burbidge* 3426 (HO). VICTORIA: Yarra Yarra, *Mueller* (K); (?) Mt. St. Bernard, Jan. 1899, *Walker* (NSW); Mt. Hotham, Jan. 1900, *Maiden* (NSW); Buffalo Mt., 4300 ft., 19 Jan. 1913, *Cabbage* 3753 (NSW). NEW SOUTH WALES: Watcha Road, Dec. 1893, *Kretschmann* (NSW); Mt. Kosciusko, Jan. 1898, *Maiden* (NSW); Thredbo River, Jan. 1899, *Maiden & Forsyth* (NSW); Bemberi Peak, 6100 ft., 15 Jan. 1912, *Cabbage* 3441 (NSW); Kosciusko, 9 March 1949 *Skottsberg* (NSW, S); near Charlotte Pass, 14 March 1949, *Skottsberg* 174 (S).

In the original publication of *Erechtites Gunnii*, Hooker merely stated: "Hab. Alpine situations, *Gunn*." In the 'Flora Tasmaniae' he cited *Gunn* 700, and ". . . Arthur's Lakes, Marlborough, etc. *Lawrence*, *Gunn*." One sheet of *Gunn* 700 at Kew has two gatherings, "Gunn 700, Arthur's Lakes, 17/1/45, V. D. Land", and "Gunn 700/1842, Marlboro, 5/1/41." Beside the former are the diagnostic figures drawn for plate 63 in the 'Flora Tasmaniae'. Below the latter specimen is "*Erechtites Gunnii*" in Hooker's script. I interpret these gatherings as the syntypes. This same sheet has been annotated by Bentham as the variety.

The systematic status of *S. gunnii* is still somewhat uncertain. It is surely closely allied to *S. quadridentatus*. That it may be a hybrid between, say, *S. minimus* and *S. quadridentatus*, with perhaps some introgression into *S. hispidulus*, can not be ruled out entirely without cytogenetic study. The principal argument against its hybridity is its lack of variability in those features which intergrade in the group of putative hybrids between *S. hispidulus* and *S. quadridentatus*. On the other hand, Bentham may have been right in considering it a variety of *S. quadridentatus*. Pending further clarification, I side with Rodway³⁴ in considering it a species.

From the elevations given by the collectors, *S. gunnii* appears to be alpine and subalpine in distribution. The only other ecological datum available to me is that of Gunn, preserved in the type cover at Kew: "Very common on the summits of the Western Mountains, growing in moist places in the pasturage."

14. SENECEO GLOMERATUS Desf. *ex* Poiret in Lam. Encyc. Suppl. 5: 130. 1817.

Senecio glomeratus Desf. Cat. Hort. Paris. 124. 1815, *nomen nudum*; *ex* Link, Enum. Hort. Berol. 2: 325. 1822.

Erechtites glomerata and vars. *subincisa* and *polycephala* DC. Prodr. 6: 297, 1838.

Neoceis microcephala Cass. Dict. Sci. Nat. 34: 388. 1825.

Senecio argutus A. Rich. Fl. Nouv. Zél. 258, 1832; Sert. Astrolabe, 104. 1834; Endl. Prod. Fl. Norf. 51. 1833; *non* Kunth in HBK. Nov. Gen. & Spec. 4: 183, 1820.

Erechtites arguta (A. Rich.) DC. Prodr. 6: 296. 1838; Cheesm. Man. N. Z. Fl. 364. 1906; *ibid.* ed. 2, 1007. 1925; Hook. f. Fl. N. Zeal. 1: 142. 1853, *pro parte*; Fl. Tasm. 1: 219. 1860, *pro parte*; Benth. Fl. Austral. 3: 659. 1866, *pro parte*; Rodway, Tasm. Fl. 95. 1903, *pro parte*; Black, Fl. S. Austral. 4: 610. 1929, *pro parte*.

Senecio Lessonianus Sch. Bip. Flora 28: 498. 1845; *non* Steud. Nom. ed. 2, 2: 562. 1841.

Senecio plebeius Banks & Soland. *ex* Hook. f. Fl. N. Z. 1: 142. 1853, *ut syn.*, *nom. nud.*

Senecio Lessoni F. Muell. Ann. Rept. Gov't. Bot. 26. 1858, *nom. nud.* (publ. as *nom. nov.* for "E. angusta", error for *E. arguta*?).

Annual (?); stem erect, herbaceous or slightly woody at base, simple or branching above, more or less densely arachnoid-pubescent, sometimes glabrate below, often sublanate on juvenile parts and inflorescences. Leaves ovate-lanceolate to linear-lanceolate, variable in length and width and in length-width ratio but usually more than three times as long as wide, denticulate and revolute to irregularly and coarsely sharp-toothed to sinuate-lobate with obtuse sinuses and callose-denticulate deltoid lobes to more or less profoundly pinnatifid with long lanceolate denticulate or subincised acute or obtuse lobes, sessile, usually auriculate; lower leaves sometimes subpetiolate above the auricles; sparsely arachnoid to glabrate above, more densely arachnoid beneath. Inflorescences terminal and axillary, forming a congested corymbose panicle, arachnoid to lanate, rarely glabrate after anthesis, capitula small, 5 to 7 mm. long, 2 to 3 mm. wide, borne singly or in small clusters, calyculate; phyllaries 11 to 13, 3.5 to 5 mm. long, usually near 4 mm., with basal one-third to one-half usually densely short-arachnoid to lanate, or rarely glabrate after fructescence, obscurely 2- to 3-nerved, acute to acuminate, minutely ciliolate at the apex. Marginal florets pistillate, occasionally with rudimentary stamens, with corolla filiform, usually 3-fid, sometimes irregularly 2-fid and subligulate. Disc

³⁴ Tasmanian Flora. pp. 94-95. 1903.

florets hermaphroditic, with slenderly infundibuliform corolla 4-, 5-fid, and with style-arm apices truncated. Achene short-subcylindric, 1.5 mm. long or less, not attenuate-rostrate, ribbed, with short whitish or tawny subappressed hairs between the ribs. Pappus white, capillary, exceeding involucre, subequalling florets.

CULTIVATED: "*Senecio quadridentatus* Labill. *Senecio glomeratus* h. par." (FI, Hb. Webb. ex Hb. Desf., 2 pieces, right-hand one designated as neotype); "*Senecio aggregatus* hort. Paris., 1813" (P); "Jardin des Plantes . . . October 1816" (K ex Hb. Gay, det. as *S. glomeratus* Poir.); "*Senecio glomeratus* h. pl. 1815" (G Prodr., syntype of *E. glomerata* var. *subincisa* DC.).

AUSTRALIA. TASMANIA: "Nouv. Holl., détr. d'Entrecasteaux", iter *Baudin* (P, det. as *S. argutus* by Richard); "Nouv^e Hollande, côte merid^e, Mus. de Paris 1821", ex itin. *Baudin* (G Prodr., holotype of *E. glomerata* DC. var. *typica*); "Tasmania 1833", *Gunn* 408 (K, right-hand specimen only, left is a hybrid); "Van Dieman's Land, 1833", *Gunn* 408 (K); *C. Stuart* (W, 2); Adventure Bay, Feb. 1906, *Maiden* (NSW); Birch's Bay, 400 ft., Jan. 1931, *Rodway* 75 (K); Bishopsbourne Creek, Jan. 1931, *Rodway* 122 (HO, K); Bridgeport, April 1946, *Wilson* (HO); Somerset, Feb. 1948, *Curtis* (HO). WESTERN AUSTRALIA: "Riv. des Cygnes", iter *Baudin* (P); Swan River, 1839, *Drummond* (K, 2), *Drummond* 257 (W). SOUTH AUSTRALIA: "Austra. felix, Novara Expedit." *Mueller* (K; W, 2, marginal florets frequently more or less ligulate, next row sometimes perfect and infundibuliform, closely approaching true radiate structure); Aldgate, Jan. 1907, *Maiden* (NSW). VICTORIA: Wendu Vale, *Robertson* (K); S. E. of Oakleigh, Dec. 1892, *Morrison* (S); Jan. 1924, *Williamson* (F); Frankstone, Nov. 1936, *Mauritzon* (S); Sandringham, Nov. 1936, *Meebold* 21799 (NSW). NEW SOUTH WALES: Mt. Koscuisko, 5500 ft., Jan. 1898, *Maiden* (K).

NEW ZEALAND. NORTH ISLAND: "Ad riv. Punakitere, Nov. 1874", *Berggren* (S); Auckland, Panmore, *Kirk* (F); Auckland, *Cheeseman* (F); Wellington, "open places, sea to 2000 ft., common," March 1909, *Travers* (G Deless., W). SOUTH ISLAND: "Havre de l'Astrolabe, détroit de Cook" (P, holotype of *S. argutus* A. Rich.); Lake Dist. in the bush, March, *Hector & Buchanan* 3 (K). WITHOUT SPECIFIC LOCALITY: "*Senecio plebius*" 1769-70, *Banks & Solander* (BM, S, US); "Nouvelle Zélande, voyage de l'Astrolabe et de la Zélee, 1838-1840" (K); "Nlle. Zélande, Voyage de M. Bernard", 1847, *Vedele* (P).

UNITED STATES. CALIFORNIA: Vance's Camp 17, June 1911, *Smith* 3849 (F); Crescent City, June 1928, *Thompson* 4537 (F); San Francisco, July 1930, *Rose* (S); Mendocino County, July 1931, *Jones* 29097 (BM, F); San Mateo Co., open rocky hills, Sharp Park, 1936, *Rose* 13980 (W); Humboldt County, Spruce Cove, Trinidad, *Parks* 24033 (BM, F, S).

Poiret's description is rather difficult to apply literally to the herbarium material to which his epithet has been applied, the disagreement being mainly with leaf shape and pubescence. The name was based on a living plant, and there might be no holotype. I have, however, obtained from Florence a sheet with two specimens from Desfontaines' herbarium, which is ticketed "*Senecio quadridentatus* Labillard. Compos. h. p., *S. glomeratus* h. Par." The latter determination is in the same script and ink used on the holotype of *S. minimus* Poir., and is, I believe, in Poiret's writing. I therefore select the right-hand specimen on this sheet as neotype of *Senecio glomeratus* Desf. ex Poir.

The two specimens have somewhat different leaf forms. The neotype approximates Poiret's description of the leaf as linear-lanceolate, incised or toothed, but clearly shows a few pinnatifid leaves near the base. The specimen on the left accords well with the description of *S. glomeratus* Desf. ex Link as petiolate and pinnatifid. It also agrees with a number of specimens bearing determinations as

S. glomeratus Desf., most of which, like the one in the Prodrumus Herbarium, were taken from cultivation. These two specimens are in excellent agreement in floral characters; both were included in the determination, and I see no basis for separating them. Nor could I justify forming subspecific categories of this variable species on such an unstable basis as these foliar differences, when every degree of intergradation exists in the material.

Richard based *S. argutus* on a scrappy specimen, little more than an inflorescence, from New Zealand. The floral characters of this specimen, and of a somewhat larger pair of branches from Richard's herbarium, ticketed simply as "*Senecio argutus* nob., N^{lle} Zélande", are unmistakably those of *S. glomeratus*. The same is true for the sheet of six fragmentary specimens collected by the naturalists of the Baudin expedition from "Nouv. Holl. détr. d'Entrecasteaux" (Tasmania), which Richard determined as *Senecio argutus*. He rightly cited these as extending the range of this species to Australia.

The d'Urville specimen cited by de Candolle in the 'Prodrumus', in contrast to the one retained by Richard, has quite pinnatifid leaves but agrees with Richard's type and description in pubescence and floral features. This New Zealand specimen forms the basis for "*Erechtites arguta* . . . *Senecio argutus* A. Rich. et Lesson. . . . non Kunth" in the 'Prodrumus'. De Candolle also maintained *E. glomerata* as a distinct species, and even placed it in a different section of the genus! The holotype of his typical variety is a specimen "ex itin. Baudin", which is almost an exact replica of the left-hand specimen on the Baudin sheet cited by Richard as *S. argutus*. These two specimens likely are of the same gathering, possibly even from the same plant!

With this merely sinuate-dentate specimen de Candolle associated two coarsely lobate to pinnatifid specimens as *E. glomerata* var. *subincisa* DC. This was based on "*Senecio glomeratus* Desf.! hort. Paris 1824 [sic!]. Poir. Suppl. 5. p. 130. Link enum. 2. p. 325. *Neoceis microcephala* Cass. dict. 34. p. 388. (v. v. et s.)". These specimens approach the left-hand specimen from Desfontaines' herbarium, but do not quite equal it in depth of lobing and slenderness of lobes. One is ticketed as "*Senecio glomeratus* h. pl. 1815", and is probably the basis for the exclamation mark after the basonym, since with de Candolle that meant that he had seen the "type". The other specimen establishes the earliest date, 1807, which I find for this species in cultivation.

The type of *E. glomerata* var. *polycephala*, from Port Western on Bass Strait, has a somewhat larger capitulum with larger and wider bracts than usual, and three large leaves which are merely shallowly dentate. Although I have seen no other specimen which exactly duplicates this, it is definitely a part of the *S. glomeratus* complex. It is linked to the more typical state by several collections, notably the Travers specimen from Wellington, on which the phyllaries were 5 mm. long and the leaves similarly large. I therefore regard var. *polycephala* as only a luxuriant state of *S. glomeratus*.

J. D. Hooker disregarded *E. glomerata* and took up *E. arguta* in his floristic papers on Australasia. In attempting to deal with the extreme polymorphism shown by the (hybrid) material in his herbarium,³⁵ he created four varieties of *E. arguta* for Tasmanian specimens, and later³⁶ formed two varieties for New Zealand specimens. These specimens are at Kew, duly annotated.

Hooker's var. *a* of New Zealand is typified by Akaroa, *Raoul 31* (K), which I regard as a hybrid between *S. glomeratus* and *S. hispidulus* (probably var. *scaberulus*). His var. *β* of New Zealand agrees well enough with typical *S. glomeratus*. His var. *β glabrata* of Tasmania is typified by two mixed sheets at Kew, of which that part which most closely matches the brief description again appears to be another hybrid of the above parentage, while the other specimens are more like pure *S. glomeratus*. Hooker attributed his var. *γ asper* to *S. asper* Cunn. I have failed to find this name published, and if it were it would be a later homonym of *S. asper* Ait. This variety is typified by *Hooker 1125* and by "near Woolworth, 25 Nov. 1836, *Gunn 843*". These were compared with Richard's types, and agreed most closely with *S. pusillus* A. Rich., which I consider a depauperate state of another hybrid between *S. glomeratus* and *S. hispidulus*. Var *δ obovata* is good *S. glomeratus*. Var *ε*, without an epithet, typified by "Circular Head, 11 Dec. 1837, *Gunn 843/1842*", is much the same type of plant as the hybrid var. *a* of New Zealand. Thus *E. arguta* Hk. f. includes both *S. glomeratus* and some hybrids of it with *S. hispidulus*.

Bentham consolidated these errors by accepting as *E. hispidula* a mixed group of large-headed specimens including *S. squarrosus*, and by placing the then nameless specimens of *S. hispidulus*, along with hybrids of it with *S. glomeratus*, in with the true *S. glomeratus* material as *E. arguta* (*sensu Benthami*). A large part of Bentham's description of *E. arguta* applies much more to *S. hispidulus* than to *S. glomeratus*, and some parts apply only to the former and its hybrids.

Of modern authors, only Cheeseman seems to have had an accurate conception of this taxon, under the name of *E. arguta* DC. Neither his key to species nor his description reveals any confusion with *S. hispidulus*. Rodway followed Bentham exactly. Black similarly followed Bentham, even to the inclusion of his var. *microcephala*, which is better treated as a distinct species (see *S. laticostatus*).

15. *SENECIO laticostatus* Belcher, nom. nov.

Erechtites arguta var. *microcephala* Benth. Fl. Austral. 3: 659. 1866; *non Senecio microcephalus* Phil. 1894.

Stem striate, arachnoid, apparently simple below the inflorescence, basal part unknown. Leaves to 6 cm. long, 2.5 cm. wide, pinnately lobed, lobes triangular to oblong, sharply toothed, base auriculate, semiamplexicaul especially upward, sparsely hispid and arachnoid and rough above, copiously arachnoid beneath. Inflorescence a compact corymbose panicle of numerous capitula, few or solitary on

³⁵ Lond. Jour. Bot. 6:122. 1847.

³⁶ Bot. Antarct. Voy. II. Fl. N. Z. 1:142. 1853.

peduncles from 0.5 to 3 cm. long, branches striate, arachnoid, peduncles strongly striate, moderately arachnoid, the linear-lanceolate entire bracts virtually glabrous, receptacles lanate. Capitula short, comparatively broad; phyllaries of involucre about 12 to 13, slightly lanate at the base, glabrous at the apex, 3.5 to 4 mm. long, 0.5 to 0.75 mm. wide at base, the center portion about 0.1 to 0.2 mm. wide between the scarious margins which rapidly taper toward the apex so that the apical 0.75 to 1.0 mm. is essentially without scarious margins and is long and slenderly acuminate, even in early bud, when the phyllaries may equal or exceed 3 mm. while the florets are still less than 1 mm. long. Marginal florets pistillate, 20 to 25, corolla slender, 3- or 4-fid, 2.5 to 2.75 mm. long. Disc florets hermaphroditic, 3 or 4 in number, corolla 3.0 to 3.25 mm. long, thick, apex 1.5 mm. in circumference, with 4 obtusely deltoid lobes, each 0.4 mm. wide and 0.3 mm. long, anthers 1 mm. long; florets at anthesis exceeding phyllaries by about 1 mm. Achene (somewhat immature) olive-green, 1.5 mm. long, cylindrical, non-attenuate, glabrous, having 5 extremely narrow thin high ridges extending its full length. Pappus hairs white, unequal in length but mostly equaling or slightly exceeding the phyllaries, shorter than the florets.

Known to me only from the holotype collection.

AUSTRALIA: Flats beyond the Brodribb River, Jan. 1855, *Mueller* (MEL holotype).

Mueller gave to the type specimen a manuscript name in *Erechtites*; *Bentham* adopted his trivial as the varietal epithet. The new epithet, *laticostatus*, alludes to the unique fin-like ribs of the achene. The type specimen has a somewhat anomalous growth pattern, as though it had been broken over prior to flowering. The leaves are highly suggestive of the more coarsely lobate forms of *S. glomeratus*, differing unreliably in having somewhat coarser denticulations on the median lobes. The floral features, however, are unique, particularly the short broad 4-fid corolla of the few disc florets, with bluntly deltoid lobes, the short phyllaries with acuminate non-scarious apices, and the five-finned short achene. Furthermore, the peduncles of *S. glomeratus* are shorter and more lanate than those of *S. laticostatus*, and the involucre of the former is much more pubescent than that of the latter.

It is possible that the type specimen is a hybrid between *S. glomeratus* and some discoid species of *Senecio*, in some of which there is an approach to this type of corolla. But I have yet to encounter any species which might have contributed the unique features of the phyllaries and the achene. Furthermore, the pollen grains are well formed, lacking the abortive grains one would expect from a wide cross. I have seen no other specimen of this taxon, which in itself is suspicious, but I see no alternative to treating it as a good species, perhaps related to but certainly distinct from *S. glomeratus*.

16. *SENECIO HISPIDULUS* A. Rich. Sert. Astrolabe, 92, tab 34. 1832.

Annual herb; stem erect, simple or sparingly branched below the inflorescence, sometimes subscapose, glabrous or minutely puberulous or sometimes densely clothed with crisped multicellular hairs. Leaves 3 to 7 (to 11) cm. long, 0.5 to 1 cm.

wide (to 2.5 cm. or more in vars. *dissectus* and *scaberulus*), linear-lanceolate to ovate-lanceolate, sessile, auriculate with coarsely bidentate auricles, or the lowest leaves sometimes subpetiolate with minute linear auricles, more or less coarsely and irregularly sharp-toothed, sometimes deeply pinnatisect and the segments sharply denticulate, densely hispid beneath with multicellular hairs, less densely to sparsely hispid above or sometimes glabrate, upper surface frequently roughly wrinkled or scabrid after drying, with the hairs subtuberculate. Inflorescences terminal and axillary, corymbose, usually rather congested, sometimes diffusely paniculate, glabrous, minutely puberulous, or rarely hispid; bracts greatly reduced, sublinear or long-triangular, subentire, erect. Capitula slender, calyculate with triangular bracteoles about 1.5 mm. long and 0.4 mm. wide; phyllaries of involucre 11 to 13, 4.5 to 6 mm. long, glabrous or sparsely puberulous, not arachnoid, strongly keeled and prominently 2-nerved, scarious on the margins, acute or acuminate; corollas of the filiform pistillate marginal florets usually 4-fid, a few 3-fid or 5 fid, of the less numerous slenderly infundibuliform perfect disc florets 5-fid, the lobes all obtusely papillose-thickened on the inner aspect of the apex, the style-arm apices truncated. Achene 1.5 to 2 mm. long, plump, cylindrical, without attenuate neck but with callose-annulate apex, blackish-brown with whitish subappressed hairs in rows of variable width between the low rounded ribs. Pappus white, exceeding phyllaries, subequalling the florets.

In temperate Australia and New Zealand.

16a. *SENECIO HISPIDULUS* var. *hispidulus*

Senecio hispidulus A. Rich.

Erechtites hispidula (A. Rich.) DC. Prodr. 6: 296. 1838; *non* Hook. f. Fl. Tasm. 1: 220. 1860; *non* Benth. Fl. Austral. 3: 660. 1866; *non* Rodway, Tasm. Fl. 94-95. 1903; *non* Black, Fl. S. Austral. 610. 1929.

Erechtites arguta Benth. Fl. Austral. 3: 659. 1866, *pro majore parte*.

Leaves linear-lanceolate to lanceolate, denticulate to coarsely toothed, neither pinnatifid nor lobed, upper leaf surfaces scabrid with subtuberculate-based hairs. Achenes 1.5 to 1.75 mm. long, beset with hairs in narrow rows in the grooves.

AUSTRALIA. TASMANIA: "*Senecio hispidulus* No. 18. Van Diemen, 1828, Voy. Astrolabe" (P, holotype); Port Dalrymple, R. Brown 2278 (K); between National Park and Westerway, in railway cutting, Nov. 1929, Comber 1756 (HO, 2; K); Knocklofty, Hobart, Dec. 1937, Olsen (HO); Adamsfield "in tussock of *Restio australis* in tea tree swamp, 1400 ft.", Dec. 1942, Gordon (HO); N. Parkside, St. Helens, Nov. 1945, Curtis (HO). WESTERN AUSTRALIA: near Perth, Andrews 486 (K); Smith (K); Midland Junction, Nov. 1902, Fitzgerald (NSW). SOUTH AUSTRALIA: Lowden, South West, Oct. 1910, Koch (NSW). VICTORIA: Melbourne, Brunswick, Feb. 1894, Morrison (K); S. E. of Oakleigh, Dec. 1895, Morrison (US, one piece with leaves deeply pinnatifid, approaching var. *dissectus*); Boyamp, Oct. 1896, Morrison (K); Midland Junction, Dec. 1898, Morrison (US). NEW SOUTH WALES: Sydney, U. S. Expl. Exped. (US); Dec. 1902, Camfield (US, left-hand specimen only, right a hybrid with *S. quadridentatus*); Kiama, Harvey (K).

NEW ZEALAND. NORTH ISLAND: Coromandel, Petrie (K, 2). SOUTH ISLAND: without specific data, ex Hb. T. Kirk (F). Bay of Islands, U. S. Expl. Exped. (US, aspect of var. *hispidulus*, but only 8 phyllaries, depauperate, leaf bases non-auriculate, leaves oblong or ovate-lanceolate).

Senecio hispidulus is a species whose identity in Australian floras has been thoroughly submerged in "*E. arguta*", while other taxa have masqueraded under its name as "*E. hispidula*".

Richard's description and figure of *S. hispidulus*, on the whole, agree well with the holotype, but erred slightly. The marginal florets are pistillate, not staminate, as pointed out by de Candolle, and are more usually 4-fid than 3-fid. The artist portrayed the leaves as entire above the bidentate auricles; actually they are rather regularly callose-dentate, as I found by use of detergent solution, but are so strongly rolled as to appear entire. De Candolle had no specimen of this taxon, but drew the diagnosis for the 'Prodromus' directly from Richard, merely correcting the description of the pistillate floret.

Hooker, however, had the misfortune to receive from Gunn, and later from other collectors on Tasmania, a curious assortment including hybrids of *S. hispidulus* with both *S. glomeratus* and *S. quadridentatus*. The former group he referred to "*E. arguta*", and attempted to treat them as varieties, as discussed above under *S. glomeratus*. The latter group he first distributed, in the "Florae Tasmaniae Spicilegium", as unnamed varieties of *E. hispidula* and *E. glabrescens* (i. e., a glabrate state of *S. quadridentatus*). Both varieties were queried as to whether they might belong to the other species!

In properly assigning Cunningham's, d'Urberville's, and his own specimens from New Zealand to *E. hispidula* in the 'Flora Novae Zelandiae', Hooker compared them to this mixed Tasmanian group: "This is also a New Holland and Tasmanian plant, but the specimens from the latter country are wooly as well as hispid. Those figured by Richard have the leaves nearly entire." This concept is epitomized by the Kew specimen, "Circular Head, 23/11/37, Gunn 508", which is annotated "*E. glabrescens* DC.", and beneath that, "*E. hispidula* DC.", both in Hooker's script. (Bentham rejected this determination, and cited this specimen in the 'Flora Australiensis' as *E. quadridentata* var. *glabrescens*, which it is not, either.) This specimen has the combined pubescence of *S. hispidulus* and of *S. quadridentatus* (hence, "Wooly as well as hispid"); the longer phyllaries and long and attenuate-rostrate achene of the latter; and the bidentate auricles and callose-dentate leaf margin of the former.

In the 'Flora Tasmaniae' Hooker merged his varieties of *E. glabrescens* and *E. hispidula* into what must be called *E. hispidula* Hk. f., non DC., and rewrote the description to fit the Tasmanian plants in his herbarium. To the Circular Head specimen he added others, which, as far as I could find at Kew, did not include a single specimen of typical *E. hispidulus* but did include the Launceston gathering of Gunn 508, which definitely is *S. squarrosus*. Hooker accurately compared his New Zealand material with this Tasmanian mixture in the 'Handbook of the Flora of New Zealand': "This differs from the Tasmanian *E. hispidula* in the achene only 1/12 in. long and not attenuate at the top, also in the smaller glabrous heads and short involucre scales." He thus correctly concluded that the two groups were not conspecific, and set the New Zealand material apart as a new

species, *E. scaberula*! Actually, by direct comparison of types, *E. scaberula* and *S. hispidulus* A. Rich. are very similar and can only with some difficulty be separated into varieties.

A careful examination of the specimens determined as *E. hispidula* by Bentham for the 'Flora Australiensis' reveals that the misinterpretations initiated by Hooker were only further entrenched. I believe that all of the specimens now remaining at Kew which were determined by Bentham as *E. hispidula* are in fact not that species at all. "Gunn 508 Circular Head," he returned to *E. quadridentata* as var. *glabrescens*. To "Gunn 508 Launceston" and other material of *S. squarrosus* he added other large-headed specimens collected by Backhouse and by Robertson, and called the lot *E. hispidula* (Benth., non DC.). His description largely applies to *S. squarrosus*, which he included in the synonymy. He also included *S. hispidulus*, but wrote: "from the description, but scarcely the figure, t. 34." As noted above, the plate actually is in good agreement with both specimen and description.

To find *S. hispidulus* of Richard in the 'Flora Australiensis' one must look under *E. arguta*, which is described as: "more or less scabrous-hirsute with crisped hairs and occasionally with white cottony wool on the underside of the leaves and about the inflorescences, rarely nearly or even quite glabrous," and "involucre in the normal form about 3 lines long". Most of this applies to *S. hispidulus* rather than to *S. glomeratus*, and the second quotation quite excludes *S. glomeratus*! In effect, Bentham treated the *S. hispidulus* and the *S. argutus* of Richard as synonyms, although he did not realize it, having already mistakenly identified the former with *S. squarrosus*.

This confusion in *E. arguta* Benth. becomes even more obvious when Bentham's synonymy and comment are considered. *E. Bathurstiana* DC., treated as a variety of *E. arguta*, is definitely related to *S. hispidulus* instead. *S. multicaulis* A. Rich. is, by examination of the type, unquestionably part of the *S. hispidulus* complex, with phyllaries 6 mm. long and entirely glabrous, but with the achenes also glabrous instead of hairy. *S. apargiaefolius* Walp. is most likely a hybrid of *S. hispidulus* with *S. quadridentatus* (see below). *S. pusillus* A. Rich. is, from the type, definitely a hybrid between *S. glomeratus* and *S. hispidulus*, with the characters of the latter predominating, and is essentially equivalent to *E. arguta* var. *asper* Hk. f. The non-existent *S. pumilus* Poir. (*E. pumila* DC.) is an error on de Candolle's part for *S. minimus* Poir.

Rodway followed Bentham closely in his treatment of *Erechtites*. He characterized *E. hispidula* as having 16 to 24 phyllaries about 4 lines long, the capitula few and stout. This appears to be *S. squarrosus*. His *E. arguta*, with phyllaries 3 lines long or less, is certainly meant to include *S. hispidulus* as well as *S. glomeratus*. Black also included *S. hispidulus* in his *E. arguta*, but he appears to have followed Hooker in part, rather than Bentham, in applying the name *E. hispidula* to the group of specimens more resembling *S. quadridentatus* but with larger slender capitula and more numerous phyllaries.

16b. *SENECIO HISPIDULUS* var. *dissectus* (Benth.) Belcher, comb. nov.*Erechtites arguta* var. *dissecta* Benth. Fl. Austral. 3: 659. 1866.*Erechtites Bathurstiana* DC. Prodr. 6: 297. 1838.*Senecio Bathurstianus* (DC.) Sch. Bip. Flora 28: 498. 1845.

Differing from the typical variety in having deeply pinnatisect leaves with obtuse sinuses, lobes 5 to 8 (to 10) on each side and broadly linear to oblanceolate, more or less acute-denticulate; marginal florets irregularly 3-fid, with one cleft or two much deeper, inner florets 4-fid.

AUSTRALIA. NEW SOUTH WALES: "Rocky Hills in the neighborhood of Bathurst", *A. Cunningham* 135 (G Prodr., holotype), *A. Cunningham* 102 (K, isotype?); "Rocky Hills in the country N. E. from Lachlan River", *A. Cunningham* 46 (K); Hunter River, *U. S. Expl. Exped.* (US); Warrumbungle Ranges, Oct. 1899, *Forsyth* (NSW); Narrabri, Nov. 1899, *Maiden* (NSW); Capertee, Jan. 1900, *Boorman* (NSW); Brunswick River, Dec. 1903, *Maiden & Boorman* (NSW); top of Mt. Dangar, Gungahlin, Sept. 1904, *Boorman* (NSW); Burrinjuck, Feb. 1911, *Boorman* (NSW); Coonor's Creek, Barroba, Aug. 1913, *Rupp* 6 (NSW); Bell's Paddock, Black Mountain, June 1932, *McKie* 454 (NSW). VICTORIA: Wimmera, *Dallachy* (K, immature); Lake Albacutya, 1901, *D'Alton* (NSW); Goorman, Euroa, Dec. 1901 *Williamson* (NSW). SOUTH AUSTRALIA: "Austr. felix", *Mueller* (K).

Bentham's placement of *E. Bathurstiana* DC. as a variety of *E. arguta* Benth. was a logical consequence of his concept of that species as virtually identical with *S. hispidulus*. It has a much closer affinity with *S. hispidulus* proper than with *S. glomeratus*, when the pubescence and general facies are considered. It is not impossible that genetic analysis will reveal this variety as another hybrid, with *S. glomeratus* the other parent, as is suggested by the irregular corolla of the marginal floret and the addition of arachnoid pubescence on the leaf over the multicellular crisped hairs. But the general characters are closer to *S. hispidulus*, and I leave it in that species pending further study.

Croizat³⁷ cited this variety (as *E. arguta* var. *dissecta*) as occurring on Lombok in the Lesser Sunda Islands, without giving the authority for this record. In view of the confusion over the identity of *S. glomeratus* and of *S. hispidulus*, I hesitate to accept this extreme extension of range until I have examined the specimen.

16c. *SENECIO HISPIDULUS* var. *scaberulus* (Hook. f.) Belcher, comb. nov.*Erechtites scaberula* Hook. f. Handb. Fl. N. Z. 157. 1864.*Senecio hispidulus* Cunn. Ann. Nat. Hist. 2: 121. 1838; non A. Rich.*Erechtites hispidula* Hook. f. Fl. N. Zeal. 142. 1853; non DC.? *Erechtites pumila* Armst. Trans. N. Z. Inst. 13: 338. 1881, *vide* Kirk, Student's Fl. N. Z. 334. 1899; non DC.

Leaves lanceolate, the lower oblanceolate and coarsely toothed or irregularly lobed, the upper surfaces beset with coarse but non-tuberculate hairs. Achenes 2.0 mm. long, hairy in broad bands in the grooves.

I did not see Armstrong's type, cited as "McKenzie Country, Mr. J. F. Armstrong, December 1877".

³⁷ Manual of Phytogeography. p. 538. 1952.

NEW ZEALAND. SOUTH ISLAND: Akaroa (K ex Hb. Hk., lectotype); Bay of Islands, 1853, Hooker (K, 2 sheets, syntypes); Dunedin, Kirk 333 (US). NORTH ISLAND: "Among ferns at Wangeroo", 1833, R Cunningham (K); Wellington, open places, 1500 ft., 1909, Travers (W). Also reported by Cheeseman (l.c. 1007. 1925) from Stewart Island and the Chatham Islands.

Neither Cunningham's nor Hooker's original descriptions of this taxon gave any clue to the distinctions between it and the typical Australian variety. Hooker described it as a distinct species only on the basis of differences between it and what he mistakenly supposed *E. hispidula* to be, as described above. Since in the description of *E. scaberula* Hooker cited no specimens, but referred to his treatment of 1853, the specimens cited in the earlier work must be the syntypes. The Akaroa specimen, presumably supplied by d'Urville, is selected as lectotype because it is determined in Hooker's script as *E. scaberula*. The Cunningham specimen of this variety was not annotated by Hooker. The two sheets of Hooker's own gathering are included in the syntypes because they bear his determination as *E. scaberula*. All are in good agreement.

Dissection of a capitulum from Hooker's specimen revealed that all 18 florets contained stamens, either vestigial or functional. The lobing of the corollas also varied considerably. Most of the florets were 4-fid, some with 4 and some with 5 stamens, functional or not; two were 3-fid, one with 3 vestigial stamens, the other, non-marginal, one with 4 functional ones; only three 5-fid florets had 5 functional stamens each. No tendency toward ligules was discernible, the picture being entirely one of partial emasculation accompanied by reduction in size of corolla limb and number of lobes. This specimen thus offers an intermediate stage between the truly discoid *Senecio* with all florets perfect and infundibuliform, and the extreme erechthitoid state with all outer florets strictly pistillate and filiform. (In some other specimens, however, which also had staminodes in 4-fid marginal florets, there were some corollas with some sinuses much more shallow than others, thus approaching the ligulate condition.)

This variety appears to be confined to New Zealand, where it largely replaces the typical variety. The latter is adventive in New Zealand to some extent. The specimens from Coromandel, for example, were sent to Kew by Petrie with a note saying that they were new to the island. The determination at Kew was: "*E. scaberula* with slightly different achenes"!

SENECIO GLOMERATUS × S. HISPIDULUS

Senecio pusillus A. Rich. Sert. Astrolabe, 99. 1834.

Erechtites arguta (A. Rich.) DC. var. *α* Hk. f. Fl. N. Z. 142. 1853 (prob. × *S. hispidulus* var. *scaberulus*); vars. *β glabrata*, *γ aspera*, and *ε*, Hk. f. Fl. Tasm. Spicil. 122. 1847; Fl. Tasm. 1: 219. 1860.

Senecio glomeratus and *S. hispidulus* appear to hybridize so freely over much or all of their largely overlapping range that determination of material in this complex is exceedingly difficult. This is a situation which urgently requires investigation by as many varied techniques as can be brought to bear.

In my own determinations the following criteria have prevailed. For *S. glomeratus* I associate arachnoid pubescence, simple auricles, lanate receptacles, bracts, pedicels, and phyllary bases, small capitula, short (3.5 to 4 to 5 mm.), obscurely nerved phyllaries, usually 3-fid pistillate florets, with slightly irregular corollas, and short (1.5 mm.) brownish achenes. For *S. hispidulus* I associate hispid multicellular pubescence, with the bases of the hairs usually subtuberculate, bi-dentate auricles, glabrous or minutely puberulous inflorescence, larger capitula, longer (4.5 to 6 mm.), strongly 2-nerved, glabrous phyllaries, usually 4-fid regular pistillate corollas, and slightly longer (1.5 to 2 mm.) blackish-brown achenes.

Many specimens are intermediate in some degree in one or another or several of these characteristics, and I have felt obliged to call such specimens hybrids. If this entire complex is considered as one vast polymorphic species, which is what Bentham in effect did, one is left with the problem of appropriate subspecific categories for the many intermediate forms and the cause for such extreme variability is ignored. Hooker's reaction to contact with limited numbers of examples of these hybrid swarms was to form varieties for each; Bentham's response to a somewhat larger suite was to merge them. Later authors have largely followed Bentham.

Determination of specimens of *S. glomeratus* is further complicated by the rather extreme range of foliar variation of the species and by certain trends in the floral features as well. I strongly suspect this species of crossing rather frequently with *S. quadridentatus*, although this is much more difficult to detect because of their similarities in pubescence. I also suspect introgression, less commonly, with one or more radiate species of *Senecio*, but I am not sufficiently acquainted with these to name the probable offenders. Indeed, cursory examination of the material laid in under the several names in both the discoid and the radiate groups of Australasian *Senecio* leads me to fear that there is as much confusion of identity in those taxa as in the erechthitoid material!

SENECIO HISPIDULUS × S. QUADRIDENTATUS

Erechtites tenuiflora DC. Prodr. 6: 296. 1838.

(?) *Senecio apargiaefolius* Walp. Linnaea 14: 309. 1840.

Senecio tenuiflorus (DC.) Sieb. ex Sch. Bip. Flora 28: 495. 1845.

Erechtites apargiaefolia (Walp.) Sond. Linnaea 25: 524. 1852.

Erechtites Muelleri Lange, Ind. Sem. Hort. Hafn. 28. 1861; Jour. Bot. 1874: 5, t. 3. 1874.

The evidence of hybridization between these two species is presumptive, based on the existence of specimens intermediate in some particulars. Three related collections from Tasmania, "between National Park and Westerway, in railway cutting, 500 ft. alt., 30 Nov. 1929" (K!) are of especial interest: (1) *Comber 1756*, the first of these, is annotated: "*Erechtites arguta* DC. Tall erect perennial, 2-4 ft. high with shrubby base; whole plant green; flowers yellow". This specimen matched precisely the holotype of *S. hispidulus*. (2) *Comber 1757* is annotated: "*Erechtites quadridentata* DC. Tall erect perennial 2-6 ft. high

with a shrubby base; leaves and stems white wooly; flowers yellow". This specimen is *S. quadridentatus*, quite typical except for slightly more glabrate phyllaries than usual. (3) *Comber 1758* is annotated: "*Erechtites tenuiflora* DC. Intermediate between above numbers; 3 – 5 ft. high; involucre purple". This specimen is not quite identical with the type of *E. tenuiflora*, although the resemblance is quite close. The leaf is shaped like that of *S. quadridentatus* but is broader and auriculate at the base, although the auricle is not bidentate. The leaf is hispid above, arachnoid and hispid beneath. The stem is cottony below, glabrate above and on the inflorescence. The phyllaries are glabrate as in *S. hispidulus* but 7 to 8 mm. long, slender, and not strongly keeled. The achenes, however, are short and non-attenuate. The general aspect is that of *S. quadridentatus*, but it has several of the features of *S. hispidulus*. It is undoubtedly a hybrid, and quite possibly the offspring of numbers *1756* and *1757* themselves!

With this clearly intermediate specimen as a guide, re-examination of a large suite of specimens revealed numerous other individuals which were intermediate in various degrees in the several features in which the two species differ, and which I interpret as also being of hybrid origin.

One such hybrid, which has been dignified as a species, is *E. tenuiflora*. The type material, *Sieber* "Fl. Novae Holl. no. 435" (BM!, G!, K!, P!), shows appreciable variation among the several specimens. They agree, however, in having rather short phyllaries (6 rather than 7 to 8 mm. long), achenes of intermediate length without necks, small but definite auricles, very little arachnoid pubescence and more or less abundant hispid multicellular pubescence, features indicative of an admixture of *S. quadridentatus* with *S. hispidulus*, with the former predominating.

Another such hybrid is *E. apargiaefolia* Sonder, the type of which (Fiedler's Section, *Behr*, MEL *ex* Hb. Sond. !) was located for me by Mr. J. H. Willis. Its connection with *S. hispidulus* is shown in the auriculate leaf bases, the crisped multicellular hairs on the lower leaf surfaces beneath the arachnoid pubescence and the roughened and scabrous-haired upper leaf surface, the glabrous 2-nerved phyllaries, and the short cylindric achene. Its relationship to *S. quadridentatus* is seen in the moderately long slender phyllaries, arachnoid pubescence, narrowly lanceolate leaves, and 4-fid florets with thickened glandulose apices. It resembles *E. tenuiflora* but has a somewhat shorter achene and broader and more scabrid lower leaves.

Sonder published *E. apargiaefolia* as a new combination for *Senecio apargiaefolius* Walp., although based on a different collection. Walpers' type, cited as "Nova Hollandia Lhotsky legit", is supposed to be in Herb. Lucaeni at the Botanische Institut, of Kiel University. Although the greater part of the herbarium was saved in the destruction of the Institut during the war, it (as of 1952) was in temporary storage and inaccessible. Although Sonder stated that he compared *Behr's* specimen with Walper's type and found them conspecific, I have reduced *S. apargiaefolius* with a query, pending examination of the type, if it still exists.

Walper's description actually applies very well to the Behr specimen except for four points: (1) the widest leaf is only $3\frac{1}{2}$ lines instead of 5 to 6, and is not repand-dentate; (2) the capitula are heterogamous, not homogamous; (3) the leaf base has small semi-clasping auricles and is not simply attenuate; and (4) the achenes are not all glabrous. The difference in leaf width may mean only that Walper's specimen is larger, or, more likely, that its leaf configuration trends more toward that of *S. hispidulus*. Walpers stated: "Flores homogami tubulosi hermaphroditi". Sonder, after examining the type, wrote: "Flores marginales feminei tubulosi!", and so transferred Walper's name to *Erechtites*. This is certainly true for the Behr specimen, and I accept it for the Lhotsky specimen until it is available for further study. Walpers possibly overlooked the auricles, which is easily done, especially if there is much arachnoid pubescence around the node. It is also possible that the Lhotsky specimen has auricles lacking or very slightly developed, for this is a very variable character. The sheets of *Sieber 435*, for example, vary among themselves from no auricles to auricles as long as 2 or 3 mm. This suggests a multiple-allelic character appearing in varying degrees, and is one of the lines of evidence in support of the hybridity of this complex.

All the achenes in the packet on the Behr specimen are definitely hairy on their ridges, after the manner of *S. hispidulus*, and are approximately 2 mm. long. Most of the achenes visible in the capitula, and all of the obviously immature ones, are also hairy. A few achenes, however, apparently the most mature ones retained, are certainly glabrous. This coincides with other observed instances, both in this genus and others, of achenial pubescence diminishing with increasing maturity. Accordingly, I accept Walper's characterization as based upon the most mature and accessible achenes and not in actual disagreement with Sonder's type.

My inquiry to Copenhagen concerning the type of *E. Muelleri* Lange went unanswered, but two sheets so determined and said to have been raised from seed from Copenhagen were included in the loan from Vienna. These agreed well with Lange's emended description and plate (1874), and may be presumed authentic. (I was unable to locate the 1861 seed list in which Lange originally published.) Their achenes ranged from 2.4 to 3 mm. long, and were heavily ribbed and only slightly attenuated. The leaves were long and rather wide, regularly denticulate to sinuate-dentate or with an occasional long-exserted linear-lanceolate tooth. The phyllaries were glabrous or glabrate, the leaves variably arachnoid, mostly glabrous above. From these features I conclude that this represents another hybrid between *S. hispidulus* and *S. quadridentatus*, essentially stabilized near the latter parental line. The relative uniformity of these plants and their immediate ancestors is not necessarily an effective argument against their hybrid nature; as pointed out by Anderson³⁸: "variation between [hybrid] individuals will lessen as parental combinations are approached".

I have not cited specimens of hybrid nature, except those indicated above, for lack of space. They are, however, quite common in all the herbaria examined.

³⁸ Anderson, E. *Introgressive hybridization*. New York. 1949.

ARRHENECHTHITES

ARRHENECHTHITES Mattf. Engl. Bot. Jahrb. 69: 288. 1938.

Perennials with shoots herbaceous or suffruticose. Capitula heterogamous with few florets. Involucre of 5 to 8 sub-biseriate phyllaries, the narrow scarious margins of the exterior ones inserted into grooves beneath the lateral nerves of the interior phyllaries. Marginal florets pistillate, as many as or slightly more than the phyllaries and opposite them; corolla filiform with base inflated and more or less indurated, oblique and truncate at the apex, minutely and irregularly toothed, or subligulate; style exerted, arms short and glabrous; achene subcylindric, with a callose rim base at the apex and also sometimes callose-annular at the base. Disc florets fewer than or as many as the marginal florets, structurally perfect but functionally staminate, corolla with limb infundibuliform, deeply 5-lobed, lobes recurved; style arms erect, short and astigmatic, or style apex subentire, papillose-hairy over the outer faces; achene narrowly cylindric or stipiform, slightly longer than that of the pistillate floret, usually with abortive embryo. Pappus filiform, white, exceeded by disc florets.

Genus characterized by functionally staminate disc florets with style arms reduced, astigmatic, and papillose over the outer faces.

Erechthitoid *Senecio* differs in having all florets fertile, perfect florets with short erect corolla lobes and style arms glabrous except for a terminal marginal fringe of papillae. *Brachyglottis* Forst. of New Zealand approaches most closely in composition of the capitulum, having marginal florets 8, opposite the phyllaries, functionally pistillate with sterile stamens; disc florets 2, apparently perfect.

Endemic in the higher mountains of New Guinea, with an extended outlier in the Australian Alps and Blue Mountains. Six species are known.

Type of the genus: *A. tomentella* Mattf.

KEY TO SPECIES OF ARRHENECHTHITES*

- A. Phyllaries 5, pistillate florets 5; disc florets solitary1. *A. tomentella*
 AA. Phyllaries 7 or 8, pistillate florets as many or slightly more numerous; disc florets more than oneB
 B. Capitula 2.0 to 2.5 cm. long; achene 6 to 7 mm. long; corolla of marginal florets subligulate; medial leaves deeply pinnatifid2. *A. mixta*
 BB. Capitula about 1 cm. long; achenes 2 to 3 mm. long; corolla of marginal florets minutely 3-, 4-denticulate or irregularly cleft and obliquely truncated; leaves entire or merely toothedC
 C. Style of central florets scarcely bifid, clavate with shallow notch and a crown of papillose hairs; leaves 2.5 to 5 cm. long3. *A. haplogyna*
 CC. Style of central florets deeply bifid, arms erect, uniformly papillose on the outer face; leaves 10 cm. long or longerD
 D. Leaves broadly elliptical, 10 to 15 cm. long, 4.5 to 7 mm. wide4. *A. mastigotbrix*
 DD. Leaves narrowly lanceolate, 15 cm. long or longer, about 3 cm. wideE
 E. Leaves acute, 15 to 16 cm. long; disc florets 25 *A. novoguineensis*
 EE. Leaves caudate-acuminate, 20 cm. long or longer; disc florets 4 to 6
6. *A. dolichocephala*

*Modified from Mattfeld, Engl. Bot. Jahrb. 69:288-289. 1938.

1. *ARRHENECHTHITES TOMENTELLA* Mattf. Engl. Bot. Jahrb. 69:290. 1938.

Known to me only from Mattfeld's description. Apparently collected only once.

Holotype: Northeast New Guinea, "Bezirk Morobe: Sarawaket, Busu Tamunac, an offenen Grasland, 24-2700 M. ü. M.", 31 Jan. 1937, *Clemens 5251* (B, destroyed).

2. *ARRHENECHTHITES mixta* (A. Rich.) Belcher, comb. nov.

Senecio mixtus A. Rich. Sert. Astrolabe, 112, t.36. 1832.

Erechtites mixta (A. Rich.) DC. Prodr. 6:297. 1838; *non* Benth. Fl. Austral. 3:659. 1866; *non* Black, Fl. S. Austral. 4:610. 1929.

Stem herbaceous, erect, simple or sparingly branched, purpurascens, sparsely arachnoid. Leaves glabrous to sparsely arachnoid above, with sparse arachnoid hairs overlying numerous short strigose multicellular hairs beneath, sometimes purpurascens; lowest leaves alate-petiolate, abruptly broad-lanceolate to ovate, with large coarse teeth; medial leaves with attenuated portion progressively shorter and sinuses between teeth progressively deeper so that within 5 or 6 nodes the blade has become lobate to pinnatisect, the segments notably variable in size and shape, borne essentially at right angles to the midrib, more or less denticulate, shortly acuminate, acute, or rarely obtuse; sinuses equalling or exceeding the segments in width; leaf abruptly reduced below first node of inflorescence to a linear to ensiform bract; bracteoles of peduncle about 4 mm. long and 0.2 mm. wide. Inflorescence cymose-paniculate, much branched, lax; capitula solitary on elongate peduncles to 5 cm. long, ecalyculate but surrounded by 3 to 5 linear bracteoles 5 to 7 mm. long and 0.5 mm. wide, which arise from the terminal 2 or 3 mm. of the peduncle; end of peduncle above bracteoles abruptly doubled in diameter from 1.0 mm. to form a very short receptacle. Involucre (12 to) 20 to 24 mm. long, sub-biseriate; phyllaries long, linear-lanceolate, tightly appressed in bud, becoming widely separated in fruit or sometimes adhering tightly over the undeveloped achenes to simulate an elongated receptacle, flat-keeled, usually indistinctly 4-nerved, with mixed pubescence similar to that of leaf, often purplish, acute to acuminate, ciliolate; outer phyllaries narrower (0.71 mm.), non-scarious, frequently edged with purple; inner phyllaries wider (1.25 mm.) with light scarious margin 0.3 mm. wide on either side; intermediate phyllaries scarious on one margin, non-scarious and sometimes purple-edged on the other. Marginal florets pistillate, or having corolla with the base about 1 mm. long and 0.4 mm. in diameter, the tube 12 to 14 mm. long, 0.2 mm. in diameter, the oblique limb 1.0 to 1.5 mm. long, 0.4 to 0.5 mm. wide, and, imperfectly 2- or 3-dentate; style slender, slightly exceeding the tube; style arms divergent at an angle between 45° and 90° at full anthesis, about 0.5 mm. long, glabrous or minutely pubescent, stigmatic on the adaxial faces. Central florets 2 or 3, structurally perfect but not ripening achenes, corolla about 17 mm. long, the tube above the incrassate base slender, 14 mm. long and 0.2 to 0.3 mm. in diameter, the limb 3 mm. long and 1 mm. in diameter, regularly 5-fid with lobes deltoid, 1 to 1.25 mm. long, 0.5 mm. wide at base; anthers about 2 mm. long, 1/2 to 2/3 exserted, minutely sagittate, the terminal portion non-polliniferous and

broadly flattened, 0.5 mm. long; style scarcely exerted; style arms brief, appressed, clavate, non-stigmatic, long-papillose over all the abaxial surfaces. Achene of pistillate floret fusiform to subcylindric, callose-annulate at base and apex, 6-7 mm. long, 1 mm. in diameter in the middle, 0.5 mm. in diameter at either end, about 12-ribbed, brown, glabrous or with a single row of short slender hairs down the middle of each groove. Achene of central floret flattened, 6 mm. long, 0.2 mm. in diameter in the middle, 0.5 mm. in diameter at either end. Pappus white, scarcely barbed, subequalling florets and phyllaries.

AUSTRALIA. NEW SOUTH WALES: Port Jackson, *Gaudichaud* 6 (P, holotype); Blue Mountains, *Fraser* (BM); between Blackheath and Katoomba, Dec. 1883, *Betche* 56 (MEL), *Betche* (P); Fitzroy Iron Mines, Sept., *L. Atkinson* 18 (MEL); Mt. Victoria, Nov. 1893, *Fletcher* (NSW); Dec. 1896, *Maiden* (NSW); Wingello, Nov. 1899, *Boorman* (NSW); Jenolan Caves, Dec. 1899, *Blakely* (NSW); Nethercote Rd., Eden, Dec. 1903, *Cheel* (NSW); Eskbank, Jan. 1915, *Hamilton* (NSW); Mt. Tomah, *Gregson* (NSW). VICTORIA: East Gippsland, spurs north of Mt. Drummer, Dec. 1937, *Hunter* (MEL); Bidwell, Feb. 1943, *Hunter* 9 (MEL); Genoa Peak, Jan. 1947, *Willis* (MEL). "Australia orient.", *Hugel* (W, very meagre specimen).

Richard interpreted the subligulate marginal floret of this species as indicating a transitional form between the discoid and radiate sections of *Senecio*. He accurately described the unusual style arms of the central florets but did not recognize their uniqueness. The achenes of his specimen unfortunately were quite immature and he did not note the abortive development of those of the central florets. Mature specimens, however, show the imperfect central florets, reduced number of florets, and erect style arms with pubescent outer faces which together characterize *Arrhenechthites*. I therefore transfer Richard's species to this genus, although this requires emending Mattfeld's diagnosis to admit pistillate florets subligulate and more numerous than the phyllaries. These are minor changes when the excellent agreement in other respects is noted.

Mr. J. H. Willis has very kindly written as follows on the ecology of *A. mixta*: "It is a perennial with fleshy rooting system and bright reddish purple coloration on the stems and undersides of the leaves, and it favors well-watered stony hillsides in montane forests, from about 1000 to 4000 feet altitude." Inclusion of this species in *Arrhenechthites* extends the range of this genus, formerly known only from the higher mountains of New Guinea, by some 27 degrees of latitude.

The holotype at Paris apparently has not always been recognized as such. An original label as *S. sonchoides* A. Rich. was only corrected by an annotation by Joret in 1949! I find no explanation for the earlier epithet. The specimen, although undoubtedly in much poorer condition now than when illustrated, is certainly the one from which the plate was prepared. The plate, however, fails to show that the phyllary margins are free to the base, even though in firm contact with one another in the lower half of the involucre. Also, the corolla lobe in the detail of the pistillate florets is shown as too short. Most of the capitula shown, and some of the leaves, are now gone, apparently clipped off and distributed to other herbaria.

Very probably the leaves and capitula of this species which were admixed with the fragments of *S. squarrosus* in the packet labeled *E. Richardiana* in the Prodr-omus Herbarium came from this specimen at Paris. De Candolle left no specimen identified as *E. mixta* in the Prodr-omus Herbarium, no. 15 under *Erechtites* being omitted. The diagnosis in the 'Prodr-omus' is taken entirely from Richard, except for the data on number of phyllaries and length of capitulum. These he must have derived from a study of Richard's plate, for it would seem that if he had recognized the fragments mixed in with *E. Richardiana* he would have separated them, as I did, and identified them in the proper sequence.

Bentham's description of *E. mixta* resembles that of de Candolle but is original, based on *Fraser*, Piper's Hill, New South Wales (K!). This specimen is *S. runcini-folius*, as discussed above in that connection. Black's description, drawn from Bentham's, is of the same.

3. ARRHENECHTHITES HAPLOGYNA (F. Muell.) Mattf. Engl. Bot. Jahrb. 69: 292. 1938.

Senecio haplogynus F. Muell. Trans. Roy. Soc. Victoria 1:14. 1889.

Erechtites haplogyna (F. Muell.) Mattf. Engl. Bot. Jahrb. 62: 422. 1929.

Peduncle glabrate, narrowly and sharply ridged. Bracteole linear-lanceolate, 2 mm. long, subtending capitulum immediately below receptacle. Capitulum 9 mm. long, technically ecalyculate, with sub-biseriate involucre of 8 phyllaries 6 mm. long, 0.7 to 1.2 mm. wide, with about 10 narrow and sharply ridged nerves, acute, minutely ciliolate. Marginal florets 8, almost 6 mm. long; corolla 0.7 mm. in diameter at inflated base, with tube 4 mm. long and gradually tapered and indurated in lower 3 mm., apically slightly expanded, irregularly and briefly 3- or 4-fid with one sinus much more deeply cleft than the others; style exerted, coarse; style arms about 0.3 mm. long, recurved, glabrous, blunt; achene (immature) 2.25 mm. long, about 0.4 mm. in diameter. Disc florets 8; corolla 6 mm. long, infundibuliform, with inflated base indurated and 0.7 mm. in diameter, tube 3.5 mm. long and abruptly reduced in diameter to 0.3 mm. and then gradually enlarged to throat diameter of 0.5 mm., regularly 5-lobed with lobes acute and multinerved, 2 mm. long and 0.5 mm. wide; anthers 5, polliniferous, 1.75 mm. long, with bases obtuse and apices long-appendaged and narrower; style subequalling corolla lobes, almost undivided, abruptly dilated at apex to about 0.5 mm. in diameter and marginally papillose, probably non-stigmatic; achene very slender, about 2.5 mm. long and 0.2 mm. wide, immature and probably abortive. Pappus slightly tawny, barbellate, equalling phyllaries, exceeded by central florets but not by marginal ones.

Known only from a single collection in the Owen Stanley Range of New Guinea. Summit of Mt. Knutsford, 1889, *McGregor*, holotype (MEL). Material examined: A single capitulum of the holotype.

The above description is based on an examination of this capitulum after moistening it with detergent solution, and is intended only to supplement Mueller's description.

This species is quite similar to *A. novoguineensis* (S. Moore) Mattf. Indeed, in transferring Mueller's species to *Erechtites* in 1929, Mattfeld stated that they might be identical. Later, in transferring them both to *Arrhenechthites*, he kept them separate on the basis of a difference in leaf size. I at first supposed that the species named by Moore might simply be based on a more luxuriant shade form of Mueller's plant, a supposition gaining some support from ecological data in the two reports. After comparing the florets from the two types, however, I believe that the following differences in floral characteristics reinforce the imperfectly known vegetative differences:

	<i>A. haplogyna</i>	<i>A. novoguineensis</i>
Central florets	8, with corolla lobes 2 mm. long, 0.4 mm. wide	2, with corolla lobes 1.5 mm. long, 0.35 mm. wide
Corolla tube of marginal florets	Rigidly incrassate, gradually tapering for about $\frac{3}{4}$ its length	Rigidly incrassate for about $\frac{1}{4}$ to $\frac{1}{3}$ its length and abruptly reduced in diameter
Achene	Apparently about 2.5 mm. long when mature	About 2 mm. long
Style-arm apex	Extremely short, almost undivided, and abruptly dilated	0.42 to 0.45 mm. long, little or not at all dilated

4. *ARRHENECHTHITES MASTIGOTHRIX* Mattf. Engl. Bot. Jahrb. 7: 477. 1940.

Known to me only from Mattfeld's description. Apparently collected only once so far. This is the only one of the species of this genus for which Mattfeld explicitly stated: "Typus in Herb. Berol."

Holotype: New Guinea, Saruwaged Mts., Masak river, am Wasser, 1800-2400 meters, 10 Nov. 1937, *Clemens 7509* (B, destroyed).

5. *ARRENECHTHITES NOVOGUINEENSIS* (S. Moore) Mattf. Engl. Bot. Jahrb. 69: 292. 1938.

Erechtites novoguineensis S. Moore, Trans. Linn. Soc. 9: 86. 1916.

Marginal florets pistillate, 8 to 10; corolla base inflated and indurated, abruptly softened and reduced in diameter, tube slender, obliquely truncate or irregularly briefly toothed. Central florets 2, with 5 corolla lobes 1.5 mm. long, 0.35 mm. wide; anthers polliniferous; style scarcely exerted, arms only 0.42 to 0.45 mm. long (rather than 1 mm., as given by Moore) and slenderly clavate, nonstigmatic, and papillose-hairy on the abaxial sides only.

Apparently known only from the type collection from northwestern New Guinea.

Holotype: New Guinea, Nassau Mountains, Carstensz Peak, 6551 to 7956 ft., 27 Jan. 1913, *Boden-Kloss* (BM!).

The holotype, and only, specimen is a small fragment, consisting of a short apical length of stem with two main leaves, their axillary (and flowering) bran-

ches, the large terminal corymb, and an additional large leaf (detached). It agrees well with the generic characterization as given by Mattfeld for *Arrhenechthites*, especially the structure of the capitulum, except for one minor detail. Whereas Mattfeld specified that the marginal florets should be of the same number as the phyllaries and opposite them, the marginal florets in this specimen number from 8 to 10 per capitulum, whereas the number of phyllaries is 8. As pointed out in the discussion of *A. mixta*, there is also in that species an excess number of marginal pistillate florets, for the accomodation of which I have slightly expanded the generic limits. It appears that Mattfeld did the same by implication when he included Moore's species in the new genus. The supplementary description given above deals only with the finer structure of the capitulum, which was inadequately treated by Moore.

6. *ARRHENECHTHITES DOLICHOCEPHALA* Mattf. Engl. Bot. Jahrb. 69: 289. 1938.

Known to me only by Mattfeld's description. Apparently not again collected.

Holotype: Northeast New Guinea, "Bezirk Morobe, Sarawaket, Busu Tamunac, an offenen Stellen," 2100 to 2400 m., 30 Jan. 1937, *Clemens* 5287 (B, destroyed).

SPECIES TO BE EXCLUDED FROM *ERECHTITES*

In addition to the Australasian species of *Erechtites* which I have placed in an erechthitoid group of *Senecio*, and the three species referred to *Arrhenechthites*, six other taxa have been described as *Erechtites* which do not belong to that genus. One is a *Blumea*. The other five belong in *Senecio*; one is erechthitoid, one is radiate, and three are discoid. These six are discussed here. In addition, a seventh name, a *nomen nudum*, is shown to be based most probably on still another discoid *Senecio*.

BLUMEA TENERA Merr. Philip. Jour. Sci. Bot. 7: 250. 1912.

Erechtites Bukaensis Rech. & Muschl. in Rech. Denkschr. Akad. Wiss. Wien 89: 620. 1914.

Rechinger 4043 (W!), syntype of *E. Bukaensis*, has a pluriseriate involucre, caudate anthers, and other features of the tribe Inuleae, genus *Blumea*. Among the Indonesian sheets of *Blumea* at Kew was an undetermined sheet from the Solomons and two sheets from the Philippines which agreed with the Rechinger specimen in fullest detail. The Philippine sheets included *Merrill* 7363, isotype of *Blumea tenera*, and agreed fully with the description. This species is now seen to have a wide, if spotty, distribution from Luzon to the Solomons. It appears to be a low-growing member of the rank-grass or "cogonal" association. Further search in such habitats should reveal additional stations.

PHILIPPINE ISLANDS. LUZON: Prov. Rizal, between La Loma and Maypajo, near Manila, Dec. 31, 1910, "in open grasslands a few meters above sea-level, not common", *Merrill* 7363 (K, isotype of *Blumea tenera* Merr.); Palawan, Taytay, May 1913, *Merrill* 9397 (K). NEW GUINEA: "am Ramm Fluss", Jan. 1902, *R. Schlechter* 13900 (K). SOLOMON IS.: Buka, "in Alang-Alang (*Imperata*)", Sept. 1905, *Rechinger* 4043 (W, syntype of *E. Bukaensis*); New Pomerania, Simpsonhafen, Sept. 1905, *Rechinger* 4205, 4267 (W, both det. as *E. prenanthoides* DC.).

Merrill also cited "*Merrill* 679 from Culion, and *For. Bur.* 5874 *Curran*, from Zambales Province, Luzon, both small forms", but I have not seen them. In addi-

tion, *Rechinger 4044*, from the same station as *Rechinger 4043*, the other syntype of *E. Bukaensis*, is most probably *B. tenera* also, but I have not seen the specimen, which is at Vienna.

SENECIO LEPTANTHUS Phil. Anales Univ. Chile 88:15. 1894; *emend.* Reiche, Fl. Chile 4: 225-226. 1905.

Erechtites leptantha (Phil.) Cabr. Not. Mus. La Plata 14 (Bot. No. 69): 75-78. fig. 1. 1949.

CHILE: Prov. Antofagasta, Taltal, Oct. 1925, *Werdermann 825* (K, 2); Desert of Atacama, 1890, *Morong 1292* (K).

I have not seen Philippi's type (*Geisse*, near Caldera). The specimens cited above, however, agree with his description except for the achenes, which are very densely clothed with short blunt white hairs, rather than glabrous. This is reconciled by Reiche: "Aquenios cortamente blanco-peludos (no peludos, como se dice en la diagnosis original.)" Cabrera also describes the achenes as "densa y cortamente papiloso-pubescentes".

In *Werdermann 825* the first row of marginal florets was filiform and pistillate, those of the second row functionally pistillate but with rudimentary stamens, and those of the third and subsequent rows perfect with functional stamens. *Morong 1292* had some florets in the outermost marginal row with rudimentary stamens and others without, while those in the second and subsequent rows were all functionally perfect. Of more importance, all of the specimens agreed as to style-arm apices. The tips of the style arms in the marginal florets were blunt, without dorsal protruding papillae. In the perfect florets the style-arm apices were sharply truncate with a half-crown of moderately enlarged but non-fused papillae fringing the apex (cf. Cabrera, fig. 1-H).

Cabrera transferred this species to *Erechtites* because of the pistillate filiform marginal florets. In view of the lack of the appendage of fused papillose hairs which characterizes *Erechtites*, I believe it better to return this species to *Senecio*. In structure and size of capitula it strikingly resembles erechthitoid species of *Senecio* in Australasia. This resemblance is reinforced by the unusual velutinous achene, quite like that of certain Australian species, which is so very different in shape, size, ribbing, color, and pubescence from the distinctive achene of the genus *Erechtites*.

SENECIO glossanthus (Sond.) Belcher, comb. nov.

Erechtites glossantha Sond. Linnaea 25:524. 1852.

Senecio brachyglossus F. Muell. *ex* Benth. and var. *major* Benth. Fl. Austral. 3:670. 1866; *excl.* var. *elatior* Benth. 1. c.; *non* *S. brachyglossus* Turcz. Bull. Soc. Nat. Mosc. 24II: 87. 1851.

Annual; stem erect, 20 cm. tall, sparingly branched above, glabrate, faintly striate, purplish below. Leaves 2 mm. broad at the base, alate, broader toward apex, bearing on either side one or more narrow lobes at an angle of from 45° to 60° and approximately 5 times as long as wide, their width being about one-half that of the rachis, the margins all minutely and irregularly callose-denticulate, glabrate or with occasional long coarse isolated hairs, especially along the nerves

beneath, lower leaves sessile and neither auriculate nor clasping. Upper leaves similar to the lower but more lobate and smaller, with base auriculate and semi-amplexicaul. Inflorescence compactly cymose, capitula rather few, peduncles short, primary floral bracts equaling or exceeding the branches. Involucre of 8 to 10 (to 12) phyllaries 4 to 6 mm. long, inconspicuously 2- to 4-nerved, with margins scarious and apex acute, sphacelate and minutely papillose; calyculus of 6 to 8 broadly lanceolate short bracteoles, 1.5 to 2 mm. long and 0.5 to 0.6 mm. wide, margins laciniate, apex sphacelate; peduncles long-haired in the axils. Marginal florets few, ligulate, pistillate, without rudimentary stamens; corolla tube slender, 2.5 to 2.75 mm. long, 0.25 mm. in diameter, 4-nerved; ligule up to 2 mm. long and 0.5 mm. wide, 2-nerved, lanceolate, apex acute, revolute; style arms ca. 1 mm. long, bluntly truncate or slightly rounded on apex, without encircling papillae, exerted. Disc florets perfect, about 25; corolla very slenderly infundibuliform, 4 mm. long, 0.4 mm. in diameter, minutely and regularly 5-fid, teeth about 0.3 mm. long; style arms about 1 mm. long, not exerted, apices slightly rounded, marginally papillose. Achene 2 to 2.5 mm. long, very densely clothed with appressed tawny hairs about 0.5 mm. long which completely conceal the slender achene and extend beyond its apex. Pappus white, capillary slightly exceeding phyllaries.

AUSTRALIA. S. AUSTRALIA: "ad litus sinus St. Vincent", *Mueller* (MEL, syntype); Mt. Lyndhurst, Sept. 1898, *Koch* 220 (K). VICTORIA: Aug. 1843, *Robertson* 468 (K); Melbourne, 1854, *Adamson* 342 (K); Point Nepean, *Mueller* (K, syntype of *S. brachyglossus* var. *major*). WESTERN AUSTRALIA: Swan River, *Drummond* 44 (K); *Drummond* 377 (K); Klondinin, Sept. 1932, *Young* (K).

This briefly ligulate and rather variable species bridges the gap between erechthitoid species with irregular corollas in the marginal florets and definitely ligulate eusenecionoid species. It was assigned to *Erechtites* section PLAGIOTOME by Sonder, despite his description, "ligulis stylum aequantibus vel superantibus." This might indicate that he also felt the vagueness of the boundary between *Senecio* and the Australian species assigned to *Erechtites*. Sonder described the capitulum as 3 lines long with about 12 phyllaries and 20 to 30 florets. Bentham described *S. brachyglossus* as having capitula 2 lines long with about 8 phyllaries and 16 to 18 florets, and then wrote: "var. (?) *major*. Flower-heads larger. Involucres about 3 lines long with about 12 bracts. Florets also more numerous." Thus var. *major* agrees exactly with Sonder's description of *E. glossantha*.

The syntype from St. Vincent's Gulf has phyllaries 6 mm. (3 lines) long, as stated by Sonder, but the number ranges from 8 to 10, usually 9, and never reaches 12. The other syntype collection by Mueller, cited by Sonder as "ad agros prope urbem Adelaide", may be the specimen cited by Bentham for his typical variety as "near Adelaide, *F. Mueller*". If so, it probably has 8 phyllaries 4 to 5 mm. long, as do the other specimens at Kew which Bentham determined as typical *S. brachyglossus*. The Pt. Nepean specimen, cited by Bentham for var. *major*, agrees exactly with the one from St. Vincent's Gulf except that it does have 12 phyllaries. *Drummond* 377, cited by Bentham for var. *major*, differs from both the above in having

only 8 phyllaries, much broader leaves, and the corolla merely obliquely truncated, but since the achene is characteristically pubescent I consider it a variant of *S. glossanthus*. The Wilson Promontory specimen is to be excluded from the species altogether, as it had a bifid ligule 2.5 mm. long, a glabrate achene with an oblique annulus, and leaves with broadly amplexicaul bases. Thus Bentham's var. *major* is based on a mixture of unrelated elements and should not be maintained.

I conclude that *Senecio glossanthus* is best interpreted as a variable species distinctively characterized by its unusually hairy achene. The variation of the phyllaries from 8 to 12 in number, and from 4 to 6 or 7 mm. in length, may be an edaphic response, which would make it unwise to make varietal distinctions without further information.

Bentham also published a var. *elatior*, based on a specimen from the Blue Mountains. The type specimen at Kew and isotypes sent from Melbourne and Sydney agree in having the ray florets with a trifid ligule only 1 mm. long, 10 to 12 phyllaries, and a leaf much larger and more dissected than that of *S. glossanthus*. In addition, their achenes are distinctively different in size, shape, and pubescence from those of *S. glossanthus*. Var. *elatior* is to be excluded from this species.

SENECIO GEORGIANUS DC. Prodr. 6: 371. 1838; *non* Greenm. Ann. Mo. Bot. Gard. 25: 803. 1938.

Erechtites candicans Hook. f. Lond. Jour. Bot. 6: 122. 1847.

Hooker did not specify a type in his description of *E. candicans*, stating merely: "Hab.? (*Gunn* in Herb. Hook.)". There is a sheet at Kew from Hooker's herbarium on which the right-hand specimen bears the following annotation: "Van D[ieman's] L[and], Gunn", "*Erechtites candicans* nob." (in Hooker's script), and "701. *Senecio Georgianus* DC.". I take this to be the holotype, and it agrees with the description given by Hooker. Dissection of a capitulum at the bud stage showed it to have marginal florets 5-fid with polliniferous stamens; that is, it is a discoid rather than an erectitoid *Senecio*. Comparison of this specimen with both the isotype (K!) and the holotype (G!) of *S. georgianus* DC. shows them to be conspecific, as later concluded by Hooker and as given in the 'Index Kewensis'.

Senecio georgianus Greenm. was published as a new name for *S. Hallii* Hieron., 1895, *non* Britton, 1889. Apparently Greenman overlooked the anterior Candollean name. Britton's plant was from Wyoming, Hieronymus' from South America. As far as I am aware, the latter still requires re-naming, but that I leave to students of *Senecio* of South America, if indeed they have not already done so.

SENECIO POLYPODIOIDES (Greene) Greene *ex* Greenm. Monogr. Senecio, T. 1: 25. 1901; Engl. Bot. Jahrb. 32: 21. 1902.

Senecio polypodioides Greene, Pittonia 3: 90. 1896, *nom. prov.*

Erechtites polypodioides Greene, Pittonia 3: 90. 1896, *nom. nov.* for *S. gracilipes* Robins. & Greenm.

Senecio gracilipes Robins. & Greenm. Amer. Jour. Sci. 50: 156. 1895; *non* A. Gray, Proc. Amer. Acad. 5: 142. 1862

Senecio polypodioides Robins. & Greenm. *ex* Jacks. Ind. Kew. Suppl. 1:393. 1906, error.

The isotype at Kew has functional stamens in all florets and belongs in *Senecio*, section MULGEDIFOLII, where Greenman finally placed it.

Type: Mexico, State of Oaxaca, Sierra de Clavellinas, 9000 ft., 24 Oct. 1894, Pringle 6010 (GH; K!).

SENECIO RUNCINATUS Less. *Linnaea* 6: 410. 1831.

Erechtites ? *runcinata* (Less.) DC. *Prodr.* 6: 295. 1838.

This species has uniformly homogamous capitula. Not one filiform pistillate floret was found among several hundred florets which I examined from scores of heads from many different specimens (K, BM, P, G, W, MICH). The style-arm apices are truncated, with a lateral whorl of stubby pollen-presentation papillae but with no terminal tuft of fused hairs such as characterizes the genus *Erechtites in sensu strictiore*. This species is, in fact, a discoid *Senecio*, section MULGEDIFOLII. Its delimitation and synonymy will be treated in a separate publication.

Type: Mexico, Vera Cruz, "Malpays de la Joya, Novbr.", Schiede & Deppe (B, destroyed).

ERECHTITES ELONGATA A. Gray ex Jacks. *Ind. Kew.* 2: 860. 1893, *nomen nudum*; DC. *Prodr.* 6: 294, 1838, *nomen nudum*.

As pointed out in the discussion of *Erechtites*, this "*E. elongata*", in the light of Rafinesque's letter to de Candolle, refers most probably to *Senecio elongatus* Pursh, *Fl. Am. Sept.* 2: 529. 1814. This was treated by Torrey and Gray as a discoid form of *S. aureus* var. *obovatus* Torr. & Gray, and now appears in 'Gray's manual' (8th ed.) as *S. obovatus* forma *elongatus* (Pursh) Fern. It is as unrelated as possible to *E. hieracifolia*.

At least four other names have been published in *Erechtites* as *nomina nuda*. These are: *E. senecioides* Turcz. (*Bull. Soc. Nat. Mosc.* 24: 201. 1851), probably an error for *E. sonchoides*, as explained on page 48; *E. macroglossa* Muell. (*Rept. Gov't. Bot.* 1853, p. 15. 1853), entirely unidentified; and *E. pauciflora* and *E. uniflora* Raf. (*Herb. Raf.* 68. 1833), both of which most probably were applied to depauperate forms of typical *E. hieracifolia*.

INDEX TO SCIENTIFIC NAMES

Previously published valid names are in ordinary type; new names and the final members of new combinations are in bold face type; synonyms are in *italics*.

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<i>tomentella</i>	74, 75	<i>hieracifolia</i>	19
<i>Blumea tenera</i>	79	sect. <i>Hieraciifoliae</i>	11, 15
<i>Cacalia prenanthoides</i>	30	<i>hispidula</i>	48, 66, 69
<i>Crassocephalum valerianaefolium</i>	26	<i>ignobilis</i>	36
<i>Erechtites</i>	10	<i>incana</i>	57
<i>agrestis</i>	20	<i>Labillardieri</i>	46
<i>ambigua</i>	31	<i>lacerata</i>	51
<i>angusta</i>	61	<i>leptantha</i>	80
<i>apargiaefolia</i>	71	<i>macroglossa</i>	83
<i>arguta</i>	51, 61, 66	<i>megalocarpa</i>	18
var. <i>a</i>	64, 70	<i>minima</i>	46
var. <i>asper</i>	64, 70	<i>missionum</i>	32
var. <i>dissecta</i>	69	<i>missionum</i>	34
var. <i>glabrata</i>	64, 70	var. <i>lanceolata</i>	32, 34
var. <i>microcephala</i>	64	<i>mixta</i>	54, 75
var. <i>obovata</i>	64	<i>Muelleri</i>	71
var. <i>e</i>	64, 70	<i>novoguineensis</i>	78
<i>Atkinsoniae</i>	41	<i>organensis</i>	29
<i>Bathurstiana</i>	69	<i>pauciflora</i>	83
<i>Bukaensis</i>	79	<i>papuana</i>	53
<i>cacalioides</i>	19	<i>petiolata</i>	31
<i>candicans</i>	82	<i>picridioides</i>	48, 54
<i>carduifolia</i>	19	<i>polypodioides</i>	82
var. <i>latifolia</i>	20	<i>praealta</i>	2
<i>diversifolia</i>	56	<i>prealta</i>	10, 14
<i>elongata</i>	83	<i>prenanthoides</i>	31, 43, 46
<i>erechthitoides</i>	53	var. <i>minor</i>	55
<i>erecta</i>	57, 59	var. <i>picridioides</i>	48
<i>Gardneriana</i>	26	<i>pumila</i>	46, 69
<i>glabrescens</i>	55, 57	<i>pyrophila</i>	49
<i>glandulosa</i>	57	<i>quadridentata</i>	49, 57
<i>glomerata</i>	61	var. <i>glabrescens</i>	57
var. <i>polycephala</i>	61	var. <i>Gunnii</i>	60
var. <i>subincisa</i>	61	<i>Richardiana</i>	48
<i>glossantha</i>	80	<i>runcinata</i>	83
sect. <i>Goyazenses</i>	11, 15, 34	<i>scaberula</i>	69
<i>goyazensis</i>	11, 34	<i>senecioides</i>	83
<i>Gunnii</i>	60	Senecioneae	7
<i>haplogyna</i>	77	Senecioninae	7, 8
<i>hieracifolia</i>	11, 12	<i>sonchoides</i>	43
var. <i>cacalioides</i>	19	<i>sulcata</i>	19
var. <i>cacalioides</i>	19	<i>tenuiflora</i>	71
f. <i>pubescens</i>	19	<i>uniflora</i>	83
var. <i>carduifolia</i>	19	<i>valerianaefolia</i>	25

f. <i>organensis</i>	29	<i>beterophylla</i>	46
var. <i>organensis</i>	29	<i>hieracifolius</i>	13, 19, 46
f. <i>prenanthoides</i>	30	var. <i>gigantea</i>	14
f. <i>reducta</i>	30	<i>hispidulus</i>	65
f. <i>valerianaefolia</i>	26	var. <i>dissectus</i>	69
<i>Erechtites</i>	10	var. <i>hispidulus</i>	66
<i>Gynura</i>		var. <i>scaberulus</i>	69
<i>aspera</i>	20	<i>hispidulus</i>	66, 69
<i>malasica</i>	20	<i>hispidulus</i> × <i>quadridentatus</i>	71
<i>papuana</i>	53	<i>ignobilis</i>	36
<i>rosea</i>	26	<i>kermadecensis</i>	45
<i>zeylanica</i> var. <i>malasica</i>	20	<i>laceratus</i>	51
<i>Neoceis</i>	10	<i>lactuoides</i>	31
<i>carduifolia</i>	19	<i>laticostatus</i>	64
<i>hieracifolia</i>	14	<i>leptanthus</i>	80
<i>microcephala</i>	61	<i>Lessoni</i>	61
<i>rigidula</i>	14	<i>Lessonianus</i>	61
<i>tomentosa</i>	57	<i>microcephalus</i>	64
<i>Ptileris</i>	10	<i>minimus</i>	46
<i>hieracifolia</i>	14	var. <i>minimus</i>	46
<i>Senecio</i>	3, 37	var. <i>picridioides</i>	48
<i>albiflorus</i>	31	<i>mixtus</i>	75
<i>apargiaefolius</i>	71	<i>Mülleri</i>	46
<i>argutus</i>	61	<i>multicaulis</i>	68
<i>Atkinsoniae</i>	41	<i>papuana</i>	53
<i>Bathurstianus</i>	69	<i>plebeius</i>	61
<i>bipinnatisectus</i>	41	<i>polypodioides</i>	82
<i>biserratus</i>	43	<i>polypodioides</i>	82
<i>brachyglossus</i>	80	<i>prenanthoides</i>	57
var. <i>elatior</i>	80	<i>pumilus</i>	46, 68
var. <i>major</i>	80	<i>pusillus</i>	70
<i>cacalioides</i>	19	<i>pyrophilus</i>	49
<i>carduifolius</i>	19	<i>quadridentatus</i>	57
<i>Decaisnei</i>	3	<i>runcinatus</i>	83
<i>diversifolius</i>	56	<i>runcinifolius</i>	48, 54
<i>dunedinensis</i>	56	<i>seminudus</i>	14
<i>elongatus</i>	5, 83	<i>sonchoides</i>	14
<i>erechthitoides</i>	53	<i>squarrosus</i>	48
<i>Fischeri</i>	19	<i>tenuiflorus</i>	71
<i>flaccidus</i>	43	<i>valerianaefolius</i>	25, 26
<i>georgianus</i>	82	<i>Vukotinovici</i>	14
<i>glabrescens</i>	57	<i>wairauensis</i>	55
<i>glandulosus</i>	57	<i>Warscewiczii</i>	46
<i>glomeratus</i>	61	<i>Senecio</i>	10
<i>glomeratus</i>	61	<i>Sonchus</i>	
<i>glomeratus</i> × <i>hispidulus</i>	64, 70	<i>agrestis</i>	19
<i>glossanthus</i>	80	<i>brasiliensis</i>	19
<i>Goyazensis</i>	34	<i>erythropappus</i>	26
<i>gracilipes</i>	82	<i>laevis</i>	13
<i>gunnii</i>	60	<i>occidentalis</i>	19
<i>haplogynus</i>	77		

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No. 2

THE AUSTRALIAN AND NEW ZEALAND SPECIES OF *PITTOSPORUM**

ROBERT C. COOPER**

Many of the Australian and New Zealand species of *Pittosporum* have long been treasured in gardens of Australia, New Zealand, France, and England, for their flowers, foliage and sweet scent, and several are common hedge plants and ornamentals in California and Florida. In addition to an aesthetic appeal, the species have scientific interest and potential economic value.

The most recent inclusive treatment of *Pittosporum* is in the treatment of the family Pittosporaceae by Pritzel,¹ who found it was impossible to make a satisfactory arrangement or classification of the genus and relied upon the geographic distribution of the species. He wrote as follows:

Etwa 160 Arten in den Tropen und Subtropen der östlichen Hemisphäre von West-Afrika bis zu den Inseln des Pazifik. Da eine befriedigende natürliche Gliederung der Gattung noch nicht gegeben werden kann, so bleibt nichts anderes übrig, als sie nach ihrer Verbreitung zu behandeln. Ein künftiges System der Gattung wird sich vor allem auf die Frucht zu gründen haben, und diese ist bei vielen Arten noch nicht genügend bekannt.

He discussed and keyed the species separately of the following regions:

Malaysia	Australia	Other Polynesian Islands	China and Japan
Philippine Islands	Solomon Islands and Bismarck	New Zealand	Africa
New Guinea	Archipel.	Hawaiian Islands	Macronesia
New Caledonia	Fiji and Tonga Islands	India	Madagascar Terr.

The species of New Caledonia were treated by Guillaumin² in 1940, and a key to them was published in 1948³. The Hawaiian species were revised by Sherff⁴ in

¹ Pritzel, E. In Engler & Prantl's, Nat. Pflanzenfam. ed. 2. 18a:273-281. 1930.

² Bull. Soc. Bot. Fr. 87:333. 1940.

³ Fl. Analyt. et Synopt. Nouv. Calédonie. Phanérogames. pp. 134-136. 1948.

⁴ Field Mus. Nat. Hist. Bot. Ser. 22:467. 1942.

*An investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University, and submitted as a thesis in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

** Botanist, Auckland Institute and Museum, Auckland, New Zealand.

Issued July 19, 1956

1942. A preliminary account of the African species by Cufodontis⁵ appeared in 1951, and a fuller revision⁶ in 1952. A study of the East Asian species by Gowda⁷ was published in 1951, and a criticism of this work by Li⁸, in connection with the Formosan species, followed in 1953. The species of the Malayan Archipelago will be revised by one of the authors of 'Flora Malesiana'⁹, and those of the Central Pacific Islands will be dealt with in A. C. Smith's "Studies of Pacific Plants"¹⁰. The species which occur in Australia and New Zealand are revised in this study, and an attempt is made to reconcile some of the divergent views of other workers.

HISTORY OF THE GENUS

William Dampier, navigator and sometime buccaneer, was the first European to collect a specimen of *Pittosporum* in the Australasian region. Between August 6 and September 2, 1699, he cruised along the northwest Australian coast in H.M.S. Roebuck, from Shark's Bay northward to 18° 21' S. latitude. The few specimens of plants he collected at Shark's Bay went to Dr. William Sherard and are preserved in the Sherardian Herbarium at Oxford, England. They were described by John Ray assisted by Sherard,¹¹ and Plukenet.¹² Among them was the species we now know as *Pittosporum phillyraeoides* DC. Linnaeus did not list the plant in his 'Species Plantarum' (1753) and although Robert Brown examined the Shark's Bay collection subsequent workers did not mention it.

The type specimens of the type species of the genus *Pittosporum* were collected by Banks and Solander, who accompanied Cook as naturalists on his first voyage of discovery. Between October 1769 and February of 1770 they collected four species in New Zealand, and in May and June of 1770 they obtained another species at Palm Island and Bustard Bay on the coast of Queensland, Australia. During the voyage Solander had written descriptions of the plants collected which were revised and systematically arranged prior to his death in 1782. Banks had prepared excellent plates to accompany his manuscript, but publication was delayed and finally abandoned. In 1788 Gaertner¹³ published the description of *Pittosporum* from the manuscript prepared by Solander, and described and illustrated the fruits and seeds of two species made available to him by Banks¹⁴.

The subsequent history of the collection of new species in Australia and New Zealand, like the history of botanical discovery in these regions, may be divided

⁵ Österr. Bot. Zeitschr. 98:105. 1951.

⁶ Fedde's Rep. Sp. Nov. 55¹:27. 1952.

⁷ Jour. Arnold Arb. 32:263. 1951.

⁸ Jour. Wash. Acad. Sci. 43:43. 1953.

⁹ Personal communication from Dr. C. G. G. J. Van Steenis, general editor of "Flora Malesiana".

¹⁰ Personal communication.

¹¹ Hist. Pl. Vol. 3, and Appendix. 1704.

¹² Almath. Bot. 1705.

¹³ Fruct. et Sem. Pl. 1:286. t. 59. 1788.

¹⁴ The five species collected by Banks and Solander were: *Pittosporum tenuifolium* Gaertn., *P. umbellatum* Gaertn., *P. ralphii* Kirk, *P. cornifolium* A. Cunn., all from New Zealand, and *P. ferrugineum* Ait. from Australia.

into two periods: 1, the period of investigations by travellers or naturalists attached to voyages of discovery or survey; 2, the period of investigation by resident botanists. Dampier, Cook, d'Urville, Wilkes, Robert Brown, and J. D. Hooker are a few of the distinguished men who visited Australia and New Zealand during the first period. The second period followed when systematic white settlement of the two countries began. Bentham¹⁵, F. M. Bailey¹⁶, Maiden¹⁷, Lee¹⁸ and Willis¹⁹ have dealt adequately with the Australian collectors of both periods, and J. D. Hooker²⁰, Cheeseman²¹ and Cockayne²² have given full accounts of the New Zealand botanists.

The descriptions of species of *Pittosporum* from Australia and New Zealand are scattered widely in the extensive literature on the floras of these regions, but have been brought together from time to time by European and local workers. In 1839 Putterlick²³ recognised thirty-six species of which twelve were recorded from Australia and seven from New Zealand. Bentham²⁴, whose study was based on the extensive Australian collections of Robert Brown, Preiss, Sieber, Allan Cunningham, Ferdinand Mueller and others recognized nine species. J. D. Hooker²⁵ revised the New Zealand species in 1853 and again in 1864 and recognized thirteen species. His study was based on the extensive collections of Colenso, Sinclair, Dieffenbach, Buchanan, Bidwill, Richard and Allan Cunningham, Hector, Lyall, Travers, and others.

Hooker was far from satisfied regarding the status of several of the species, and wrote²⁶: "I have restored the var. *reflexum* of Fl. N.Z. as a different species, but with some doubt: better specimens are wanted of both"; and again²⁷, "It is with great reluctance that I add another *Pittosporum* to the series, already very difficult of discrimination, that consists of *tenuifolium*, *colensoi* and *fasciculatum*."

Kirk²⁸ published a revision of the New Zealand species in 1872, based on his own extensive collections and field observations. He did not have access to the early literature on the genus, or to the important collections at the Royal Botanic Gardens, Kew, but in spite of these handicaps he made a very valuable contribution

¹⁵ Fl. Austr. 1: pref. 1863.

¹⁶ Proc. Roy. Soc. Queensland 8:xvii, xlv. 1891.

¹⁷ Jour. & Proc. Roy. Soc. N.S.W. 42:60. 1908. 1st. Suppl. Rept. Austr. Assoc. Adv. Sci. 13: 224. 1912. 2nd Suppl. Jour. & Proc. Roy. Soc. N.S.W. 55: 150. 1921.

¹⁸ Early explorers in Australia. 1925.

¹⁹ Vict. Nat. 66^{5,6,7}. 1949.

²⁰ Handb. N.Z. Fl. Pref. 1864-1867.

²¹ Man. N.Z. Fl. p.xi. 1906: ed. 2. p.xv. 1925.

²² Vegetation of New Zealand. In Die Vegetation der Erde 14:8. ed. 2. 1928.

²³ Syn. Pittosp. pp. 5-18. 1839.

²⁴ Fl. Austr. 1: 109. 1863.

²⁵ Fl. Nov. Zel. 1: 21. 1853; Handb. N.Z. Fl. p.18. 1864, and p. 725. 1867.

²⁶ *loc. cit.* p.21. 1864.

²⁷ *loc. cit.* p.725. 1867.

²⁸ N.Z. Inst. Trans. & Proc. 4:260. 1872.

to our knowledge of the New Zealand species. Cheeseman²⁹, who worked under similar difficulties, recognized nineteen species in 1906 and twenty-three in 1925, but expressed doubts regarding the status of many of these entities.

The most recent study which is of importance to us is that of the small-leaved species of *Pittosporum* in New Zealand, published by Laing and Gourlay³⁰ in 1935. This was based on extensive field observations and a considerable number of specimens cultivated in the authors' gardens, and includes complete descriptions of seedling and juvenile stages. They observed the similarity of one of the small-leaved New Zealand species of *Pittosporum* to the Australian species of *Bursaria* but left the question of nomenclature changes to future workers. Pax³¹ treated the genus as a whole for the 'Die Natürlichen Pflanzenfamilien' in 1891 and recognised the species described by Bentham for Australia and by J. D. Hooker and Kirk for New Zealand. Similarly, Pritzel³², in the second edition of 'Die Natürlichen Pflanzenfamilien', adopted the Australian species from Bentham and subsequent authors, and the New Zealand species from Cheeseman, with little change.

ECONOMIC USES

From the wealth of observation published on the uses of different species of *Pittosporum* two generalizations can be made: (1) that certain medicinal and poisonous properties are common throughout the range of the genus; (2) that these properties were known to several primitive races of people who lived in communities which were widely separated, if not completely isolated.

The Australian aborigines soaked the seeds and pulp of the fruit of *P. phillyraeoides* in water and used the bitter infusion internally for pains and sprains³³. The Filipinos used a decoction of the leaves of *P. pentandrum* as an aromatic bath after childbirth, and the powdered bark of the same tree as a febrifuge and for bronchitis. They also used the fruits of *P. resiniferum* as a universal medicine³⁴. The Malaysians applied the leaves and roots of *P. ferrugineum* as poultices in the treatment of malaria³⁵, and some South African natives employed the bark of *P. viridiflorum*³⁶ as a febrifuge and as a bitter emetic. Again, on Réunion Island the natives used the bark and leaves of *P. senacia* in medicine³⁷.

The Malaysians macerated the leaves and fruit of *P. ferrugineum* for fish poison³⁸, and the Javanese treated *P. ferrugineum* and *P. javanicum* for the same

²⁹ Man. N.Z. Fl. pp. 51, and 1134. 1906; ed. 2, p. 486. 1925.

³⁰ Trans. Roy. Soc. N.Z. 65:44. 1935.

³¹ Engler & Prantl, Nat. Pflanzenfam. 3 (2a):106. 1891.

³² *loc. cit.* ed. 2. 18a:265. 1930.

³³ Maiden, For. Fl. N.S.W. 3¹:161. 1908.

³⁴ Valenzuela, Concha and Santos. Jour. Philipp. Pharm. Assoc. 34:34. 1947.

³⁵ Burkill, Dict. Econ. Prod. Malay Penin. 2:1763. 1935.

³⁶ Githens, Drug Pl. Afr. p.100. 1949.

³⁷ Niederlein, Resources Veg. des Colon. Franc. p.55. 1902.

³⁸ Burkill, *loc. cit.* 1935.

purpose³⁹. The Fijians used the fruits of *P. arborescens*, *P. brackenridgei*, and *P. rhytidocarpum* as a fish poison, the fruits of *P. rhytidocarpum* as a dye, the leaves of *P. arborescens* as a remedy for stomach troubles, and the bark and leaves of *P. arborescens* and *P. brackenridgei* for witchcraft. A cherished sheet of *P. arborescens* in the herbarium of the Department of Agriculture, Suva, Fiji, is from a plant which was "Exhibit A" at the trial of a poisoner charged with ritual murder.

It is possible that these medicinal and poisonous properties will be of economic value in the future. For example, the bitter properties of *P. phillyraeoides* (Australia) and *P. viridiflorum* (South Africa) have been mentioned. Since the dawn of history all sorts of virtues have been ascribed to bitter or "strong" medicine, but bitters still have a place in medicine as general tonics, in the control of diarrhoea, and in wound dressings.

The presence of saponins has been reported by a number of workers. Klein⁴⁰ states that the following species contain the saponin "pittosporin" of unknown formula. He gives no reference, but the information is probably taken from Greshoff⁴¹.

REGION	SPECIES	MATERIAL TESTED
Sino-Japanese Region	<i>Pittosporum tobira</i>	Leaves
Madeira-Teneriffe	<i>Pittosporum coriaceum</i> <i>Pittosporum densiflorum</i>	Leaves and bark Leaves
Malayan Archipelago	<i>Pittosporum javanicum</i>	Bark
South Africa	<i>Pittosporum floribundum</i> <i>Pittosporum viridiflorum</i>	Bark Bark
Australia	<i>Pittosporum erioloma</i> <i>Pittosporum phillyraeoides</i> <i>Pittosporum rhombifolium</i> <i>Pittosporum undulatum</i>	Leaves Fruit Leaves Leaves and bark
New Zealand	<i>Pittosporum cornifolium</i> <i>Pittosporum crassifolium</i> <i>Pittosporum eugenioides</i> <i>Pittosporum buttonianum</i>	Leaves Leaves Leaves Leaves

³⁹ Hayne, Nutt. Plant. Ned. Ind. p. 688. 1927.

⁴⁰ Handbuch der Pflanzenanalyse. 3²:1135. 1932.

⁴¹ Kew Bull. p. 414. 1909.

The presence of saponins probably accounts for most of the medicinal and poisonous properties of the species. Githens⁴² says:

The saponins constitute a very large and diverse group of glucosides which have the property of causing foaming when added to water. [*P. coriaceum* and *P. viridiflorum* are known as soap substitutes in their native countries.] They find an extensive use in shampoos, toothpastes and similar cosmetic preparations. Some have no marked action on the body, but many of them induce nausea or vomiting. This is accompanied by increased secretion in the respiratory passages and a greater fluidity of the mucus, leading to loosening of coughs or expectorant action. The nausea is often accompanied by sweating leading to lowering of febrile temperature. Saponins are therefore used as emetics, expectorants and febrifuges. Many saponins act on the gills of fish and interfere with respiration and are therefore used as fish poisons. A few saponins are locally irritant and act as purgatives . . . some (sapotoxins) cause death.

Saponins have been found suitable for insecticides, but neither the Department of Insecticides at Rothamstead Experimental Station, England, nor the Section for Insecticide Investigations at the U. S. Department of Agriculture Research Station, Beltsville, Md., has examined any species of *Pittosporum*. The only information I have on their insecticidal properties is to be found in "A Survey of Plants for Insecticidal Activity" by Heal and others⁴³. These workers found that aqueous extracts of the branches, leaves, and roots of *P. senacia* were toxic to American cockroaches when injected into the bloodstream, but were inactive against German cockroaches and milkweed bugs. Alcohol and petroleum ether extracts of *P. senacia* branches leaves were toxic to black carpet beetles, but non-toxic to other insects tested. An extract of *P. viridiflorum* bark was non-toxic to all insects tested. *Pittosporum ferrugineum* of Malaya and Australia, and *P. arborescens*, *P. brackenridgei* and *P. rhytidocarpum* of Fiji appear, from their record as fish poisons, to be more promising than the species tested.

The essential oils of several species have been examined and described, and the papers are listed:

Malayan Archipel.....	{	<i>Pittosporum monticolum</i>	A. J. Altee. in Pharm. Weekblad, 74:666. 1937
		<i>Pittosporum resiniferum</i>	I. Garcia-Reyes, in Rev. Filip. Med. Farm. 28:448. 1937.
Australia.....		<i>Pittosporum undulatum</i>	J. W. Cornworth & J. C. Earl, in Jour. Roy. Soc. N.S.W. 72:249. 1939.
New Zealand.....	{	<i>Pittosporum eugenioides</i>	C. L. Carter & W. V. Heazlewood, in Jour. Soc. Chem. Ind. 68: 34. 1949.
		<i>Pittosporum tenuifolium</i>	A. J. Calder & C. L. Carter, loc. cit. 68:355. 1949.

⁴² Githens, loc. cit. 1949.

⁴³ Lloydia 13:89. 1950.

Essential oils⁴⁴ usually are the source of scent in flowers, and have many uses as flavors and condiments in food. Frequently they have the property of checking bacterial growth and are used for food preservatives, and even as wound dressings. They are also valuable in medicine to regulate intestinal movements and for respiratory, kidney and urinary infections. In 1889 Maiden⁴⁵ recommended the cultivation of *P. undulatum* on a commercial scale for its essential oil, but his suggestion has never been followed, and the possibilities of this and other species remain unexplored.

The gum-resins of *P. bicolor*, *P. rhombifolium* and *P. undulatum* of Australia and of *P. eugenioides* and *P. tenuifolium* of New Zealand have been described by Maiden⁴⁶, who suggested that they might be found useful in medicine.

The woods of the Australian species have been described by Mueller⁴⁷, Bailey⁴⁸ and Maiden⁴⁹, and the woods of the New Zealand species have been dealt with by Kirk⁵⁰ and others. They are not available in sufficient size or quantity for commercial use but are much esteemed for special purposes. The wood of *P. undulatum* is preferred by some to any other timber for golf sticks⁵¹. The wood of *P. bicolor*, which was once used for clubs or "waddies" by the aborigines of Tasmania, is now much esteemed for axe handles and billiard cues⁵². The replacement of "waddies" by billiard cues will be deplored by all lovers of the truncheon and shillelagh.

Pittosporum has made a small but valuable contribution to horticulture. The cultivation of species of *Pittosporum* began when *P. coriaceum* was brought to England from Madeira in 1787 and introduced into gardens by James Webster; *P. undulatum* was introduced into England from Australia by Sir Joseph Banks about two years later; and *P. tobira* was sent to Kew from Canton, China, in 1804. Splendid living collections are maintained today at the Royal Botanic Gardens, Kew, the Villa Thuret, in southern France, and Golden Gate Park, San Francisco, California. Many Australian and New Zealand species are represented in these collections and are grown in the surrounding districts as street trees, garden ornamentals, hedge plants, and shelter trees. The Australian *P. undulatum* is probably the most widely cultivated and has been reported in gardens in Ceylon, Italy, the Azores, France, England, the United States (Florida and California), Bermuda, Hawaii, India, China, New Zealand and, of course, Australia. In the Azores it was introduced as a shelter tree for the orange groves and is now naturalized. In Bermuda and Hawaii it has also become naturalized and is an attractive addition to the local flora.

⁴⁴ Finnemore, H. The essential oils. pp. 347-349. 1926.

⁴⁵ Useful Nat. Pl. Austr. p.292. 1889.

⁴⁶ Proc. Austr. Assoc. Adv. Sci. 4:289. 1893.

⁴⁷ Select Extra-Trop. Pl. p.258. 1881.

⁴⁸ Queensland Woods. p.11. 1888.

⁴⁹ Useful Nat. Pl. Austr. p.588. 1889.

⁵⁰ N.Z. Inst. Trans. & Proc. 4:260. 1872.

⁵¹ Maiden, For. Fl. N.S.W. 7:129. 1920.

⁵² Maiden, For. Fl. N.S.W. 8:47. 1923.

The widespread use of the Australian and New Zealand species in horticulture has been accompanied by the usual nomenclatural problems. Horticulturists have created, and persist in using, several specific epithets which have been ignored or reduced to synonymy by taxonomists concerned only with the "wild forms". I have attempted to solve the nomenclatural problems by citing published horticultural names in the synonymy of the species concerned and in the discussion following the description.

TAXONOMIC CRITERIA

The principal criteria for the classification of the Australian and New Zealand species of *Pittosporum* are based on comparative morphology and geographic distribution. The chromosome number of only one species, the Chinese *P. tobira* ($2n = 24$), is known⁵³, and the embryology of the genus has not been investigated⁵⁴. The anatomy of thirty-six species of *Pittosporum*, and a representative of each of the allied genera, *Hymenosporum*, *Bursaria*, *Sollya*, and *Citriobatus*, has been examined by Guenot, who commented:⁵⁵ "La structure anatomique du genre *Pittosporum* s'est montrée dans les espèces que nous avons examinées d'une constance remarquable."

Gowda⁵⁶ examined the pollen of twenty-six species of *Pittosporum* and a representative of each of the other genera in the family, and found that they varied in size but did not show any marked difference in form and sculpture. Lucy Watson-Smith⁵⁷ has informed me that the New Zealand species vary in size and thickness of the exine but generally are very much alike. In the preceding chapter on economic uses I mentioned that certain chemical properties of the genus are remarkably constant.

A study of living and herbarium specimens has convinced me that *Pittosporum* is an assemblage of very homogeneous forms and that many of its morphological characters are constant throughout its range from Hawaii to South Africa. All the evidence suggests that it is a tropical and subtropical genus which is most specialized and reduced at the extreme limits of its distribution, especially at the southern boundaries in Australia and New Zealand.

MORPHOLOGY

SHOOT SYSTEM:

The Australian and New Zealand species are evergreen trees and shrubs with verticillate and simple branching. Gowda⁵⁸ described the behaviour of the leading shoot as follows:

⁵³ Darlington, C. D. and Janaki Ammal, E. K. Chromosome atlas of cultivated plants. p. 112. 1945.

⁵⁴ Johansen, D. A. Plant embryology. p. 174. 1950

⁵⁵ Guenot, J. F. Contribution à l'étude anatomique des Pittosporacées. Doct. Diss. Univ. Paris. Ser. A. No. 523, p.52. 1906.

⁵⁶ Jour. Arnold Arb. 32:277. 1951.

⁵⁷ Personal communication.

⁵⁸ *loc. cit.* p. 265. 1951.

1. Vegetative in the first year.
 - a. Producing terminal leafy inflorescences in the second year and also a new leading vegetative shoot or shoots from the lower axils; or
 - b. Producing leafless pseudoterminal inflorescences the second year from the buds congested at the apex, and also a new leading vegetative shoot or shoots.
2. Vegetative and terminating in an inflorescence the first year, and the second year producing a new leading vegetative shoot or shoots from its lower axils.

A plant of the Australian *P. undulatum* was observed in the Linnaean house of the Missouri Botanical Garden from February 1952 until April 1953. In February inflorescences developed in a terminal position on leading shoots. During April and May buds appeared in the axils of the leaves beneath the inflorescences, and some of these developed rapidly and assumed a leading position while others developed more slowly and formed a whorl of lateral branches. Similar behaviour was observed in the Chinese *P. tobira* and on both plants two phases of growth, reproductive and vegetative, were accomplished in the growing season.

The plants bore female flowers which were not fertilized, and the dead flowers were forced to one side and shed when an axillary shoot assumed a leading position. On several branches of both plants one or two axillary vegetative shoots developed at the same time as, and immediately below, the terminal inflorescences. In several instances one of these vegetative shoots immediately assumed a leading position and the inflorescence was left behind in a lateral position. On other branchlets the vegetative shoots formed an irregular whorl and the inflorescence was left behind in a terminal position.

An examination of herbarium material of *P. undulatum* showed that the vegetative buds remain dormant in the axils of the subtending leaves when fruit develop and the cluster of fruit persists for some time as a terminal structure. Herbarium material of *P. umbellatum*, *P. tenuifolium*, *P. crassifolium*, *P. cornifolium*, and *P. dallii* showed that where a terminal inflorescence developed fruit, the fruit stalks were occasionally forced to one side by the leading shoot and persisted in a lateral position.

Agnes Arber⁵⁹ has remarked that in shoot systems, "the subordination of parent shoots to lateral shoots is, indeed, quite common; it is the essential feature of all sympodial and cymose branching."

The development of the leading vegetative shoot prior to the inflorescence shoot involves a change in timing which has occurred in the allied Australian genus *Sollya*. In *S. heterophylla* the inflorescence develops in a lateral position but is not subtended by a leaf. There is a leaf on the side of the shoot opposite to the inflorescence, however, indicating that the shoot above the inflorescence is really a lateral axillary structure.

In *Pittosporum divaricatum* and *P. crassicaule* of New Zealand the branchlets are almost spinose, but bear leaves and occasionally an inflorescence. Spines are

⁵⁹ The natural philosophy of plant form. p.94. 1950.

well developed in the Australian *P. o'reillyanum* and the allied Australian genera *Bursaria* and *Citrobatus*, and their derivation from short shoots is indicated by the occasional presence of leaves on them.

In the New Zealand *Pittosporum divaricatum*, *P. crassicaule*, and *P. anomalum* the flowers are borne on "arrested branchlets" which may attain several millimetres in length. These are lateral structures and appear to be miniature forms of the reproductive shoots on which the flower stalks are borne in many other species.

In the Australian *P. phillyraeoides* and *P. bicolor*, and in the New Zealand *P. obcordatum* and *P. rigidum*, the inflorescence consists of a solitary flower, or a fascicle of flowers, which is usually borne in the axil of a leaf. *Pittosporum phillyraeoides* rarely has several flowers in a cyme, and *P. obcordatum* and *P. rigidum* frequently have flowers on minute arrested branchlets. The New Zealand *P. tenuifolium* and *P. buttonianum* bear both terminal and axillary inflorescences which consist of a fascicle of flowers or of a solitary flower.

In all species mentioned the flowers may be considered as terminal on a shoot which is reduced and sometimes is represented only by the scales at the base of the flower stalks. Occasionally, in *P. tenuifolium* and *P. buttonianum* the shoot is well developed and bears a whorl of cataphylls or 1-2 leaves beneath the terminal fascicle of flowers. Rarely, the subtending cataphylls and leaves are suppressed and the inflorescence appears to be compound. Other aspects of this reduction in the reproductive shoot are discussed below.

The presence of terminal inflorescences, axillary inflorescences, and of both terminal and axillary inflorescences is fairly constant within a species or subspecies and is a valuable criterion for classification. However, it must be borne in mind that the inflorescence may be pushed from a terminal to a lateral position by the development of a leading shoot. Furthermore, in some species several reduced forms of the fertile shoot (e.g. a cyme, fascicle, or solitary flower) may be found together on a branchlet.

LIFE FORMS:

The life forms of the Australian and New Zealand species and subspecies, according to the system of Du Rietz⁶⁰, are summarized in the following table:

In compiling this table difficulty has been experienced in fitting the species to the various categories defined by Du Rietz. His definition of "trees" is holoxyles with a distinct main trunk remaining unbranched in its lower part", and of "shrubs," "holoxyles higher than 0.8 m., not developing a distinct main trunk, with the stem branched from its basal part above or below the soil surface". Some species of *Pittosporum* develop both a main trunk and branches from the base. *Pittosporum undulatum*, for example, when grown in an open situation usually has branches from the base as well as a main trunk. Difficulty has also been experienced with the size classes of Du Rietz. Again *Pittosporum undulatum* may

⁶⁰ Life forms of terrestrial flowering plants. Acta Phytogeogr. Suec. 31. 1931.

Life Form	Australian	Norfolk and Lord Howe Islands	New Zealand	
	BIVALVAE	TRIVALVAE	BIVALVAE	TRIVALVAE
Tall trees (8 - 30 m. in height)	6	..	2	2
Low trees (2 - 8 m.)	1	2	4	3
Dwarf trees (0.8 - 2 m.)	1	..
High shrubs (2 - 8 m.)	4	..	3	2
Ordinary shrubs (0.8 - 2 m.)	1	..
Dwarf shrubs (under 0.8 m.)	2	..
Epiphytic shrubs	2	..

be cited as an example: in barren exposed localities it is a shrub 2-3 m. high but in favorable situations it is a tree 10-30 m. tall. Similarly, *P. bicolor*, *P. rhombifolium*, and *P. crassifolium* are very variable in habit and size.

In spite of these difficulties the summary does show: (1) that the New Zealand species of the series TRIVALVAE are conservative in form; (2) that the New Zealand species of the series BIVALVAE are more diverse in shrub forms; and (3) that the Australian species of the BIVALVAE are a relatively conservative group.

The Australian species belonging to genera allied to *Pittosporum* have 2-valved fruits, and if these were included in the table the number of shrub species would be much higher, and the number of life form classes would be increased by the addition of dwarf-shrubs, dwarf half-shrubs, and twiners with a woody base.

Although the life forms of members of the Pittosporaceae have evolved along closely parallel lines in Australia and New Zealand, the New Zealand species are placed without difficulty in the genus *Pittosporum* while the Australian species are so specialized in other characters that they are classified in separate genera. A possible explanation of the different rates of evolution in the two countries is given later.

Laing and Gourlay⁶¹ considered that the small-leaved New Zealand species of the BIVALVAE are a natural group and commented:

It should first be noted that all the species dealt with . . . are highly polymorphic in length and rigidity of branchlets, leaf shape and size, and in habit generally. In addition to the polymorphic mature plant, each of the species . . . has also a distinct juvenile and shade form, differing in habit, leaf size and shape, from the corresponding adult plant. Sometimes there is more than one adult form, and the juvenile may go through many changes.

⁶¹ Trans. Roy. Soc. N.Z. 65:46. 1935.

There are a number of species, however, which lie between the two extremes represented by Laing and Gourlay's polymorphic small-leaved section of BIVALVAE and the more conservative members of the BIVALVAE and TRIVALVAE. For example, *Pittosporum turneri* is a shrub or tree 2-9 m. tall, with sharply divaricating and matted branchlets at the juvenile stage and on the lower part of the adult stem, and ascending branches on the upper part of the stem. The leaves are relatively small below and large above, and the plant combines the distinguishing characters of the two sections suggested by Laing and Gourlay.

Cockayne and Allan⁶² recorded about 200 New Zealand species as showing more or less strongly marked dimorphy or even polymorphy as they progress from the juvenile to the adult stage, and they suggested that an explanation based on hybridism and the "somatic segregation" in hybrids of chimaeras of various types might be the correct one. There is, however, no evidence to support their hypothesis.

ONTOGENETIC DEVELOPMENT OF THE SHOOT:

The vegetative shoot develops from a bud which is protected by cataphylls. The term "cataphyll"⁶³ is used here to include both bud scales and transitional leaves. Usually the latest-formed cataphylls become quite leaf-like but with the elongation of the shoot they are shed and only a whorl of leaves near the apex of the shoot matures. The sequence of cataphylls from one whorl of mature leaves to the next is illustrated in fig. 1. for the Australian *P. undulatum*, the New Zealand *P. umbellatum*, and the Chinese *P. tobira*.

Usually the cataphylls are missing from herbarium specimens but their scars have been found in most species of *Pittosporum* that I have examined. In the allied Australian genus *Hymenosporum* the cataphylls are shed, but in *Sollya*, *Bursaria*, *Pronaya*, *Billardiera*, *Citriobatus*, *Cheiranthera*, and *Mariantbus* they are retained.

Stebbins⁶⁴ and others have remarked that the presence of an apical meristem and the serial differentiation of organs result in two types of ontogeny; one is that of the various lateral appendages, starting from the time when they become differentiated from the apical meristem of the shoot, and the other is that of the embryo and seedling. Agnes Arber⁶⁵ pointed out that recent work by Miller and Wetmore⁶⁶ showed that the development of the shoot from the meristematic apex is merely a modification of the original pattern in the relevant part of the embryo. The embryo has not been investigated, but there are many observations on the development of *Pittosporum* seedlings and juveniles.

Generally variations in size and shape are more marked in seedling and juvenile leaves than in the cataphylls between two whorls of mature leaves, but the resemblance between the two ontogenies is marked.

⁶² Jour. Ecol. 15:239, 245. 1927.

⁶³ Foster, in Amer. Jour. Bot. 16:475. 1929.

⁶⁴ Variations and evolution in plants. p. 488. 1950.

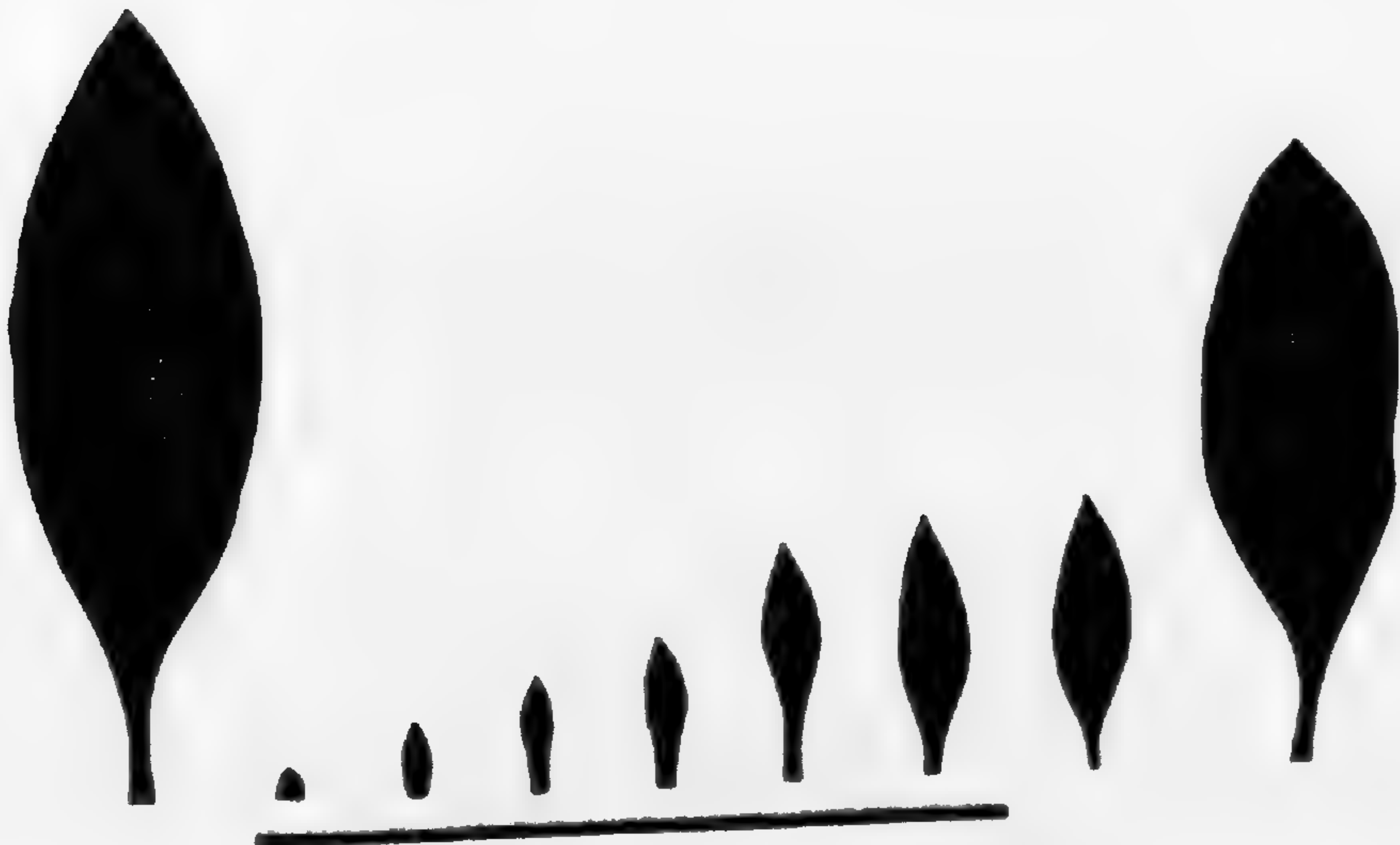
⁶⁵ The natural philosophy of plant form. p. 162. 1950.

⁶⁶ Amer. Jour. Bot. 33:1. 1946.



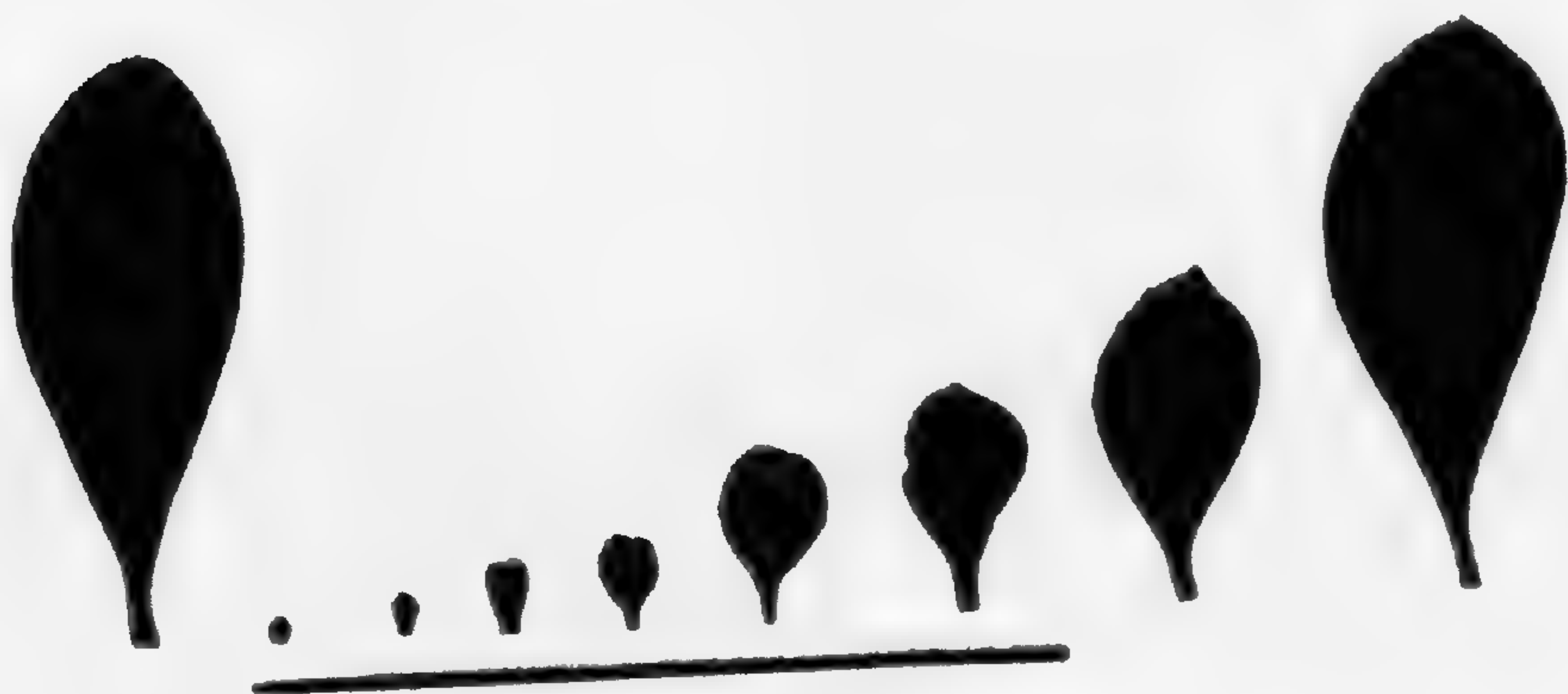
P. UMBELLATUM

NEW ZEALAND



P. UNDULATUM

AUSTRALIA



P. TOBIRA

ASIA

Fig. 1. Sequence of cataphylls and leaves of three species of *Pittosporum*. Previous mature whorl of leaves at left; new whorl at right; caducous cataphylls indicated by horizontal black line. About one-third natural size. Further explanation in the text.

The following summary of seedling, juvenile, and adult foliage in representative Australian and New Zealand species of *Pittosporum* and in *Billardiera longiflora* is based on the descriptions of Lubbock⁶⁷, Cockayne⁶⁸, Sainsbury⁶⁹, Hardy⁷⁰, Laing and Gourlay⁷¹, as well as my own observations.

Species	Seedling leaves	Juvenile leaves	Adult leaves
Australia			
<i>P. phillyraeoides</i>	Entire, lanceolate-oblong	As for adult	Entire, linear-oblong
<i>P. undulatum</i>	Entire, lanceolate-oblong	As for adult	Entire, elliptic-oblong
<i>B. longiflora</i>	Entire, linear	Trilobed, obovate	Trilobed, lobes serrate, ovate
New Zealand			
<i>P. tenuifolium</i>	Entire, ovate	As for adult	Entire, oblong-ovate
<i>P. umbellatum</i>	Entire, obovate	Lobed, pinnatifid, obovate	Entire, elliptic
<i>P. divaricatum</i>	Irregularly double, serrate, linear	Lobed, oblong or obovate to linear	Entire or dentate, crenate or lobed, linear-oblancoate to linear-oblong
<i>P. eugenioides</i>	Entire, lanceolate-elliptic	Variouly notched at base, oblong-elliptic	Entire, oblong-elliptic

From the above summary and the descriptions given later, it is clear that marked changes in seedling, juvenile, and adult foliage are due to differences in size and general outline, and frequently to variation in the leaf margins.

Following Arber⁷², I am using the term "heterophylly" to describe the occurrence of two or more different types of leaf upon one individual. Heterophylly has been reported in almost all the New Zealand species of *Pittosporum*. It is slight in the TRIVALVAE (e.g. *P. tenuifolium*) but is well marked in the BIVALVAE (e.g. *P. umbellatum* and *P. divaricatum*). Several heterophyllous species of *Pittosporum* have been reported from New Caledonia⁷³, but none are known from Australia. The allied Australian genera, *Pronaya*, *Marianthus*, and *Billardiera* have species with

⁶⁷ A contribution to our knowledge of seedlings. p. 200. 1892.

⁶⁸ N.Z. Inst. Trans. & Proc. 31:362. 1899; and 33:265. 1901.

⁶⁹ N.Z. Inst. Trans. & Proc. 54:572. 1923.

⁷⁰ Proc. Roy. Soc. Vict. 28:240. 1916.

⁷¹ Trans. Roy. Soc. N.Z. 65: 44. 1935.

⁷² Water plants. p.143. 1920.

⁷³ Guillaumin, in Bull. Mus. Hist. Nat. Paris 25:214. 1919.

lobed or notched leaves, however, and their resemblance to juvenile forms of the New Zealand species of *Pittosporum* is striking.

Distinct sun and shade forms in *P. divaricatum*, *P. crassicaule*, and *P. anomalum* have been described by Cockayne⁷⁴, and Laing and Gourlay⁷⁵; and Michie has supplied me with sun and shade forms of *P. pimeleoides* var. *major*. It is clear from the records and specimens that leaves exposed to the sun tend to be entire, and that shaded leaves are variously lobed, toothed, and pinnatifid; but exposure and shade are obviously not the cause of heterophylly. Stebbins⁷⁶ discussed heterophyllous leaves from the ecological viewpoint but admitted that similar lobed and pinnatifid leaves in *Quercus* had no apparent selective value. Ashby⁷⁷ studied the changes in size and shape from leaf to leaf on a shoot of *Ipomoea caerulea* and remarked:

On the basis of these fragments of evidence it is suggested that lobing is determined very early in leaf ontogeny by a growth substance which changes in concentration or composition during development, . . . and which is suppressed at low light intensities and also in short days with uninterrupted nights.

Elsewhere⁷⁸, he summarized past research as follows:

In some plants no correlation has been discovered between leaf shape and external conditions. In these plants (e.g. species of *Ipomoea* and *Hedera*) leaf shape is a function of the age of the plant and the position at which the leaf arises. Heteroblastic^[79] development is presumably controlled by unknown internal factors.

Both leaf shape and rate of heteroblastic development are influenced by genes. For *Gossypium* the effects of some specific genes on heteroblastic development have already been worked out.

In the New Zealand *P. umbellatum* the change from lobed and pinnatifid leaves is abrupt, but in *P. virgatum* it is gradual; in fact, lobed leaves are frequently found in the adult foliage. There are not two phases, juvenile and adult, in this species, but a series of phases in which the leaves differ markedly in size and form. Ross Michie, of Kaitaia, N.Z., a keen amateur botanist, has a number of plants of *P. virgatum* in cultivation on which two, three and four types of foliage are present at different levels on the trunk, and he observes that some plants develop entire leaves after the first phase of lobed and pinnatifid leaves, while others pass through two or three more or less distinct leaf forms before reaching the adult foliage.

Leaf forms of juvenile and adult plants of *P. umbellatum*, *P. virgatum*, *P. patulum*, *P. turneri* and *P. pimeleoides* are illustrated in fig. 2, and measurements of their flowers and fruits are given in the chapter on Taxonomy. There is some similarity between the adult leaves of *P. pimeleoides*, and the juvenile leaves of *P. patulum*, *P. turneri*, and *P. virgatum*, and some resemblance between the adult

⁷⁴ Rept. Austr. Ass. Adv. Sci. 13:219. 1912.

⁷⁵ Trans. Roy. Soc. N.Z. 65:44. 1935.

⁷⁶ Variation and evolution in plants. p.490. 1950.

⁷⁷ New Phytol. 49:386. 1950.

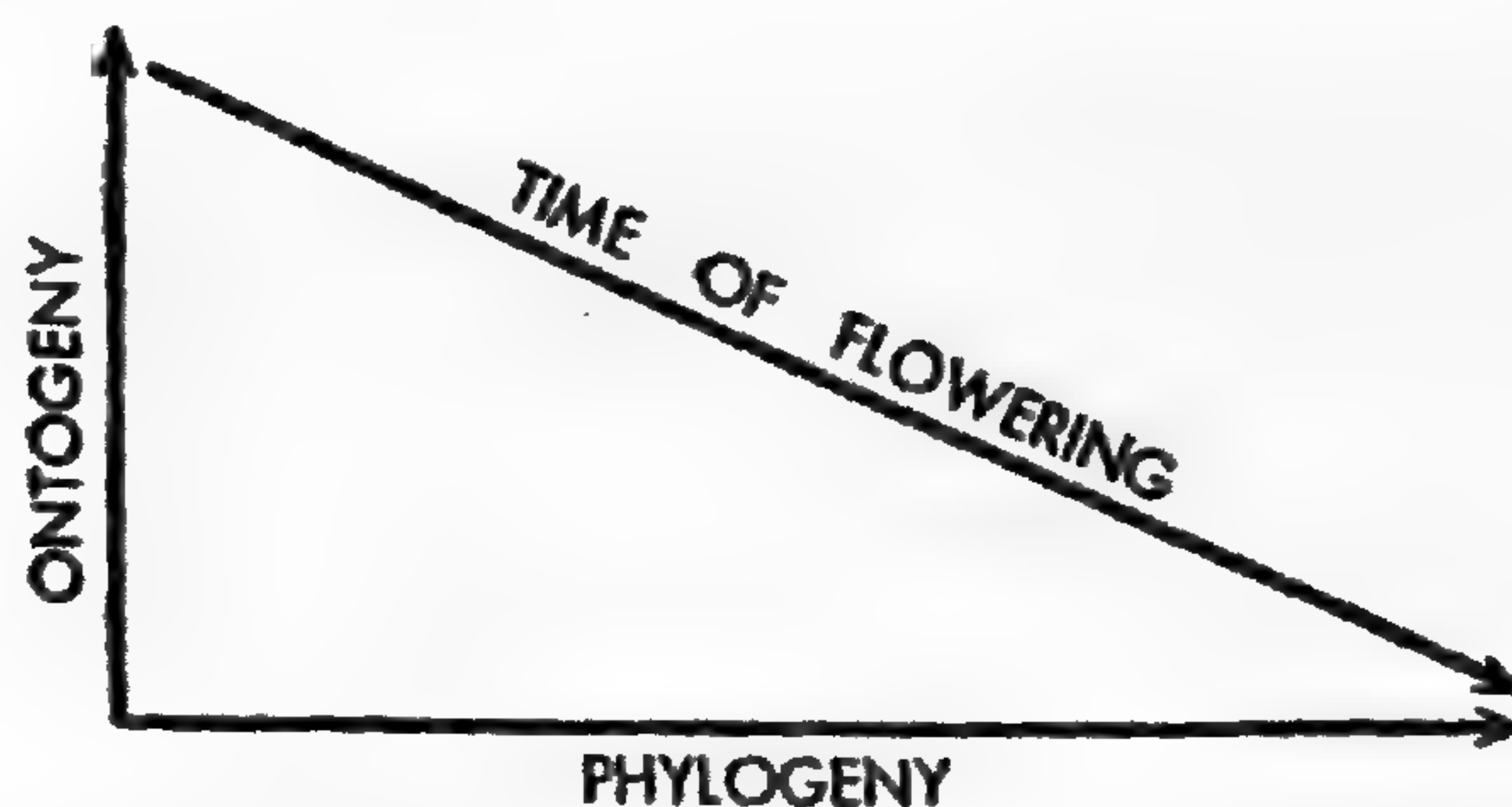
⁷⁸ *loc. cit.* 47: 174. 1948.

⁷⁹ The term "heteroblastic" is used by Ashby in the sense given it by Goebel (*Organographie der Pflanzen*, ed.1. p.123. 1898) and is synonymous with "heterophyllous" in this discussion.

leaves of *P. patulum* and *P. turneri* and the juvenile leaves of *P. virgatum*. There is closer similarity between the adult leaves of *P. virgatum* and the juvenile leaves of *P. umbellatum*. In habit, *P. pimeleoides* is a slender shrub to 2.5 m. tall; *P. umbellatum* is a spreading tree to 10 m. tall; and *P. virgatum*, *P. patulum*, and *P. turneri* are trees intermediate in height between these two extremes.

In size of inflorescence, flowers and capsules, the species show a similar gradient from *P. umbellatum* to *P. pimeleoides*. In other morphological characters and in their geographical ranges the five species are distinct; but a comparison of leaf forms, flowers, and capsules suggests that they may be of common origin and represent a series in which increase, or more probably reduction, in size has been of evolutionary significance.

Flowering on semi-juvenile and shade forms has been observed in *P. virgatum*, *P. turneri*, *P. patulum*, *P. pimeleoides*, *P. pimeleoides* var. *major*, *P. divaricatum*, *P. obcordatum*, *P. crassicaule*, and *P. anomalum*, and the phenomenon is not rare in heterophyllous species⁸⁰. The possibility that some of the reproductive juvenile forms have become permanently fixed during the history of *Pittosporum* is suggested to account for the resemblance in leaf form and leaf ontogeny, and may also be relevant in the comparative interpretations of plant forms in the family. In the diagram below I hesitantly present a representation of the hypothesis, adapted from De Beer⁸¹.



Takhtajan⁸² discussed similar phenomena in higher plants in relation to phylogeny, and concluded that:

In the evolution of the organism new characters arise as hereditary changes of the most varied stages of their development, beginning from the initials and terminating with the last phases. The most differentiated and, consequently, least plastic are the last stages of the development of an organism or organ. The latter end, particularly the terminating stages, can produce small insignificant variations only. At the last phases arise asymmetry of the leaf, zygomorphy of the flower, the increase and decrease in the size of the organs, . . . The changes in the terminating stages of development give rise to various kinds of regressive phenomena as well. Having set in the last stages of development the change can gradually move on deep into more earlier stages of ontogenesis. Just in this way great evolutionary transformations of the organs usually take place.

⁸⁰ Cockayne, *Vegetation of New Zealand*, In *Die Vegetation der Erde*. ed. 2. 14:140. 1928.

⁸¹ *Embryos and ancestors*, ed. 2. p. 32. 1951.

⁸² *Trans. Molotov State Univ. Erevan* 22:168. 1943.

Regarding embryological investigations from the standpoint of comparative morphology Jepsen, Mayr, and Simpson⁸³ remarked:

Morphological embryologists are agreed on recognizing a principle of *heterochrony*, alteration of the sequence of ontogenetic stages in the phylogeny of a structure. Obviously this is merely a morphologist's phrasing of the geneticists' conclusion that mutation may alter the relative velocity of ontogenetic processes.

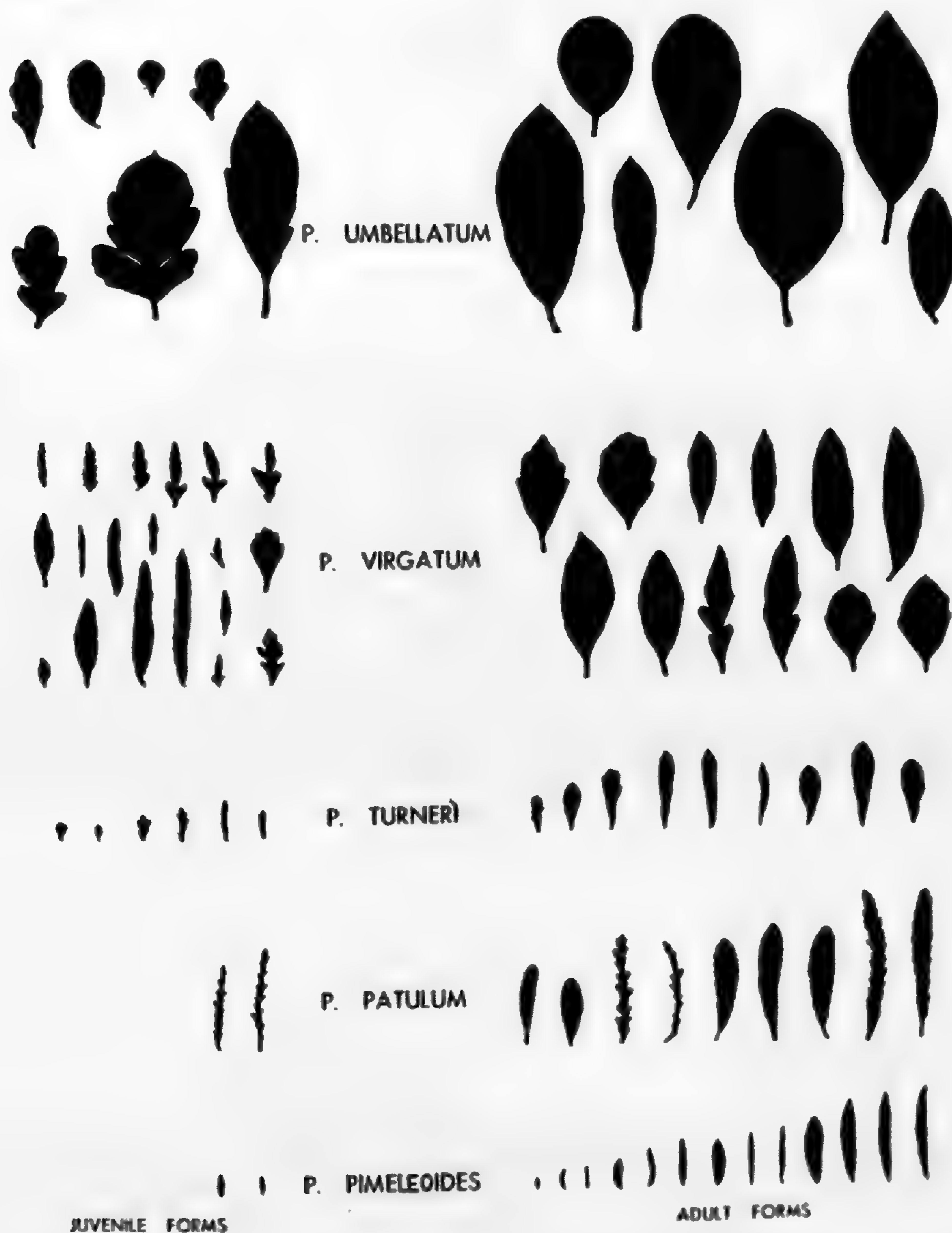


Fig. 2. Variation in leaf forms of five species of *Pittosporum*: juvenile forms at left; adult forms at right. One fourth natural size. Further explanation in the text.

THE INFLORESCENCE:

The basic unit of the inflorescence of *Pittosporum* is the cyme. In *P. undulatum* (fig. 3) the flower-stalks bear one to four flowers. The first flower to open is the terminal one, after which flowering is frequently from the base of each flower-stalk upwards, although the order is variable.

⁸³ Genetics, palaeontology and evolution. p.71. 1949.

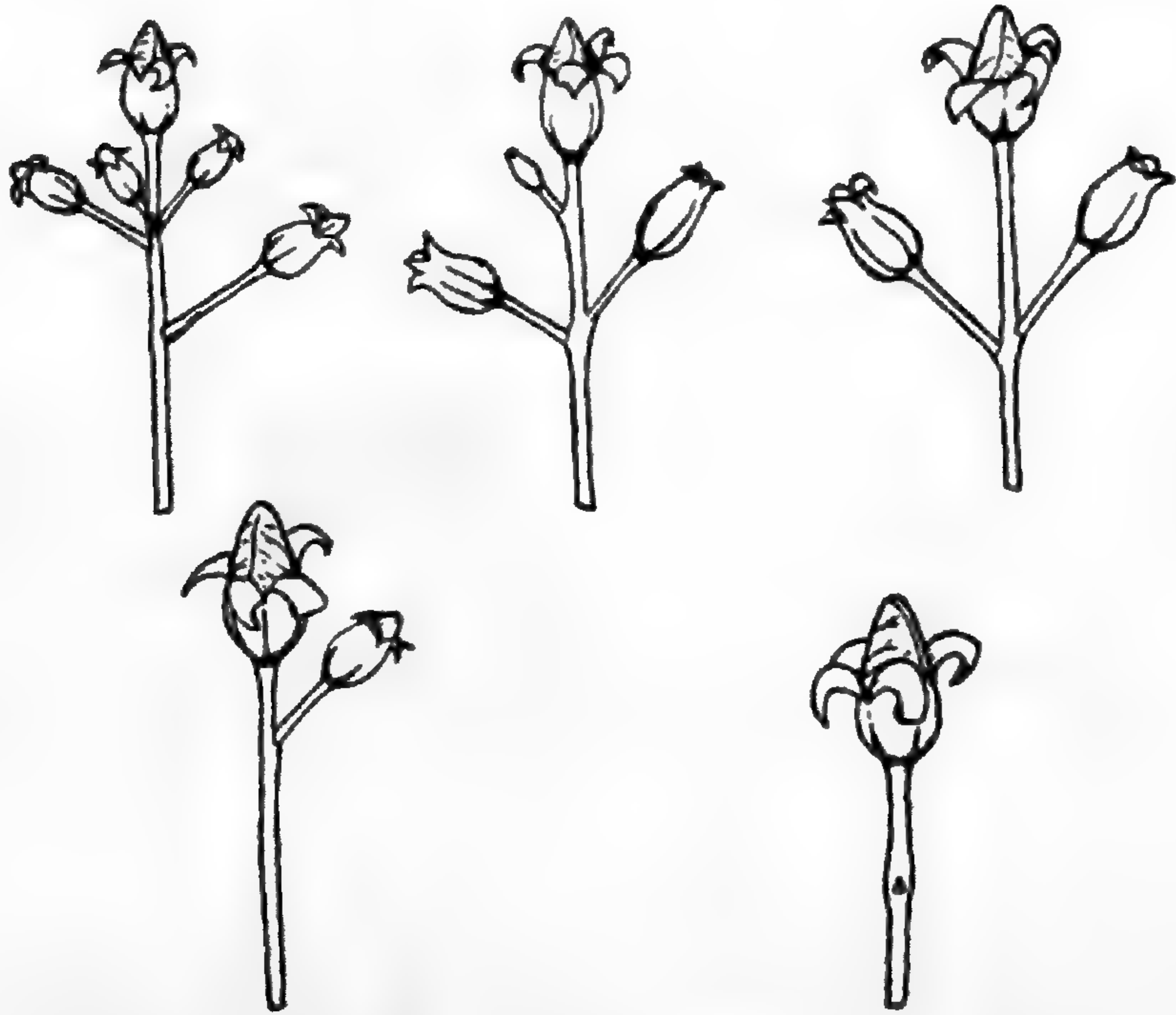


Fig. 3. Variation in the inflorescence of *P. undulatum*, Australia. $\times 1\frac{1}{2}$.

Gowda⁸⁴ placed the series TRIVALVAE before the series BIVALVAE in his key to the genus as plants of the former have certain characters (e.g. large 3-valved capsules, many seeds, funicles from the base to near the apex of the capsule valve) from which the characters of the BIVALVAE were derived. He considered that the evolution of the inflorescence in the genus "is from the well branched paniculate [i.e. paniculiform] to the simple cymose type and eventually to the solitary flower with all intermediate stages present." But none of the East Asian or New Zealand species of the TRIVALVAE have well-branched paniculiform inflorescences. In the Australian and New Zealand species the following trends have been recognised:

1. Reduction from a cyme to a solitary flower, e.g. *P. undulatum*.
2. Reduction from a fascicle to a solitary flower, e.g. *P. tenuifolium*.
3. Condensation of a compound inflorescence, e.g. *P. dallii*.

Presumably the spreading compound inflorescence of *P. ferrugineum* and its allies has been derived by aggregation of fertile shoots and reduction of subtending leaves to cataphylls or bracts. The increase in the number of flowers in the inflorescence has been balanced by reduction in the size of the capsule and in the number of seeds.

PUBESCENCE:

Hairs are most common on young shoots, leaves, and inflorescences; and persist on petioles and undersides of leaves, pedicels, sepals and ovaries. The two main types in the Australian and New Zealand species are icacinaceous and malpighaceous hairs as defined by Heintzelman and Howard⁸⁵. Forms intermediate

⁸⁴ *loc. cit.* p.271. 1951.

⁸⁵ *Amer. Jour. Bot.* 35:43. 1948.

between the two types are found. The absence of hairs, or the presence of hairs on parts usually bare, is a criterion for the recognition of particular species or subspecies. Hair color is also useful in the recognition of several species, e.g. *P. buttonianum*, although in other species it is most variable, e.g. *P. bicolor*.

THE FLOWER:

Kirk⁸⁶ reported dimorphic flowers in several New Zealand species of *Pittosporum*, and Petrie⁸⁷ described male and female flowers of *P. cornifolium*. Several notes on the sexual behaviour of the Australian species of *Pittosporum* were published by Maiden⁸⁸, and the pollination of the New Zealand species was discussed by Thomson⁸⁹.

In most of the Australian and New Zealand species I have found flowers which appear to be functionally unisexual. The male flowers have weakly capitate to truncate stigmas, long styles, slender ovaries, oblong anthers 2-4 mm. long borne on slender filaments. Usually the anthers are level with the stigma or exserted. The flowers which I think may be female have 2-, 3- or 4-lobed capitate stigmas, slightly shorter styles, plumper ovaries, apparently abortive, sagittiform anthers 1-2 mm. long, borne on filaments 1 mm. or more broad at the base, tapering distally. Usually the anthers are borne below the stigma. Flowers with oblong, apparently functional anthers 3-4 mm. long, capitate stigmas, and plump ovaries occur (i.e. hermaphroditic), as do flowers with 4 functional anthers 3-4 mm. long and one apparently abortive anther 1-2 mm. long.

Ross Mitchie, of Kaitaia, N. Z., has observed the flowers of a number of species over a period of years and considers that some plants have female and others male flowers, but the female plants sometimes shed a little pollen and the males occasionally set a few fruit. In a letter to Dr. Woodson⁹⁰ I recently recorded my own studies as follows:

I have observed four self-sown trees of *Pittosporum tenuifolium* ssp. *tenuifolium* for three years in my garden at Blockhouse Bay, New Zealand, where there is an acre of rapidly regenerating coastal scrub and forest. All the trees flower profusely in the spring (August to October) and two, which bear flowers with functional anthers and slender ovaries, have not set fruit. The other two trees, which bear flowers with aborted anthers and plump ovaries, are laden with fruit each autumn and the seeds germinate freely—there being a carpet of seedlings under both trees.

Over the same period I have watched the behavior of planted trees of *P. obcordatum* and *P. umbellatum* in the Auckland Domain, adjacent to the Museum where I work. The trees appear to be female (i.e. the flowers have apparently aborted anthers and plump ovaries, and fruit develop each year) but there are no "male" trees in the neighborhood. Possibly some of the anthers shed sufficient pollen to fertilize the ovaries, but this has not been observed.

Again I have received specimens of flowers and fruit from a plant of the Australian *P. undulatum*, planted in the grounds of the Middlemore Hospital, near Auckland. The flowers have plump ovaries and apparently aborted

⁸⁶ N.Z. Inst. Trans. & Proc. 4:260. 1872.

⁸⁷ N.Z. Inst. Trans. & Proc. 53:365. 1921.

⁸⁸ For. Fl. N.S.W. 7:124. 1920.

⁸⁹ N.Z. Inst. Trans. & Proc. 13:254. 1881, and 57:115. 1926.

⁹⁰ Personal communication.

anthers. The fruit are fully developed and the seeds germinate each year. There is no male plant of the species in the neighborhood, however, and the source of pollen is not known. More observations on all the Australian and New Zealand species of *Pittosporum* are required to determine the extent of dicliny.

Cufodontis⁹¹ stressed the value of the sepals as a criterion for the recognition of species and subspecies and described and illustrated five types of sepal arrangement. Only four of these types are found in the Australian and New Zealand species of *Pittosporum*: 1, sepals free or slightly coherent at base, not imbricate, e.g. *P. dallii*; 2, sepals free and clearly imbricate, e.g. *P. bicolor*; 3, sepals coherent, e.g. *P. melanospermum*; and 4, sepals connate in a tube splitting into 2 parts, one 1- to 2-lobed, the others 3- to 4-lobed, e.g. *P. undulatum*.

Occasionally in *P. phillyraeoides* and *P. cornifolium* one or two pairs of sepals are coherent from base to apex and the arrangement of the sepals varies slightly in most species examined. Size, shape, and pubescence of the sepals also vary, but are as valuable as sepal arrangement in the recognition of species.

The usual number of sepals and petals is five, but extra sepals and petals have been found rarely in *P. revolutum* and *P. phillyraeoides* (Australia), *P. erioloma* (Lord Howe Island), and *P. crassifolium* and *P. umbellatum* (New Zealand).

Petal color is constant in most of the Australian and New Zealand species of *Pittosporum* and is a useful character in the classification of the species. For about half of the species of the genus the flower color is not known, but in the remainder the colors usually found are white, greenish-white, and yellow. Red or purple flowers have been reported in three species in New Guinea, three species in New Caledonia, one species in the Tonga Islands, one species in Australia, and in most of the species in New Zealand. In the allied Australian genera there are a number of species with red, purple, and blue petals, and these colors seem to be associated strongly with small leaves, heterophylly, and reduced forms.

THE FRUIT:

Gowda⁹² recognized two major series in the Asiatic species which he termed the BIVALVAE and the TRIVALVAE, according to the carpel number. Cufodontis⁹³ did not discuss valve number but it is clear from his descriptions and illustrations that all the species he dealt with belong to the BIVALVAE. The character is somewhat variable, but the group to which a species belongs can be determined if sufficient fruits are available and cognizance is taken of associated characters.

Cufodontis⁹⁴ considered that valve shape is a valuable character and recognized four basic types based on cross-sections of the valves:

1. Valvae convexae—more or less evenly convex or with a flat middle portion.
2. Valvae concavae—between the convex edges lies a concave middle zone.
3. Valvae gibbosae—between the convex borders is a longitudinal dorsal thickening.
4. Valvae sulcatae—resembling 3, but with a longitudinal groove down the dorsal thickening.

⁹¹ Österr. Bot. Zeitschr. 98:109. 1951.

⁹² *loc. cit.* p.278. 1951.

⁹³ *loc. cit.* 1951.

⁹⁴ *loc. cit.* p.109. 1951.

As the four types represent the variation in cross-sections of two-valved fruits it was necessary to examine as many three-valved fruits as possible to determine whether the classification applied to these. Generally the four basic types are present in the TRIVALVAE but within some species more than one valve type is found. A rapid survey of the valve shape throughout the range of the genus gives the impression that the character is useful for the recognition of the Hawaiian species as a whole; the capsule valves of the Hawaiian species have a distinct longitudinal thickening with a median longitudinal groove. The character is also of value in the classification of species and subspecies.

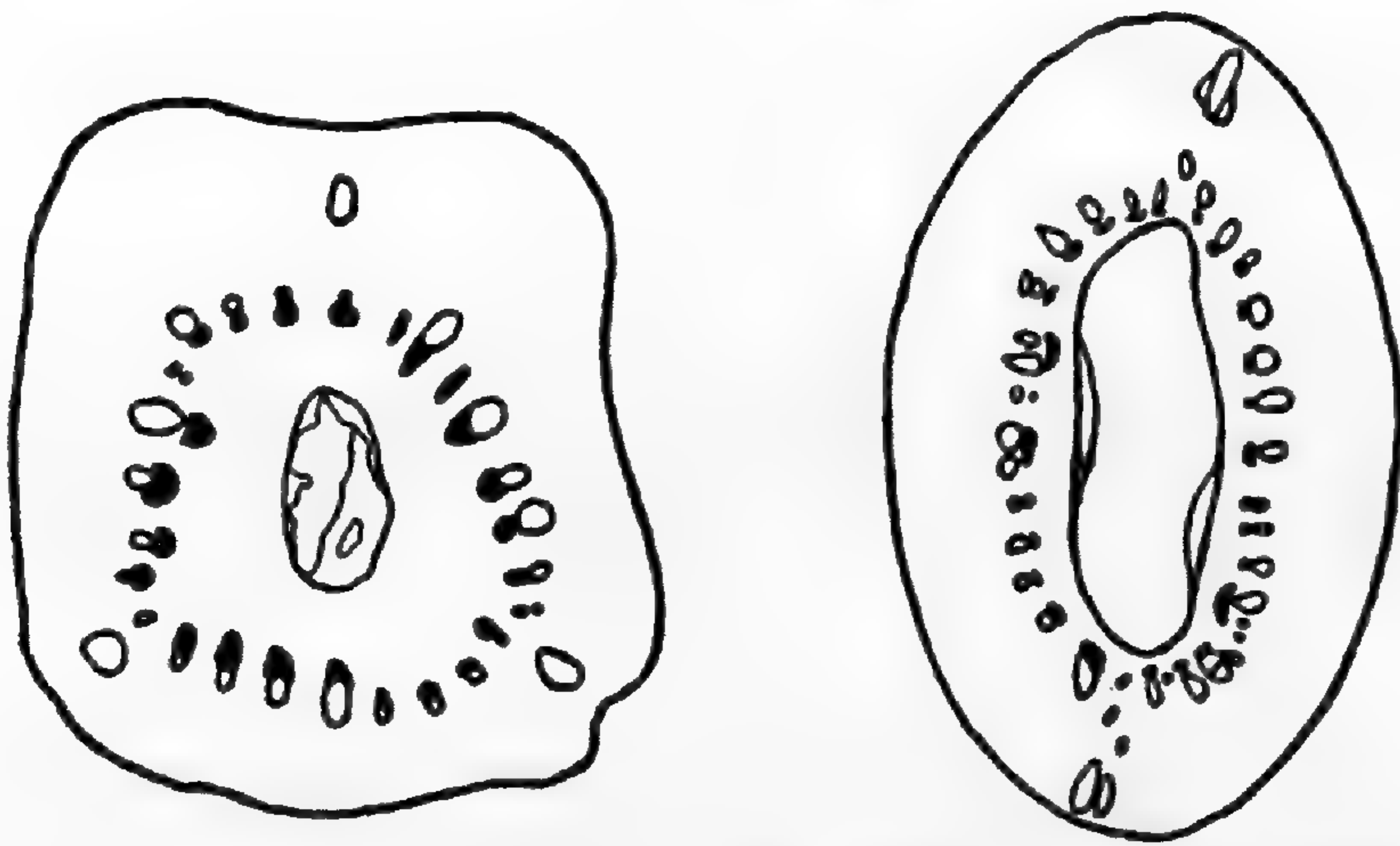


Fig. 4. Ovary sections of *P. crassifolium* (left) and *P. eugenioides* (right), New Zealand. Resin canals indicated by hollow circles; vascular strands indicated in black. $\times 23$.

Moore and Adams⁹⁵ described and figured a papery endocarp in the New Zealand *P. dallii*, *P. eugenioides*, and *P. anomalum*. Fruit of *P. crassifolium* and *P. eugenioides* both show (fig. 4) a more or less complete circle of large resin canals lying outside, rarely inside, the vascular supply which branches to all parts of the valve. In *P. eugenioides* the canals fuse more than they do in *P. crassifolium* and finally the endocarp, vascular supply, and mesocarp separate in the former species. Apart from the valve number and the resin canal development, no marked differences were found in the anatomy of the fruits of the two species. On boiling the fruits of *P. crassifolium* and *P. fairchildii*, I have found the endocarp partly or completely free from the vascular supply and mesocarp, and the separation of the tissues can be effected without difficulty in several species. No great significance can be placed on the presence or absence of a papery endocarp, although it is a useful character for the recognition of *P. dallii*, *P. eugenioides*, and *P. anomalum*. *Pittosporum dallii* and *P. eugenioides* may be related but there is nothing apart from this character to suggest a close relationship with *P. anomalum*; in fact all three are isolated and highly specialized members of the genus.

Gowda⁹⁶ used the placenta and funicles for the recognition of complexes of

⁹⁵ Trans. Roy. Soc. N.Z. 77: 250. 1949.

⁹⁶ *loc. cit.* 280. 1951.

East Asian species, and *Cufodontis*⁹⁷ has illustrated these characters for the African species. In the classification of the Australian and New Zealand species they are valuable, although in most species there is some variation in the length and thickness of the placenta and in the size and arrangement of the funicles. Emphasis is placed on the placenta and funicles as characters rather than the ovules, because the funicles persist whereas the ovules are frequently disarranged or missing on herbarium material.

GEOGRAPHY

The literature on the past history of the Australian and New Zealand flora and fauna is extensive and the conclusions of the most eminent authors frequently conflict. Raup⁹⁸ and Cain⁹⁹ have suggested that such varying points of view might be unified if plant geographers would use more inductive methods. With this good advice in mind, I have presented below the facts I have regarding the distribution of *Pittosporum* and its allies in Australia and New Zealand. I have included information about the distribution of the Pittosporaceae elsewhere as I am convinced that the family must be studied on a world basis, not on a regional one.

DISTRIBUTION OF THE PITTOSPORACEAE:

As at present understood the family Pittosporaceae comprises nine genera and about 276 species, the distribution of which is illustrated in fig. 5.

The species were defined originally by divers botanists, and it is improbable that they exercised taxonomic judgment to the same degree. A semblance of uniformity has been introduced by the general treatments of Pax¹⁰⁰ and Pritzell¹⁰¹, but further study will undoubtedly result in some of the species being relegated to synonymy and others being separated into new categories. Indonesia, New Guinea, and the Melanesian Islands will probably yield more forms when their floras are better known, and the revision of the Polynesian Island species will shed further light on the evolution of the family in the Pacific area.

From the figures available it is possible that the main centre of development is Australia (9 genera and 48 species) and that important secondary centres are the Hawaiian Islands (1 genus, 23 species), New Caledonia (1 genus, 46 species), New Zealand (1 genus, 20 species), southeast Asia (1 genus, 52 species), and Africa (1 genus, 10 species).

DISTRIBUTION OF HIGHER CATEGORIES:

Bentham¹⁰² Pax¹⁰³ and Pritzell¹⁰⁴ recognised two sub-families in the Pitto-

⁹⁷ Fedde's Rep. Sp. Nov. 55¹:27. 1952.

⁹⁸ Assoc. Amer. Geogr. Ann. 32:320. 1942.

⁹⁹ Foundations of Plant Geography. p. 210. 1944.

¹⁰⁰ Engl. & Prantl, Nat. Pflanzenfam. 3^{3*}:106. 1891.

¹⁰¹ Engl. & Prantl, Nat. Pflanzenfam. ed. 2. 18a:265. 1930.

¹⁰² In Benth. et Hook.f., Gen. Pl. 1:131. 1862.

¹⁰³ *loc. cit.* 1891.

¹⁰⁴ *loc. cit.* 1930.

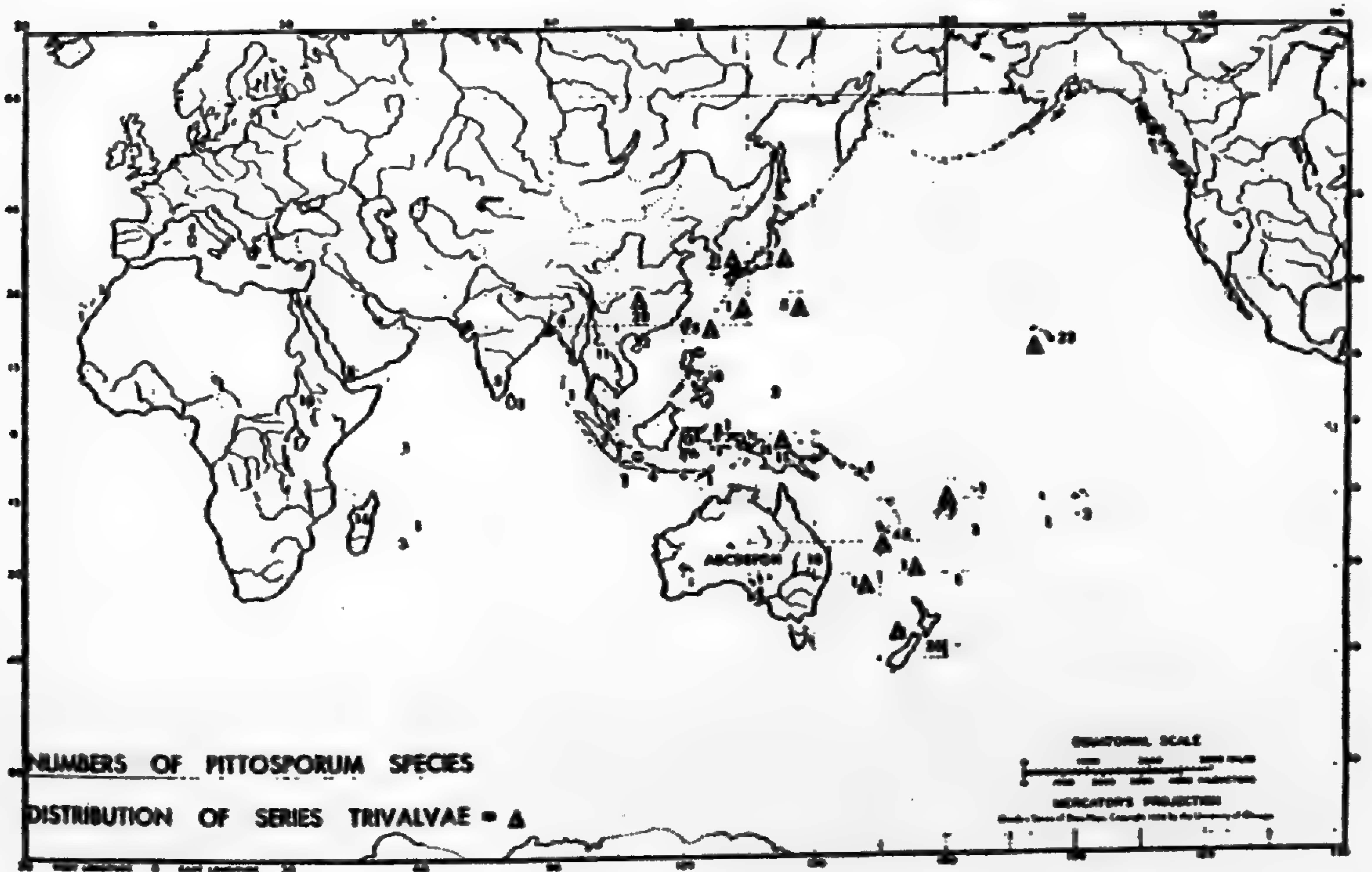


Fig. 5. World distribution of the Pittosporaceae. Figures indicate the number of *Pittosporum* species in that locality. Letters represent the following genera: A, *Billardiera* (8 species), B, *Bursaria* (2 species), C, *Cheiranthra* (4 species), D, *Marianthus* (16 species), E, *Pronaya* (1 species), F, *Sollya* (2 species), G, *Citriobatus* (4 species), H, *Hymenosporum* (1 species).

sporaceae, the PITTOSPOREAE, characterized by woody and leathery capsules, and the BILLARDIEAE, distinguished by succulent berries. In the PITTOSPOREAE, the genus *Pittosporum* is wide-ranging, *Hymenosporum* occurs in Australia and New Guinea; and *Marianthus*, *Cheiranthra* and *Bursaria* are known only from Australia. In the second subfamily, the BILLARDIEAE, the genus *Citriobatus* occurs in Australia, Java, Luzon, and the Celebes, while *Sollya*, *Billardiera* and *Pronaya* are known, so far, only from Australia. The regions where members of the two subfamilies have been found together are Australia, Java, Luzon, and the Celebes.

In the genus *Pittosporum*, the series BIVALVAE ranges from Hawaii to Africa and is present in all regions where the family is found, except the Ryu-kyu, Lord Howe, and Norfolk islands. The series TRIVALVAE is known from the mainland of China, Formosa, the Ryu-kyu and Bonin islands, Japan, South Korea, New Guinea, New Zealand, Lord Howe and Norfolk islands, Fiji, and Hawaii. The regions where members of the two series of *Pittosporum* have been found together are Upper Burma and Assam, western and southwestern China, Formosa, the Bonin Islands, New Guinea, New Zealand, Fiji, and Hawaii.

I do not know of any region where both subfamilies of the Pittosporaceae and both series of *Pittosporum* occur.

DISTRIBUTION OF WIDE-RANGING SPECIES:

The wide-ranging members of the family and the regions in which they occur are:

- Hymenosporum flavum*—Australia, New Guinea.
Pittosporum ramiflorum—Philippines, Java.
 var. *parviflorum*—New Guinea, Solomon Islands.
P. ferrugineum—Australia, New Hebrides, New Guinea, Java, Sumatra, Nicobar Islands.
P. podocarpus—China, Indo-China, Burma, India.
P. oligocarpum—Formosa, China.
P. sabnianum—Formosa, China.
P. tobira—Japan, Korea, China.
 var. *sukurai*—Bonin Islands.
P. baileyianum—China, Hainan, Indo-China.
P. ceylanicum—Ceylon, southern India.
P. neelgherrense—Ceylon, southern India.
P. nervosum—China, Indo-China.
P. formosum—Formosa, Indo-China.
 var. *hainanense*—Indo-China, Hainan.
P. napaulense—Nepal, Sikkim, Tibet, Bhotaun, Assam.
 var. *rawalpindiense*—Sikkim, Dehra Dun, Punjab.
P. floribundum—India, Madagascar.
P. kerrii—China, Indo-China, Siam, Burma.
P. johnstonianum—China, northern Burma.
P. tetraspermum—China, India.
P. viridiflorum—Arabia (Yemen), Ethiopia, central and southern Africa.

Gowda¹⁰⁵ considered *Pittosporum ferrugineum* to be an extremely variable and poorly understood species, but I have found it too coherent to allow separation of the Australian, New Guinean, and Indonesian forms with the material available. At present it is the only species of *Pittosporum* known which extends from Australia to Asia but it does not reach the Asiatic mainland. Gowda¹⁰⁶ found that none of the eastern Asiatic species of *Pittosporum* occurred in Indonesia, New Guinea, or Australia, but Li¹⁰⁷ believed that Gowda was mistaken and that some species extend from Asia to Indonesia.

I am tempted to speculate on the past land connections indicated by some of these ranges, but it is possible that diaspores of the species have been carried to their present areas by birds, hurricanes, and ocean currents. I must emphasize, too, the probability that these populations will undergo further revision in the future.

DISTRIBUTION OF INTERGRADING SPECIES:

The species of *Pittosporum* found in Hawaii are evidently very closely related. Sherff¹⁰⁸ wrote:

Much of the trouble in making a workable key for Hawaiian *Pittospora* lies in the fact that numerous subspecific entities, namely varieties and forms

¹⁰⁵ Jour. Arnold Arb. 32: 322. 1951.

¹⁰⁶ loc. cit. 1951.

¹⁰⁷ Jour. Wash. Acad. Sci. 43:43. 1953.

¹⁰⁸ Field Mus. Nat. Hist. Bot. Ser. 22:472. 1942.

(formae), occur. While these have their individual criteria by which they usually can be recognized, they nevertheless afford so many intermediate characters as to make their respective species seem to intergrade or even overlap.

Similar remarks have been made regarding the species of *Pittosporum* which occur in New Zealand. J. D. Hooker has been quoted previously; Kirk¹⁰⁹ commented of *P. tenuifolium*, *P. colensoi*, and *P. fasciculatum*: "These forms vary considerably in all their parts, so that it would not be difficult to obtain a connected series of specimens which should include the whole."

In the taxonomic treatment I have discussed *P. ellipticum* var. *decorum*, which appears to be intermediate between *P. ellipticum*, *P. buttonianum* and *P. ralphii* and have mentioned *P. intermedium*, which resembles large forms of *P. tenuifolium* in foliage, while the capsule partakes of the characters of *P. crassifolium* and the sepals and petals match *P. umbellatum* in size and shape.

Pittosporum rigidum, *P. divaricatum*, *P. crassicaule*, and *P. anomalum* contain a bewildering series of polymorphic and heterophyllous forms most of which occur in small areas at high elevations. Another series of intergrading forms occurs in North Auckland, and has been variously treated by different authors; I suspect that *P. reflexum* and *P. pimeleoides* are sun and shade forms of the same species but have seen too few living specimens to be certain. The large linear-leaved forms of *P. pimeleoides* resemble juvenile plants of *P. virgatum*, and some of the adult plants of *P. virgatum* are very similar to juvenile plants of *P. umbellatum*.

The problem of intergrading forms in the Australian species of *Pittosporum* is slight. Small-leaved forms of *P. undulatum* have been misidentified as glabrous forms of *P. bicolor* and some are close to small-leaved specimens of *P. revolutum*, but generally the species are easily recognised by their morphological characters.

Gowda¹¹⁰ indicated a number of closely allied species of *Pittosporum* in eastern Asia, the most noteworthy being *P. kerrii* (Siam, China), *P. floribundum* (southern India, Madagascar), and *P. ripicola* (central and eastern Africa). Three groups of intergrading species are mentioned: (1) *P. napaulense*, *P. floribundum*, and *P. kerrii*; (2) *P. truncatum* and *P. heterophyllum*; and (3) *P. trigonocarpum* and *P. sabnianum*.

I have been unable to determine the frequency of intergrading forms in the species of *Pittosporum* described from other areas, and any conclusions are premature. So far the evidence indicates that intergrading forms are more frequent in the Hawaiian Islands and New Zealand than in Australia and Asia. Gowda¹¹¹ recognised 52 species of *Pittosporum* in southeastern Asia, and the intergrading species amount to about a seventh of the total. The proportion of intergrading species in the New Zealand and Hawaiian species is much higher.

¹⁰⁹ N.Z. Inst. Trans. & Proc. 4:262. 1872.

¹¹⁰ Jour. Arnold Arb. 32:284. 1951.

¹¹¹ *loc. cit.* 1951.

DISTRIBUTION OF ENDEMIC SPECIES IN AUSTRALIA AND NEW ZEALAND:

All species of *Pittosporum* in New Zealand are endemic, but only *P. tenuifolium* and *P. eugenioides* are found throughout the country. The other New Zealand members of the TRIVALVAE and BIVALVAE occupy smaller areas. For example, *P. turneri* is known only from one locality on the Central Volcanic Plateau of the North Island, and a closely allied species, *P. patulum*, occurs in a few localities in the mountains of northwest Nelson, in the South Island. *Pittosporum fairchildii* is restricted to the Three Kings Islands, a group of rocks some 30 miles off the coast, and *P. dallii* is known only from one locality where about a dozen plants have been found. A number of the ranges of the New Zealand species are disjunct and most of the small-leaved heterophyllous species have been found in small isolated populations. For example, *P. obcordatum* is known only from three isolated localities several hundred miles apart, the total population being about 15 trees.

All Australian species of *Pittosporum* are endemic, except *P. ferrugineum* which is also found in the New Hebrides, New Guinea, and Indonesia. *Pittosporum bracteolatum* is restricted to Norfolk Island and *P. erioloma* is known only from Lord Howe Island. *Pittosporum bicolor* is most common in Tasmania, but occurs in Victoria and New South Wales. An allied species, *P. phillyraeoides*, is found in every state, except Tasmania. The most widespread of the remaining species is *P. revolutum*, which extends from Queensland to Victoria, a distance of 1000 miles. Within this range are the areas of *P. rhombifolium*, *P. rubiginosum*, *P. undulatum*, and *P. o'reillyanum*. *Pittosporum venulosum* is found on the coast of Queensland farther to the north, and *P. melanospermum* has been collected from the same coast and from the Northern Territory. No one species occupies the whole of the Australian continent, but the majority of species occupy relatively large areas; and all have continuous ranges, except possibly *P. melanospermum*. Furthermore, if the populations of Norfolk and Lord Howe islands are excluded from the Australian species, the number of individuals comprising an Australian species is far greater than the number of a New Zealand population.

CLIMATE:

The climatic regions of Australia and New Zealand, according to Thornthwaite's classification¹¹², and the number of species of *Pittosporum* in each are plotted in fig. 6. The species of *Pittosporum* in the twelve climatic areas are listed below, each species being indicated by its number in the present taxonomic treatment.

The concentration of *Pittosporum* species in eastern Australia (Queensland, New South Wales, and Victoria) and the relative paucity of species in central and western Australia, specifically the desert and steppe climate areas, is noteworthy. *Pittosporum phillyraeoides*, the only species which is found throughout southern, central, and western Australia, is xeromorphic as are some of the species of the

¹¹² Geog. Rev. 28: 433. 1933.

Climatic type*	Australian Species	Norfolk and Lord Howe Islands	New Zealand Species
A A'r	24, 25, 27, 30		
B A'w	24, 25, 27, 28, 29, 30		
B B'r	9, 10, 24, 26	1, 2	3, 4, 5, 6, 7, 8, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 31, 32
C A'w	9, 28		
C B'd	9, 11, 24, 26, 29		
C B'r	9, 10, 24, 26		
C B's	9		
D A'w	9		
D B'd	9		
D B's	9		
E A'd	9 (coastal only)		
E B'd	9 (coastal only)		

* The first letter of the climate type indicates the vegetation transitions due to diminished effective rainfall: (A) rain forest, (B) forest, (C) grassland, (D) steppe, and (E) desert. The second letter indicates the vegetation transitions due to diminished temperature efficiency: (A') tropical rain forest, and (B') temperate rain forest. The third letter indicates the seasonal distribution of precipitation: (r) precipitation at all seasons, (s) scanty rainfall in summer, abundant in winter, (w) scanty rainfall in winter, abundant in summer, and (d) dry at all seasons.

allied genera which occur in the desert and steppe. The development of the allied genera mainly in the southern parts of Australia is linked with the development of the so-called Australian elements in the flora and arid periods in the Post-Pleistocene.¹¹³ Stebbins¹¹⁴ has presented evidence in favour of a hypothesis that environments limiting or deficient in one all-important factor, moisture, often have promoted rapid evolution. The variety of life-forms in the allied genera is strikingly different from the general uniformity of *Pittosporum* and may be the result of evolution under the stimulus of aridity. The northerly concentration of the New Zealand species is illustrated by grouping the species according to the two major geographical units. Until the close of the Pliocene period Cook Strait, which separates the North and South Islands, was closed and there was no barrier to the spread of species north and south.

Species found in the North Island only	11
Species found in the South Island only	2
Species common to both islands	7

20

Owing to its relatively small size, New Zealand has only one climatic type,

¹¹³ Crocker and Wood, in Trans. Roy. Soc. S. Austr. 71:91. 1947.

¹¹⁴ Amer. Nat. 86:33. 1952.

but generally the North Island has warmer summers and milder winters than the South Island. Zotov¹¹⁵ studied the correlation between vegetation and climate in New Zealand and commented:

On the continents where annual variation of temperature is great, the absolute minimum value of temperature—i.e. degrees of frost—may become a very important limiting factor for the distribution of many species. In New Zealand, however, the minimum temperature does not appear to be of importance for the great majority of species, since they reach their summer "limiting temperature" in places well outside the boundaries of limiting winter temperature.

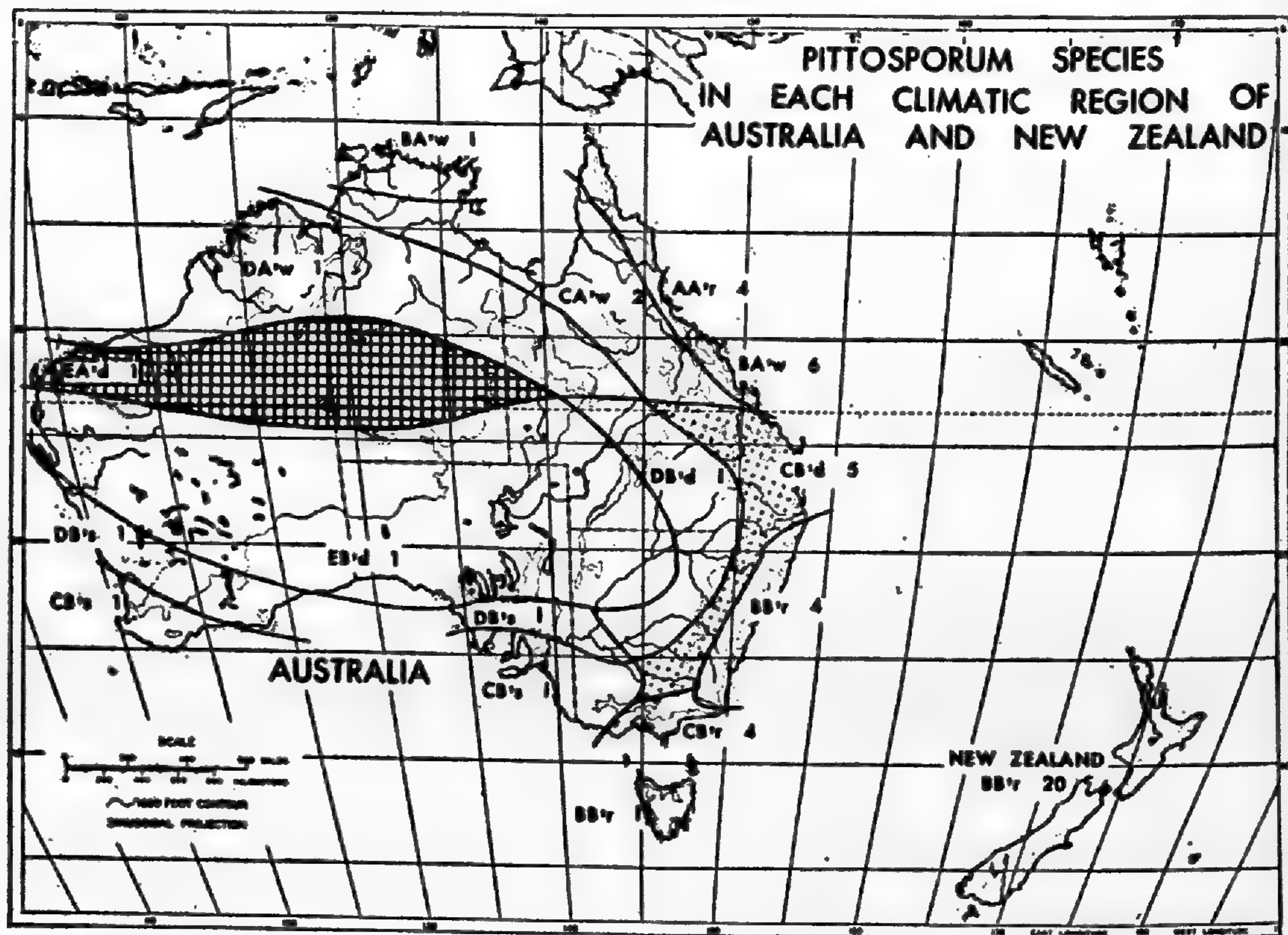


Fig. 6. Number of species of *Pittosporum* in each climatic region of Australia and New Zealand. For explanation see text and table on preceding page.

On Thornthwaite's¹¹⁶ maps of climatic types the regions occupied by the species of *Pittosporum* outside Australia and New Zealand are generally in the rain forest, forest, or grassland classes, for effective rainfall, and in the tropical and temperate rain forest classes, for temperate efficiency. Over much of the range of the genus the isothermal difference between extreme months is relatively small.

In the Pittosporaceae the largest plants are *Pittosporum brackenridgei* of Fiji (tree to 25 m. tall), *P. undulatum* of Queensland, Australia (tree to 30 m. tall), and *P. viridiflorum* of Africa (tree to 25 m. tall). These species occur in tropical rain forests. The smallest plants are those of *Marianthus procumbens* of Australia (a low shrub to 30 cm. tall) and its allies, *Pittosporum anomalum* of New Zealand (semi-prostrate shrub to 1 m. tall) and its allies, and *P. saxicola* of Western Szechwan (prostrate shrub 0.3 - 2.0 m. tall) and its allies. These species are found in

¹¹⁵ N.Z. Jour. Sci. Tech. 19: 474. 1938.

¹¹⁶ *loc. cit.* 1933.

various habitats at the extreme northern and southern boundaries of the family and are dwarfed in all organs.

In the evolution of these forms low temperatures may have been significant, but it is also possible that aridity has played a role. For example, the small-leaved xeromorphic *P. pimeleoides* is found on strongly leached podzolized and skeletal soils where *Agathis australis* grows or formerly grew, and the small-leaved xeromorphic *P. divaricatum*, *P. rigidum*, *P. crassicaule*, and *P. anomalum* occur on skeletal mountain and volcanic soils.

GEOLOGICAL HISTORY:

The literature on past land connections of Australia and New Zealand is large (Benson¹¹⁷, David^{118, 119}, Marwick¹²⁰, Merrill¹²¹, Oliver¹²², Skottsberg¹²³), and the diastrophic paleontologic, faunal, and floristic evidence is substantial. It is generally accepted that there have been no land connections between Australia and Asia in Tertiary and recent times (David¹²⁴, Diels¹²⁵, Merrill¹²⁶), and it is usually implied or stated that the present land area of the Australian continent has remained above water throughout Tertiary and Recent periods, save for temporary marginal incursions. The scanty relics of Upper Cretaceous floras are sufficient to show that flowering plants were established on the Australian land area prior to the Tertiary, and studies of more recent floras indicate that the flowering plants experienced significant climatic modifications in the post-Tertiary.¹²⁷

I can find no reference to fossil forms of the Pittosporaceae in Australian paleobotanical papers. Cookson and Couper¹²⁸ informed me that pollens of the Pittosporaceae are not used as indicators in Australian and New Zealand Tertiary pollen studies, and that their absence from published species lists has no significance. The well-marked morphological characters of the Australian species and the large geographical areas of most of the populations indicate that the group has evolved in isolation over a comparatively long period. I suggest that these morphological and geographical characteristics are indicative, and perhaps typical, of evolution under continental conditions.

In a recent discussion of the geological history of New Zealand with reference to the origin and history of the fauna and flora, Fleming¹²⁹ emphasized that the New Zealand area has long been a relatively isolated archipelago of islands. He

¹¹⁷ Gedenboek, Dr. R.D.M. Verboek, etc. p.53. 1925.

¹¹⁸ Geology of the Commonwealth of Australia. 3 vols. 1950.

¹¹⁹ Tuatara 2:72. 1949.

¹²⁰ N.Z. Jour. Sci. & Tech. 11: 202. 1929.

¹²¹ Far Eastern Quart. 2:66. 1942.

¹²² Jour. Linn. Soc. Lond. Bot. 47: 99. 1925.

¹²³ Plant World 18:129. 1915.

¹²⁴ *loc. cit.* chap. 15. 1950.

¹²⁵ Essays on Geobotany in honor of W. A. Setchell. p.194. 1936.

¹²⁶ *loc. cit.* 1942.

¹²⁷ David, *loc. cit.* p. 650. 1950; Gill, in Austral. Jour. Sci. 15: 47. 1952; Crocker and Wood, in Trans. Roy Soc. S. Austr. 71:91. 1947.

¹²⁸ Personal communications.

¹²⁹ Tuatara 2:72. 1949.

pointed out that the frequent changes in the size and relations of the islands may have played a significant role in the formation of races species of plants and animals. Marked climatic changes since the Cretaceous epoch are indicated by faunal changes in the fossil record¹³⁰, and several post-glacial, climatic fluctuations are reflected in the sequence of pollens found by Von Post and Cranwell¹³¹ in peat deposits and in profiles of soils studied by Raeside¹³².

Arber¹³³ found two dicotyledons in rocks of Jurassic or lower Cretaceous age, and Couper¹³⁴ found Angiosperm pollens in coals of early Cretaceous-Eocene age. *Pittosporum* leaves have been found in beds of lower Oligocene, lower Miocene and upper Pliocene age by Oliver¹³⁵, and in beds of upper Pliocene or lower Pleistocene age by McQueen¹³⁶.

In the discussion of the distribution pattern of New Zealand species of *Pittosporum* it was noted that endemism is high, intergrading forms are common, and geographic ranges are small. Apparently these characteristics are the result of a long period of evolution in a changing and relatively isolated archipelago under fluctuating climatic conditions, and I suspect that they are typical of most species formed under insular conditions. It is possible, of course, that the differences noted between the species of *Pittosporum* occurring in Australia and those found in New Zealand are due mainly to the continental outlook of Australian taxonomists and the more insular attitude of New Zealand botanists!

In a discussion of the floras of Madagascar and New Caledonia, Good¹³⁷ observed that the relative situations of the two groups of islands to the continents of Africa and Australia respectively are very similar, that the physiographic structure of the main islands is curiously alike, that the climatic types correspond, and that both possess floras with a large number of endemic species. Twenty Old World (African-Asiatic-Australian) genera have complexes of endemic species in Madagascar and New Caledonia, and Good cited *Pittosporum* as the most interesting of them, a citation which I heartily endorse. He suggested, however, that these curious similarities are the result of past land movements, or continental drift, and this I must question. If the distribution of the genus *Pittosporum* is used as evidence, the range of all species should be considered. Lists of closely allied species given previously link the various centers of development of the genus and suggest that extensive movements of the land horizontally are not required to explain the present distribution of the genus in Madagascar and New Caledonia.

¹³⁰ Fleming, in Tuatara, *loc. cit.* 1949.

¹³¹ Geograf. Ann. Heft. 3-4: 308. 1936.

¹³² Trans. Roy. Soc. N.Z. 77: 153. 1948.

¹³³ N.Z. Geol. Surv. Pal. Bull. 6. 1917. McQueen (Nature 175:177. 1955) said that the slab studied by Arber came from Upper Cretaceous beds and that the earliest New Zealand angiosperms are Cretaceous in age.

¹³⁴ N.Z. Sci. Rev. 9: 5. 1951, and N.Z. Geol. Surv. Pal. Bull. 22 (in press).

¹³⁵ N.Z. Inst. Trans. & Proc. 23: 276. 1891; and 59: 287. 1928; Tuatara 3: and 1 and 8, 1950.

¹³⁶ Personal communication.

¹³⁷ Blumea 6: 470. 1950.

Chevalier¹³⁸ considered *Pittosporum* to be a South Oceanic genus and remarked:

. . . le grande foyer de dispersion du genre *Pittosporum* ce sont l'Australie et les îles du Pacifique. Du reste, sur 10 genres que compte la famille des Pittosporées, 8 sont endémiques en Australie, le genre *Pittosporum* est aussi en grande partie pacifico-australien, le dixième genre *Tribeles* phil. (= *Chalepoa* Hook. f.) avec une unique espèce *Tribeles australis* Philippi (= *Chalepoa antarctica* Hook. f.) est confiné à la partie extrême Sud de l'Amérique (sud du Chili jusqu'à l'île Chiloé, Patagonie et île Clarence). Il semble donc que les *Pittosporum* ont essaimé des terres australes vers l'Asie, d'une part, et vers l'Afrique, d'autre part; une seule Pittosporée est parvenue en Amérique australe, à sa pointe extrême.

Engler¹³⁹ placed *Tribeles* in the subfamily ESCALLONIOIDEAE of the Saxifragaceae, however, and while that family may be related to the Pittosporaceae, there is no certain evidence that the Pittosporaceae are represented in South America. Furthermore, the development of the Pittosporaceae in Australia and New Zealand is not evidence that the family originated in that part of the world. The determination of the center of origin for the family must await the progress of paleobotany, cytology, and possibly plant exploration. For example, further field work in the New Guinea-New Caledonia area is likely to yield further novelties and throw new light on the distribution of the Pittosporaceae.

INTERRELATIONS OF THE SPECIES

Methods by which a pictorialized scatter diagram is developed are explained in Anderson^{140, 141} and Anderson and Gage¹⁴². The figures listed in Table I are the maximum measurements made of capsule width and the averages of the measurements made of petal length, sepal length and petal width for the taxonomic treatment. The averages are the means of the actual measurements made on the herbarium material cited in the text.

The measurements have been plotted as a pictorialized scatter diagram (fig. 7), to facilitate an understanding of the relationships of the species and subspecies of *Pittosporum*. Petal width and capsule width were chosen as abscissa and ordinate respectively because they varied consistently within each species and could be measured accurately. The other three characters were indicated by rays from each dot on the diagram. The number alongside each dot refers to the species in the taxonomic treatment. Limits of the three grades of each character were chosen so that extremes associated with higher values for petal width and capsule width are indicated by long rays and extremes associated with lower values for petal width and capsule width are represented without rays.

¹³⁸ Bull. Soc. Bot. Fr. 93: 205. 1946.

¹³⁹ Engl. & Prantl's, Nat. Pflanzenfam. ed. 2. 18a: 213. 1930.

¹⁴⁰ Introgressive hybridization. 1949.

¹⁴¹ Plants, Man and Life. 1952.

¹⁴² Amer. Jour. Bot. 39: 399. 1952.

At one extreme, the upper right-hand corner of each diagram, are the species with petals and sepals which are markedly long and capsules which are three-valved and markedly broad. In the New Zealand diagram most of the species at this extreme are in the series TRIVALVAE. In the Australian diagram the species numbered 1 and 2 (*P. bracteolatum* of Norfolk Island and *P. erioloma* of Lord Howe Island) are in the TRIVALVAE; the other species of this extreme are in the BIVALVAE, but approach the TRIVALVAE closely.

At the other extreme, the lower left-hand corner of the diagram, are the species with petals and sepals which are markedly short and capsules which are two-valved and markedly narrow. In the New Zealand diagram most of the species at this extreme are small-leaved, dwarf members of the BIVALVAE with small fascicles or solitary flowers. In the Australian diagram most of the species at this extreme are large-leaved tall members of the BIVALVAE with spreading compound inflorescences. Species numbered 12, 15, 13, 16, and 14 on the New Zealand diagram (*P. umbellatum*, *P. patulum*, *P. virgatum*, *P. turneri* and *P. pimeleoides* respectively) show a proportionate reduction in all characters illustrated, from the upper right-hand extreme to the lower left-hand extreme, and may connect the series TRIVALVAE and the small-leaved dwarf members of the BIVALVAE. The variety of leaf-forms in these five species has been illustrated previously and the suggestion has been made that the leaf forms indicate the direction of evolution in the New Zealand species.

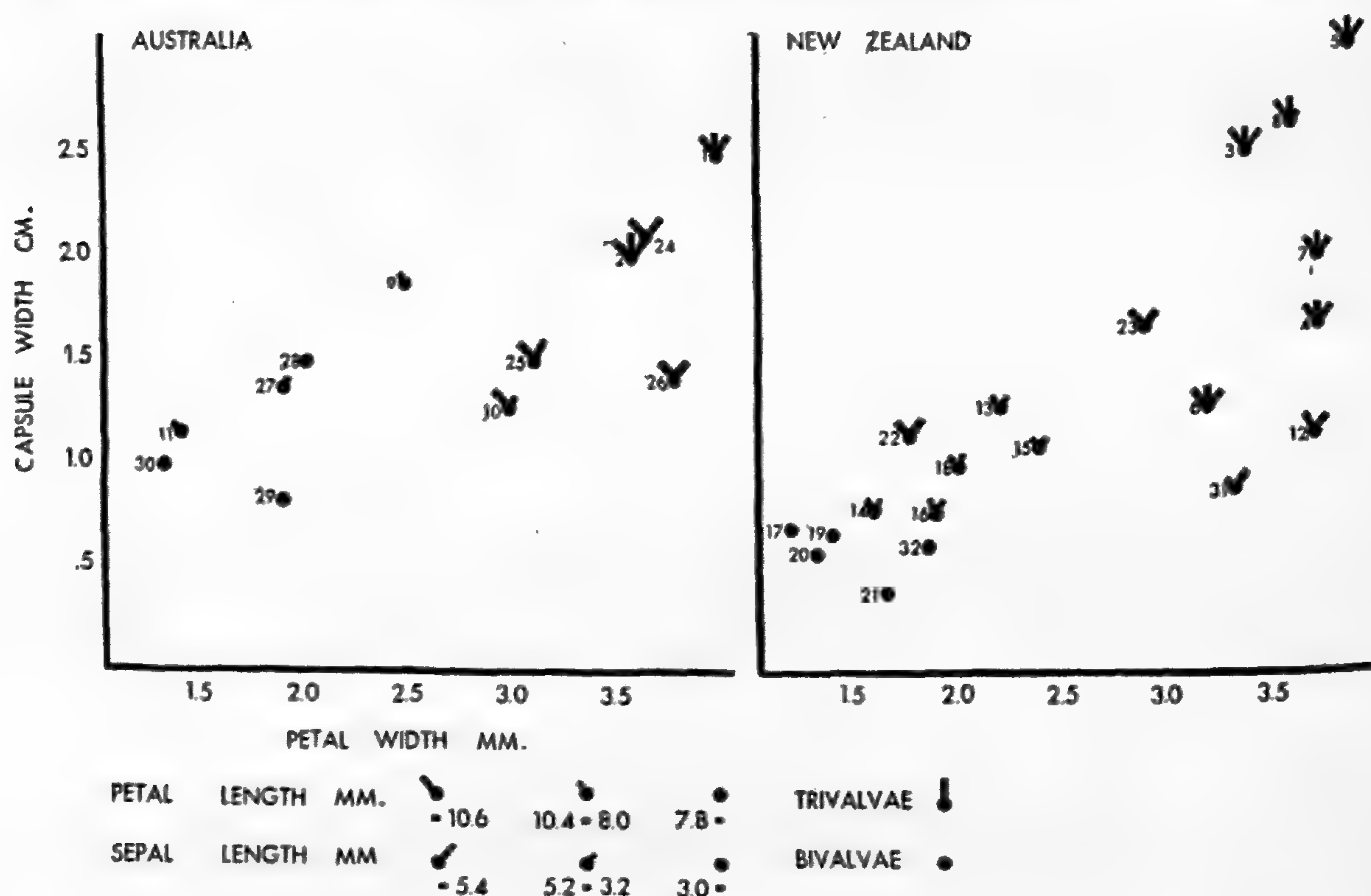


Fig. 7. Pictorialized scatter diagram of information contained in Table I, showing relationships of 32 species of *Pittosporum* as indicated by capsule width and by measurements of petals and sepals. Horizontal axis, petal width; vertical axis, capsule width. Petal length and sepal length are diagrammed by rays as explained on the diagram. Numbers beside dots refer to the position of the species in the taxonomic treatment.

TABLE I
AVERAGE MEASUREMENTS OF THE AUSTRALIAN AND NEW ZEALAND
SPECIES OF *PITTOSPORUM*

Species	Petal length mm.	Petal width mm.	Sepal length mm.	Valve number	Capsule width cm.
1. <i>P. bracteolatum</i>	17.0	4.0	10.7	3	2.5
2. <i>P. erioloma</i>	16.0	3.6	6.2	3	2.0
3. <i>P. fairchildii</i>	11.8	3.4	5.6	3	2.5
4. <i>P. ellipticum</i>	15.3	3.7	9.3	3	1.7
5. <i>P. crassifolium</i>	13.6	3.9	9.3	3	3.0
6. <i>P. ralphii</i>	14.8	3.2	8.7	3	1.3
7. <i>P. buttonianum</i>	15.6	3.7	7.1	3	2.0
8. <i>P. tenuifolium</i>					
ssp. <i>tenuifolium</i>	10.8	3.6	4.5	3	2.6
ssp. <i>colensoi</i>					
9. <i>P. phillyraeoides</i>	10.1	2.5	2.6	2	1.9
10. <i>P. bicolor</i>	11.2	3.0	4.2	2	1.3
11. <i>P. o'reillyanum</i>	9.2	1.4	1.9	2	1.2
12. <i>P. umbellatum</i>	11.5	3.7	7.1	2	1.2
13. <i>P. virgatum</i>	10.0	2.2	4.6	2	1.3
14. <i>P. pimeleoides</i>					
ssp. <i>pimeleoides</i>	9.7	1.6	4.0	2	.8
ssp. <i>major</i>					
15. <i>P. patulum</i>	10.0	2.4	4.9	2	1.1
16. <i>P. turneri</i>	8.1	1.9	4.0	2	.8
17. <i>P. obcordatum</i>	5.8	1.2	2.1	2	.7
18. <i>P. rigidum</i>	9.8	2.0	3.9	2	1.0
19. <i>P. crassicaule</i>	5.4	1.4	1.5	2	.7
20. <i>P. divaricatum</i>	5.2	1.3	1.9	2	.6
21. <i>P. anomalum</i>	3.4	1.7	1.9	2	.4
22. <i>P. cornifolium</i>	11.1	1.8	5.7	2	1.2
23. <i>P. kirkii</i>	17.6	2.9	8.6	2	1.7
24. <i>P. revolutum</i>	15.1	3.7	6.0	2	2.1
25. <i>P. rubiginosum</i>					
ssp. <i>rubiginosum</i>	13.0	3.1	6.8	2	1.5
ssp. <i>wingii</i>					
26. <i>P. undulatum</i>	13.7	3.8	7.9	2	1.4
27. <i>P. venulosum</i>	7.9	1.9	4.1	2	1.4
28. <i>P. melanospermum</i>	7.6	2.0	1.7	2	1.5
29. <i>P. rhombifolium</i>	6.3	1.9	1.6	2	.8
30. <i>P. ferrugineum</i>	7.5	1.3	2.9	2	1.0
31. <i>P. dallii</i>	8.7	3.3	5.7	2	.9
32. <i>P. eugenoides</i>	6.2	1.8	2.3	2	.6

Species numbered 22 and 23 (*P. kirkii* and *P. cornifolium*) are rather isolated, very similar in their rays, and are both epiphytic. Species numbered 31, 32 and 21, (*P. dallii*, *P. eugenoides* and *P. anomalum*), are somewhat isolated and are the three species in which capsules with a persistent papery endocarp are found.

In the Australian diagram, species numbered 10, 9, and 11 (*P. bicolor*, *P. phillyraeoides*, and *P. o'reillyanum*) show a similar proportionate reduction to that noted for the New Zealand *P. umbellatum* - *P. pimeleoides* group. The remaining Australian species fall into two groups. The first group is characterized by petals and sepals which are long and broad. Associated characters are few flowers and lobed, ellipsoid or ovoid capsules. The second group is characterized by petals and

sepals which are small and narrow. Associated characters are very numerous flowers and usually smaller globose or obovoid capsules.

Group 1

24. *P. revolutum*
25. *P. rubiginosum*
26. *P. undulatum*

Group 2

27. *P. venulosum*
28. *P. melanospermum*
29. *P. rhombifolium*
30. *P. ferrugineum*

Many years ago, Bentham¹⁴³ recognized that *P. revolutum*, *P. rubiginosum* and *P. undulatum* had characters in common, and that *P. rhombifolium*, *P. melanospermum* and *P. ferrugineum* had some general affinity, but, apart from his key and arrangement of species, he did not express his views on the relationship of the species.

The significance of the pictorialized scatter diagram is that it shows a high degree of correlation among the characters employed, and strongly supports the key and taxonomic arrangement. Moreover, since the diagram is based on actual measurements, the results expressed therein are repeatable.

STUDY MATERIALS

Specimens from the herbaria of the following institutions have been studied, and the symbols¹⁴⁴ employed in their citation are indicated.

- A —Arnold Arboretum of Harvard University, Cambridge, Mass.
AK —Auckland Institute and Museum, Auckland, New Zealand.
BH —Bailey Hortorium, Cornell University, Ithaca, N.Y.
BISH —Bernice P. Bishop Museum, Honolulu, Hawaii.
BM —British Museum (Natural History), London, England.
BRI —Department of Agriculture, Brisbane, Australia.
CANB —Division of Plant Industry, CSIRO, Canberra, Australia.
CANTY —Canterbury Museum, Christchurch, New Zealand.
CU —Wiegand Herbarium, Cornell University, Ithaca, N.Y.
F —Chicago Natural History Museum, Chicago, Ill.
GH —Gray Herbarium of Harvard University, Cambridge, Mass.
HO —University of Tasmania, Hobart, Tasmania.
ILL —Department of Botany, University of Illinois, Urbana, Ill.
K —Royal Botanic Gardens, Kew, England.
MASS —Department of Botany, University of Massachusetts, Amherst, Mass.
MEL —National Herbarium of Victoria, Melbourne, Australia.
MO —Missouri Botanical Garden, St. Louis, Mo.
NSW —National Herbarium of New South Wales, Sydney, Australia.
P —Muséum National d'Histoire Naturelle, Laboratoire de Phanérogamie, Paris.
U —Botanical Museum and Herbarium, State University of Utrecht, Netherlands.
UMEL —Department of Botany, University of Melbourne, Melbourne, Australia.
US —Department of Botany, U. S. National Museum, Washington 25, D. C.
W —Naturhistorisches Museum, Wien, Austria.

¹⁴³ Fl. Austr. 1: 110. 1863.

¹⁴⁴ Lanjouw & Stafleu, Reg. Veg. Index Herbariorum Pt. 1. The herbaria of the world, ed. 2. 1954.

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I wish to acknowledge my indebtedness to the curators of the herbaria listed above for the loan of specimens and other courtesies. The Director and staff of the Auckland Museum, and many Australian and New Zealand friends, have supplied me with specimens and information. I am also indebted to Dr. Egbert Walker of the U.S. National Museum and to Dr. F. Raymond Fosberg of the U.S. Geological Survey for sponsoring my visit to the United States, and to the Director and staff of the Missouri Botanical Garden, and to the Dean and staff of the Henry Shaw School of Botany, for many kindnesses during my stay. Finally, I must express my great obligation to Dr. Robert E. Woodson, Jr., of the Missouri Botanical Garden, who made my visit to the United States possible and for whose assistance and advice I cannot be sufficiently grateful.

TAXONOMY

PITTOSPORUM Banks & Soland. ex Gaertn. Fruct. et Sem. 1: 286. *t.* 59. 1787-88
(*T.*: *P. tenuifolium*). Banks & Soland.

Pittosporoides Banks & Soland. ex Gaertn. Fruct. et Sem. 1: 286. 1787-88, *nom. nud. in synonym.*

Erect trees or shrubs, rarely prostrate or epiphytic, pubescent or glabrous, unarmed or spinose. Leaves alternate, occasionally subverticillate, usually entire, petiolate, rarely sessile. Inflorescence terminal, terminal and lateral, or axillary, few to many-flowered, in fascicles or in umbelliform to paniculiform cymes, or solitary. Sepals 5, free, coherent or rarely connate. Petals 5, free or connivent, tips spreading or recurved. Stamens 5, erect; anthers 2-celled, introrse. Ovary sessile or stipitate, incompletely 2- to 4-celled; stigma capitate to truncate; style usually short. Capsule globose, ovoid, or obovoid, 1-celled; valves 2 - 5, woody or coriaceous, with a median longitudinal parietal placenta. Seeds immersed in a resinous viscid fluid.

The synonymy of *Pittosporum* is given in full by Pritzel¹⁴⁵.

KEY TO THE SERIES

- Capsules 3-valved, rarely 4- or 2-valved; seeds many; sepals and petals relatively large; sepals pubescent (puberulent to glabrous in *P. tenuifolium*). Norfolk Island, Lord Howe Island, and New Zealand. I. TRIVALVAE
Capsules 2-valved, rarely 3-valved; seeds few; sepals and petals relatively small; sepals minutely puberulent or glabrous (pubescent in *P. rubiginosum*, *P. venulosum* and *P. virgatum*). Australia and New Zealand II. BIVALVAE

¹⁴⁵ Engler & Prantl, Nat. Pflanzenfam. ed. 2. 18a:273. 1930.

SERIES I. TRIVALVAE

SERIES I. TRIVALVAE Gowda, in Jour. Arnold Arb. 32:284. 1951.

KEY TO THE SPECIES

- a. Petals cream-white or yellow-green; sepals glabrous or scantily pubescent without; flowers terminal, 1-8, fascicled; capsules globose to pyriform; valves usually convex in transverse section with a placenta bearing funicles from the base to the apex. Norfolk and Lord Howe Islands.
- b. Trees to 7 m. tall; leaves acuminate, 5-11 cm. long, 2.0-3.6 cm. broad; sepals linear, acuminate, 10.0-13.5 mm. long, 2.5-3.0 mm. broad, with a few hairs on the main vein without, glabrous within; petals yellow-green; capsules globose to pyriform, 2.0-3.5 cm. long, 1.5-2.5 cm. broad, without persistent dried sepals. Norfolk Island1. *P. bracteolatum*
- bb. Shrubs to 5 m. tall; leaves acute, 3-5 cm. long, 1.0-1.8 cm. broad; sepals lanceolate, acute, 4-8 mm. long, 1.5-2.5 mm. broad, glabrous without, brown-tomentose within; petals cream-white with a reddish claw; capsules usually globose, 1.3-2.0 cm. in diameter, often with persistent dried sepals. Lord Howe Island.....2. *P. erioloma*
- aa. Petals purple, reddish-brown, or red; sepals pubescent without (scantily puberulent to glabrous in *P. tenuifolium*); flowers terminal or axillary, 1-10, fascicled or solitary; capsules subglobose or trigonous, rarely 2- or 4-lobed; valves convex to concave in transverse section with a placenta bearing funicles from the base to about the middle (to the apex in *P. fairchildii*). New Zealand
- b. Flowers in terminal fascicles of 2-10, rarely solitary; capsules relatively large and thick.
- c. Capsules subglobose; valves convex in transverse section, 1.5-2.0 mm. thick at margins; flowers up to 6 per fascicle; petals purple, reddish-brown, or chocolate.
- d. Shrubs 3-5 m. tall; flowers 2-4; sepals lanceolate, acute, 4-7 mm. long, brown-tomentose without, glabrous within; petals purple; capsules 3-valved; valves not markedly thickened at apex, bearing minute funicles from the base to the apex; seeds black, round. Three Kings Islands.....3. *P. fairchildii*
- dd. Trees to 8 m. tall; flowers 2-6; sepals linear, acuminate, 8-11 mm. long, rusty-tomentose without and to near the base within; petals reddish-brown to chocolate; capsules 3- or 2-valved; valves much thickened at apex, bearing flattened funicles up to 1 mm. long from the base to the middle; seeds reddish-black, irregular. North Auckland, Auckland, Thames and East Cape4. *P. ellipticum*
- cc. Capsules trigonous, rarely 2- or 4-lobed; valves concave in transverse section, 2-3 mm. thick at margins; flowers up to 10 per fascicle; petals dark red to purple.
- d. Shrubs to small trees 1-10 m. tall; leaves obovate to oblanceolate, 3-8 cm. long, 1-3 cm. broad, attenuate at base, with strongly thickened and revolute margins, secondary veins about 5 per side; flowers 1-10; sepals oblong to linear-lanceolate, acute, brown-tomentose without and above the middle within; capsules 1-3 cm. long and broad; valves 2-3 mm. thick, woody, with a placenta bearing conspicuous funicles. North Auckland, Auckland, and Thames, on the coast. Kermedec Islands.....5. *P. crassifolium*
- dd. Shrubs 2.5-4.0 m. tall; leaves oblong to obovate, 4-12 cm. long, 2-4 cm. broad, acute to obtuse at base, with unthickened flat or revolute margins, secondary veins 9-12 per side; flowers 2-10; sepals linear, acuminate, white-tomentose without, tomentulose within; capsules 1.1-1.7 cm. long, 9-13 mm. broad; valves about 2 mm. thick, subwoody to coriaceous, with a placenta bearing inconspicuous funicles. Wanganui, Central Volcanic Plateau, East Cape and Hawkes Bay, on the coast and inland.6. *P. ralphi*
- bb. Flowers in axillary fascicles of 3, or solitary, or on very reduced lateral shoots if terminal; capsules relatively small and thin.
- c. Shrubs or trees to 10 m. tall; young leaves, petioles, and sepals white-floccose-tomentose; flowers 1-3, usually subtended by 1 to several cataphylls; pedicels up to 2 cm. long; sepals oblong, acute; petals red to magenta; capsules trigonous, 1.2-2.0 cm. in diameter; valves slightly convex to flat in transverse section. Great Barrier Island and the Coromandel Peninsula.7. *P. buttonianum*

cc. Trees to 10 m. tall; young leaves and petioles brown-tomentose, sepals scantily puberulent to glabrous; flowers 1, rarely 2-3, usually subtended by a leaf; pedicels up to 1 cm. long; sepals ovate to oblong, sub-acute to obtuse; petals usually purple, occasionally maroon, pink, or white; capsules subglobose, 1.0-1.2 cm. in diameter; valves convex in transverse section. Throughout New Zealand8. *P. tenuifolium*

1. *PITTOSPORUM BRACTEOLATUM* Endl. Prodr. Fl. Norf. p. 78. 1833. (T.: *Bauer s.n.!*).

Trees to 7 m tall; branchlets grayish-brown, the young parts sparsely tomentulose, soon glabrate. Leaves alternate, frequently crowded at the tips of the branches, lanceolate-oblong to oblanceolate, acuminate, acute to attenuate at base, entire, 5 - 11 cm. long, 2.0 - 3.6 cm. broad, dark green above, paler beneath, glabrous, membranous, margins slightly revolute and undulate, costa immersed above, raised beneath, secondary veins 8 - 14 per side, anastomosing, obscure above, distinct beneath; petioles 4 - 9 mm. long, 1 - 2 mm. broad, sparsely tomentulose when young. Flowers terminal, 1 - 8, fascicled; pedicels 2 - 3 cm. long, accrescent and recurved in fruit, sparsely tomentulose when young, usually bearing a linear bract and subtended by a loose whorl of leaves and caducous, sparsely ciliolate bud scales about 1 cm. long. Sepals free to the base, linear, acuminate, 10.0 - 13.5 mm. long, 2.5 - 3.0 mm. broad, with a few hairs on the main vein without; petals linear, acute, 1.5 - 2.0 cm. long, 4.0 - 4.5 mm. broad, free, spreading from the base, yellow-green; stamens 7.5 - 10.0 mm. long, anthers linear-oblong or sagittiform, 1.5 - 3.0 mm. long, 0.5 - 0.8 mm. broad. Pistil at anthesis slightly shorter than the stamens; ovary 4 - 7 mm. long, 1.5 - 5.0 mm. broad, tomentose; style 4.0 - 4.5 mm. long; stigma truncate. Capsules globose to pyriform, 3-valved, 2.0 - 3.5 cm. long, 1.5 - 2.5 cm. broad, brown-tomentose, glabrate, rugose; valves convex to slightly sulcate in transverse section, 3 - 5 mm. thick, woody, light yellow within, with a conspicuous placenta bearing 2 rows of short stout funicles from the base to the apex; seeds about 70, reddish-black, round to irregular.

Found only on Norfolk Island. Flowers in the winter months (June to August).

NORFOLK ISLAND: *Bauer s.n.* (K); in woods, *A. Cunningham* 26 (K); *Backhouse* 669 (K); on the margins of woods, *A Cunningham s.n.*, 138 (K); *Mueller s.n.* (K); *Maiden & Boorman s.n.* (BM, K); *Paterson s.n.* (BM).

A flower which may have been female had a plump ovary 7 mm. long and 5 mm. broad, stamens 7.5 mm. long, and sagittiform, probably abortive, anthers 1.5 mm. long. The style was missing. Flowers which may have been male had slender ovaries 3.5 - 4.5 mm. long, 1.5 - 2.0 mm. broad, stamens 8.5 - 10.0 mm. long, and linear-oblong anthers 2.5 - 3.5 mm. long. The styles were 3.5 - 4.5 mm. long and the stigma was truncate.

2. *PITTOSPORUM ERIOLOMA* Moore & F. Muell. in F. Muell. Frag. Phyt. Austr. 7: 139. 1871. (T.: *Fullager s.n.!*).

Shrubs 2 - 5 m. tall; branchlets grayish-brown, the young parts brown-tomentose, soon glabrate. Leaves approximately verticillate, oblanceolate to obovate,

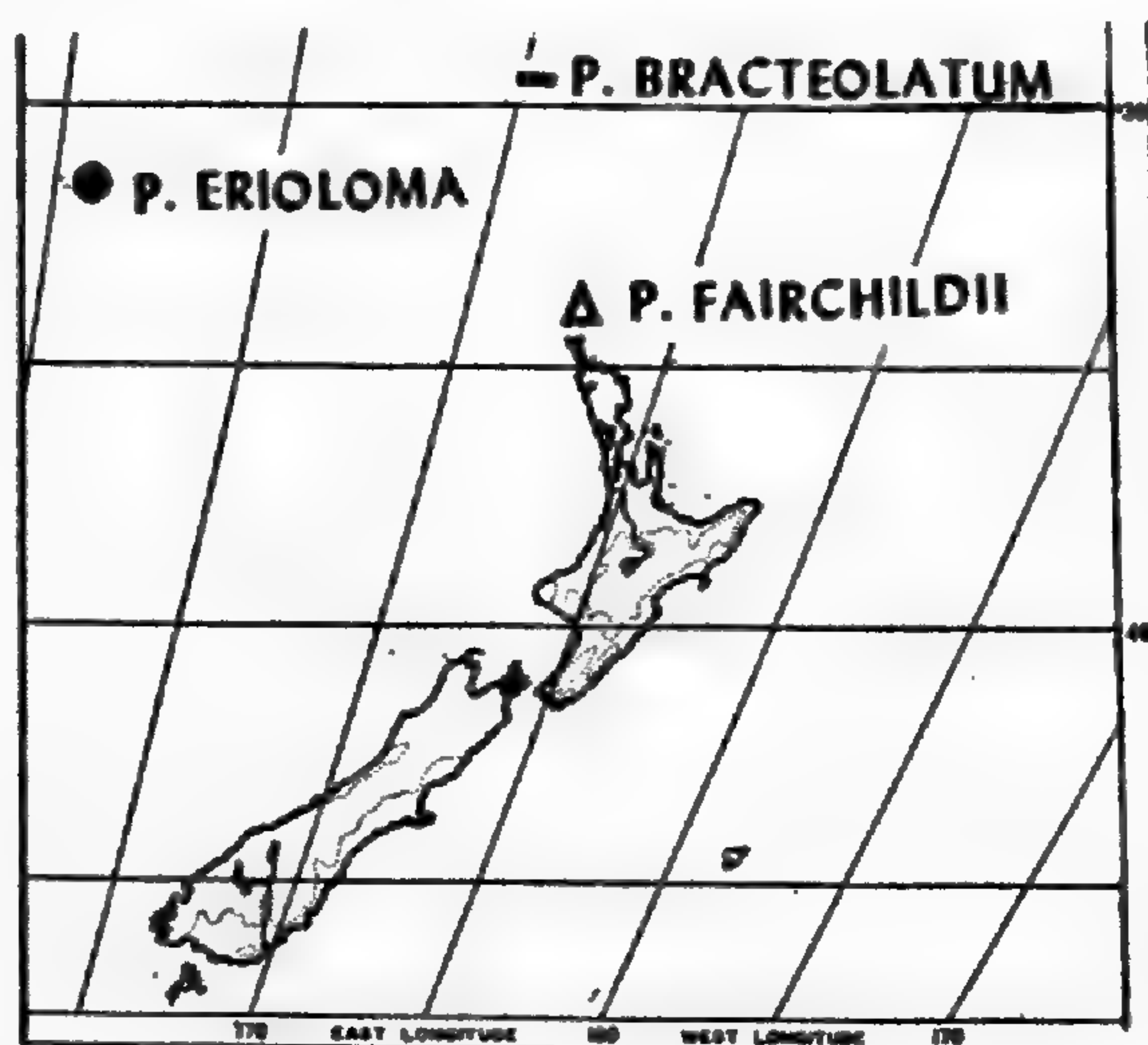


Fig. 8. *P. bracteolatum*, *P. erioloma*, and *P. fairchildii*.

acute at the apex and base, entire, or occasionally toothed or lobed when juvenile, 3-5 cm. long, 1.0-1.8 cm. broad, dark green above, paler beneath, glabrous, coriaceous, margins ciliate when young, glabrate, thickened and revolute when mature, costa raised above and beneath, secondary veins 7 - 9 per side, anastomosing, obscure above, distinct beneath; petioles 2 - 7 mm. long, 1 - 2 mm. broad, brown-tomentose when young. Flowers terminal, 2 - 7, fascicled; pedicels 1 - 2 cm. long, accrescent and recurved in fruit, brown-tomentose, subtended by a whorl of leaves and caducous, ciliate bud scales about 3 mm. long. Sepals imbricate at base, lanceolate, acute, 4 - 8 mm. long, 1.5 - 2.5 mm. broad, ciliate, glabrous without, brown-tomentose within; petals lanceolate-oblong, subacute, 15 - 18 mm. long, 3 - 4 mm. broad, free or coherent at the base, spreading from above the middle, cream-white with a reddish claw; stamens 7 - 11 mm. long, anthers sagittiform or elliptic-oblong, 1.5 - 3.5 mm. long, 0.5 - 1.00 mm. broad. Pistil at anthesis slightly shorter or longer than stamens; ovary 3 - 6 mm. long, 1 - 3 mm. broad, tomentose; style 2.0 - 4.5 mm. long; stigma 3-lobed and capitate, or truncate. Capsules globose, rarely subglobose or 3-lobed, 3-valved, 1.3 - 2.0 cm. in diameter, glabrous, rugose to slightly rugose, often accompanied by the persistent dried sepals; valves usually convex in transverse section, 3 - 6 mm. thick, coriaceous, light yellow within, with a conspicuous placenta bearing 2 rows of short stout funicles from the base to near the apex; seeds 11 - 23, black, round to irregular.

Mounts Lidgebird and Gower on Lord Howe Island; most common at elevations above 300 m. in "moss forest". Flowers during September and October.

LORD HOWE ISLAND: summit of Mt. Lidgebird, *Fullager s.n.* (MEL); *Fitzgerald s.n.* (AK); *King s.n.* (NSW); 600' to 1800', Mt. Lidgebird, *McComish 136, 136a* (K, NSW); summit of Mt. Gower, *Hedley & Dunn s.n.* (NSW); 1000', *Boorman s.n.* (NSW); Howe's Island, *Moore 9, 23* (K).

Flowers with 3-lobed capitate stigmas which protrude beyond the stamens, broad filaments, and small sagittiform anthers may be female as the anthers appear to be abortive. Flowers with truncate stigmas which do not protrude beyond the

stamens, narrower filaments, and larger elliptic-oblongoid anthers may be male as the ovary is small and thin.

Vernacular name: Lord Howe Island's Hedge Laurel.

3. *PITTOSPORUM FAIRCHILDII* Cheesem. in N.Z. Inst. Trans. & Proc. 20: 147. 1887. (T.: *Cheeseman s.n.*!).

Shrubs 3 - 5 m. tall; branchlets gray to brownish-gray, the young parts white-tomentose, soon glabrous. Leaves alternate, frequently crowded at the tips of the branches, obovate, elliptic-obovate or elliptic-oblong, obtuse or acute at apex, acute at base, entire, 4 - 7 cm. long, 2.0 - 3.5 cm. broad, light green above, paler beneath, white- to brown-tomentose when young, soon glabrous above but tomentulose beneath when mature, coriaceous, revolute, costa raised, secondary veins 7 - 11 per side, anastomosing, distinct; petioles 3 - 8 mm. long, 0.5 - 2.0 mm. broad, white- to brown-tomentose. Flowers terminal, 2 - 4, fascicled; pedicels 12 - 20 mm. long, accrescent in fruit, brown-tomentose, subtended by a whorl of leaves and caducous ciliate bud scales 5 - 10 mm. long. Sepals imbricate at base, lanceolate, acute, 4-7 mm. long, 2.0-3.5 mm. broad, brown-tomentose without, glabrous within, ciliate; petals lanceolate-oblong, subacute, 9 - 14 mm. long, 2.5 - 4.5 mm. broad, free, spreading from above the middle, purple; stamens 7.0 - 8.5 mm. long anthers sagittiform or elliptic-oblong, 1.5 - 2.5 mm. long, 0.5 - 1.3 mm. broad. Pistil at anthesis slightly longer to slightly shorter than the stamens; ovary 2.5 - 6.0 mm. long, 2 - 4 mm. broad, brown-tomentose; style 3 - 4 mm. long; stigma weakly capitate to truncate. Capsules subglobose, 3-valved, 2.0 - 2.5 cm. in diameter, tomentose, glabrate, rugose; valves convex in transverse section, 1.5 - 2.0 mm. thick, coriaceous, with a conspicuous placenta bearing two rows of minute funicles from the base to the apex; seeds 19 - 22, black, round.

Flowers in August.

NEW ZEALAND: THREE KINGS ISLANDS: Great Island, *Cheeseman, s.n.* (AK, BM, K); *Baylis 22797* (AK); *Turbott 23023* (AK); *Turbott & Bell 22925* (AK); North East Island, *Buddle 22894* (AK).

Flowers which may be female have sepals up to 6.5 mm. long, petals up to 14 mm. long, sagittiform anthers only about 1.5 mm. long, weakly capitate stigmas exserted beyond the anthers, thin styles up to 3 mm. long, and stout ovaries 6 mm. long and 4 mm. broad. Flowers which may be male have sepals 4 - 7 mm. long, petals 9 - 13 mm. long, elliptic-oblong anthers about 2.5 mm. long, truncate stigmas level with or below the anthers, thicker styles 3.5 - 4.0 mm. long, and thin ovaries about 3.5 mm. long and 2.0 - 2.5 mm. broad.

Cultivated specimens from the Botanic Gardens, Cambridge (England), have been seen, *without collector s.n.* (K).

4. *PITTOSPORUM ELLIPTICUM* Kirk, in N.Z. Inst. Trans. & Proc. 4: 267. 1872. (T.: *Kirk s.n.*!).

Pittosporum ellipticum Kirk ssp. *ellipticum* Kirk, *loc. cit.* 1872. (T.: *Kirk s.n.*!).
Pittosporum ellipticum Kirk var. *decorum* Cheeseman, Man. N.Z. Fl. ed.2. p. 491. 1925. (T.: *Cheeseman s.n.*!).

Trees to 8 m. tall; branchlets dark brown, covered with appressed rusty tomentum when young, ultimately glabrate. Leaves alternate, crowded at the tips of the branches, elliptic-oblong to ovate or obovate, acute to obtuse at apex and base, entire, 3.5 - 9.7 cm. long, 1.5 - 4.8 cm. broad, covered with appressed rusty tomentum when young, soon glabrate above, sparsely tomentose to glabrate beneath, coriaceous, margins unthickened and slightly revolute, costa raised, secondary veins 7 - 10 per side, anastomosing, obscure above, distinct beneath; petioles 4 - 15 mm. long, 1.5 - 2.0 mm. broad, rusty-tomentose. Flowers terminal, 2 - 6, fascicled; pedicels 5 - 14 mm. long, accrescent in fruit, tomentose, subtended by a whorl of cataphylls and several caducous rusty-tomentose bud scales 1 - 2 mm. long. Sepals slightly imbricate at base, linear, acuminate, 8 - 11 mm. long, 2.0 - 2.7 mm. broad, rusty-tomentose without and to near the base within, ciliate; petals oblanceolate-linear, subacute, 14.0 - 19.5 mm. long, 3.0 - 4.5 mm. broad, free, recurved at the tips, reddish-brown to chocolate; stamens 7.2 - 11.0 mm. long, anthers sagittiform to oblong, 1.2 - 3.0 mm. long, 0.5 - 1.2 mm. broad. Pistil at anthesis slightly shorter or longer than the stamens; ovary 2.5 - 7.5 mm. long, 1.5 - 4.5 mm. broad, rusty-tomentose; style 1.5 - 6.5 mm. long, stigma capitate or truncate. Capsules subglobose, 3- or 2-valved, 1.5 - 2.0 cm. long, 1.3 - 1.7 cm. broad, rusty-tomentose to glabrate, slightly rugose; valves convex in transverse section, up to 1.5 mm. thick at the margins, much thickened at the apex, almost woody, with a thin raised placenta fused at the base, bearing flattened funicles up to 1 mm. long from the base to the middle; seeds 27 - 32, reddish-black, irregular.

Occurs in the hills in the North Auckland, Auckland, South Auckland, Thames and East Cape districts of the North Island of New Zealand. Flowers from August to November.

NEW ZEALAND: NORTH AUCKLAND: Whangaroa North, *Kirk s.n.* (AK); Mt. Manaia, *Kirk s.n.* (A, AK, GH, MO), 122 (K); same locality, *Cheeseman s.n.* (AK); Whangarei, *Kirk s.n.* (A), 623 (BM). AUCKLAND: Waitakere Ranges *Cheeseman s.n.* (AK, BISH, BM, K, US); same locality, *Meebold 5389* (BISH); same locality, Nihotapu, *Matthews, LeRoy & Carse s.n.* (AK); same locality, eastern side, *Bishop s.n.* (AK); Titirangi Ranges, *Cheeseman s.n.* (GH, K); roadside cliff, Huia, *Wood 27210* (AK); Anawhata, West Coast, *Cranwell s.n.* (K). THAMES DISTRICT: Ohinemuri Gorge near Karangahake, *Cheeseman s.n.* (AK); same locality, *Petrie s.n.* (AK); Gordon Settlement, near Te Aroha, *Downard s.n.* (AK). EAST CAPE: Hawaii River, inland from Opotiki, *Field s.n.* (AK); 3000', Aorangi Scenic Reserve near Hikurangi, *Williams s.n.* (AK).

Flowers which may be male have truncate stigmas, styles 5.0 - 6.5 mm. long, ovaries 3.0 - 3.5 mm. long, about 2.5 mm. broad, and long stamens with oblong anthers up to 3 mm. long. Flowers which may be female have capitate stigmas, styles about 3 mm. long, ovaries 7.5 mm. long, 4.5 mm. broad, and short stamens with sagittiform anthers 1.2 - 1.5 mm. long, and about 0.5 mm. broad. Male flowers in which the pistil is only 4 mm. long also occur. It is difficult to decide whether this species belongs to the TRIVALVAE or BIVALVAE; Michie¹⁴⁶ has found trees with 3-valved fruits but the specimens I have seen in the Waitakere Ranges

¹⁴⁶ Personal communication.

have mostly 2-valved fruits. A yellow-flowered form is in cultivation in New Zealand.

Pittosporum ellipticum Kirk ssp. *ovatum* Kirk¹⁴⁷ is based on fruiting specimens collected at Whangaroa North over 80 years ago. Kirk¹⁴⁸ also cited Cheeseman's specimens from the Manaia Hills and the Titirangi district, but none of these match the description and the type collection from Whangaroa North. The Whangaroa district seldom has been visited by botanists and until more material is available the status of the subspecies is obscure. A specimen labelled var. *ovatum* in the Herbarium of the Royal Botanic Gardens, Kew (*Kirk 105*) resembles a broad-leaved form of *P. virgatum*.

Pittosporum ellipticum Kirk var. *decorum* Cheeseman was based on the collectings of Cheeseman, Petrie, Downard, Field, and Williams, from the Thames and East Cape districts. Cheeseman wrote:

I am greatly puzzled with var. *decorum* which agrees exactly with the type in ferruginous tomentum, but differs in the inflorescence being both terminal and lateral. It has some points of agreement with *P. buttonianum* but never has the white floccose tomentum which is such a distinctive character when *P. buttonianum* is in bloom.

Cockayne identified Petrie's specimens from Karangahake as *P. buttonianum*, but a comparison of the characters of *P. ellipticum*, Cheeseman's var. *decorum*, *P. buttonianum*, and *P. ralphii* shows that var. *decorum* has some characters in common with each of the other three species. *Pittosporum buttonianum* and *P. ellipticum* are found to the north, and *P. ralphii* to the south of Cheeseman's var. *decorum*; and this last may possibly be representative of a heterozygous population derived through introgressive hybridization of the three species. *Pittosporum buttonianum*, *P. ellipticum*, and *P. ralphii* occur mainly in areas which were not submerged in recent geological time. On the other hand, Cheeseman's var. *decorum* is found in localities which were beneath the sea during the Castlecliffian (upper Pliocene)¹⁴⁹, and it is possible that past geographical changes have been significant in the formation of the three peripheral species and the population represented by Cheeseman's var. *decorum*.

5. PITTOSPORUM CRASSIFOLIUM Banks & Soland. ex A. Cunn. in Ann. Nat. Hist. 4:106. 1839. (T.: R. Cunningham s.n.).

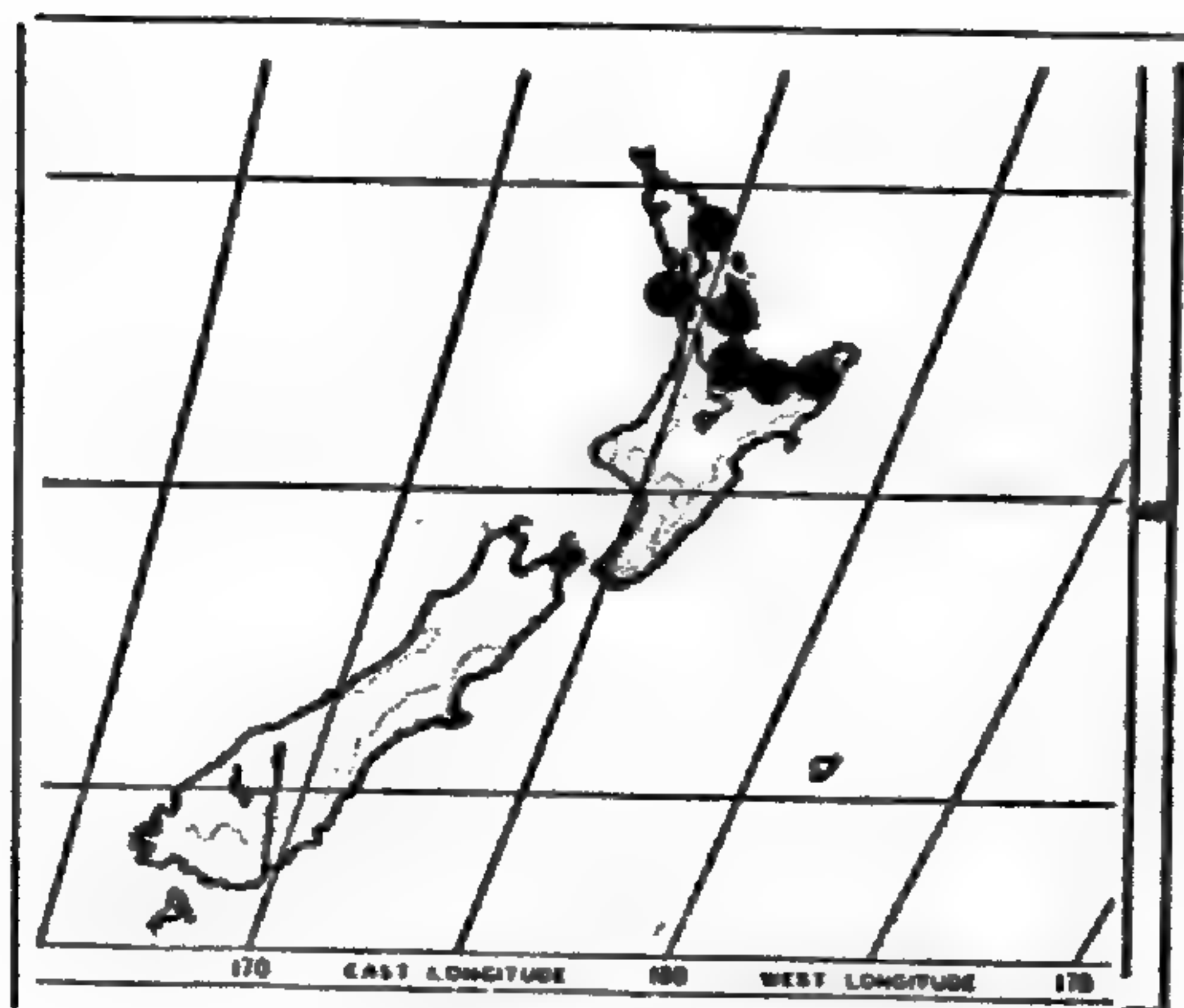
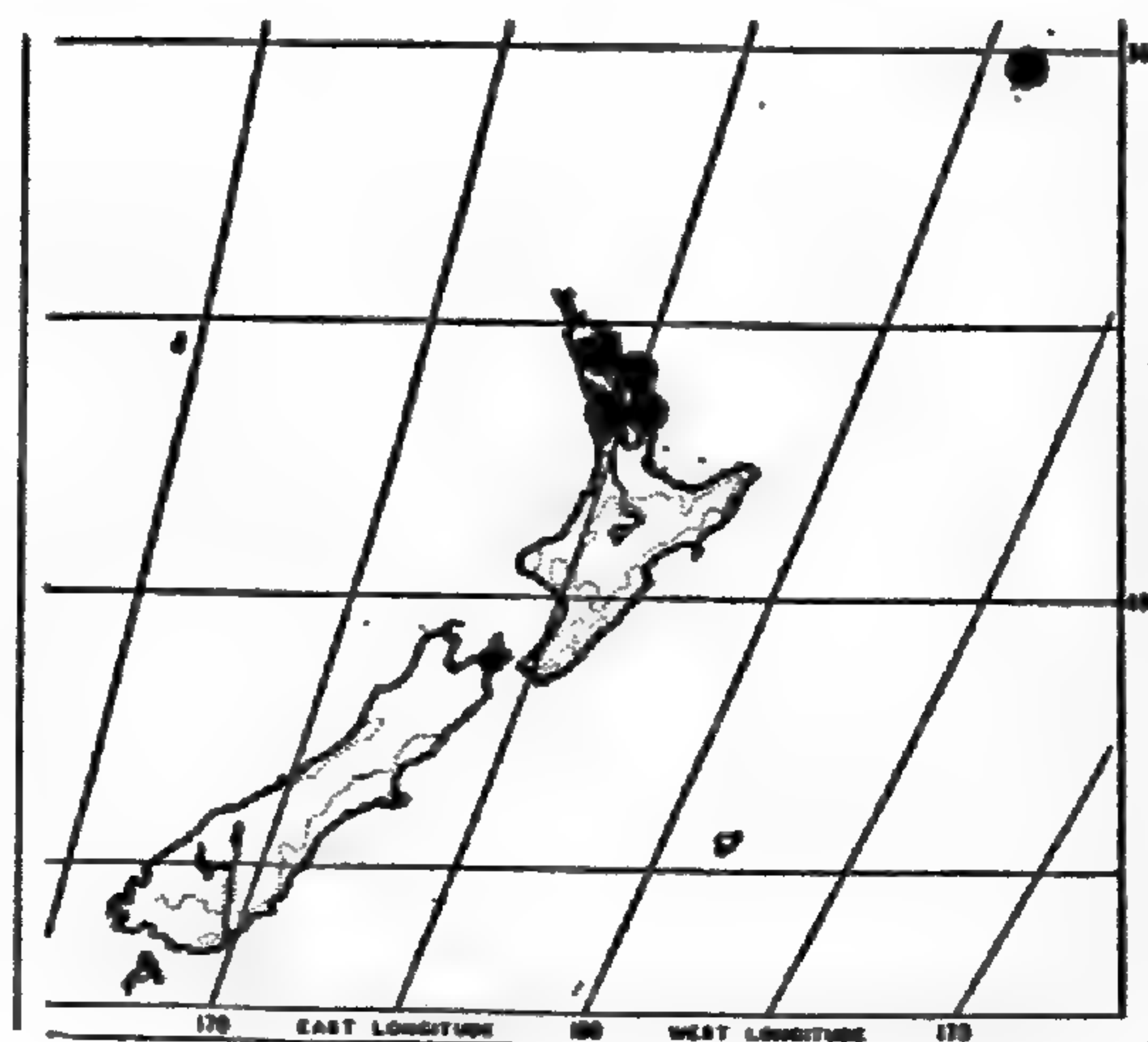
Pittosporum crassifolium var. *strictum* Kirk, in N.Z. Inst. Trans. & Proc. 4:266. 1872. (T.: Kirk s.n.).

Shrubs to small trees 1 - 10 m. tall; branchlets dark brown, the young parts white- or rusty-tomentose, becoming black. Leaves alternate, frequently crowded at the tips of the branchlets, obovate to oblanceolate, obtuse to acute at apex, attenuate at base, entire, 3 - 8 cm. long, 1 - 3 cm. broad, white- or brown-tomentose when young, soon glabrate above but densely appressed-tomentose beneath, coriaceous, margins thickened and strongly revolute, costa raised, secondary veins

¹⁴⁷ N.Z. Inst. Trans. & Proc. 4: 267. 1872. (T.: Kirk s.n.).

¹⁴⁸ loc. cit. 1872.

¹⁴⁹ Fleming, in Tuatara 2: 80. 1949.

Fig. 9. *P. ellipticum*.Fig. 10. *P. crassifolium*

about 5 per side, anastomosing, usually obscure; petioles 4 - 14 mm. long 1 - 3 mm. broad, brown-tomentose. Flowers terminal, 1 - 10, fascicled; pedicels 0.6 - 5.0 cm. long, accrescent in fruit, tomentose, subtended by a whorl of leaves and numerous caducous, brown-tomentose, ciliate bud scales 3 - 15 mm. long. Sepals imbricate at base, oblong to linear-lanceolate, acute, 7 - 11 mm. long, 1.5 - 3.0 mm. broad, brown-tomentose without, and to above the middle within, ciliate; petals oblanceolate to lanceolate, subacute, 10 - 16 mm. long, 3 - 5 mm. broad, free, recurved at the tips, dark red to purple, becoming black on drying; stamens 5 - 9 mm. long, anthers sagittiform or elliptic-oblong, 1 - 3 mm. long, 0.5 - 1.5 mm. broad. Pistil at anthesis slightly shorter or longer than the stamens; ovary 3 - 6 mm. long, 2 - 5 mm. broad, tomentose; style 3.0 - 4.5 mm. long; stigma capitate and obscurely 3-lobed or truncate. Capsules trigonous, rarely 2- or 4-lobed, 3-valved, rarely 2- or 4-valved, 1 - 3 cm. long and broad, white- to brown-tomentose, rugose; valves concave in transverse section, 2 - 3 mm. thick, woody, with a conspicuous placenta bearing short stout funicles from the base to near the apex; seeds 20 - 36, black, irregular to round.

Common on the coast of Sunday Island in the Kermadec Islands group and on the coast of the northern portion of the North Island of New Zealand. Flowers in September and October.

KERMADEC ISLANDS: SUNDAY ISLAND: northern shore, *Cheeseman s.n.* (AK, K).
 NEW ZEALAND: NORTH AUCKLAND: Waiya—Rum Bay, *Wilkes s.n.* (K); on Flat Island, one of the Cavallos, *Hamilton s.n.* (K); Bay of Islands, *R. Cunningham s.n.* or 612 (K); at Matauri, opposite the Cavallos, *R. Cunningham s.n.* or 612 (K, two labels, one *s.n.* and the other 612 are attached); Taranga (Hen) Island, *Moore & Cranwell s.n.* (AK); S.W. Island of Chickens group, *Moore & Cranwell s.n.* (AK); Southern Knight Island, Poor Knights Group, *Moore & Cranwell s.n.* (AK); Crayfish Island, 3 miles south of Helena Bay, *Olsen 10* (AK); Matakana, *Kirk s.n.* (P). AUCKLAND: Great Omaha, *Kirk s.n.* (A, GH, MO), 25 (BM); Kawau Island, *Kirk s.n.* (AK), 116 (K); David Island, *Molesworth 23320* (AK); coast near Auckland, *Cheeseman s.n.* (AK, BISH, K, NEW); same locality, *Petrie 6417* (A, NSW); Lake Pupuke, *Cheeseman s.n.* (AK, GH, NSW, US); Auckland, *Chapman s.n.* (A). THAMES: Tryphena Harbour, Great Barrier Island, *Osborne s.n.*

(AK) Great Barrier Island, *Matthews 1822* (AK); Little Barrier Island, *Kirk s.n.* (AK), 123 (K); Cape Colville, *Kirk s.n.* (US); Kennedy Bay, Coromandel, *Matthews s.n.* (AK, MO). WITHOUT DEFINITE LOCALITY: *Allison s.n.* (A, NSW); *Bidwill 198* (K); *Colenso s.n.* (K); *Cunningham 43* (U); *C. [Cunningham] 2* (NSW); *Mueller s.n.* (CU, GH); *Wilkes s.n.* (GH); *Sinclair s.n.* (BM, MO).

Flowers which appear to be female have capitate, obscurely 3-lobed stigmas, styles about 3 mm. long, and plump ovaries about 6 mm. long and 5 mm. broad. The anthers are only about 1 mm. long, sagittiform, and the filaments are about 4 mm. long, markedly broad at the base. In the material which I have examined the flowers are solitary. On *Molesworth s.n.* two or three fruits occur together, and *Cheeseman*¹⁵⁰ describes female inflorescences as 1- to 5-flowered. Pedicels are markedly shorter at anthesis but elongate in fruit. Flowers which appear to be male have truncate stigmas, styles about 3.5 - 4.5 mm. long, slender ovaries about 3 mm. long and 2 mm. broad. The anthers are 2 - 3 mm. long, elliptic-oblong, and the filaments are 5 - 6 mm. long. In the material which I have examined the inflorescences are 2- to 8-flowered but *Cheeseman*¹⁵¹ describes them as 5- to 10-flowered. The pedicels of "male" flowers are markedly longer than those of "female" flowers.

Banks and Solander collected specimens of a species of *Pittosporum* on the east coast of New Zealand in 1769 and named it *P. crassifolium in herb.* but did not publish its description and figure. Allan Cunningham applied the name to specimens collected by his brother Richard, in 1833, "on Flat Island, one of the Cavallos Group, and at Matauri, etc." In the Herbarium of the Royal Botanic Gardens, Kew, the specimens are labelled:—"On Flat Island, one of the Cavallos, *Hamilton s.n.* [Dr. Hamilton of H.M.S. Buffalo, Dec. 1833]; Bay of Islands, *R. Cunningham s.n.* [612]; at Matauri, opposite the Cavallos, *R. Cunningham s.n.* [612]". Unfortunately, these collectings were of a different species from that discovered by Banks and Solander. Plants similar to those collected by Banks and Solander were subsequently described as *P. ralphii* by Thomas Kirk (N.Z. Inst. Trans. & Proc. 3: 161. 1871).

Kirk¹⁵² described *P. crassifolium* var. *strictum* from Little Barrier Island as a variety distinguished by having several erect fruiting pedicels clustered together, and smaller capsules. Solitary and clustered fruits occur on the same plants, however, and similar small-fruited plants, which grade into the larger-fruited form, have been found in a number of localities, e.g.: on Hen and Chicken Islands (*Moore & Cranwell s.n.!*, AK); Poor Knights Islands (*Moore & Cranwell s.n.!*, AK); Great Barrier Island (*Matthews s.n.!*, AK); and Crayfish Island, 3 miles south of Helena Bay (*Olsen 10!*, AK). *Kirk 123* (K), from Little Barrier Island, is also remarkable in having pedicels up to 5 cm. long but only one collection is available. Specimens collected on the Kermadec Islands (*Cheeseman s.n.*) also have markedly

¹⁵⁰ Man. N.Z. Fl. ed. 2. p.493. 1925.

¹⁵¹ *loc. cit.* 1925.

¹⁵² N.Z. Inst. Trans. & Proc. 4: 266. 1872. (T.: *Kirk s.n.!*).

narrow leaves, strict erect fruiting pedicels clustered together, and smaller capsules as in var. *strictum*. All these collections may be distinct but in the absence of flowers of the Kermadec plants and an adequate sample of the Little Barrier population they had best be left with *P. crassifolium*.

Two horticultural varieties are available to gardeners, but are not different in any important characters. A plant with yellow flowers was found at Tryphena Harbour, Great Barrier Island, some years ago (*Osborne s.n.!*) and is known in the trade as var. *album*. A form with variegated leaves is available as var. *variegatum* (Duncan & Davies Cat. Choice Nursery Stock, 47. 1947), but is not as vigorous as plants with green leaves. The latter are extensively used in New Zealand, the south of England, Spain, and California, as ornamentals and hedge plants.

Vernacular name: *Karo*.

6. *PITTOSPORUM RALPHII* Kirk, in N.Z. Inst. Trans. & Proc. 3:161. 1871, ex char. (T.: *Ralph s.n.*).

Pittosporum crassifolium Banks & Soland. ex Kirk, Students' Flora N.Z. p. 51. 1899, *nom. nud. in synonym.*

Shrubs 2.5 - 4.0 m. tall; branchlets grayish-brown, white- to buff-tomentose, glabrate. Leaves alternate, frequently crowded at the tips of the branchlets, oblong to obovate, occasionally oblanceolate or elliptic, obtuse or acute at apex, acute or obtuse at base, entire, 4 - 12 cm. long, 2 - 4 cm. broad white- to buff-tomentose when young, soon glabrate above but densely appressed-tomentose beneath, coriaceous, margins unthickened, flat, or revolute, costa raised or immersed above, raised beneath, secondary veins about 9 - 12 per side, anastomosing, distinct in juvenile leaves, obscure in adult leaves; petioles 8 - 22 mm. long, 1 - 3 mm. broad, white- to brown-tomentose. Flowers terminal on long leading or short axillary shoots, 2 - 10, fascicled; pedicels 6 - 14 mm. long, accrescent in fruit, tomentose, subtended by a single leaf or several cataphylls and tomentose bud scales 3 - 18 mm. long, apparently pedunculate on the shedding of leaves, cataphylls, and bud scales. Sepals imbricate at base, linear, acuminate, 7 - 11 mm. long, 1.5 - 3.0 mm. broad, white-tomentose without, tomentulose within, ciliate; petals oblanceolate-linear to oblong-linear, obtuse to subacute, 11 - 18 mm. long, 2 - 4 mm. broad, free, recurved at the tips, dark red to purple; stamens 4.5 - 9.0 mm. long, anthers sagittiform to oblong, 1.0 - 3.5 mm. long, 0.5 - 1.0 mm. broad. Pistil at anthesis slightly shorter or longer than the stamens; ovary 2.5 - 4.0 mm. long, 1 - 2 mm. broad, white-tomentose; style 2 - 5 mm. long; stigma capitate. Capsules trigonous, rarely 2-lobed, 3-, rarely 2-valved, apiculate, 11 - 17 mm. long, 9 - 13 mm. broad, white-tomentose, glabrate, rugose; valves concave in transverse section, about 2 mm. thick, coriaceous to slightly woody, with a conspicuous placenta bearing minute funicles from the much-thickened base to above the middle; seeds 9 - 17, black, irregular to round.

Found from Patea and Wanganui on the west coast to East Cape and Cape Kidnappers on the east coast of the North Island of New Zealand. Flowers from October to December.

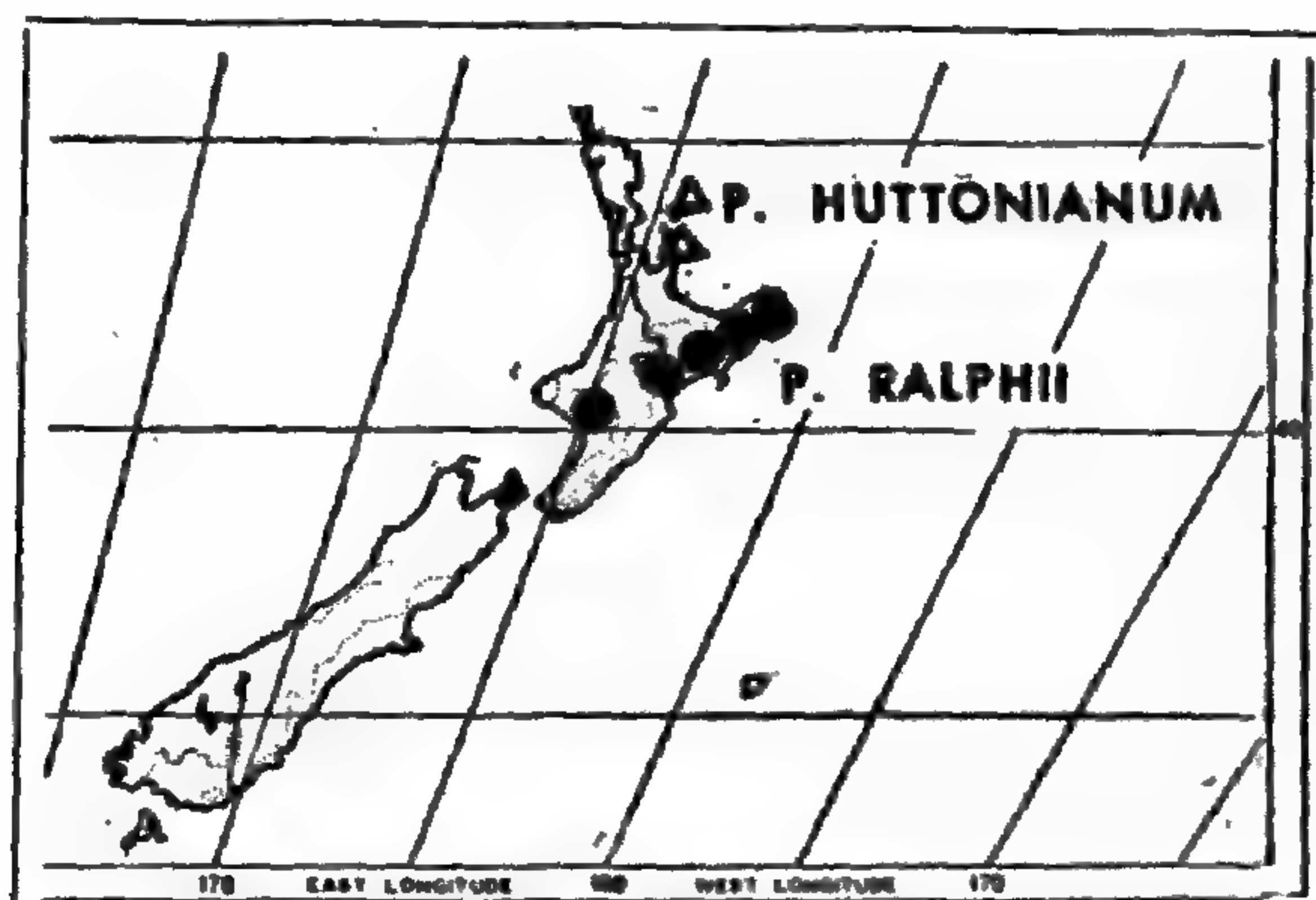


Fig. 11. *P. ralphii* and *P. huttonianum*.

NEW ZEALAND: EAST CAPE: Hendley Station, *Hodgson s.n.* (AK); bridge beyond Okawa, *Meebold 18279* (BISH); prope Tolaga, Oपुरagi and Totaranui, *Banks & Solander s.n.* (BM); Tolaga Bay, East Cape, *Banks & Solander s.n.* (AK, MO, US); coast near Gisborne, *Townson s.n.* (AK, BM); Patangata, *Hamilton s.n.* (AK); Havelock North, *Meebold 4823, 5564* (BISH); Pourere, *Kirk s.n.* (MO); Pitane, *Kirk s.n.* (A, GH); 700', Te Reinga Falls, near Waikaremoana, *Sainsbury s.n.* (AK); Wairoa, *Sainsbury 164, 622, 623, 624, 708, 709, 710, 711* (AK, MO); Waikaremoana, *Cranwell & Moore s.n.* (AK); same locality, near outlet, in forest, *Oliver s.n.* (AK); road bank near Te Araroa, *Moore & Cranwell s.n.* (AK); Mokopeka, *Meebold 18280* (BISH). WANGANUI: near Taumarunui, *Kirk s.n.* (AK); Upper Wanganui River, *Allison s.n.* (A, NSW); Patea, *ex hort.*, *Cheeseman s.n.* (GH); same locality, *ex hort.*, *Hector s.n.* 176 (K); same locality, *ex hort.*, *Kirk 656* (K). WITHOUT LOCALITY: *Colenso 206, 344* (K); *Kirk s.n.* (P).

Flowers which may be female have capitate stigmas, styles about 2 mm. long, and plump ovaries about 4 mm. long and 2 mm. broad. The anthers are probably sterile, sagittiform, 1.0 - 1.5 mm. long, and the filaments are 3.0 - 3.5 mm. long, markedly broad at the base, tapering distally. Flowers which appear to be male have weakly capitate stigmas, styles 3.5 - 5.0 mm. long, and slender ovaries 2.5 - 3.5 mm. long, and 1 - 2 mm. broad. The anthers are oblong, 3.0 - 3.5 mm. long, and the filaments are 4 - 6 mm. long, not markedly broad at the base. On one specimen (*Cheeseman s.n. ex hort*), several flowers were found with 4 functional stamens about 9 mm. long and one apparently sterile stamen about 6 mm. long. The functional stamens had oblong anthers about 3 mm. long while the apparently sterile stamens had sagittiform anthers only 1 mm. long. The stigmas were weakly capitate, the styles long, and the ovaries slender as in male flowers. Godley¹⁵³ has informed me that the species is dioecious.

It has long been known that Banks and Solander collected specimens of *P. ralphii* at Tolaga Bay on the east coast of the North Island of New Zealand during Cook's first voyage to the South Seas in 1769-1772, and named it *P. crassifolium in herb*, but their description and plate were never published and the name *P. crassifolium* was later applied by A. Cunningham to specimens of another species collected by his brother, R. Cunningham, in North Auckland. *Banks & Solander (s.n., BM)* consists, however, of two sheets of *P. ralphii* Kirk and one sheet of *P.*

¹⁵³ Personal communication.

crassifolium A. Cunn (sterile). The type of *P. ralphii* is a collection made by Dr. Ralph at Wanganui about 1870 and forwarded to Kirk for description.

A form with variegated leaves is available in the trade in New Zealand. The species is cultivated in England (Isles of Scilly, Penzance, Allerford, etc.).

7. *PITTOSPORUM HUTTONIANUM* Kirk, in N.Z. Inst. Trans. & Proc. 2: 92. 1870. (T.: Kirk s.n.).

Pittosporum huttonianum Kirk var. *fasciatum* Kirk, Students' Fl. N.Z. p. 48. 1899. (T.: Kirk s.n.).

Shrubs or trees to 10 m. tall; branchlets dark brown, covered with floccose white tomentum when young, glabrate. Leaves alternate, frequently crowded at the tips of the branchlets, elliptic-oblong to obovate-oblong, acute to obtuse at apex and base, entire, 4.2 - 12.0 cm. long, 2.1 - 5.0 cm. broad, covered with floccose white tomentum when young, glabrate, slightly coriaceous, margins unthickened, flat or undulate, occasionally revolute, costa level or sunken above, raised beneath, secondary veins about 12 per side, anastomosing, obscure above, distinct beneath; petioles 5 - 15 mm. long, 1.0 - 2.5 mm. broad, covered with appressed white tomentum when young, glabrate. Flowers terminal and axillary, solitary or in fascicles of 3; pedicels up to 2 cm. long, accrescent in fruit, white-tomentose, usually subtended by 1 to several cataphylls and caducous tomentulose or glabrous bud scales 2 - 10 mm. long. Sepals slightly imbricate at base, oblong, acute, 6 - 9 mm. long, 2.2 - 3.0 mm. broad, covered with floccose white tomentum without, glabrous within; petals oblanceolate-linear, obtuse to subacute, 12 - 18 mm. long, 3.0 - 4.2 mm. broad, free, recurved above the middle, red to magenta; stamens 6 - 10 mm. long, anthers sagittiform to oblong, 1.5 - 4.5 mm. long, 0.8 - 1.5 mm. broad. Pistil at anthesis slightly shorter or longer than the stamens; ovary 2.6 - 5.0 mm. long, 1.0 - 3.5 mm. broad, white-tomentose; style 2.0 - 5.5 mm. long; stigma weakly capitate or truncate. Capsules trigonous, 3-valved, rarely 2-valved, apiculate, 1.2 - 2.0 cm. in diameter, white-tomentose, glabrate, weakly rugose; valves slightly convex to flat in transverse section, about 1 mm. thick, coriaceous, with a thin placenta, fused at the base, bearing flattened funicles up to 1 mm. long from the base to above the middle; seeds 18 - 23, reddish-black to black, irregular.

Occurs on the Great Barrier Island and the Coromandel Peninsula in the North Island of New Zealand. Flowers from October to November.

NEW ZEALAND: THAMES: Great Barrier Island, Kirk s.n. (A, K, US), 86 (K), 518 (BM); Kaiarara, same locality, Kirk s.n. (AK, GH, MO); Kaiwiriki, same locality, Kirk s.n. (AK); timber track, Whangaparapara, same locality, Molesworth s.n. (AK); same locality, Matthews & Carse s.n. (AK); same locality, Hynes 26567 (AK, MO); Kennedy Bay, Coromandel, Matthews s.n. (AK, MO); 1600', Castle Rock, Coromandel, Cheeseman s.n. (AK, GH); same locality, Petrie 6418 (A); same locality, Cranwell & Moore s.n. (AK); Table Mountain behind Thames, Adams s.n. (AK); Pakirerehi, Adams s.n. (AK); same locality, Cheeseman s.n. (US); Kawaeranga, Hector 176 (K).

Pittosporum huttonianum var. *fasciatum* was characterized by flowers in terminal cymes and peduncles white with floccose tomentum. The "peduncles" are the young shoots which have not developed a subtending whorl of leaves or

cataphylls. This phenomenon occurs in the development of the inflorescence of other species and does not merit varietal status.

Flowers which may be female have weakly capitate stigmas on styles about 2 mm. long, plump ovaries 4.8 - 5.0 mm. long, 3.5 mm. broad, and short stamens 6 mm. long, with sagittiform anthers 1.5 mm. long, 0.8 mm. broad. Flowers which may be male have truncate stigmas on styles 3.5 - 5.5 mm. long, slender ovaries 2.6 - 4.0 mm. long, 1 - 2 mm. broad, and stamens 6.8 - 10 mm. long with oblong anthers 2.8 - 4.5 mm. long, 1.0 - 1.5 mm. broad.

8. *PITTOSPORUM TENUIFOLIUM* Banks & Soland. ex Gaertn. Fruct. et Sem. 1: 286. *t.* 59. 1787-88. (T.: *Banks & Solander s.n.*!).

Trees to 10 m. tall; branchlets grayish-brown, tomentose when young, glabrate. Leaves alternate, frequently crowded at the tips of the branchlets, oblong, obovate or elliptical, acute to obtuse at apex and base, entire, 1.5 - 12.2 cm. long, 1.2 - 4.7 cm. broad, green above, sometimes marked with purple, paler beneath, sparsely tomentose when young, soon glabrate, slightly to strongly coriaceous, margins unthickened, flat, revolute, or undulate, costa sunken above, raised beneath, secondary veins 6 - 12 per side, anastomosing, obscure above, distinct or obscure beneath; petioles 3 - 12 mm. long, 0.5 - 2.5 mm. broad, glabrous. Flowers axillary, 1 - 3, solitary or fascicled, subtended by a whorl of caducous bud scales, occasionally terminal on short axillary shoots and subtended by 1 - 2 cataphylls or leaves, and several caducous linear bracts, sessile or on pedicels up to 1 cm. long, tomentose, accrescent in fruit. Sepals slightly imbricate at base, ovate to oblong, subacute to obtuse, 3 - 7 mm. long, 1.4 - 4.5 mm. broad; petals oblanceolate-linear to spatulate and clawed, obtuse, 8 - 16 mm. long, 2 - 5 mm. broad, free, reflexed from the middle, dark purple, maroon, pink or white; stamens 3.6 - 8.0 mm. long, anthers sagittiform to oblong, 1 - 4 mm. long, 0.5 - 1.0 mm. broad. Pistil at anthesis slightly shorter or longer than the stamens; ovary 2.5 - 4.5 mm. long, 1 - 3 mm. broad, tomentose; style 2.0 - 3.5 mm. long, stigma capitate or truncate. Capsules subglobose, apiculate, 3-valved, rarely 2- or 4-valved, 9 - 14 mm. in diameter, tomentose, glabrate, weakly rugose; valves 1.0 - 1.5 mm. thick, coriaceous, convex in transverse section, with a placenta raised and fused at the base, bearing peg-like or flattened funicles from the base to above the middle; seeds 6 - 31, black, irregular.

KEY TO THE SUBSPECIES

- Leaves oblong-ovate to elliptic-obovate, obtuse to shortly acuminate, 1.5-6.0 cm. long, 1-3 cm. broad, membranous to slightly coriaceous, frequently marked with purple when young, margins often undulate; sepals usually obtuse, 2.5-5.5 mm. long, 1.5-3.6 mm. broad, tomentose to glabrate. Throughout New Zealand, at lower elevations8a. *P. t. tenuifolium*
- Leaves lanceolate-oblong to obovate-oblong, acute to shortly acuminate, 3.9-12.2 cm. long, 1.1-4.7 cm. broad, coriaceous, not marked with purple, margins usually flat; sepals subacute, 4.5-6.0 mm. long, 2.5-4.0 mm. broad, tomentulose to glabrate. From the Waikato and Volcanic Plateau southwards, at higher elevations.8b. *P. t. colensoi*

8a. *PITTOSPORUM TENUIFOLIUM* ssp. *tenuifolium*

Trichilia monophylla A. Rich. in Less. & A. Rich. Voy. l'Astrolabe, Bot. Ess. Fl. N. Zel. p. 306. pl. 34. 1832, ex char. & icon. (T.: d'Urville s.n.).

Pittosporum translucens Hook. ex Putterl. Syn. Pittosp. p. 13. 1839, nom. nud. in synonym.

Pittosporum mayi Hort. Regel, Cat. Pl. Hort. Aksakow, p. 112. 1860, nom. nud.

Pittosporum enderi Regel, in Gartenfl. 17: 226. t. 587. 1868, ex char. & icon.

Pittosporum bidwillianum Regel, loc. cit. 1868, nom. nud.

Pittosporum tenuifolium Gaertn. var. *tenuifolium* Kirk, Students' Fl. N.Z. p. 47. 1899.

Pittosporum nigricans Hort. Davy in Bailey, Cycl. Amer. Hort. 3: 1360. 1901, nom. nud. in synonym.

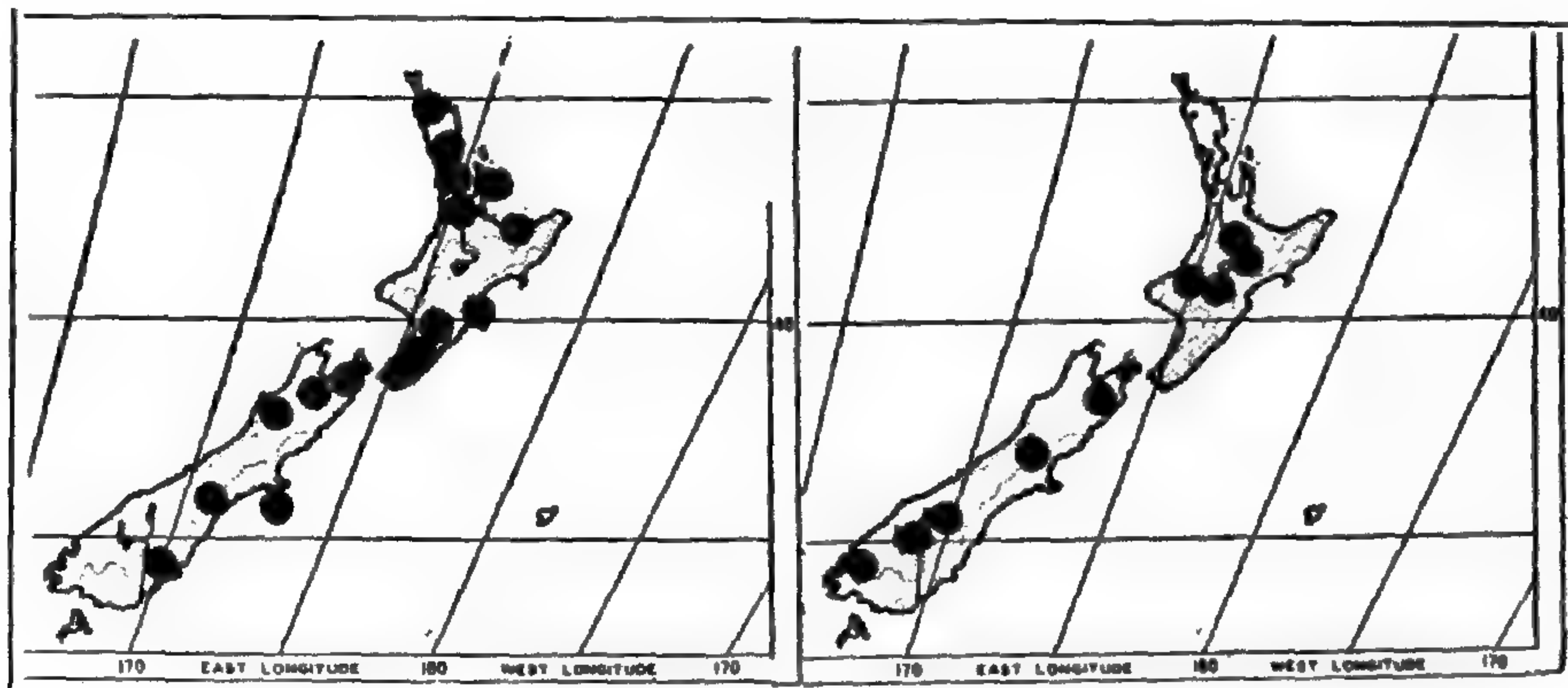
Occurs from the North Auckland district in the North Island to the Otago District in the South Island of New Zealand, at lower elevations than ssp. *colensoi*. Flowers from September to November.

NEW ZEALAND: NORTH AUCKLAND: Kaitaia, R. H. Matthews s.n. (AK); same locality, H. B. Matthews s.n. (AK); same locality, Kelly's Bush, R. H. Matthews s.n. (AK, MO); Kaiaka, Trig Track, Carse s.n. (AK, MO); near sea level on south bank of Oruru River, Taipa, in remnant of *Agathis* forest, Cooper 36006, 36014 (AK, MASS, MO); Bay of Islands, A. Cunningham s.n. (BM); same locality, Wilkes s.n. (K, US); Wangaroa, R. Cunningham 43 (K); Maungatapere, near Whangarei, Carse s.n. (AK). AUCKLAND: Omaha, Kirk 83 (GH), 85 (BM); Glenfield, Birkdale, H. B. Matthews s.n. (AK, MO); Auckland, Hector s.n. (GH); same locality, Kirk 85 (US); same locality, Kirk 54 (AK); Waitakere, Cheeseman s.n. (US); Titirangi Ranges, Cheeseman s.n. (AK); 1300', same locality, Meebold 5410 (BISH, K); Huia, Wood s.n. (AK). THAMES: Coromandel Peninsula, Adams s.n. (AK); Tapapa, Cheeseman s.n. (AK, BISH, NSW). WAIKATO: Buckland, H. B. Matthews s.n. (AK). EAST CAPE: Te Whaiti, Urewera, H. B. Matthews s.n. (AK); Lake Waikaremoana, Moore & Cranwell s.n. (AK); Wairoa South, Cheeseman s.n. (AK); 2000', Blowhard, Meebold 18277 (BISH); 1500', Tongoio, Meebold 18282 (BISH); Havelock North, Meebold 18283 (BISH). VOLCANIC PLATEAU: Murimohu, Ohakune, Attwood s.n. (AK). WAIRARAPA: 70 Mile Bush, Colenso s.n. (K). WELLINGTON: Palmerston North, Allan s.n. (BH); Lower Hutt, Kirk s.n. (NSW); in dry woods, sheltered valley, Day's Bay, 150', MacDaniels s.n. (CU). MARLBOROUGH: Kenepuru, Pelorus Sounds, MacMahon 205 (AK). NELSON: Maitai Valley, Mellor 27212 (AK); 500', same locality, near stream on damp graywacke soil, Neal 10 (BISH). CANTERBURY: Banks Peninsula, Kirk 54 (AK); same locality, Haast 69 (K); same locality, Lyttelton Hills, Meebold 4739 (BISH); same locality, Akaroa, Belligny s.n. (GH, K); Peel Forest, Meebold 4096 (BISH); 800', Waiau River, Morrison 33 (A); Ashley Gorge, Meebold 5845 (BISH); in mixed forest, Orari Gorge, Anderson 75 (A, K, MO, US). WESTLAND: Cape Foulwind, Townson 670 (AK); foot of Mt. Rochfort, Townson 669 (AK); without definite locality, Armstrong s.n. (AK). OTAGO: Arrowtown, Petrie s.n. (AK); Dunedin, Hector s.n. (K). WITHOUT LOCALITY: Banks & Solander s.n. (AK, BM labelled "prope Tolaga, Oपुरagi, Ouhuragi, Totaranui, MO, US"); Colenso s.n. (AK), s.n., 714 (K); A. Cunningham 11 (U), s.n., 615 (K); Kirk s.n. (A, MO, NSW, US); Sinclair s.n. (BM, MO); Raoul s.n. (A).

Flowers which may be female have capitate, obscurely lobed stigmas, styles about 2 mm. long, ovaries about 3 mm. long, 2 mm. broad, stamens 3.6 - 4.5 mm. long, slightly shorter than the pistil, and sagittiform, possibly abortive anthers about 1.4 mm. long. Flowers which may be male have truncate stigmas, styles 2.5 - 3.0 mm. long, ovaries 2.5 - 4.0 mm. long, 1.0 - 1.5 mm. broad stamens 6.0 - 7.5 mm. long, slightly exceeding the pistil, and oblong, probably functional anthers 2 - 4 mm. long. Godley¹⁵⁴ has informed me that the species is dioecious.

Vernacular names: *Mapauriki* (Sinclair s.n.), *Kobuhu*, *Tawhiwhi*.

¹⁵⁴ Personal communication.

Fig. 12. *P. tenuifolium* ssp. *tenuifolium*.Fig. 13. *P. t.* ssp. *colensoi*.

8b. *PITTOSPORUM TENUIFOLIUM* ssp. *COLENZOI* (Hook.f.) Kirk, in N.Z. Inst. Trans. & Proc. 4: 262. 1872.

Pittosporum colensoi Hook. f. Fl. N.Z. 1: 22. 1853. (T.: *Colenso s.n.*!).

Pittosporum viride Hook.f. loc. cit. 1853, nom. nud. in synonym.

Pittosporum uniflorum Hook. f. loc. cit. 1853, nom. nud. in synonym.

Pittosporum fasciculatum Hook.f. loc. cit. 24. 1853. (T.: *Colenso s.n.*!).

Pittosporum tenuifolium Gaertn. ssp. *fasciculatum* (Hook.f.) Kirk, in N.Z. Inst. Trans. & Proc. 4: 262. 1872.

Pittosporum tenuifolium Gaertn. var. *colensoi* (Hook.f.) Kirk, Students' Fl. N.Z. p.47. 1899.

Pittosporum tenuifolium Gaertn. var. *fasciculatum* (Hook.f.) Kirk, loc. cit. 1899.

Pittosporum tenuifolium Gaertn. var. *fasciculatum* (Hook.f.) Kirk, sub. var. *cymosum* Kirk, loc. cit. 1899. (T.: *Williams s.n.*!).

Pittosporum buttonianum Kirk var. *viridiflorum* Kirk, loc. cit. 1899. (T.: *Kirk s.n.*!).

Pittosporum colensoi Hook. f. var. *fasciculatum* (Hook.f.) Cheesem. Man. N.Z. Fl. 53. 1906.

Occurs from the Waikato and Volcanic Plateau in the North Island to the Otago district in the South Island of New Zealand, usually at higher elevations than ssp. *tenuifolium*. Flowers in November.

NEW ZEALAND: WAIKATO: Hora Hora, *Petrie* 764/4 (K). TARANKI: Urenui, *Cheeseman s.n.* (AK); roadside near Tarata, *Carse* 764/6 (K). VOLCANIC PLATEAU: Rotorua, *Petrie & H. B. Matthews s.n.* (AK); same locality, *Turner* 159 (AK); same locality, Kohuturoa Creek, *Kirk* 54 (AK), 564 (K); Patetere Plateau, *Cheeseman s.n.* (AK); near Taupo, *Colenso s.n.* (AK), 2361 (K as *P. viridum*, type of *P. fasciculatum*); in jungle filled gorge dominated by tree ferns, near the Raurimu spiral, National Park, *Walker* 4316 (MO, US); 3500', base of Ngauruhoe, *Cheeseman s.n.* (AK); near Tongariro, *Kirk s.n.* (MO); same locality, *Hodgkins s.n.* (AK); 4000', 1/2 m. west of Chateau Tongariro, *Attwood s.n.* (AK); near Haunted Whare, Waimarino, *H. B. Matthews s.n.* (AK); Waimarino Plains, *H. B. Matthews* 764/11 (K); same locality, *Zotov s.n.* (BH); Makino Valley, Manganui-a-te-ao, Waimarino, *Attwood s.n.* (AK); 1200', Ohakune, *MacDaniels* 1225 (BISH); 2000', same locality, *Meebold* 18276 (BISH). NELSON: between Nelson and Havelock, *Sledge* 266 (K). MARLBOROUGH: Awatere River, *H. J. Matthews s.n.* (AK); same locality, *Petrie s.n.* (AK); same locality, 2000', in bush, *Travers s.n.* (GH). CANTERBURY: Arthurs Pass, Halpin's, *Moore & Cranwell s.n.* (AK). WESTLAND: Otira Gorge, *Cheeseman s.n.* (AK); Anita Bay, Dusky Sound, *Aston s.n.* (AK). OTAGO: Pigeon Island, Lake Wanaka, *Hunnewell* 13466 (GH); Lake Wanaka District, *Hector s.n.* (GH); Paradise, near Lake Wakatipu, *Turner* 816 (AK); Wakatipu, *Meebold* 4442 (BISH); Clinton Valley, Lake Te Anau, 800', *Petrie* 140 (K);

Chalky Bay, *Lyall s.n.* (K); Otago, not common N. of Dusty Bay, *Hector & Buchanan 22* (K). WITHOUT LOCALITY: *Bell s.n.* (NSW); *Colenso s.n.*, (*P. uniflorum*, AK), *s.n.* (*P. viride*, K), 2367 (*P. uniflorum*, K); *Dieffenbach s.n.* (K).

Flowers which may be female have capitate stigmas, styles 1.6 - 2.0 mm. long, ovaries about 4 mm. long, 2.5 - 3.0 mm. broad, stamens about 4.5 mm. long, slightly shorter than the pistil, and sagittiform, possibly abortive anthers 1.0 - 1.2 mm. long. Flowers which may be male have truncate stigmas, styles 3.0 - 3.5 mm. long, ovaries 3.0 - 4.5 mm. long, 1.5 - 2.0 mm. broad, stamens 6 - 8 mm. long, slightly exceeding the pistil, and oblong, probably functional anthers 2 - 3 mm. long.

Vernacular name: *Mountain Kobuhu*.

The two subspecies of *P. tenuifolium* are used in New Zealand, the United States (California), France, southern England, and the Scilly Islands, the Channel Islands (Guernsey), Italy, and Australia, for hedges and ornamental trees. In New Zealand the two subspecies have been so mixed in plantings and so extensively planted that it is difficult to determine their original distribution. Furthermore, they intergrade and it is sometimes impossible to determine the subspecies to which a specimen belongs. Transplantings of trees selected from wild populations at different altitudes are required to determine the extent to which variation in the species is caused by the habitat.

Pittosporum fasciculatum Hook. f. was established to include forms which have flowers in terminal and axillary fascicles. Both *P. t. tenuifolium* and *P. t. colensoi* occasionally have fascicled flowers, and fascicled and solitary flowers are frequently found together in the other species of *Pittosporum* with simple inflorescences. Consequently I do not think that the plants with fascicled flowers should be treated as a distinct species.

Pittosporum buchmanii Hook. f. was based on specimens from a plant cultivated at Wellington by Buchanan and reputed to come from near Tongariro. The type specimen at Kew has only "New Zealand" as the locality. Specimens identified as *P. buchmanii* were subsequently collected, possibly at Kaitaia, by Buchanan, on Mt. Egmont, by Hector, and by Kirk in the Wellington district. The specimen at Kew, collected by Buchanan, as noted "... the exact place where found is uncertain but probably between Hokianga and Bay of Islands." In the last 50 years the Kaitaia, Mt. Egmont, and Wellington districts have been thoroughly explored but no further specimens have been obtained. I have treated the name *P. buchmanii* as doubtful because the specimens are too few and imperfect to determine the status of it.

Pittosporum intermedium Kirk was based on specimens from a single tree on Kawau Island. The tree was subsequently destroyed and no others have been found. In describing the species Kirk¹⁵⁵ wrote:

¹⁵⁵ N.Z. Inst. Trans. & Proc. 4: 266. 1872.

I give this well-marked form specific rank with some hesitation; in foliage it resembles large forms of *P. tenuifolium*, while the capsule partakes of the characters of *P. crassifolium* and *P. ellipticum*. Dr. Hooker and Mr. Colenso consider it a new species, still it is possible that further observation may show the wisdom of uniting it with one or other of the above. I have been tempted to attribute its peculiarities to hybridisation.

A sheet at British Museum is noted by H. H. Allen: "very probably *P. ellipticum* × *tenuifolium*". The few specimens available to me match *P. umbellatum* in the size and shape of the sepals and petals, but lack the typical large terminal inflorescence and lobed capsules. I have treated the name *P. intermedium* as doubtful under the circumstances.

The following cultivated forms of *P. tenuifolium* are available in New Zealand:

P. tenuifolium "garnettii". Duncan & Davies, Catalogue of trees, shrubs and climbers, p. 62. 1950-51.—Leaves edged with white, flecked or tinged with red.

P. tenuifolium "purpureum". *loc. cit.* Suppl. list 1950-51.—Leaves deeply tinged with purple.

P. tenuifolium "variegatum". *loc. cit.* p. 62. 1950-51.—Leaves edged with white or cream.

P. tenuifolium "argenteum". *loc. cit.* p. 32. 1953-54.—This form has been offered for sale as *P. tenuifolium* "Silver Matipo". *loc. cit.* p. 62. 1950-51, and p. 81. 1954-55, but no description is given. It may be the same as *P. nigricans* var. "Silver Queen" which is described (R.H.S. Dictionary of Gardening, 3: 1595. 1951), as having silvery-gray foliage, but I have not seen specimens of "Silver Queen". *Pittosporum tenuifolium* "argenteum" and "variegatum" were introduced into cultivation prior to 1950 but the references are to the earliest dated catalogues which I have found.

Davy¹⁵⁶ lists *P. nigra* Hort? as a horticultural name of *P. tenuifolium* and Hector noted on a sheet in the herbarium of the Royal Botanic Gardens, Kew (*Hector s.n.*) that *P. tenuifolium* was named *P. nigrum* by the Sydney Botanic Gardens in 1862. Lord¹⁵⁷ gives *P. nigrescens* as another horticultural name for *P. tenuifolium*. A form with markedly undulate leaves is available in Europe as *P. mayi*, and its origin and status are described in detail by Gadeceau¹⁵⁸.

¹⁵⁶ Davy in Bailey, Cycl. Amer. Hort. 3: 1360. 1901.

¹⁵⁷ Lord, Shrubs & Trees for Australian Gardens, p. 34. 1948.

¹⁵⁸ Bull. Soc. Bot. Fr. 67: 153. 1920.

SERIES II. BIVALVAE

SERIES II. BIVALVAE Gowda, in Jour. Arnold Arb. 32:285. 1951

KEY TO THE SPECIES

- a. Inflorescences simple; flowers solitary or in fascicles of few to many (rarely in 3- to 4-flowered cymes in *P. phillyraeoides*).
- b. Terrestrial trees or shrubs; flowers terminal and axillary; petals purple, red or yellow; capsules globose to ovoid (ellipsoid in *P. obcordatum*). Australia and New Zealand.
- c. Plants without persistent diverse juvenile foliage. Australia.
- d. Unarmed trees and shrubs; flowers subterminal and axillary, solitary or in fascicles of 2-4.
- e. Shrubs or small trees 3-10 m. tall; branches pendulous; leaves glabrous; petals yellow or white; capsule valves woody, 1.0-3.5 thick. Throughout continental Australia 9. *P. phillyraeoides*
- ee. Shrubs or small trees 6-16 m. tall; branches ascending; leaves tomentose beneath; petals yellow marked with red to purplish-red; capsule valves coriaceous, less than 1 mm. thick. New South Wales, Victoria, and Tasmania. 10. *P. bicolor*
- dd. Spinose shrubs; flowers axillary or terminal, on arrested branchlets, solitary. Southeast Queensland, at high altitudes. 11. *P. o'reillyanum*
- cc. Plants with persistent diverse juvenile foliage (juvenile and adult leaves linear in *P. pimeleoides*). New Zealand.
- d. Flowers large, terminal on normal branchlets, 1-20; capsules 6-16 mm. long; seeds up to 18, black, irregular.
- e. Branchlets never sharply divaricate or matted.
- f. Trees to 8 m. tall or more; sepals usually acute; capsule valves concave or sulcate to convex in transverse section.
- g. Trees to 10 m. tall; flowers up to 20; sepals, pedicels, young leaves, and petioles glabrous; petals red; capsules usually 4-lobed; valves usually concave in transverse section. North Auckland and Thames. 12. *P. umbellatum*
- gg. Trees to 8 m. tall; flowers 1-6; sepals, pedicels, young leaves and petioles rusty-tomentose; petals usually dark red to purple; capsules subglobose; valves sulcate to convex in transverse section. North Auckland and Thames 13. *P. virgatum*
- ff. Shrubs 0.5-5.0 m. tall; sepals usually acuminate; capsule valves convex to weakly sulcate in transverse section.
- g. Shrubs 0.5-2.0 m. tall; male flowers 6-9, female flowers 1; petals cream to yellow with a red stripe; capsules ovoid, acuminate or almost beaked at apex. North Auckland. 14. *P. pimeleoides*
- gg. Shrubs 1-5 m. tall; flowers 3-7; petals purple; capsules globose to subglobose, obtuse at apex. Nelson. 15. *P. patulum*
- ee. Branchlets sharply divaricating and matted at juvenile stage or on lower part of adult stem; shrubs or trees 2-9 m. tall; flowers 4-12; petals pink to purple; capsules globose. Volcanic Plateau. 16. *P. turneri*
- dd. Flowers minute, axillary or terminal, on arrested branchlets (terminal on normal branchlets in *P. rigidum*), in few-flowered fascicles or solitary; capsules 4.5-10.0 mm. long; seeds 1-9, reddish-black to black, round to irregular.
- e. Trees or shrubs 2-6 m. tall; petals linear-oblong, usually purple; capsule valves dehiscent without, leaving a persistent papery endocarp.
- f. Adult leaves orbicular to obovate, obcordate to obtuse at apex, with 2-4 usually distinct secondary veins per side; petioles usually narrowly winged; flowers 1-5, axillary or terminal, on minute arrested branchlets; sepals persistent, tomentulose; petals pale purple, yellow, or white; capsules ellipsoid to sub-ovoid; placentas with funicles from the base to the middle. North Auckland, Hawkes Bay, and Canterbury. 17. *P. obcordatum*
- ff. Adult leaves rarely orbicular to obovate, obtuse to subacute at apex, with obscure secondary veins; petioles without wings; flowers usually solitary (1-3 in *P. crassicaule*), axillary or terminal, on normal or arrested branchlets; sepals caducous, glabrous; petals purple; capsules cordate or subglobose to globose; placentas with funicles near the middle.

- g. Shrubs to 3 m. tall; branchlets ascending, not spinose; leaves obtuse at base; pedicels 0.5–4.0 mm. long; flowers solitary, terminal or axillary on normal branchlets; sepals 3.5–6.0 mm. long, 1.0–1.5 mm. broad; petals 8–12 mm. long, 2 mm. broad; ovary tomentose; capsules subglobose, 8–10 mm. long, 6–10 mm. broad. Hawkes Bay, Wellington, and Marlborough.18. *P. rigidum*
- gg. Shrubs 4 to 6 m. tall; branchlets divaricate, almost spinose; leaves acute to attenuate at base; pedicels minute; flowers 1–3, terminal on short arrested branchlets; sepals 1.2–2.5 mm. long, 0.5–1.0 mm. broad; petals 3.0–7.5 mm. long, 1.0–1.5 mm. broad; ovary tomentulose or glabrous; capsules subglobose, 4.5–7.0 mm. long and broad.
- h. Shrubs to 4 m. tall; main branches usually fastigate; adult leaves (exposed) elliptic-oblong, 3.5–17.0 mm. long, 1–4 mm. broad, entire, (in shade) usually with 1–5 lobes or teeth on each side; flowers 1–3 sepals 1.2–1.5 mm. long, 1 mm. broad; petals 4.0–7.5 mm. long, 1.2–1.5 mm. broad; ovary tomentulose; capsules subglobose to globose, rugose. Marlborough, Nelson, Canterbury, and Westland19. *P. crassicaule*
- hh. Shrubs to 6 m. tall; main branches usually interlaced; adult leaves (exposed) linear-oblong to linear-oblong or ovate, 4–10 mm. long, 2–7 mm. broad, entire, occasionally crenate; adult leaves (shade) usually with 1–3 lobes or teeth on each side; flowers solitary; sepals 1.5–2.5 mm. long, 0.5–1.0 mm. broad; petals 4–6 mm. long, 1.0–1.5 mm. broad; ovary glabrous; capsules cordate or subglobose, weakly rugose. Hawkes Bay, Volcanic Plateau, Nelson and Canterbury20. *P. divaricatum*
- ee. Shrubs completely prostrate in the open, a tangled mass up to 1 m. tall in shade; flowers solitary, terminal on short arrested branchlets; petals obovate to oblanceolate, variously colored; capsule valves dehiscent in part, leaving a persistent papery endocarp covering the seeds. Volcanic Plateau, Nelson, and Canterbury.21. *P. anomalum*
- bb. Epiphytic shrubs, seldom terrestrial; flowers terminal; petals yellow; capsules ellipsoid. New Zealand.
- c. Slender branched shrub 0.5–1.5 m. tall, polygamous or dioecious; leaves obovate to ovate-elliptic; male flowers about 10; female flowers 1–2; capsules about 1.7 cm. long, 1.2 cm. broad. North Auckland to Marlborough.....22. *P. cornifolium*
- cc. Stoutly branched shrub 1–5 m. tall, monoecious; leaves linear-obovate to oblong-elliptic; flowers 3–10; capsules 2.6–3.9 cm. long, 1.1–1.7 cm. broad. North Auckland to Wanganui23. *P. kirkii*
- aa. Inflorescence cymose.
- b. Capsules without a persistent papery endocarp. Australia.
- c. Flowers few (1–32), and relatively large; sepals 4.0–10.5 mm. long; petals 11–18 mm. long, connate or connivent in a cylindrical or urceolate tube, tips spreading to reflexed; capsules lobed, ellipsoid, or ovoid.
- d. Shrubs 1.5–6 m. tall; leaf margins flat or revolute; sepals slightly imbricate at base; petals yellow; capsules 1.3–2.8 cm. long.
- e. Shrubs to 3 m. tall; branchlets rusty-tomentose when young, glabrescent; leaves 4–19 cm. long, subcoriaceous to coriaceous, with appressed rusty tomentum beneath, acute to shortly acuminate, margins thickened and revolute; bud scales persistent; inflorescence 1- to 11-flowered; sepals sparsely tomentulose to glabrate; capsules 4- to 6-lobed, 2- to 4-valved, 1.5–2.8 cm. long, coarsely rugose, sessile; valves woody, 2–3 mm. thick, placentas bearing funicles from the base to near the apex; seeds 20–76. Queensland, New South Wales and Victoria.24. *P. revolutum*
- ee. Shrubs 1.5–6 m. tall; branchlets rusty-tomentose, not glabrescent; leaves 6.0–33.5 cm. long, membranous with sparse erect red hairs beneath, rusty-tomentose on the veins, acutely acuminate to cuspidate, margins flat, unthickened, sometimes irregularly revolute; bud scales caducous; inflorescence 3- to 32-flowered; sepals tomentose; capsules ellipsoid to ovoid, 2-valved, rarely 3-valved, 1.3–2.1 cm. long, minutely rugose, stipitate; valves coriaceous, under 1 mm. thick; placentas bearing funicles from the base to the middle; seeds 3–14. Queensland.25. *P. rubiginosum*
- dd. Shrubs or trees 5–13 m. tall; leaf margins markedly undulate; sepals frequently connate in a tube splitting into 2 parts, one 1- to 2-lobed, the other 3- to 4-lobed;

- petals white; capsule subglobose, 2-valved, 1.0–1.4 cm. in diameter. Queensland, New South Wales and Victoria.26. *P. undulatum*
- cc. Flowers very numerous and relatively small; sepals 1.1–3.5 mm. long; petals 5.5–9.0 mm. long, connivent in a cylindrical tube, or free and patent; capsules globose to obovoid.
- d. Sepals oblong to ovate, obtuse to acute; capsules subglobose to obovoid, 2-valved, rarely 3-valved, stipitate; valves woody or coriaceous, about 1 mm. thick.
- e. Leaves lanceolate to ovate-lanceolate; sepals oblong, obtuse, rusty-tomentose; capsules subglobose to obovoid, 1–2 cm. long, 2- or rarely 3-valved; valves 1–2 mm. thick, woody, convex in transverse section; placentas much thickened and fused at base, bearing 6–8 funicles about the middle; trees to 10 m. tall; petals white; seeds 6–14, reddish-black to black. Queensland.....27. *P. venulosum*
- ee. Leaves oblanceolate, oblong, rhombic, or ovate; sepals ovate, acute to subacute, white-tomentulose or glabrous; capsules obovoid, 2-valved; valves less than 1 mm. thick, woody, usually sulcate in transverse section; placentas much thickened at base and apex and fused more or less completely to form two chambers, bearing several funicles from the base to the middle or at the base.
- f. Shrubs or small trees to 6 m. tall; leaves oblanceolate to oblong, entire; petals yellow; capsules 6–15 mm. in diameter; valves with a placenta bearing several short stout funicles between the base and the middle; seeds 2–6, black. Northern Territory and Northern Queensland28. *P. melanospermum*
- ff. Trees 13–30 m. tall; leaves rhombic to ovate, usually coarsely serrate; petals white; capsules about 5–10 mm. long, 5–8 mm. broad; valves with a placenta bearing 1 or 2 minute funicles near the base; seeds 1–3, black. Queensland and northern New South Wales.29. *P. rhombifolium*
- dd. Sepals linear to linear-lanceolate, acute to acuminate; capsules globose to subglobose, 2-valved, sessile, 7–10 mm. in diameter; valves coriaceous, less than 1 mm. thick, convex in transverse section; placentas with funicles from the base to the middle; seeds about 16, black; trees or shrubs 8–20 m. tall; petals yellow. Queensland and Malay Archipelago.30. *P. ferrugineum*
- bb. Capsules with a persistent papery endocarp. New Zealand.
- c. Trees 4–6 m. tall; leaves coarsely serrate to entire; inflorescences condensed, about 40-flowered; petals white with red veins; capsules about 15 mm. long, 9 mm. broad; placentas bearing about 12 funicles from the base to near the apex. Northwest Nelson.31. *P. dallii*
- cc. Trees 6–13 m. tall; leaves entire; inflorescences spreading, 30- to 70-flowered; petals yellow; capsules 9–10 mm. long, 5–6 mm. broad; placentas bearing 2–4 funicles near the middle. North Auckland to Otago.32. *P. eugenioides*

9. *PITTIOSPORUM PHILLYRAEOIDES* DC. Prodr. 1:347. 1824. (T.: *Leschenault s.n.*!).

Pittosporum angustifolium Lodd. Bot. Cab. 19: t. 1859. 1832, ex icon. ♂ char.

Pittosporum ligustrifolium A. Cunn. ex Loud. Hort. Brit. Suppl. 1: 597. 1832, nom. nud.

Pittosporum longifolium Putterl. Syn. Pittosp. p.15. 1839, ex char. (T.: *Roe s.n.*).

Pittosporum roeanum Putterl. loc. cit. p.16. 1839, ex char. (T.: *Roe s.n.*).

Pittosporum ligustrifolium A. Cunn. ex Putterl. loc. cit. p. 16. 1839. (T.: *A. Cunningham s.n.* [30, 142] ! Rottneest Is.).

Pittosporum oleaefolium A. Cunn. ex Putterl. loc. cit. p. 17. 1839. (T.: *A. Cunningham s.n.* [31, 32, 143] ! Dick Hartog Is.).

Pittosporum acacioides A. Cunn. in Ann. Nat. Hist. 4: 109. 1839. (T.: *R. Brown s.n.* [5447]!).

Pittosporum salicinum Lindl. in Mitch. Jour. Exped. Int. Trop. Austr. p. 97. 1848. (T.: *Mitchell 273*!).

Pittosporum lanceolatum A. Cunn. in Mitch. loc. cit. p. 272, 291. 1848, nom nud.

Pittosporum phillyraeoides DC. var. *microcarpa* S. Moore in Jour. Bot. 35: 163. 1897. (T.: *Spencer Moore s.n.*!).

Shrubs to small trees 3–10 m. tall; branches pendulous; branchlets grayish-brown, tomentose when young, soon glabrate. Leaves alternate, linear-oblong to linear-oblanceolate, rarely elliptic-oblong, acute and apiculate at apex, attenuate at base, entire, 2.5 – 12.6 cm. long, 2 – 15 mm. broad, tomentose when young, soon

glabrate, very coriaceous, margins flat or revolute, costa raised to sunken above and below, secondary veins usually obscure; petioles 4 - 15 mm. long, 0.5 - 1.0 mm. broad, glabrous. Flowers pseudoterminal and axillary, 1 - 4, solitary or fascicled, rarely in 3- to 4-flowered cymes, clustered at the ends of leafy branchlets; peduncles and pedicels 3 - 15 mm. long, accrescent in fruit, sparsely tomentulose, glabrate, subtended by a single leaf and a whorl of caducous bud scales 1 - 2 mm. long. Sepals imbricate or coherent at base, 1 - 2 pairs occasionally fused to apex, lanceolate, subacute to acute, 2 - 3 mm. long, 1.1 - 2.0 mm. broad, glabrous; petals linear-oblong to linear-oblongate, sometimes slightly pandurate, obtuse, 8 - 11 mm. long, 2.0 - 3.5 mm. broad, coherent in a cylindrical or somewhat urceolate tube for about two-thirds of their length, tips spreading to reflexed, yellow to white; stamens 4.2 - 8.0 mm. long, anthers sagittiform, ovoid or oblong, 1.0 - 3.3 mm. long, 0.8 - 1.3 mm. broad. Pistil at anthesis slightly shorter or longer than the stamens; ovary 3.0 - 5.5 mm. long, 1 - 3 mm. broad, tomentose, sometimes glabrate above; style 1.5 - 3.0 mm. long; stigma capitate, sometimes obscurely lobed. Capsules ovoid to globose, obtuse to subacute, 2-valved, rarely 3-valved, apiculate, 1 - 2 cm. long, 9.5 - 19.0 mm. broad, glabrate, smooth, dark red or orange without, yellow within; valves convex to sulcate in transverse section, 1.0 - 3.5 mm. thick, woody, with a conspicuous placenta, fused at the base, bearing short stout funicles from the base to above the middle; seeds 4 - 24, red, irregular.

Occurs throughout Australia. Flowers from July to October.

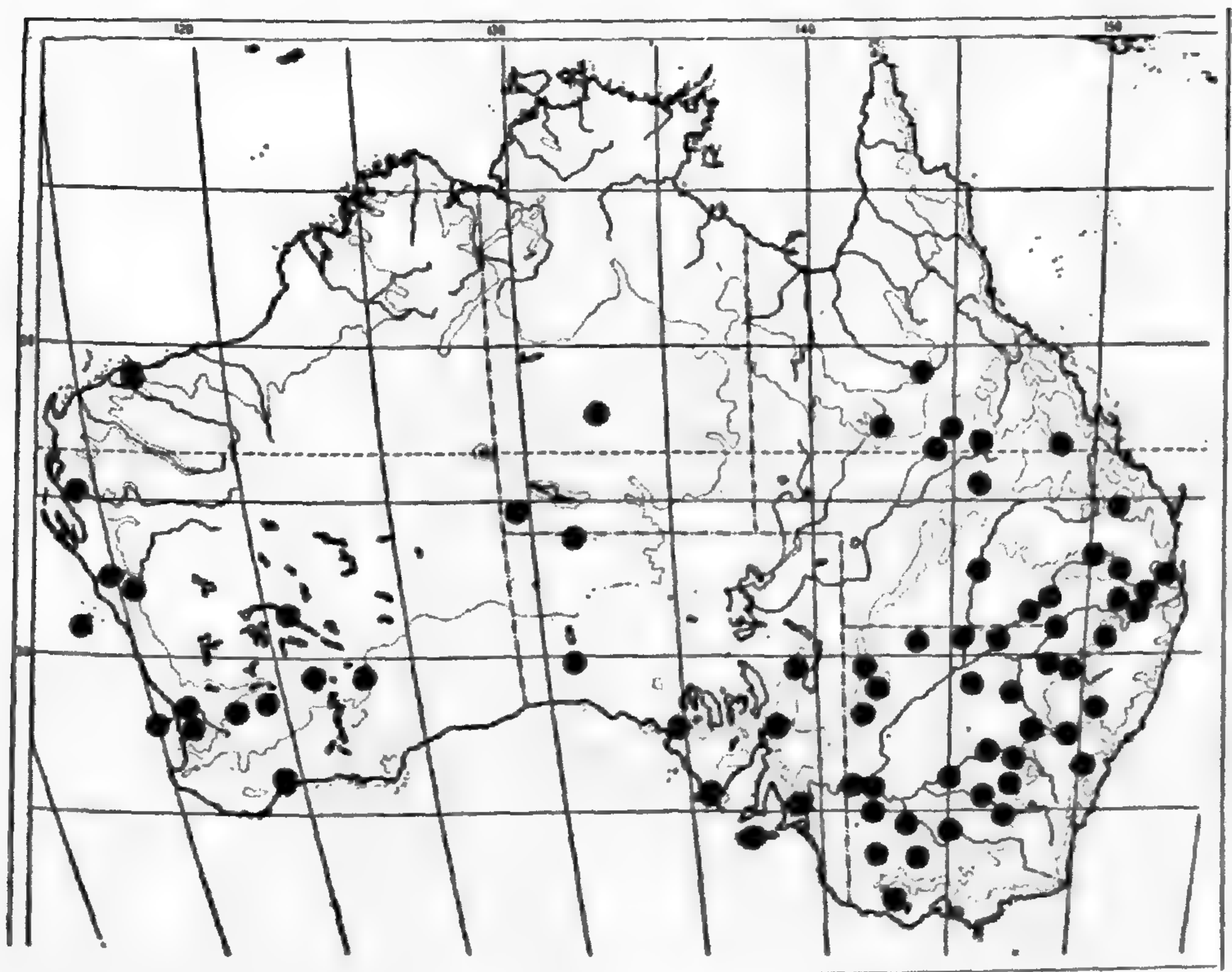


Fig. 14. *P. phillyraeoides*.

AUSTRALIA: NORTHERN TERRITORY: 60 miles N.E.C.2. [near Macdonnell Ranges, between Stuart Bluff Range and the Lander], *Hill* 283 (MEL); Northwest Petermann Ranges, *Basedow* 159 (K); Petermann Ranges *Basedow* 171 (K); without locality, *Hill* 98 (NSW). QUEENSLAND: Burdekin, *Mueller s.n.* (K); Hughenden, *Longman s.n.* (A, K); on stony ridges between Aramac and Muttaborra, *Brass & White* 44 (A, K); between Bowen Downs and Mueller's Range, *Birch s.n.* (MEL); Texas, *Boorman s.n.* (A); Mitchell, *Edwards s.n.* (A); Barcoo, *Schneider s.n.* (MEL); Eidsvold, *Bancroft s.n.* (A); in red-brown fine sand, Glenber, C. 40 miles S.E. Charlesville, Warrego District, *Everist* 3397 (K); Barunga, north of Miles, *Belson s.n.* (A); in brigalow scrub in heavy soil, C. 890', Wandoan, *Hubbard* 5024 (K); Wallumbilla, *Francis s.n.* (A, K); Dalby, *White* 9032 (A, K); Moreton Bay, *Mallard s.n.* (GH); Ipswich, *Nernst* 35 (MEL); Bumble Station, 70 miles north of Mungindi, *Cabbage* 4404 (NSW); 558', in heavy black soil in open *Eucalyptus* forest, Dirranbandi, *Hubbard* 5572 (A, K); Noondoo, Maranoa District, *Everist* 786 (A, K); apparently epiphytic in an Eucalypt (*E. corymbosa?*) near Warwick, *E. Thomson* 16 (K); Silverwood, *White* 1712 (A); Inglewood, *Boorman s.n.* (NSW); Goondiwindi, *Colclough s.n.* (K). NEW SOUTH WALES: Moru-Mungundi District, *Kerry s.n.* (NSW); Uriseno-Thurloo Downs, *Boorman s.n.* (NSW); Middle Warrego, *Bullock s.n.* (MEL); between 40 and 50 miles N.W. of Collarenebri, *Jackson s.n.* (NSW); Bingara, *Boorman s.n.* (BISH); New Angledool, *Paddison s.n.* (A); Narrabi W., *Boorman s.n.* (NSW); same locality, *Lyne s.n.* (NSW); plains country north of the Namoi River, *Taylor s.n.* (NSW); Pilliga, *Rupp s.n.* (NSW); roadside, Baradine, *Lamont* 201 (BM); Bogan River District, *without collector s.n.* (NSW); Castlereagh, *Woolls s.n.* (MEL); Nyngan Exp. Farm, *Downing s.n.* (BISH, NSW, US); Cobbora-Boomley Rd., 1700', on quartzite in rocky scrub-land, *Johnson & Constable s.n.* (NSW); Currabubula, *Cabbage* 3575 (NSW); Cobar, *Hadley s.n.* (NSW); Trangie, *Maclean* 6 (NSW); Barrier Range, *Irvine s.n.* (BM, MO); Broken Hill, *Morris s.n.* (NSW); in open plain, Mundi Mundi Station, Broken Hill, *Constable s.n.* (NSW); sandy flat, Wilmatha, Condobolin, *Hadley* 29 (A, NSW); Wyalong, *Boorman s.n.* (NSW); same locality, *House s.n.* (K, MO); Wollongong, *Wilkes s.n.* (US); E. Mirrool, *Campbell s.n.* (NSW); in barren country S.W. of the Lachlan River, *A. Cunningham* 35 (K); in granite soil at side of road, Ardlethan District, *Constable s.n.* (AK, K, NSW, US); Temona, *Dwyer s.n.* (MO, NSW); junction of Darling and Murray rivers, *Holding s.n.* (MEL); Wagga, *Helms s.n.* (NSW); Yenda, *Searcy s.n.* (NSW); without definite locality, *Fraser s.n.* (A, K); VICTORIA: Mildura, *Limmer s.n.* (UMEL); Lower Murray River, *Mueller s.n.* (BM, GH, K, MO); Box Ridge, Robinvale, Murray River, *Froggatt s.n.* (NSW); Benjeroop, Murray River, *C. French Jr. s.n.* (NSW); Swan Hill District, *C. French Jr. s.n.* (GH, MEL); Deniliquin, *Crawford s.n.* (NSW); Dimboola, *d'Alton* 31 (NSW); Wimmera, *Mueller* 18 (GH); same locality, *Williamson s.n.* (NSW); same locality, *Walter s.n.* (GH, NSW); scrub, Kamarooka, near Bendigo, *Paton s.n.* (MEL); Mallee, *C. French Jr. s.n.* (NSW); ranges bearing S.W. from Camp 29 [vicinity of Mt. Cole, near Ararat], *Mitchell s.n.* (BM). SOUTH AUSTRALIA: Gov. Northwest Expedition, *Basedow* 112 (NSW); Elder Expedition, Camp 10, *Helms s.n.* (K, MEL, NSW); Musgrave Range, *Lord s.n.* (MEL); Ooldea, *Kershaw s.n.* (MEL); Commonwealth Hill, near Ooldea, *Basedow* 84 (NSW); Mt. Lyndhurst, *Koch* 7 (K); Flagstaff Point, near Streaky Bay, *Rogers s.n.* (NSW); Streaky Bay, *Crocker s.n.* (CANB); Port Augusta, *Lea s.n.* (BM); Port Lincoln, *Browne* C. 29 (MEL); same locality, *Schomburgk s.n.* (US); Memory Cove, near Port Lincoln, *Maiden s.n.* (NSW); shores of Bay III, South Coast, *R. Brown* 5447 (BM, K, MO); 10 miles E. of Mannum, in mallee scrub, *Vickery s.n.* (NSW); Kangaroo Island, *Waterhouse s.n.* (MEL); Central Australia, *Sturt s.n.* (BM); without locality, *Conservator of Forest s.n.* (NSW); WESTERN AUSTRALIA: in stream-bed, Nickol Bay, *Gregory Expedition s.n.* (MEL); Sharks Bay, *Mueller s.n.* (MEL); barren sandy downs, Dirk Hartog's Island, *A. Cunningham s.n.*, 31 32 (K), 143 (BM); Murchison River, *Oldfield s.n.* (GH, K, MEL); Greenough Flat, *Gray s.n.* (MEL); Tabletop Hill, Northampton, *Campbell* 18 (K); South Island, Houtman's Abrothos, *Gilbert* 98 (BM, K, MO); Walkaway, S. of Geraldton, *Morrison* 13305 (K); saltbush plain south of Doyle's Well, *Spencer Moore s.n.* (BM); Arrino, *Fitzgerald s.n.* (NSW); arid shores of Rottnest Island, *A. Cunningham s.n.*, 30 (K), 142 (BM); in

arenosis sylvae orae occidentalis insulae Rottneest, *Preiss 1297* (GH, MO, P); Swan River, *Drummond s.n.* (K), 31 (BM, K, MO); 57, 76 (K), 76 (BM); R. des Cygnes, *Drummond 76* (P); same locality, *Preiss 1297* (P); limestone rocks, face of cliff, Claremont, *Andrews 37* (BM, K); Kellerberm, *Vachell s.n.* (NSW); Merredim, *Koch 2983* (K, MEL, NSW); near rock outcrop about 6 miles N.W. of Muntadgin, *Bailey 182* (CANB); 70 miles N. of Coolgardie, *C. A. White s.n.* (K); Main Camp, Kurrawang, *Maiden s.n.* (NSW); E. of Kalgoorlie, Transcont. Ry. Survey, *Deans s.n.* (NSW); Point Peron, on sand dunes near sea, *Burbidge 1962* (CANB); on damp flat in plain, 7 miles west of Deakin, *Calaby s.n.* (CANB); Benner Bay, *Menzel 56* (NSW); without definite locality, *Drummond 76* (MO). WITHOUT LOCALITY: Exped. Baudin, *Leschenault s.n.* (BM); N. Holl., *Lhotsky s.n.* (P); *Mitchell s.n.*, 228, 229, 273 (K); [228, 229, on the Belyando River near $147^{\circ} \times 22^{\circ}, 27'$, Mantuan Downs between Kilsyth and valley of Nogoia River $147\frac{1}{2}^{\circ} \times 24\frac{1}{2}^{\circ}$.]

Flowers which may be female have pistils slightly longer than the stamens, large capitate stigmas, styles about 1.5 mm. long, ovaries 4.0 - 5.5 mm. long, 2.5 - 3.0 mm. broad, and sagittiform to ovate anthers 1.0 - 1.5 mm. long, borne on filaments only 3 - 4 mm. long. Flowers which may be male have pistils slightly shorter than the stamens, smaller capitate stigmas, styles 3.0 - 3.5 mm. long, ovaries 3 - 4 mm. long, 1 - 2 mm. broad, and oblong anthers 2.0 - 3.3 mm. long borne on filaments 3.5 - 6.0 mm. long. Intermediate forms with large anthers and plump ovaries occur.

Pittosporum phillyraeoides is grown as a hedge, windbreak, and as an ornamental shrub in the United States (California, Arizona, and Florida), France, Australia, and New Zealand; and in the drier parts of Australia it is used as a stock food.

The variability of the leaves was noted by Bentham¹⁵⁹, who commented:

This species, apparently spread over the whole desert country of Australia, cannot be confounded with any other notwithstanding the variability of the proportions of its leaves, flowers and fruit. In some of the western specimens the leaves are barely 2 inches long, and fully an inch wide, whilst in a large number of eastern and some western ones they attain 4 or 5 inches in length with a breadth of only 2 or 3 lines.

In the material I have examined there is a specimen from Shark Bay, western Australia (*Mueller s.n.* MEL), with elliptic-oblong leaves about 3.5 cm. long and up to 1.7 cm. broad, covered with appressed tomentum beneath, but this extreme is connected with the more common form by a number of intermediates, and I am unable to define any varieties. The variability of the capsules in size and shape must be mentioned. Again the extremes are connected by intermediates and I am unable to recognize var. *microcarpa* S. Moore.

Vernacular names: Butter Bush, Willow or Willow Tree, *Berrigan*, Locket Bush, Butterwood, Bell's Orange, Quinine Tree, Weeping Pittosporum, Native Willow, Poison-berry Tree, Apricot Tree, West Australian Willow, *Macla* (Paroo River Blacks), *Derrine* (Dubbo Blacks).

¹⁵⁹ Fl. Austr. 1: 113. 1863.

10. *PITTOSPORUM BICOLOR* Hook. in Jour. Bot. 1: 249. 1834. (T.: Lawrence s.n.).

Pittosporum buegelianum Putterl. in Endl. Nov. Stirp. Dec. 43. 1839, ex char. (T.: Hügel s.n.).

Pittosporum discolor Regel in Gartenflora 1:133. t. 15. 1852, ex icon.

Shrubs to small trees 3 - 16 m. tall; branchlets ascending; branchlets grayish-brown, the young parts hoary or rusty-tomentose, soon glabrous. Leaves alternate, rarely subverticillate, oblong-lanceolate to linear, obtuse or apiculate at apex, acute or attenuate at base, entire, 2 - 7 cm. long, 3 - 18 mm. broad, glaucous-green and glabrous above, white-, yellow- to brown-tomentose beneath, coriaceous, revolute, costa and secondary nerves usually distinct above, costa distinct beneath, but secondary nerves obscure; petioles 2-5 mm. long, 1-2 mm. broad, tomentulose when young. Flowers pseudoterminal and axillary, 1 - 4, solitary or fascicled, clustered at the ends of leafy branchlets; pedicels 3 - 19 mm. long, accrescent in fruit, brown-tomentose, subtended by numerous caducous bud scales about 1 mm. long. Sepals imbricate at base, lanceolate, acute, 2-6 mm. long, 1-3 mm. broad, puberulous; petals lanceolate-oblong, subacute, 9 - 15 mm. long, 2 - 4 mm. broad, free or coherent at the base, spreading from above the middle, yellow with red veins, yellow marked with red, or reddish purple; stamens 3 - 9 mm. long, anthers elliptic-oblong, 1 - 3 mm. long, 0.5 - 1.0 mm. broad. Pistil at anthesis as long as the stamens, rarely almost twice as long; ovary 3 - 5 mm. long, 2 - 3 mm. broad, villous; style 1.5 - 5.0 mm. long; stigma capitate and obscurely 4-lobed on short-styled pistils, weakly capitate to truncate on long-styled pistils. Capsules subglobose, 2-valved, rarely 3-valved, 7 - 13 mm. in diameter, tomentose, glabrate; valves convex in transverse section, less than 1 mm. thick, coriaceous, with a conspicuous placenta bearing short stout funicles from the base to just above the middle; seeds 10 - 20, yellowish-red to reddish-black, irregular.

Fairly common from sea-level to 1300 m. in Tasmania, less common in eastern Victoria and southern New South Wales. Flowers from July to December.

AUSTRALIA: NEW SOUTH WALES: Bibbenluke, near Bombala, *Edwards s.n.* (NSW); Glenbog State Forest, *Beuzeville LI* (NSW); Brown Mountains near Littleton, *Betche s.n.* (NSW). VICTORIA: Sherbrook Forest, *Lothian s.n.* (GH); Blacks Spur, *Deane s.n.* (BISH, NSW); same locality, *Morris 1441* (NSW); Milla Milla, *Clinton s.n.* (NSW); Bonang, *Baeunton s.n.* (NSW); near Mt. Ellery, *Merrab s.n.* (MEL, NSW); Genoa District, *Baeunton s.n.* (MEL, NSW); along Dividing Range, *Stirling s.n.* (NSW); same locality, *Walter s.n.* (BISH, NSW); Matlock, *Staer s.n.* (NSW); Upper Yarra, *Staer s.n.* (NSW); Mt. Baw Baw, *C. French Jr. s.n.* (MEL, NSW); same locality, *Walter s.n.* (NSW); Mt. Disappointment and Dandenong, *Mueller s.n.* (MEL, NSW); near Melbourne, *Cecil 219* (K); Ferntree Gully, *Staer s.n.* (NSW); Emerald, *Rendle s.n.* (BM); Paradise, *Cookson s.n.* (UMEL); Korumburra, *Baker s.n.* (MEL); East Gippsland, *C. French Jr. s.n.* (GH); same locality, *Mueller s.n.* (US); same locality, *Stirling s.n.* (BM); Corner Inlet, *Mueller s.n.* (NSW); Sealer's Cove, *King s.n.* (BM, K, NSW); near Cape Otway, *Lucas s.n.* (MEL, NSW). TASMANIA: King's Island, *Sayer s.n.* (MEL, NSW); Circular Head, *Gunn 154* (K, MO, NSW), *154/1842* (BM); Penguin, *Gunn 154* (NSW); Port Dalrymple, *Paterson s.n.* (BM); Hampshire Hills, [*Gunn*] *s.n.* (K); same locality, *Milligan s.n.* (HO); Chilton, Surrey Hills, *Gunn s.n.* (K); May Day Plains, 3000-3500', in exposed open situations on the sides or tops of mountains, [*Gunn*] *651* (K); gum forest association, 2700', Dove Valley, *Weindorfer s.n.* (K); Marlborough, *Gunn s.n.* (NSW); Derby to St.

Helens, *Ford s.n.* (NSW); near St. Patrick's River, *Mueller IL19* (MEL, NSW); same locality, *Gunn 154* (NSW); top of Western Mts., 3500', *Gunn 651* (K); Launceston, *Gunn 154* (MO); same locality, *Gunn 154/1842* (BM, K); same locality, *Stuart s.n.* (MEL, NSW); Cataract Gorge, *Rupp 31* (NSW); Cora Linn, N. Esk, *Gunn 154/1842* (NSW); sides of mountains among rocks, [*Gunn*] 650 (K); Arthur's Lakes, *Gunn 651* (K, NSW); sheltered side of beach, Bicheno, *Ford s.n.* (NSW); Macquarie Harbour, *Le Grand s.n.* (MEL); same locality, in damp shaded woods on the low shores, *A. Cunningham 33* (K); beech forest between Lake Huegel and Lake St. Clair, *Burbidge 3359* (CANB); 3500', Lake Fenton National Park, *Lord s.n.* (HO, K); rocky slopes above Lake Fenton, Mt. Field National Park, *Burbidge 3280* (CANB); Maria Island, summit of mountain, c. 2000', *Gibbs 6395* (K); Hobart Town, *Siemsen s.n.* (MEL, NSW); Lenah valley near Hobart, *White 8406* (A, BM); prope Derwent, *Brown 5448* (BM, K, MO); Diabase Hill, Collins Vale in Fairy Glen, *Long 1008* (HO); open places in moist forest, 2000', Collinsvale, *Comber 1550* (K); 300', Waterworks, Hobart, *Olsen s.n.* (HO); 800', near waterworks, *Atkinson 93* (CANB, HO, K); 1000', High Peak, Hobart, *Curtis s.n.* (BH); rocky hillside above springs, Mt. Wellington, *Long 355* (HO); Mt. Wellington, *Gunn 154/1842* (NSW), *651/1842* (BM); same locality, *Verreaux 1961* (K, P); same locality, *Maiden & Cabbage s.n.* (NSW); 1200', by creek bank, New Town side, Mt. Wellington, *Long 375* (HO, K); 3000', above springs, Mt. Wellington, *Long 355* (A); Kangaroo Bottom, *Hooker 844* (K); Sassafras Valley, *Hooker 842* (K); Mt. Nelson, *Rodway s.n.* (HO); Little Plain, *Simson s.n.* (AK); Adventure Bay, [*Bligh, Wiles & Smith*] *s.n.* (BM, K); Recherche Bay, *Maiden 3991* (BH, NSW). WITHOUT LOCALITY: *Archer s.n.* (NSW); *Blyth s.n.* (NSW); *Caley s.n.* (A); *Gunn 154, 651* (GH, K); *Hannaford s.n.* (NSW); *La Billardièrè s.n.* (BM, GH, MO); *Lawrence s.n.* (K).

The variation in plant form and leaf size in this species was noticed by Hooker¹⁶⁰, who remarked:

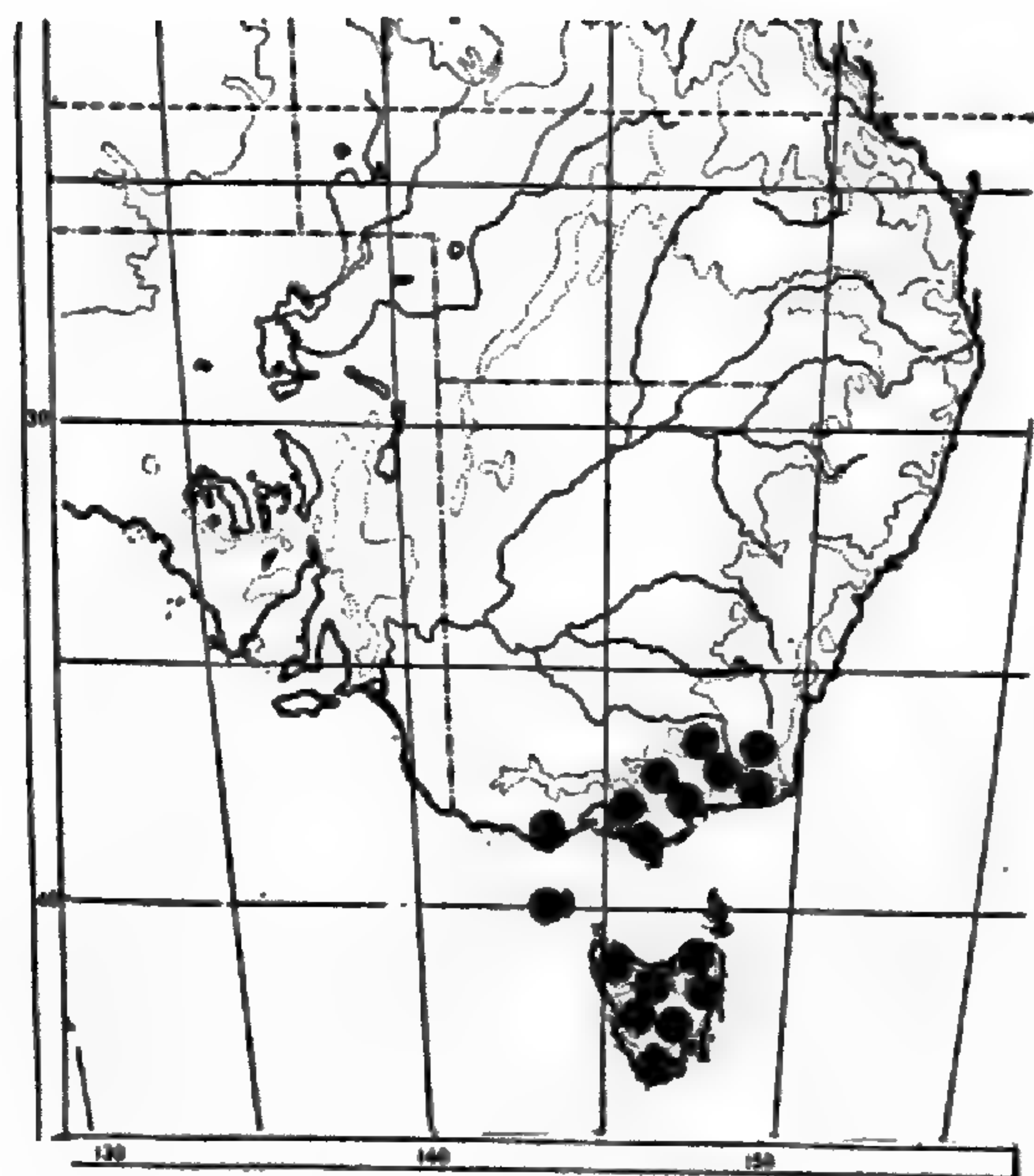
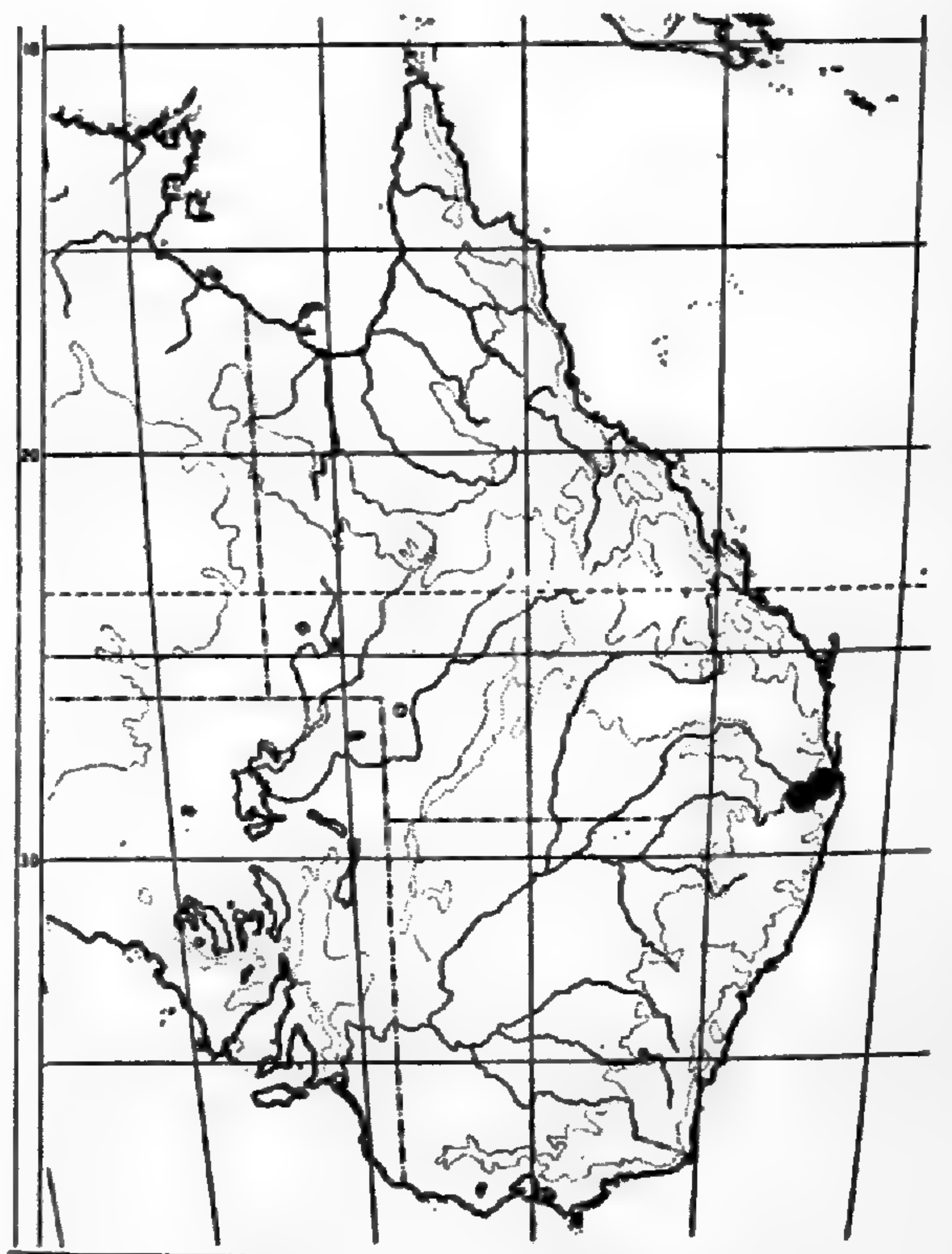
One of the most variable plants in the Island (Tasmania), forming in low grounds, a tree 30 - 40 feet high; with a trunk a foot and more in diameter, but gradually becoming a stunted scrubby bush on ascending the mountains. The changes of habit and characters on ascending are so gradual that I cannot rigidly define the varieties, of which the following are the best marked; on low ground, branches lax, twiggy, with spreading flat, linear-obovate or oblong leaves, 1-2 inches long, with slightly revolute margins and silvery grey down beneath; on ascending, the branches become short, rigid, robust, erect, leaves densely crowded, erect, shorter, blunter, with rigidly coriaceous margins very revolute, clothed below with ferruginous silky and villous hairs.

The flowers also vary in size and form. Flowers which may be female have capitate stigmas, styles 1 - 2 mm. long, plump ovaries, filaments 2 - 3 mm. long, and possibly abortive anthers about 1 mm. long. Flowers which may be male have weakly capitate to truncate stigmas, styles 3 - 5 mm. long, slender ovaries, filaments 3 - 5 mm. long, and functional anthers 2 - 3 mm. long. Pedicels of female flowers are usually shorter than those of male flowers. Between the two extremes described, intermediate forms have been found; e.g. *Lord s.n.* from 3500' at Lake Fenton National Park has a truncate stigma, style 3 mm. long, filaments 4.5 - 5.0 mm. long (i.e. it appears to have male flowers) but the anthers are only 1 mm. long, apparently abortive; *Olsen s.n.* from 300' at the waterworks, Hobart, has a capitate stigma, style 1.5 mm. long, and anthers 1.5 mm. long (i.e. it appears to have female flowers) but the filaments are 4.5 mm. long as in male flowers.

Pittosporum bicolor is cultivated in California and England.

Vernacular names: Whitewood, Tallow-wood, Tolosa-wood, Dragon's Blood Pittosporum (Tasmania), Cheesewood (Victoria), *Banyalla* (Victoria, aboriginal).

¹⁶⁰ Fl. Tasman. p. 38.. 1860.

Fig. 15. *P. bicolor*.Fig. 16. *P. o'reillyanum*.

11. *PITTIOSPORUM O'REILLYANUM* White, in Proc. Roy. Soc. Queensland 47:53. 1936. (T.: *White* 6173!).

Shrubs 1 - 2 m. tall; branchlets grayish-brown, spinose, brown-tomentulose when young, soon glabrate. Leaves alternate, sometimes clustered on arrested branchlets, ovate to elliptic-oblong, acute to cuspidate at apex, obtuse at base, entire, 2.5 - 20.0 mm. long, 2 - 5 mm. broad, green above, paler beneath, sparsely tomentulose when young, soon glabrate, margins flat or recurved, costa immersed above and beneath, secondary nerves 2 - 4 per side, anastomosing, distinct or obscure; petioles up to 1.0 mm. long, sparsely tomentulose when young, soon glabrate. Flowers axillary or terminal, on arrested branchlets, solitary; pedicels 1 - 2 mm. long, accrescent in fruit, brown-tomentulose, subtended by 1 to several leaves and caducous brown-tomentulose bud scales 0.5 - 1.0 mm. long. Sepals irregularly connivent at the base, subulate, acute, 1.7 - 2.0 mm. long, 0.5 - 0.8 mm. broad, tomentulose; petals linear to linear-oblong, subacute to acute, 6.0 - 9.5 mm. long, 1.2 - 1.5 mm. broad, connivent in a cylindrical or slightly spreading tube with reflexed tips; stamens 6.8 - 7.0 mm. long, anthers oblong to ovate, 1.8 - 2.0 mm. long, 0.7 - 1.0 mm. broad, filaments filiform, coherent to the petals. Pistil at anthesis equal to the stamens; ovary 3 - 4 mm. long, 1 mm. broad, tomentulose; style 2.5 - 3.0 mm. long; stigma subcapitate, obscurely 2-lobed. Capsules globose, 2-valved, apiculate, 7 - 12 mm. broad, glabrous, smooth; valves convex in transverse section, less than 1 mm. thick, coriaceous, with a placenta bearing 3 - 4 strap-like funicles, up to 2 mm. long, from the middle to the base; seeds about 6, light red, irregular.

Occurs at high altitudes in southeast Queensland. Flowers in September and October.

AUSTRALIA: QUEENSLAND: very common in rain forest, usually weighted down with masses of liverworts and mosses, 4000', Mt. Hobwee, Lamington National Park, *White 6173* (A, BM, K, MO); in *Nothofagus* forest, 3700', Mt. Merino, MacPherson Range, *Johnson s.n.* (NSW); MacPherson Range, *Perry 512* (CANB).

12. PITTOSPORUM UMBELLATUM Banks & Soland. ex Gaertn. *Fruct. et Sem.* 1: 286. *t. 59.* 1787-88. (T.: *Banks & Solander s.n.*!).

Pittosporoides umbellata Soland. ex Gaertn. *loc. cit.* 1787-88, *nom. nud. in synonym.*

Small trees 4 - 10 m. tall; branchlets grayish-brown, the young parts sparsely brown-tomentose when young, soon glabrate. Leaves subverticillate, dark green above, paler beneath, glabrous, coriaceous, margins thin, flat and brown-pilose when young, thickened, revolute, and glabrate when mature, costa raised above and beneath, frequently sparsely brown- to white-tomentose at base, secondary veins 8 - 15 per side, anastomosing, obscure above, distinct beneath. Juvenile leaves obovate to oblanceolate, usually crenate, lobed, or parted; adult leaves elliptic to oblong-lanceolate, entire, or rarely crenate, acute or acuminate at apex, acute to attenuate at base, 2.5 - 10.0 cm. long, 1.5 - 5.0 cm. broad; petioles 6 - 22 mm. long 1 - 2 mm. broad, brown-tomentose when young, glabrate. Inflorescences terminal or sometimes becoming lateral on development of a leading shoot from an axillary bud, in umbels up to 20-flowered; pedicels 4 - 25 mm. long, accrescent in fruit, brown-tomentose, subtended by an approximate whorl of leaves and numerous caducous, glabrous, ciliate bud scales up to 12 mm. long. Sepals slightly imbricate at base, lanceolate, acute to acuminate, 4.5 - 9.0 mm. long, 1.5 - 3.0 mm. broad, sparsely ciliate; petals linear-oblong, subacute to obtuse, 11.0 - 12.5 mm. long, 2.5 - 5.0 mm. broad, loosely coherent at the base, spreading from above the middle, dull red; stamens 4 - 8 mm. long, anthers sagittiform to elliptic-oblong, 1 - 3 mm. long, 0.6 - 1.3 mm. broad. Pistil at anthesis slightly shorter or longer than the stamens; ovary 2.5 - 3.5 mm. long, 1 - 3 mm. broad, villous; style 3 - 4 mm. long; stigma capitate and obscurely 4-lobed, or truncate. Capsules tetragonous or 4-lobed, 2-valved, 7 - 12 mm. in diameter, green to black, sparsely pubescent; valves concave in transverse section, less than 1 mm. thick, with much thickened rims, coriaceous, with a conspicuous placenta bearing short stout funicles from near the base to just above the middle; seeds 9 - 14, black, irregular.

Occasional from the North Cape to the Coromandel Peninsula, North Island of New Zealand, in forest remnants on the sea coast and coastal islands. Reputed to occur as far south as Gisborne in Poverty Bay, but I have not seen specimens from south of the Thames district.

NEW ZEALAND: NORTH AUCKLAND: summit of Ounuwahao, 950', Spirit's Bay, *Cooper 24478* (AK); at waterfall, near sea-level, Kapowairua valley, Spirit's Bay, *Cooper 24448* (AK); Spirit's Bay, *Cheeseman s.n.* (AK); at sea-level, Taipa, base of Doubtless Bay, *Walker 5364* (AK, MO, US); in *Agathis australis* forest, Saies, Whangaroa Harbour, *Cooper 35960* (AK, MASS, MO); Totara North, Whangaroa Harbour, *Carse s.n.* (AK); Koukoumiko, Baie des Îles, *Raoul s.n.* (P), 81 (K); Bay of Islands, *Wilkes s.n.* (US);

same locality, *A. Cunningham* 29/1826 (K); same locality, *Fraser s.n.* (K); same locality and Tippona, *Wilkes s.n.* (K); Opua, Bay of Islands, *Moore & Cranwell s.n.* (AK); Helena Bay, *Olsen s.n.* (AK); Whangarei Heads, *Cheeseman s.n.* (AK, GH, NSW); same locality, *Baylis s.n.* (K); same locality, *Turner s.n.* (AK); same locality, *Turbott s.n.* (AK); Taranga (Hen Island), *Moore & Cranwell s.n.* (AK). THAMES: Great Barrier Island, *Kirk s.n.* (AK), 90 (K); same locality, *Hynes s.n.* (AK); same locality, near State forest Service Station, *Lloyd & Anderson* 36309, 36310 (AK); same locality, coastal forest, Whangaparapara, *Molesworth s.n.* (AK); Little Barrier Island, *Kirk* 90 (K); same locality, *Cheeseman s.n.* (AK, US); same locality, *Shakespeare s.n.* (AK); same locality, *Adams s.n.* (AK); same locality, 1000', *Turner s.n.* (AK); Cape Colville, *Kirk s.n.* (AK); Te Moehau, near Stony Bay, c. 1000 - 1100', *Moore & Cranwell s.n.* (AK, K); Shag Bay, Coromandel Peninsula, *Moore & Cranwell s.n.* (AK, K); Coromandel, sea-level, *Mackie s.n.* (AK); Kennedy Bay, *Matthews s.n.* (AK); in sylvis prope Oपुरagi, *Banks & Solander s.n.* (BM); Mercury Bay, *Kirk* 6 (A, BM, GH, MO, US); North of Buffalo Beach, *Whetter* 1980 (AK); Tapu, Thames Coast, *Molesworth s.n.* (AK); Thames, *Cheeseman s.n.* (AK); same locality, *Adams s.n.* (AK); same locality, near sea, *Petrie s.n.* (A). WITHOUT LOCALITY: *Banks & Solander s.n.* (AK, MO, US); *Colenso s.n.* (K); *A. Cunningham* 30 (U); *R. Cunningham* 192, 613 (K); *Hooker*, 350, 351 (K); *Kirk s.n.* (K); *Wilkes s.n.* (GH).

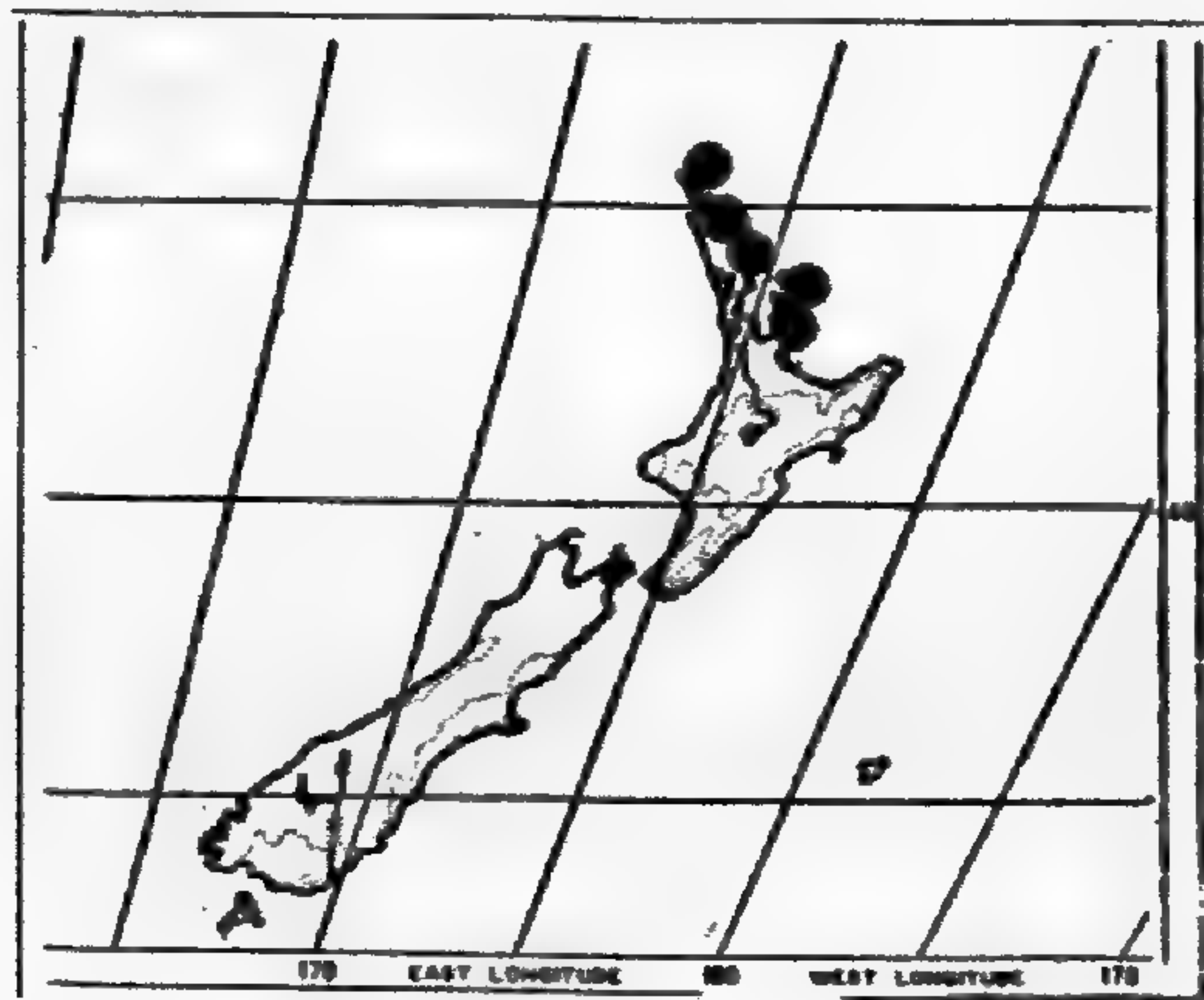


Fig. 17. *P. umbellatum*.

Heterophylly in this species has been described and illustrated in the discussion of taxonomic criteria. Flowers occur which are probably female. They have capitate, 4-lobed stigmas which are exerted 1 - 2 mm. beyond the stamens, and sagittiform anthers only 1.0 - 1.5 mm. long, which appear to be abortive. The pedicels are usually short (4 - 14 mm.). Flowers which are perhaps male have truncate stigmas, styles 1.0 - 1.5 mm. shorter than the stamens, elliptic-oblong anthers 2 - 3 mm. long, and ovaries which are slender and appear to be abortive. The pedicels are usually long (10 - 25 mm.). Intermediate forms occur with weakly capitate stigmas and pistils which are more or less equal in length to the stamens. I have not found flowers with capitate and truncate stigmas in the same inflorescence, or on the same specimen, but field studies are required to determine the significance of these morphological differences.

A form of the species having leaves gradually narrowed below and cordate capsules has been described as *P. umbellatum* var. *cordatum* by Kirk in N.Z. Inst. Trans. & Proc. 4: 264. 1872. (T.: *Kirk s.n.* A, AK, GH, MO, 90K.) The original

specimens came from the Great and Little Barrier Islands where there are several puzzling forms, and until further studies are made of these populations the status of the variety is obscure.

A cultivated specimen from the Scilly Islands has been seen, *Hill s.n.* (K).

Vernacular name: *Haekaro*.

13. *PITTOSPORUM VIRGATUM* Kirk, in N.Z. Inst. Trans. & Proc. 4: 264. 1872. (T.: *Kirk s.n.*!).

Pittosporum virgatum var. *crataegifolia* Kirk, *loc. cit.* 265. 1872. (T.: *Kirk s.n.*!).

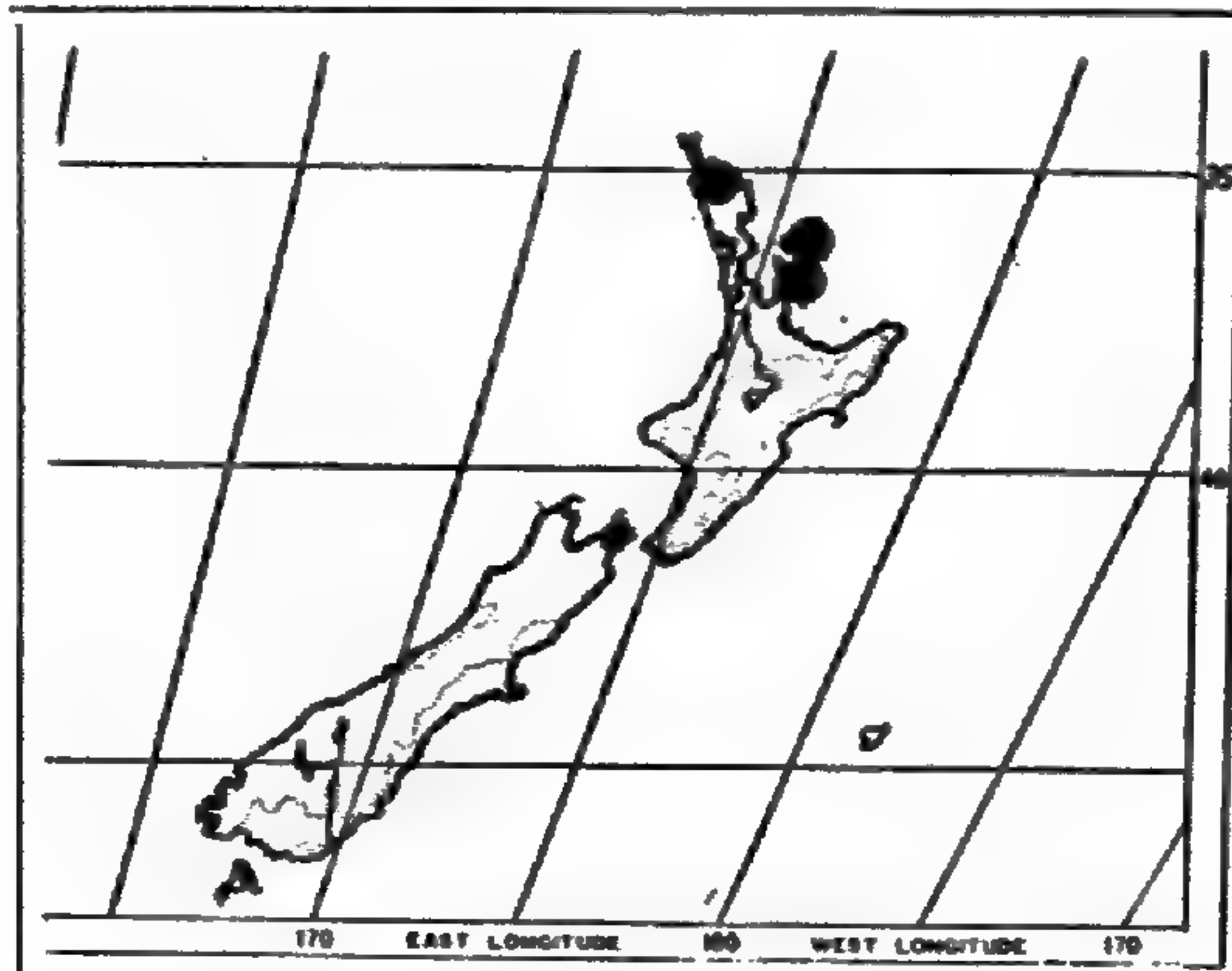
Pittosporum virgatum var. *serratum* Kirk, *loc. cit.* 1872. (T.: *Kirk s.n.*!).

Pittosporum virgatum var. *sinuatum* Kirk, Students' Fl. N.Z. p.51. 1899. (T.: *Kirk s.n.*!).

Pittosporum matthewsii Petrie, in N.Z. Inst. Trans. & Proc. 52: 17. 1920. (T.: *Matthews s.n.*!).

Small trees to 8 m. tall; branchlets brown, rusty-tomentose when young, soon glabrate. Leaves alternate, frequently somewhat crowded at the tips of the branchlets; juvenile or lower leaves linear, entire or variously lobed or parted, 1.0 - 3.8 cm. long, 1 - 7 mm. broad, rusty-tomentose, glabrate; intermediate leaves lanceolate to oblong or obovate, usually lobed or parted, 1.3 - 5.2 cm. long, 0.9 - 2.7 cm. broad; adult or upper leaves oblong, occasionally linear, oblanceolate, or elliptic-oblong, entire, rarely sinuate or lobed, 1.8 - 7.0 cm. long, 0.4 - 2.1 cm. broad; margins flat to slightly undulate, sometimes a little thickened and revolute, costa immersed above, raised beneath, tomentose, secondary veins 7 - 9 per side, anastomosing, obscure above, distinct beneath; petioles 1 - 7 mm. long, 0.5 - 1.0 mm. broad. Flowers terminal, 1 - 6, fascicled or solitary; pedicels 5 - 9 mm. long, accrescent in fruit, rusty-tomentose, subtended by an approximate whorl of leaves and several minute rusty-tomentose caducous scales. Sepals not imbricate at base, oblong to linear-lanceolate, acute, 3.5 - 6.5 mm. long, 1.0 - 2.5 mm. broad, rusty-tomentose; petals linear-oblanceolate to linear-oblong, acute, 6 - 13 mm. long, 2 - 3 mm. broad, coherent in a tube to above the middle, tips reflexed, dark red to purple, rarely yellow, pink or white; stamens 4 - 7 mm. long, anthers sagittiform or oblong-ovate, 1 - 2 mm. long, 0.4 - 1.0 mm. broad. Pistil at anthesis equal to or slightly longer than the stamens; ovary 2 - 4 mm. long, 1.0 - 2.5 mm. broad, rusty-tomentose; style 1 - 5 mm. long; stigma capitate and obscurely 2- or 4-lobed on short-styled pistils, truncate on long-styled pistils. Capsules subglobose to subpyriform, 2-, rarely 3-, valved, apiculate, 11 - 16 mm. long, 10 - 13 mm. broad, rusty-tomentose to glabrate, obscurely rugose; valves sulcate to convex in transverse section, about 1 mm. thick, coriaceous, with a thickened placenta bearing stout flattened funicles up to 2.5 mm. long from the base to above the middle or apex; seeds 1 - 16, black, irregular.

Occurs from the hills behind Ahipara on the west coast to Coromandel Peninsula on the east coast of the North Island of New Zealand. Flowers in September and October.

Fig. 18. *P. virgatum*.

NEW ZEALAND: NORTH AUCKLAND: Kaitaia, *Matthews s.n.* (AK, MO); Taumata Mahoe, near Kaitaia, *Matthews s.n.* (AK); range west of Okahu, Kaitaia, *Matthews s.n.* (AK); at edge of forest, high country, Pukepoto, *Matthews & Carse s.n.* (AK); Whangaroa, *Kirk 96* (K). THAMES: Great Barrier Island, *Kirk s.n.* (GH), 521 (BM); same locality, *Kirk 521* (US); same locality, *Matthews & Petrie s.n.* (AK); same locality, *Hynes 26568* (AK); Port Fitzroy, Great Barrier Island, *Kirk s.n.* (AK), 87, 88 (K); back of Whangaraparapara, *Molesworth 22171* (AK); Coromandel, *Cheeseman s.n.* (AK, BISH, GH, NSW); Kennedy Bay, Coromandel, *Matthews s.n.* (AK, MO); Waipuna, Kennedy Bay, *Matthews s.n.* (AK); between Kennedy Bay and Cape Colville, *Matthews s.n.* (AK).

The plants recognized by Kirk as var. *crataegifolia*, var. *serratum* and var. *sinuatum* are juvenile forms. The distinguishing characters of *P. matthewsii* from Kennedy Bay were stated to be the smaller and narrower linear-oblong leaves and the subpyriform capsules. Among the large collection left by Matthews are specimens of *P. virgatum* from both Kaitaia and Kennedy Bay with subpyriform capsules; and Michie has sent me material from the Kaitaia area with linear leaves which match those of *P. matthewsii*, collected at Kennedy Bay (the type locality). As the morphological differences are slight and both of the main populations show them I have not recognized *P. matthewsii* as a distinct population.

The flowers are of two kinds. Flowers which may be female have capitate, 2- or 4-lobed stigmas, styles 1.0 - 2.5 mm. long, ovaries about 4 mm. long and 2.5 mm. broad, short stamens 4 - 5 mm. long, with sagittiform, possibly abortive anthers about 1 mm. long. Flowers which may be male have truncate stigmas, styles 3.5 - 5.0 mm. long, ovaries 2.0 - 3.5 mm. long, 1 - 2 mm. broad, stamens 5 - 7 mm. long with oblong-ovoid, apparently functional anthers 1 - 2 mm. long.

14. *PITTIOSPORUM PIMELEOIDES* R. Cunn. ex A. Cunn. in Ann. Nat. Hist. 4: 108. 1839. (T.: R. Cunningham 40, 618!).

Shrubs 0.5 - 2.0 tall, erect or prostrate; branchlets slender, brown, the young parts white or brown-tomentulose, soon glabrous. Leaves alternate, sometimes subverticillate, elliptic, elliptic-obovate, oblanceolate, linear-oblong, or linear, acuminate to obtuse at apex, acute to attenuate at base, entire or obscurely crenulate, 0.5 - 4.3 cm. long, 0.5 - 13.0 mm. broad, pale green above, lighter beneath, sparsely tomentulose and ciliolate when young, coriaceous, margins thickened, flat,

costa raised above and beneath, secondary veins anastomosing to form large areoles, obscure above, obscure or distinct beneath, sessile or with petioles up to 0.5 mm. long. Flowers terminal or sometimes becoming lateral on development of a leading shoot from an axillary bud; male flowers 6 - 9, fascicled; female flowers solitary; pedicels filiform, 2 - 9 mm. long, accrescent in fruit, puberulent, subtended by an approximate whorl of leaves and several caducous, glabrous, ciliolate bud scales 2 - 3 mm. long. Sepals not imbricate at base, linear, acuminate, 2.5 - 5.0 mm. long, 0.5 - 1.0 mm. broad, glabrous; petals linear, acuminate, 7.5 - 11.5 mm. long, 1.0 - 2.2 mm. broad, coherent in a tube to about their middle, spreading to reflexed above, cream to yellow with a central red stripe; stamens 2.5 - 6.5 mm. long, anthers sagittiform, or ovate to oblong, 0.5 - 2.0 mm. long, 0.2 - 0.8 mm. broad. Pistil at anthesis equal to or slightly longer than the stamens; ovary 1 - 2 mm. long, 1.0 - 1.5 mm. broad, villous; style 1.5 - 3.5 mm. long; stigma capitate and obscurely 2-lobed, or almost truncate. Capsules ovoid, 2-valved, acuminate, 6 - 12 mm. long, 4 - 6 mm. broad, green to brown, rugose, pubescent when young, glabrate; valves convex in transverse section, less than 1 mm. thick, coriaceous, with a slightly thickened placenta bearing flattened funicles up to 3 mm. long from base to near the middle; seeds 7 - 17, black, irregular.

KEY TO THE SUBSPECIES

- Shrubs usually erect, 0.5-2.0 m. tall; leaves oblanceolate, linear-oblong or linear, 0.5-4.3 cm. long, 0.5-9.0 mm. broad. Sepals 2.5-4.0 mm. long; petals 7.5-9.0 mm. long. North Auckland: Kaitaia to the Kawakawa River.....14a. *P. p. pimeleoides*
 Shrubs prostrate; leaves elliptic or elliptic-obovate, 9-13 mm. long, 4.5-7.0 mm. broad in sun, 1.0-2.7 cm. long and 6-13 mm. broad in shade. Sepals 4.5-5.0 mm. long; petals 11.0-11.5 mm. long. North Auckland: Kerr Point, North Cape.....14b. *P. p. major*

14a. PITTOSPORUM PIMELEOIDES ssp. *pimeleoides*

- Pittosporum pimeleoides* A. Cunn. ex Putterl. Syn. Pittosp. p. 15. 1839, *ex char.* (T.: R. Cunningham s.n.).
Pittosporum crenulatum R. Cunn. ex Putterl. Syn. Pittosp. p. 15. 1839. (T.: Huegel 26!).
Pittosporum reflexum R. Cunn. ex A. Cunn. in Ann. Nat. Hist. 4: 108. 1839. (T.: R. Cunningham 40, 617 !).
Pittosporum radicans R. Cunn. ex A. Cunn. *loc. cit.* 1839. (T.: R. Cunningham 200, 619 !).
Pittosporum pimeleoides R. Cunn. ex A. Cunn. var. *reflexum* (A. Cunn.) Hook. f. Fl. Nov. Zel. 1: 24. 1853.
Pittosporum gilliesianum Kirk, in N.Z. Inst. Trans. & Proc. 1: 143. 1868. (T.: Kirk s.n., 95 !).
Pittosporum pimeleoides R. Cunn. ex A. Cunn. ssp. *reflexum* (A. Cunn.) Kirk, in N.Z. Inst. Trans. & Proc. 4: 263. 1872.
Pittosporum pimeleoides R. Cunn. ex A. Cunn. var. *gilliesianum* (Kirk) Kirk, *loc. cit.* 264. 1872.

Occasional from Kaitaia to Kawakawa in North Auckland, New Zealand.
 Flowers from March to May.

NEW ZEALAND: NORTH AUCKLAND: Kaitaia, H. B. Matthews s.n. (AK); in Kauri (*Agathis australis*) forest, Fairburn, Mangonui, R. H. Matthews & Carse s.n. (AK, MO); south bank of Oruru River, half-mile southwest of Taipa, 100' above sea-level, in remnant of *Agathis australis* forest, Cooper 36009 (AK, MASS, MO); same locality,

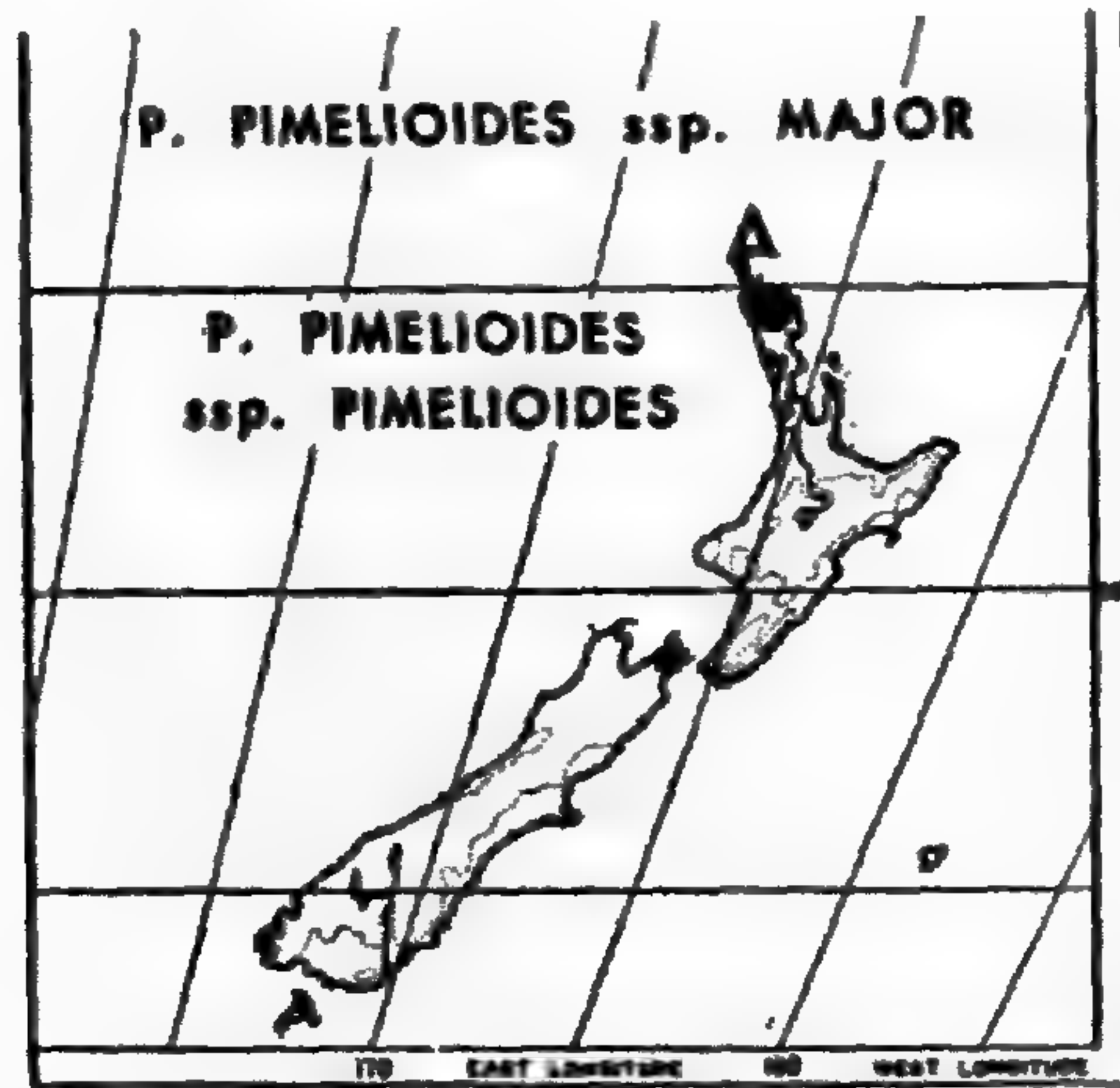


Fig. 19. *P. pimeleoides* ssp. *major* and ssp. *pimeleoides*. Names on map should read *pimeleoides*.

Powell 26437 (AK); hills north of Mangonui Harbour, Cheeseman s.n. (AK, BM); same locality, Kirk s.n. (US), 515 (BM); Waitetoki stream, near Mangonui, Cheeseman s.n. (AK); Mangonui, Kirk 95 (K, as *P. gilliesianum*); at Wangaroa and the Bay of Islands, in thickets on the slopes of hills, R. Cunningham 40, 617 (K, as *P. reflexum*); in dry woods at Wangaroa and the Bay of Islands, R. Cunningham 40, 618 (K, as *P. pimeleoides*); Bay of Islands, Wilkes s.n. (K); same locality, Hector s.n. (K); same locality, Kirk s.n. (A); in dry woods on hills, Wykari, [Hooker] 191 (K); Kawa Kawa River, Kirk s.n. (GH, MO); same locality, Kirk 538 (K); about the roots of Kauri, principally in a forest near the head of the Kawa Kawa, R. Cunningham 200, 619 (K, as *P. radicans*). WITHOUT LOCALITY: Buchanan s.n. (AK); Colenso s.n. (K); A. Cunningham 618 (K); Edgerley s.n. (K); "Auckland", Kirk s.n. (K); a small shrub in woods, Hooker 352 (K); Wilkes s.n. (US); ora septentr. Huegel 25/2, 26 (R. Cunningham) (W).

Flowers which appear to be female have capitate obscurely 2-lobed stigmas, styles only about 1.5 mm. long, and plumper ovaries 2 mm. long by 1 mm. broad. The pistil is exerted 1 mm. or more beyond the stamens, which have sagittiform probably sterile anthers only 0.5 mm. long. Flowers which appear to be male have weakly capitate stigmas, styles 3.0 - 3.5 mm. long, and thinner ovaries 1.0 - 1.5 mm. long and 0.5 - 1.0 mm. broad. The pistil is level with the anthers, which are ovoid, apparently functional, and 1.0 - 1.5 mm. long. The pedicels of "female" flowers are markedly shorter than those of "male flowers".

The ranges of *P. pimeleoides* and *P. reflexum* are not distinct, and I cannot find any constant morphological characters to separate *P. reflexum* as a species or variety. I suspect that most of the variation in leaf size and shape is caused by ecological factors, but have seen too few living plants to be certain. In the discussion of *P. eugenioides*, later in this work, the priority of the specific names of A. Cunningham (Ann. Nat. Hist. 4: 108. 1839) over those of Putterlick (Syn. Pittosp. p. 15. 1839) is discussed.

14b. *PITOSPORUM PIMELEOIDES* ssp. *major* (Cheeseman) R. C. Cooper, *stat. nov.*

Pittosporum pimeleoides R. Cunn. ex A. Cunn. var. *major* Cheeseman, Man. N.Z. Fl. p.60. 1906. (T.: Cheeseman s.n.!).

Found only on Kerr Point, North Cape, New Zealand. Flowers in June.

NEW ZEALAND: NORTH AUCKLAND: Kerr Point, North Cape, *Cheeseman s.n.* (AK); same locality, *Michie 80/45* (AK).

Kerr Point was formerly an island but now is joined to the North Island of New Zealand by a sand bar some 70 miles long, built probably during the Castlecliffian (upper Pliocene) period. Several species of plants are endemic to Kerr Point, but I hesitate to recognize *ssp. major* as a distinct species as it is very similar to *ssp. pimeleoides* in the characters of the flowers and fruits.

15. *PITTIOSPORUM PATULUM* Hook. f. *Handb. N.Z. Fl.* p. 19. 1864 (T.: *Sinclair s.n.*!).

Shrubs 1 - 5.0 m. tall; branchlets grayish-brown, the young parts brown-tomentose, soon glabrous. Leaves alternate, 2 - 6 cm. long, 3 - 10 mm. broad; juvenile leaves usually longer and narrower than the adult, linear, deeply lobed to pinnatifid, the lobes variously toothed; adult leaves linear-oblongate, entire to crenate-serrate, obtuse to acute at apex, attenuate at base, dark green above, paler beneath, glabrous, coriaceous, margins flat, rarely revolute, costa raised above and below, side veins 10 - 15 per side, anastomosing, usually obscure when juvenile but distinct above when adult; petioles 2 - 7 mm. long, brown-tomentose when young, glabrate. Flowers terminal, 3 - 7, fascicled; pedicels 7 - 15 mm. long, contracted in fruit, brown-tomentose, subtended by a whorl of leaves and numerous caducous, sparsely tomentose bud scales 1 - 2 mm. long. Sepals rarely imbricate at base, ovate-lanceolate, irregularly toothed above, acuminate, 4 - 6 mm. long, 1.5 - 2.5 mm. broad, glabrous; petals oblong, obtuse, 9 - 11 mm. long, 2 - 3 mm. broad, free or coherent at the base, spreading from above the middle, purple; stamens 4 - 7 mm. long, anthers about 1 mm. long and broad. Pistil at anthesis slightly exserted; ovary 2.5 - 3.0 mm. long, 1 - 2 mm. broad, glabrous; style 1.5 - 3.5 mm. long; stigma capitate and 2-lobed or truncate. Capsules cordate, globose to subglobose, 2-valved, 6 - 11 mm. in diameter, glabrous; valves convex to weakly sulcate in transverse section, less than 1 mm. thick, coriaceous, with a conspicuous placenta bearing 2 rows of short stout funicles from the base to just above the middle; seeds about 18 per capsule, black, irregular.

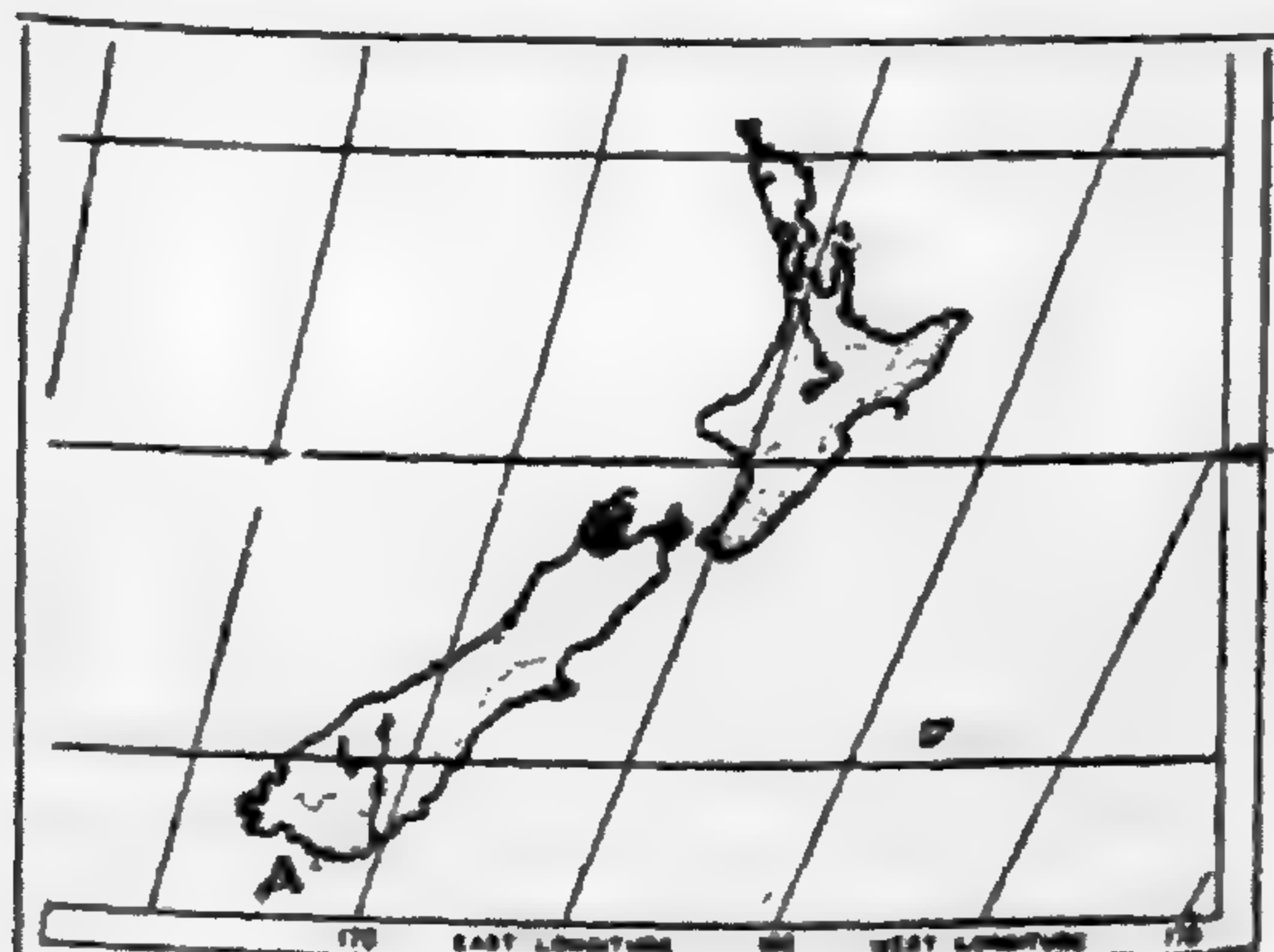


Fig. 20. *P. patulum*.

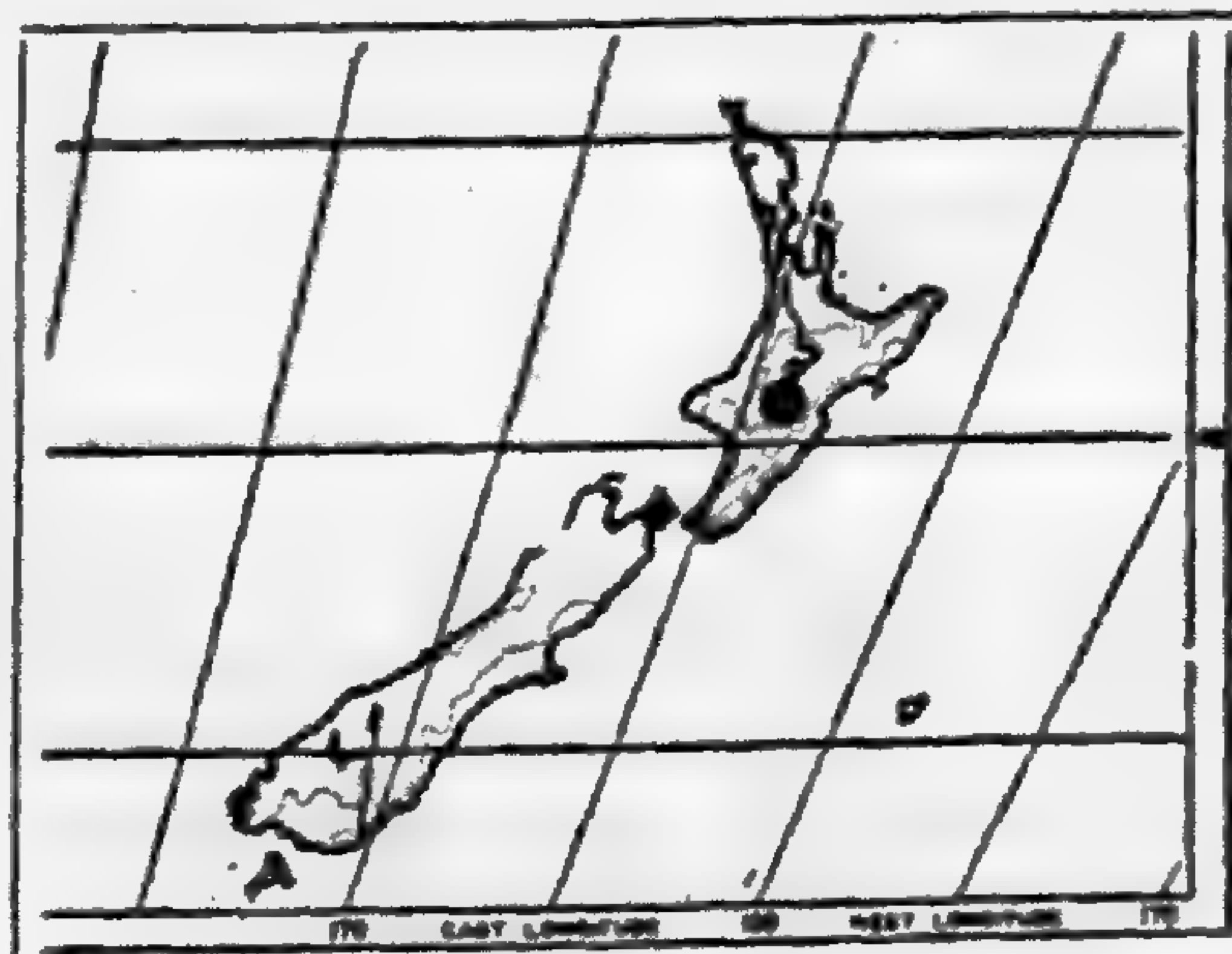


Fig. 21. *P. turneri*

Rare and local in the northern ranges of the South Island of New Zealand.

NEW ZEALAND: NORTH AUCKLAND: Kerr Point, North Cape, *Cheeseman s.n.* (AK); near Collingwood, *Gibbs s.n.* (BM); Lake Rotoiti, *Buchanan s.n.* (AK); same locality, *Cheeseman s.n.* (AK); Spencer Mountains, *Kirk s.n.* (GH, MO); Spencer Mountains, Glacier Gully, *Laing s.n.* (NSW); woods, Upper Waiau, *Travers s.n.* (K); 5000', same locality, *Sinclair s.n.* (K).

16. *PITTOSPORUM TURNERI* Petrie, in N.Z. Inst. Trans. & Proc. 55: 95. 1924.
(T.: *Matthews & Carse s.n.*!).

Shrubs or small trees 2 - 9 m. tall; branchlets dark gray or brown, sharply divaricating and matted at juvenile stage or on lower part of stem, fastigate in adult stage or on upper part of stem, white-tomentulose when young, soon glabrate. Leaves alternate, clustered at the tips of short branchlets, brownish-green above, paler beneath, tomentulose when young, soon glabrate, coriaceous, with slightly thickened and revolute margins, costa obscure above, raised beneath, secondary veins 10 - 13 per side, anastomosing, obscure above, distinct beneath. Juvenile leaves orbicular, obovate, or linear, entire or variously lobed and parted, 2 - 15 mm. long, 1 - 5 mm. broad, adult leaves obovate to oblanceolate, obtuse to acute at apex, attenuate at base, entire or obscurely crenate, 1 - 4 cm. long, 6 - 12 mm. broad; petioles 0.5 - 2.5 mm. long, 0.5 - 1.5 mm. broad, tomentulose when young, soon glabrate. Flowers terminal, 4 - 12, fascicled; pedicels 1 - 3 mm. long, accrescent in fruit, brown-tomentose, subtended by an approximate whorl of leaves and numerous caducous tomentose-ciliate bud scales 2 - 7 mm. long. Sepals slightly imbricate at base, lanceolate, acute to acuminate, 3.5 - 5.0 mm. long, 1 - 2 mm. broad, ciliolate, tomentulose; petals oblong, subacute to obtuse, 6 - 9 mm. long, 2.0 - 2.5 mm. broad, free spreading from above the middle, pink or purple; stamens 4.0 - 5.5 mm. long, anthers ovate-elliptic, 1.5 - 2.0 mm. long, 0.5 - 1.0 mm. broad. Pistil at anthesis slightly shorter than or equal to the stamens; ovary 2.5 - 3.5 mm. long, 1.0 - 1.5 mm. broad, tomentulose; style about 2 mm. long; stigma weakly capitate to truncate. Capsules globose, 2-, rarely 3-, valved, apiculate, 5 - 8 mm. in diameter, slightly rugose; valves convex or sometimes sulcate in transverse section, less than 1 mm. thick, coriaceous, with a conspicuous placenta bearing several pairs of short stout funicles between the base and the middle; seeds 3 - 10, black, irregular.

Found only on the Central Volcanic Plateau of the North Island of New Zealand, at forest margins between Erua and Waimarino, about 1000 m. above sea-level. Flowers in November and December.

NEW ZEALAND: VOLCANIC PLATEAU: Waimarino, *Matthews & Carse s.n.* (AK, MO); same locality, *Petrie & Matthews s.n.* (AK); same locality, *Turner s.n.* (AK); 3000', Erua and Waimarino, *Attwood s.n.* (AK, K, MO); forest margins, Waimarino, *Allan s.n.* (GH, K); on stream side near Erua, *Allan s.n.* (K); same locality, *Moore & Cranwell s.n.* (AK, K, MO).

17. *PITTOSPORUM OBCORDATUM* Raoul, in *Ann. Sci. Nat.* III, 2: 121. 1844.
(T.: *Raoul s.n.*!).

Shrubs to small trees 2 - 5 m. tall; branchlets divaricating, gray to reddish-brown, tomentulose when young, soon glabrate. Leaves alternate at seedling stage and on young branchlets, later restricted to the tips of arrested branchlets 1 - 2 mm. long, tomentulose to glabrous, submembranous when young, coriaceous when adult, margins entire or crenate, flat or revolute, sparsely ciliolate, costa immersed above, raised beneath, secondary veins 2 - 4 per side, anastomosing, obscure above, distinct or obscure beneath; juvenile leaves at first oblong to elliptic, entire, 5 - 9 mm. long, 2.5 - 4.0 mm. broad, soon linear to spatulate, variously lobed, toothed and parted, rarely entire, 1.3 - 3.6 cm. long, 2 - 12 mm. broad; adult leaves orbicular to obovate, obcordate to obtuse at apex, attenuate at base, 4 - 14 mm. long and broad; petioles 0.5 - 5.0 mm. long, tomentulose to glabrous, usually narrowly winged. Inflorescences axillary or terminal, on minute arrested branchlets, 1- to 5-flowered, umbelliform; pedicels up to 2 mm. long, accrescent in fruit, tomentulose, subtended by 1 - 5 leaves and numerous caducous sparsely ciliolate and tomentose bracts 1 - 2 mm. long. Sepals slightly imbricate at base, lanceolate-subulate acute, 1.5 - 3.0 mm. long, 0.5 - 1.0 mm. broad, ciliolate, tomentulose; petals linear-oblong, obtuse, 4.0 - 6.5 mm. long, 0.7 - 1.5 mm. broad, connate in a cylindrical tube with spreading or reflexed tips, pale purple, yellow, or white, sometimes with a reddish-purple stripe; stamens 2.5 - 4.5 mm. long, anthers sagittiform to ovate, 0.5 - 1.0 mm. long. Pistil at anthesis slightly shorter or longer than the stamens; ovary 1.5 - 3.3 mm. long, 0.5 - 1.5 mm. broad, tomentose; style 1 - 2 mm. long; stigma capitate and obscurely 2-lobed or truncate. Capsules ellipsoid to subovoid, 2-valved, apiculate, with persistent sepals at base, 6.5 - 10.0 mm. long, 5 - 7 mm. broad, frequently dehiscing laterally by one opening, green to black, slightly rugose, sparsely tomentose, glabrate; valves convex in transverse section, less than 1 mm. thick, coriaceous, with a slightly thickened placenta bearing 2 - 4 stout flattened funicles up to 1 mm. long from the base to just above the middle; seeds 4 - 7, reddish-black to black, irregular.

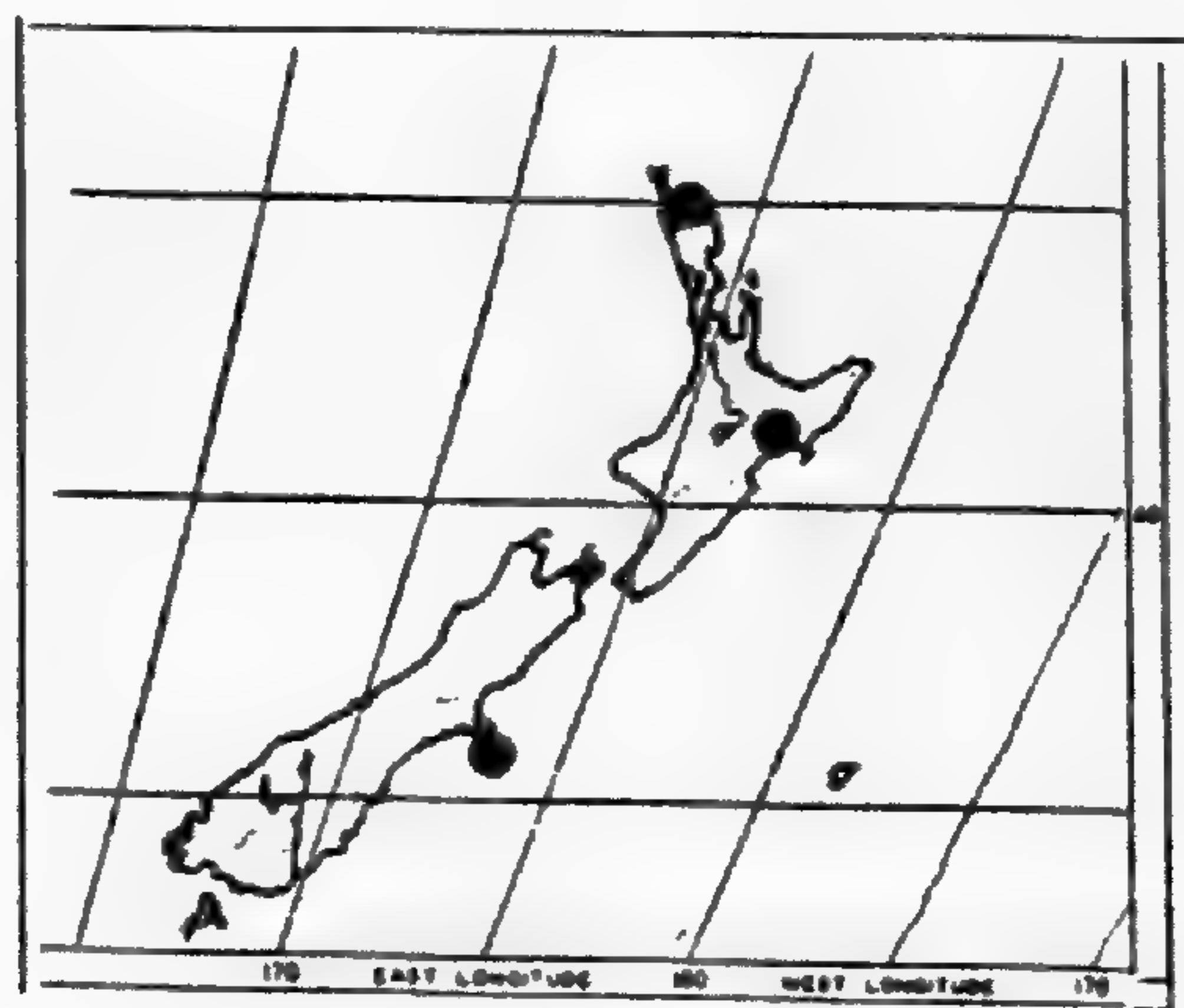
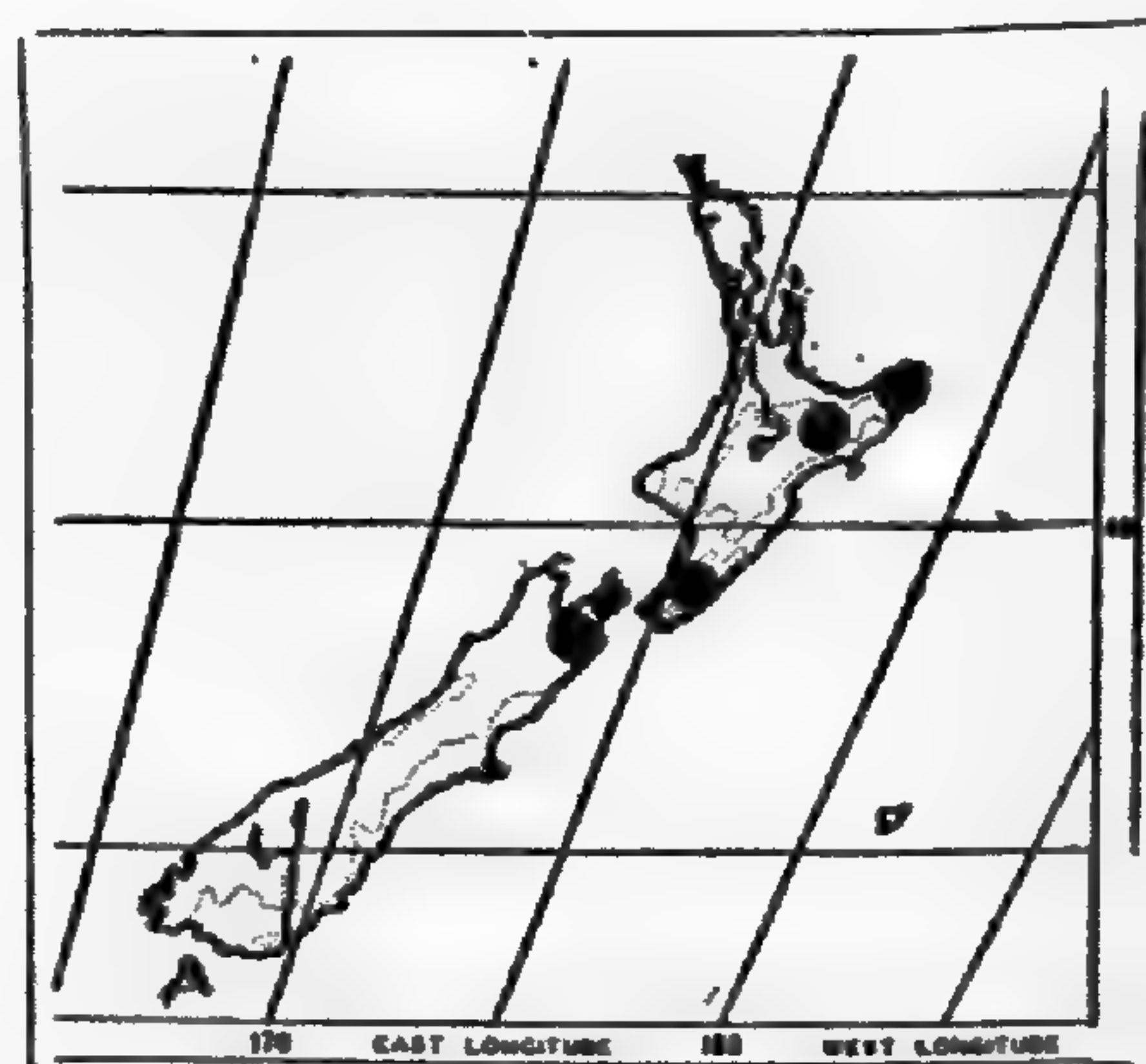
Found in three isolated localities in New Zealand. Flowers in October and November.

NEW ZEALAND: NORTH AUCKLAND: near Lake Tongongoe, Kaitaia, *H. B. Matthews s.n.* (AK, CANTY); same locality, *R. H. Matthews s.n.* (AK, BM); in open on river bank, west of wireless station, Kaitaia, *H. B. Matthews & Carse s.n.* (AK, CANTY); in alluvial land subject to flooding, in shade of river bank below Kaitaia, *R. H. Matthews & Carse s.n.* (AK, MO); Kaitaia, *H. B. Matthews s.n.* (AK, MO); 1855 (K). EAST CAPE: Wairoa River, *Sainsbury s.n.* (AK, CANTY); Hurumua, near Wairoa, *Hodgson s.n.* (CANTY). CANTERBURY: presqu'île de Banks, *Raoul s.n.* (P), 80 (K).

The type material was collected by Raoul between 1840 and 1842 at Banks Peninsula in the South Island of New Zealand, but the plant has not been found again in that locality. In 1901 *R. H. Matthews* found two or three plants at Kaitaia in the extreme north of the North Island, and about 1923 *G. O. K. Sainsbury* discovered twelve or fifteen plants near Wairoa on the east coast of the North

Island. The plants of these widely separated stands are not floristically identical and Laing & Gourla¹⁶¹ described the Kaitaia population as *P. obcordatum* var. *kaitaiaensis* but their description lacks a Latin diagnosis and is therefore invalid¹⁶². The two authors mentioned separated the Kaitaia plants as a variety on their seedling form, but I do not consider that their evidence is adequate. Cheeseman¹⁶³ noted that specimens from Kaitaia had slightly larger young leaves, and Sainsbury pointed out that the bark of the Wairoa plants is reddish-gray rather than gray, but the differences in the material which I have seen are so slight that I do not consider that varietal names are warranted.

The flowers of Kaitaia and Wairoa plants appear to be unisexual. Flowers which may be female have capitate, 2-lobed stigmas, short styles, plump ovaries 3 mm. long, 1.0 - 1.5 mm. broad, stamens 0.5 - 1.3 mm. shorter than the pistil and sagittiform probably abortive anthers under 1 mm. long. Flowers which may be male have weakly capitate to truncate stigmas, longer styles, more slender ovaries 1.5 - 2.5 mm. long, 0.5 - 1.0 mm. broad, stamens almost equal to or slightly longer than the pistil, and ovate probably functional anthers about 1 mm. long. The single Akaroa specimen has flowers which appear to be male. Godley¹⁶⁴ has informed me that the species is dioecious.

Fig. 22. *P. obcordatum*.Fig. 23. *P. rigidum*.

18. *PITOSPORUM RIGIDUM* Hook. f. Fl. Nov. Zel. 1: 22. t. 10. 1853. (T.: *Colenso s.n.*!).

Shrubs to 3 m. tall; branchlets erect, not interlaced or divaricating, grayish-brown, rusty- to gray-tomentose, glabrate. Leaves alternate, dark green above, paler beneath, costa raised or immersed above, raised beneath, secondary veins usually obscure; juvenile leaves obovate, oblanceolate, or elliptic-oblong, acute,

¹⁶¹ Laing & Gourlay, in Trans. Roy. Soc. N.Z. 65: 47. 1935.

¹⁶² Int. Code Bot. Nomencl. 1952. Art. 44.

¹⁶³ Man. N.Z. Fl. ed.2. p.490. 1925.

¹⁶⁴ Personal communication.

rarely obtuse at apex, attenuate at base, variously incised, toothed or crenate, occasionally entire, 5 - 13 mm. long, 3 - 10 mm. broad, tomentulose, soon glabrate, membranous to coriaceous; adult leaves elliptic-oblong, occasionally oblanceolate to obovate, rarely lanceolate, obtuse to subacute at apex, obtuse at base, entire, rarely toothed, 5 - 24 mm. long, 3 - 13 mm. broad, rusty-tomentose, glabrate, coriaceous, slightly revolute; petioles 1 - 3 mm. long, rusty-tomentose. Flowers terminal or axillary, solitary; pedicels 0.5 - 4.0 mm. long, accrescent in fruit, subtended by one to several leaves and a whorl of caducous brown-tomentulose bud scales 1 - 2 mm. long. Sepals not imbricate, lanceolate-oblong, acute, 3.5 - 6.0 mm. long, 1.0 - 1.5 mm. broad, sparsely ciliolate with scattered hairs; petals linear-oblong, obtuse, 8 - 12 mm. long, 2 mm. broad, free, patent with reflexed tips, dingy purple; stamens 4.0 - 6.5 mm. long, anthers sagittiform or ovate, 0.6 - 1.8 mm. long, 0.3 - 1.0 mm. broad. Pistil at anthesis slightly shorter than the stamens; ovary 2.0 - 2.5 mm. long, 1 - 2 mm. broad, tomentose; style 2.5 mm. long; stigma capitate to truncate. Capsules subglobose, 2-valved, apiculate, 8 - 10 mm. long, 6 - 10 mm. broad, tomentose, glabrate, rugose; valves convex in transverse section, less than 1 mm. thick, coriaceous, with a slightly thickened placenta bearing 1 - 5 thick strap-like funicles up to 1.5 mm. long near the middle; seeds 3 - 9, black, irregular.

Occurs from the East Cape of the North Island of New Zealand to Marlborough in the South Island, along the mountain ranges between 650 and 1400 m. Flowers in November and December.

NEW ZEALAND: EAST CAPE: Mt. Hikurangi, *Adams s.n.* (AK); 4000', same locality, *Petrie s.n.* (AK); 4300', undershrub in *Notofagus* (beech) forest, Maungapohatu, Urewera, *Moore & Cranwell s.n.* (AK). WELLINGTON: Mt. Holdsworth, 3500', *Townson s.n.* (BM); same locality, at forest line, *Cockayne 9076* (A); same locality, *Aston s.n.* (AK, NSW); same locality, *Jones s.n.* (MO); 3000'-4000', Mt. Hector, *Petrie s.n.* (AK); same locality, *Attwood s.n.* (AK); Mt. Waiopahu, *Attwood s.n.* (AK); Mt. Omega, *Turner 156* (AK); Field Hut, *Moore & Cranwell s.n.* (AK). MARLBOROUGH: Mt. Stokes, *Turner s.n.* (AK). WITHOUT LOCALITY: *Colenso s.n.*, 45, 64, 924 (K); *W. T. L. Travers s.n.* (K).

The flowers are of two kinds: those which appear to be male have truncate stigmas, styles about 2.5 mm. long, slender ovaries 2.5 mm. long, 1 mm. broad, stamens 5.5 - 6.5 mm. long, and probably functional ovoid anthers 1.5 - 2.0 mm. long, 1 mm. broad. The flowers which appear to be female have capitate stigmas, styles about 2 mm. long, plump ovaries 2.0 - 2.5 mm. long, 2 mm. broad, stamens about 4 mm. long, and probably abortive sagittiform anthers 0.6 - 0.8 mm. long, 0.3 - 0.5 mm. broad.

The flowering material available is inadequate but in the specimens seen the male flowers had pedicels up to 4 mm. long while the female flowers had pedicels only 0.5 mm. long. Godley¹⁶⁵ has informed me that the species is dioecious.

Cockayne¹⁶⁶ divided *P. rigidum* Hook. f. into two species, and kept the name

¹⁶⁵ Personal communication.

¹⁶⁶ N.Z. Inst. Trans. & Proc. 47:111. 1915.

P. rigidum for the East Cape and Tararua population, as Colenso gathered the type material in the East Cape district.

19. *PITTOSPORUM CRASSICAULE* Cockayne ex Laing & Gourlay, in Trans. Roy. Soc. N.Z. 65: 50. 1935. (T.: *Laing & Gourlay s.n.*!).

Pittosporum lineare Laing & Gourlay, *loc. cit.* 57. 1935. *in part.* (*quoad MacMabon 35!*).

Shrubs to 4 m. tall; main branches usually erect, often closely compressed; branchlets divaricating, opposite or whorled at the nodes, stout, often spinose at the tips, white-tomentose. Leaves alternate at seedling and juvenile stage, restricted to the apex of short, stout, sometimes minute branchlets at adult stage, submembranous when juvenile, coriaceous when adult, green above, paler beneath, sparsely ciliolate and tomentulose when young, glabrate, costa slightly raised above and beneath or immersed, secondary veins obscure; juvenile leaves obovate to oblanceolate, variously lobed and parted, lobes irregularly dentate, 4.5 - 12.0 mm. long, 3 - 8 mm. broad; adult leaves linear or elliptic-oblong to oblanceolate, obtuse to subacute at apex, attenuate at base, entire, occasionally lobed or toothed, especially in shade forms, 3.5 - 17.0 mm. long, 1 - 4 mm. broad; petioles 1.0 - 1.5 mm. long, glabrous. Flowers terminal, 1 - 3, solitary or fascicled, sessile on minute arrested branchlets, subtended by 1 - 6 leaves and numerous persistent tomentulose bud scales about 1 mm. long. Sepals imbricate at base, lanceolate-ovate, 1.2 - 1.5 mm. long, 1 mm. broad, glabrous, ciliolate; petals linear-oblong, obtuse, 4.0 - 7.5 mm. long, 1.2 - 1.5 mm. broad, coherent in a cylindrical tube, tips spreading, later recurved, purple; stamens 1.5 - 4.5 mm. long, anthers ovate, 0.6 - 1.0 mm. long, 0.4 - 0.6 mm. broad. Pistil at anthesis slightly shorter or longer than the stamens; ovary 1.5 - 2.5 mm. long, 1 - 2 mm. broad, tomentulose; style 1 - 2 mm. long; stigma capitate or truncate. Capsules subglobose to globose, 2-valved, apiculate, 4.5 - 7.0 mm. long, 5.5 - 7.0 mm. broad, tomentulose or glabrate, rugose; valves convex in transverse section, less than 1 mm. thick, almost woody, with a placenta thickened from the middle to the base, bearing 1 - 2 slender peg-like funicles near the middle; seeds 1 - 3, black, round to irregular.

Occurs in Marlborough, Nelson, Westland, and Canterbury, mainly on the western side of the South Island of New Zealand. Flowers in October and November.

NEW ZEALAND: MARLBOROUGH: Pelorus Valley, *MacMabon 35* (AK). NELSON: 500', Maitai Valley, *Cheeseman s.n.* (AK); Rocky River, Bainham, Collingwood, *Wall s.n.* (CANTY); Buller Valley, *Townson 445* (AK); same locality, *Cheeseman s.n.* (AK, MO). WESTLAND: 380 m. in scrub on banks of Teremakau River, near Railway Settlement, Otira, *Laing & Gourlay s.n.* (CANTY). CANTERBURY: 730 m. north side of Rough Creek, near railway cottages, Arthur's Pass, *Laing & Gourlay s.n.* (CANTY); same locality, *Laing s.n.* (K); same locality, near Jack's Hut, *Laing s.n.* (K); roadside, same locality, *Cooper 24318* (AK, US).

Flowers which may be female have capitate stigmas, and stamens 1.5 - 1.6 mm. long, with anthers 0.6 mm. long and 0.4 mm. broad. Flowers which may be male have truncate stigmas, and stamens 3.9 - 4.6 mm. long with anthers 1 mm.

long and about 0.5 mm. broad. I cannot find any consistent differences in the size of the ovaries.

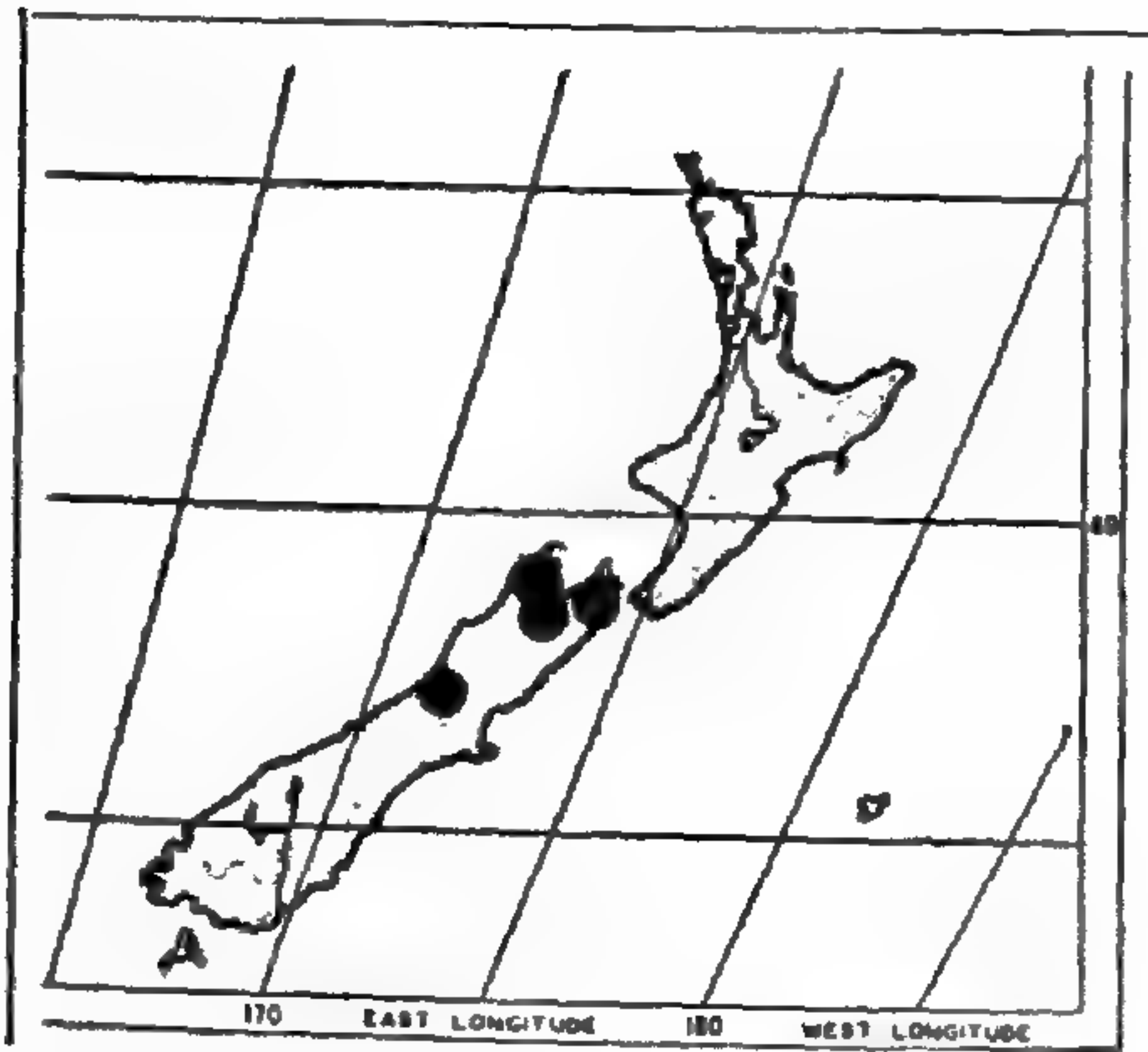


Fig. 24. *P. crassicaule*.

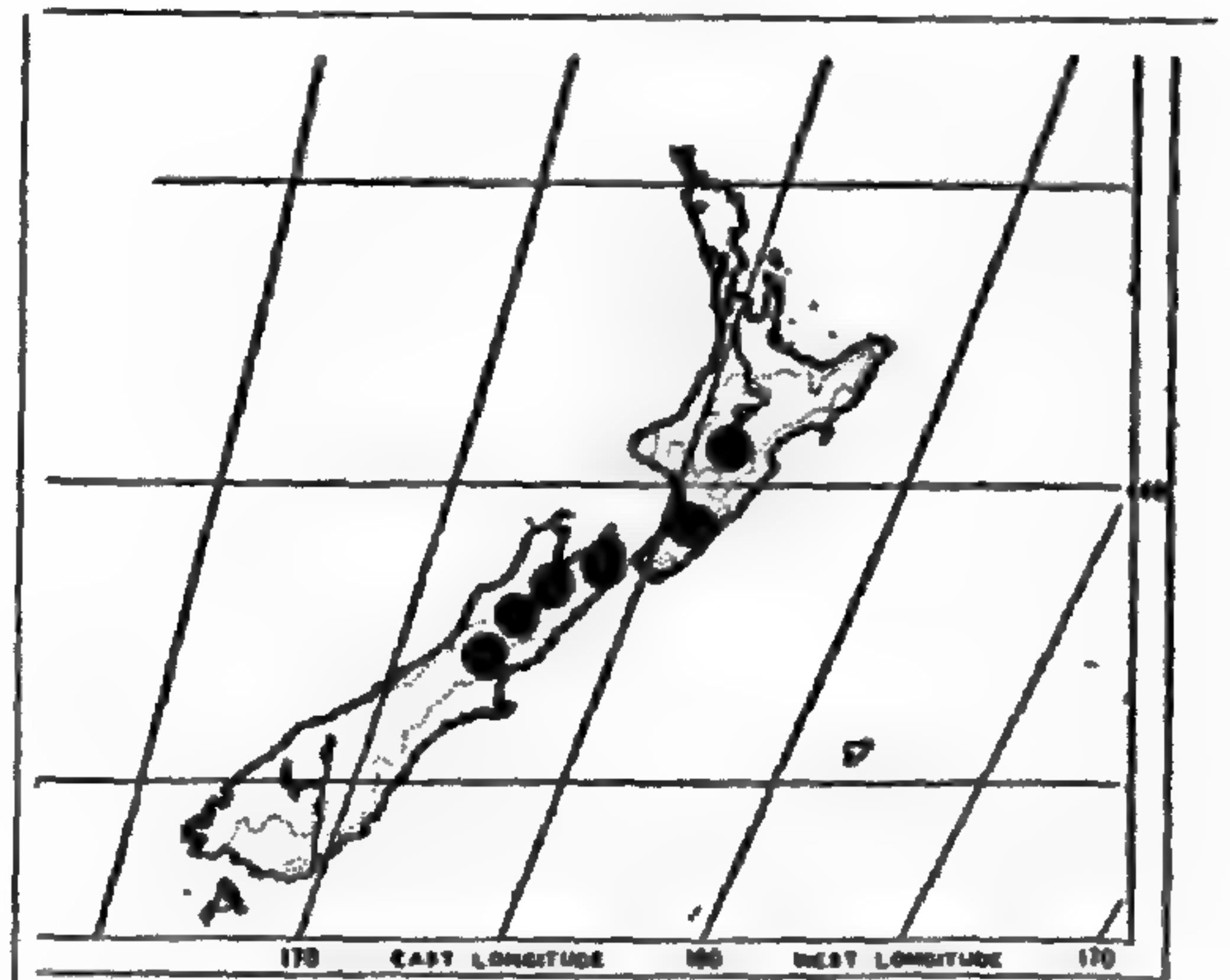


Fig. 25. *P. divaricatum*.

20. *PITTOSPORUM DIVARICATUM* Cockayne, in N.Z. Inst. Trans. & Proc. 47: 111. 1915. (T.: Cockayne 8551!).

Pittosporum rigidum Hook. f. Fl. Nov. Zel. 1: 22. 1853, in part.

Pittosporum divaricatum Cockayne, in N.Z. Inst. Trans. & Proc. 44: 20. t. 3. f. 2 & t. 8. 1912, nom nud; in Austral. Assoc. Adv. Sci. Proc. 13: 219. 1912, nom. nud.

Pittosporum lineare Laing & Gourlay, in Trans. Roy. Soc. N.Z. 65: 57. 1935, in part. (quoad Laing & Gourlay s.n. 1).

Shrubs to 6 m. tall; branches thick and woody, interlaced; branchlets divaricating, opposite or whorled at the nodes, stout, often spinose at the tips, tomentulose when young, soon glabrate. Leaves alternate at seedling stage and on young branchlets, later restricted to the tips of arrested branchlets 1 - 5 mm. long, submembranous when juvenile, coriaceous when adult, green above, paler beneath, glabrous, costa immersed above, sunken beneath, secondary veins obscure; juvenile leaves oblong, obovate to lanceolate, or almost linear, margins with 1 to several lobes or teeth on either side, occasionally crenate, 6 - 9 mm. long, 1 - 4 mm. broad; adult leaves linear-oblong to linear-oblong, or ovate, acute to obtuse at apex, acute at base, 4 - 10 mm. long, 2 - 7 mm. broad, smaller and entire in sun, larger and variously dentate, crenate, or lobed in shade; petioles about 1 mm. long, glabrous. Flowers terminal on short arrested branchlets, solitary, sessile or with minute pedicels, subtended by several leaves and caducous ciliolate bud scales about 1 mm. long. Sepals not imbricate at base, lanceolate, acute, 1.5 - 2.5 mm. long, 0.5 - 1.0 mm. broad, glabrous, ciliolate; petals linear-oblong, obtuse, 4 - 6 mm. long, 1.0 - 1.5 mm. broad, coherent in a cylindrical tube, tips spreading, purple; stamens 1.5 - 2.6 mm. long, anthers ovate or sagittiform, 0.5 - 1.4 mm. long, 0.3 - 0.7 mm. broad. Pistil at anthesis slightly exerted; ovary 1.0 - 2.2 mm. long, 0.5 - 1.0 mm. broad, glabrous; style 1.0 - 1.5 mm. long; stigma capitate to truncate. Capsules cordate or subglobose, 2-valved, acute and apiculate, 6 mm. long, 5.5 - 6.0 mm. broad, glabrous, weakly rugose; valves convex in transverse

section, less than 1 mm. thick, coriaceous, with a slightly thickened placenta bearing 1 - 2 pairs of peg-like funicles near the middle; seeds 1 - 6, black, round to irregular.

Occurs from the Ruahine Range and Central Volcanic Plateau of the North Island to Arthur's Pass on the Main Divide of the Southern Alps of New Zealand. Flowers in October and November.

NEW ZEALAND: EAST CAPE: Pukatitiri, eastern foothills of Ruahine Range, *Hodgson s.n.* (AK, CANTY). VOLCANIC PLATEAU: Lake Karioi, vicinity of Ruapehu, *Attwood s.n.* (AK, MO). WELLINGTON: Tararua Range, *Petrie s.n.* (AK). MARLBOROUGH: Picton, *MacMahon s.n.* (AK, NSW); Koromiko, *Laing & Gourlay* [The label of the Kew sheet of the Koromiko plant is noted by H. H. Allan as "col. H. Jenkins end of Oct. 1932."] *s.n.* (CANTY, K). NELSON: Dun Mountain, *Sainsbury s.n.* (CANTY); Wangapeka River, *Cheeseman s.n.* (AK); 2000', in bog forest on the Rahu Saddle, *Cockayne 8551* (A, K); without locality, *Bidwill 96* (K). CANTERBURY: Lewis Pass, *Morrison 39* (A, CANTY); Cass River, *Kirk s.n.* (GH, NSW); south side of Rough Creek, Arthur's Pass, *Laing & Gourlay s.n.* (CANTY).

It is with hesitation that I treat *P. lineare* as a synonym of *P. divaricatum* and *P. crassicaule*. Laing and Gourlay, the two authors of *P. lineare*, cultivated and studied the small-leaved New Zealand species of *Pittosporum* for many years before publishing their results, but in the material cited by them there appear to be two distinct entities: the Koromiko plants (*Laing & Gourlay s.n.*) which have flowers with sepals 2.0 - 2.5 mm. long, capitate stigmas, styles 1.0 - 1.2 mm. long, glabrous ovaries 2.0 - 2.2 mm. long, and stamens about 2 mm. long; and the Pelorus Valley plants (*MacMahon s.n.*) which have flowers with sepals 1.0 - 1.5 mm. long, truncate stigmas, styles about 1.8 mm. long, tomentulose ovaries 1.5 mm. long, and stamens nearly 4 mm. long. The linear entire leaves of the Koromiko plant give it a very different appearance from most specimens of *P. divaricatum*, but the flowers are within the range of variation of *P. divaricatum*, and similar plants with linear entire leaves and bearing the distinctive cordate glabrate fruits of *P. divaricatum* occur on the Volcanic Plateau (*Attwood s.n.*), and in cultivation (*Cooper 36299*). The tomentulose ovary of the Pelorus Valley plants is a feature of *P. crassicaule*, *P. rigidum*, and *P. obcordatum*, but the other characters of the flower, fruit, and foliage are similar to those of *P. crassicaule*. Consequently with some misgivings I have included the collection in that species.

In the material examined there are slight differences in the size and form of the flowers. Flowers which may be female have capitate stigmas, ovaries 1.5 - 2.2 mm. long, 1 mm. broad, stamens 1.5 - 2.5 mm. long and sagittiform to ovate anthers 0.5 - 0.9 mm. long, 0.3 - 0.5 mm. broad. Flowers which may be male have truncate stigmas, ovaries 1.0 - 1.5 mm. long, 0.5 - 0.6 mm. broad, stamens about 4.0 mm. long, and ovate anthers 1.0 - 1.5 mm. long, 0.6 - 0.7 mm. broad.

21. *PITTIOSPORUM ANOMALUM* Laing & Gourlay, in *Trans. Roy. Soc. N.Z.* 65: 54. 1935. (T.: *Laing & Gourlay s.n.* !).

Shrubs, prostrate in the sun and with rigid, almost spinose branches, semi-prostrate in shade and forming subglobose masses up to 1 m. tall and 2 m. in

diameter with non-spinose, interlaced branches; branchlets brownish-gray, tomentulose when young, soon glabrate. Leaves alternate on juvenile plants and young branchlets, later restricted to the tips of arrested branchlets, oblong-linear to oblanceolate-linear, obtuse to subacute at apex and base, submembranous when young, coriaceous when adult, green in summer, brownish-red in winter, paler beneath, sparsely tomentulose when young, soon glabrate, costa immersed above, raised beneath, secondary veins obscure; juvenile leaves dentate-serrate, 8 - 12 mm. long, 2 - 3 mm. broad; adult shade leaves deeply doubly dentate or serrate to crenate, occasionally entire, 5 - 10 mm. long, 1.0 - 2.5 mm. broad; adult sun leaves entire, occasionally crenate, 2 - 5 mm. long, 1.0 - 1.5 mm. broad; petioles up to 1 mm. long, glabrous. Flowers terminal on short arrested branchlets, solitary, sessile, subtended by several leaves and caducous ciliolate bud scales 2 mm. long. Sepals not imbricate at base, lanceolate, 2 mm. long, 0.5 - 1 mm. broad, glabrous, ciliolate; petals obovate to oblanceolate, obtuse to subacute, 2.5 - 4.0 mm. long, 1.2 - 2.0 mm. broad, spreading, creamy yellow, purple at the edges and tips; stamens 2 - 3 mm. long, anthers ovate to orbiculate, 0.5 - 0.8 mm. long, 0.3 - 0.8 mm. broad. Pistil at anthesis equal to the stamens; ovary 1.0 - 1.3 mm. long, 0.8 - 0.9 mm. broad, glabrous; style 0.5 - 12.2 mm. long; stigma capitate and 2-lobed or truncate. Capsules ovoid, 2-valved, acute to acuminate, apiculate, 5.5 - 7.0 mm. long, 3 - 4 mm. broad, glabrous; valves convex in transverse section, less than 1 mm. thick, subcoriaceous, splitting longitudinally on dehiscence and leaving a papery endocarp covering the seeds; placenta unthickened, bearing 1 - 2 short stout funicles about the middle; seeds 2 - 4, black, round to irregular.

Occurs on the Central Volcanic Plateau of the North Island, and at Nelson and Arthur's Pass in the South Island of New Zealand. Flowers in December and January.

NEW ZEALAND: VOLCANIC PLATEAU: shrub steppe, Mt. Hauhangatahi, *Carse & Matthews s.n.* (CANTY); Hauhangatahi, *Moore & Cranwell s.n.* (AK, MO); 3000', in tussock near Chateau Tongariro, Mt. Ruapehu, *Godley 24963* (AK). NELSON: wooded peak, *Gibbs s.n.* (CANTY). CANTERBURY: 3000', Arthur's Pass, *Laing & Gourlay s.n.* (CANTY); same locality, "Jack's Hut", *Laing s.n.* (K).

Flowers which may be female have capitate 2-lobed stigmas, styles 0.5 - 0.7

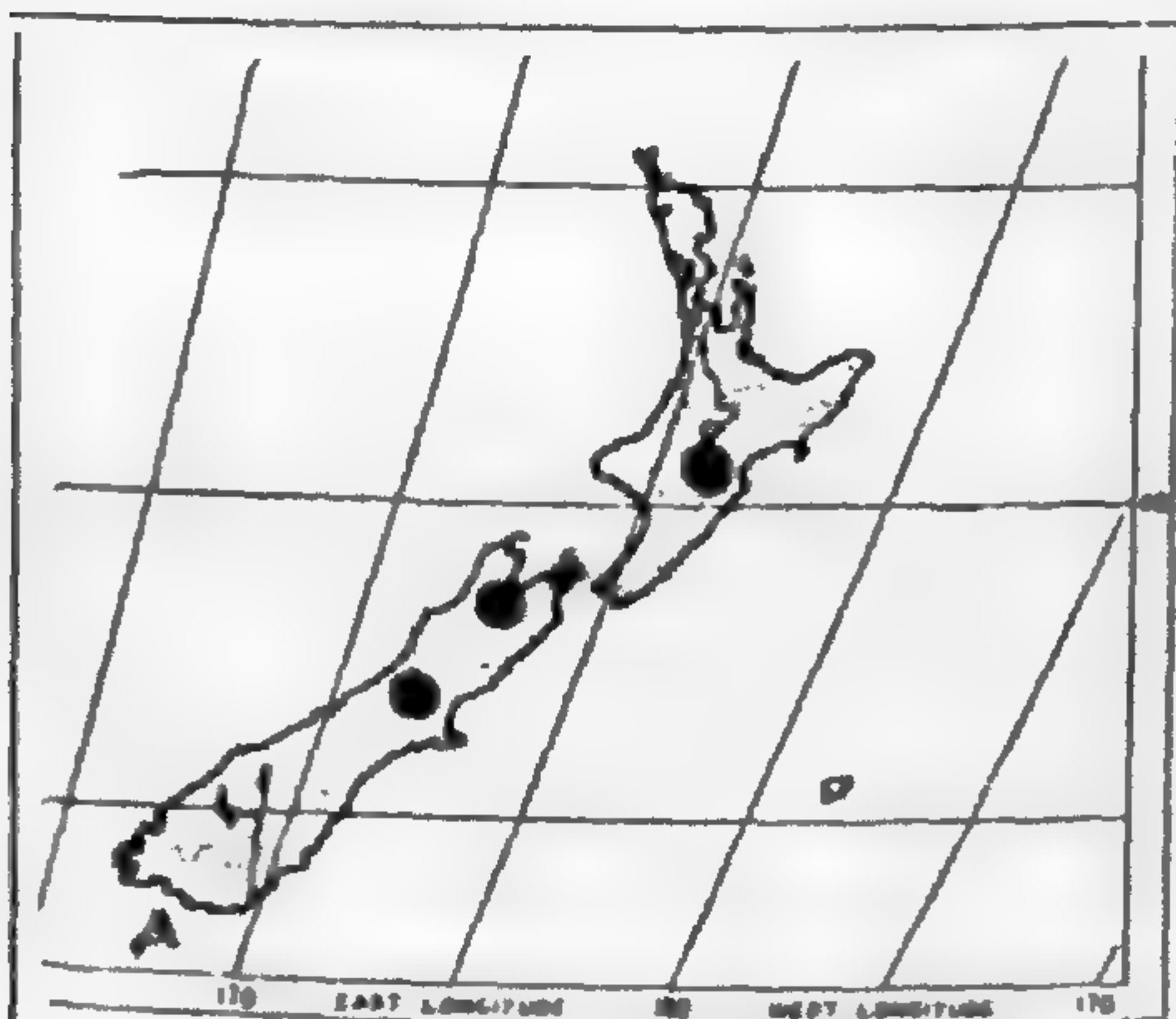


Fig. 26. *P. anomalum*.

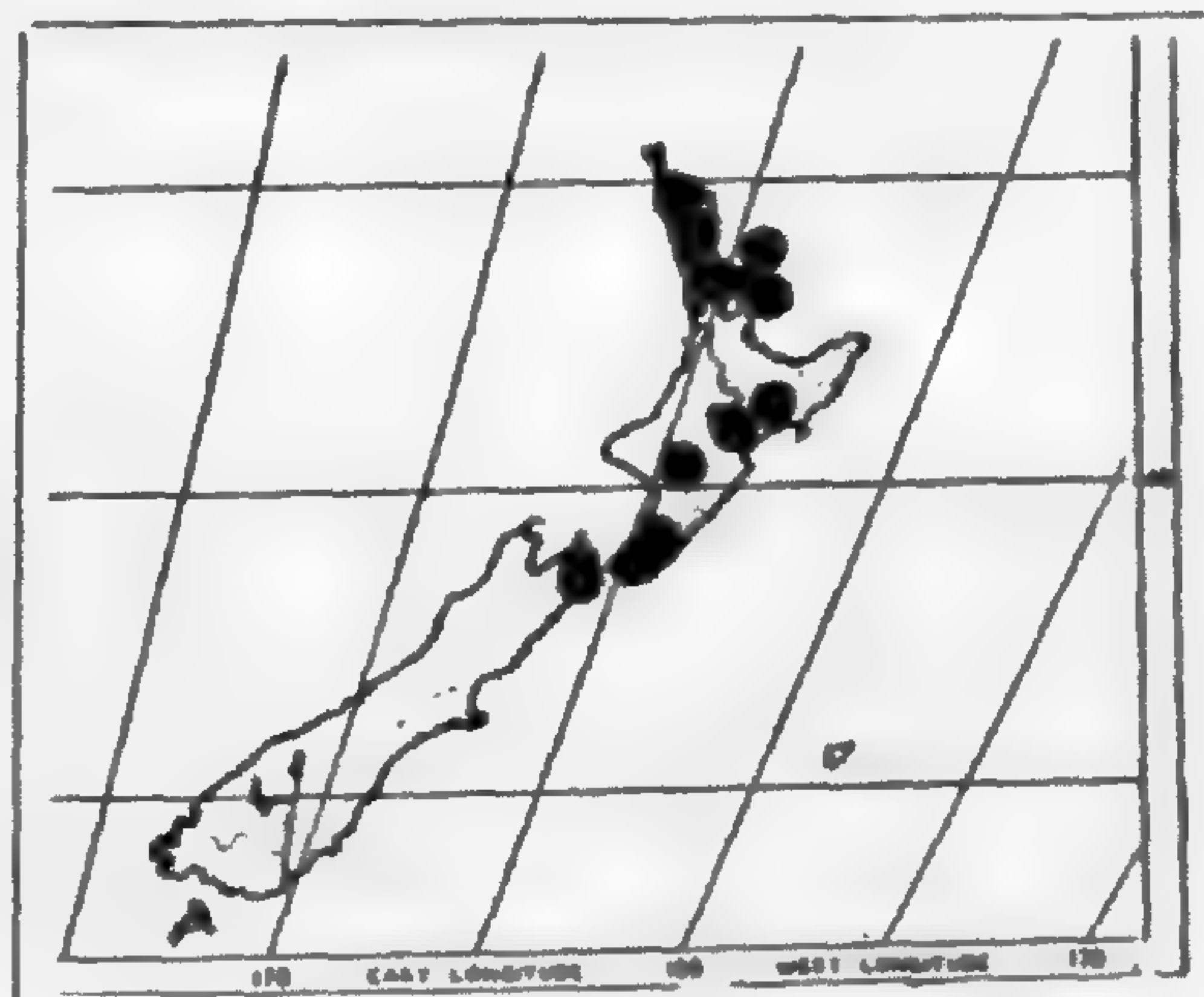


Fig. 27. *P. cornifolium*.

mm. long, and ovate anthers 0.5 mm. long, 0.3 mm. broad, on filaments about 1.5 mm. long. Flowers which may be male have truncate stigmas, styles 1.0 - 1.2 mm. long, and orbiculate anthers 0.7 - 0.8 mm. long, 0.5 - 0.8 mm. broad, on filaments 1.5 - 2.2 mm. long. There is little difference in ovary size in the specimens which I have seen

22. *PITTOSPORUM CORNIFOLIUM* A. Cunn. ex Hook. in Bot. Mag. t. 3161. 1832. (T.: *A. Cunningham* 616 !).

Pittosporoides verticillata Banks & Soland. ex A. Cunn. in Ann. Nat. Hist. 4: 107. 1839, *nom. nud. in synon.*

Shrubs 0.5 - 2.5 m. tall, epiphytic, rarely terrestrial; branchlets forked or verticillate, dark brown, glabrous. Leaves verticillate, obovate- to ovate-elliptic, acute to subacuminate at apex, acute to obtuse at base, entire, 2 - 10 cm. long, 1 - 5 cm. broad, light green above, paler beneath, ciliate when young, soon glabrate, coriaceous with thickened slightly revolute margins, costa raised above, immersed beneath, secondary nerves obscure above, distinct beneath; petioles 0.5 - 3.0 mm. long and 0.5 - 2.0 mm. broad, glabrous. Inflorescences terminal, 1- to 10-flowered, usually umbelliform; pedicels 2 - 15 mm. long, accrescent in fruit, brown-tomentose, subtended by a whorl of leaves and numerous caducous bud scales about 1 mm. long. Sepals not imbricate, narrow-lanceolate, acute, 4 - 7 mm. long, about 1 mm. broad, spreading, sparsely puberulent; petals linear-lanceolate, acute to acuminate, 8 - 12 mm. long, 1.5 - 2.0 mm. broad, coherent in a tube with reflexed tips, yellow; stamens 4 - 6 mm. long, anthers sagittiform to elliptic-oblong, 1 - 2 mm. long, 0.5 - 1.0 mm. broad. Pistil at anthesis slightly longer to slightly shorter than the stamens; ovary 1.5 - 3.0 mm. long, 0.5 - 2.0 mm. broad, villous; style 2.5 - 4.0 mm. long; stigma capitate and 2-lobed to truncate. Capsules ellipsoid, 2- or 3-valved, about 1.7 cm. long, 1.2 cm. broad, glabrate; valves convex in transverse section, less than 1 mm. thick, coriaceous, with a short basal placenta bearing several strap-like funicles up to 5 mm. long; seeds 4 - 8, black, irregular.

Occurs from sea-level to 650 m. throughout the North Island and northern part of the South Island of New Zealand; common in the northern part of the North Island, rarer to the south. Flowers from June to September.

NEW ZEALAND: NORTH AUCKLAND: Kaitaia, *Matthews s.n.* (AK, MO); Okahu, Kaitaia, *Matthews s.n.* (AK); Whangaroa, *Kirk s.n.* (GH); Bay of Islands, *Wilkes s.n.* (US); same locality, *Hooker s.n.* (K); Opuia, *Mackie s.n.* (AK); growing uniformly as an epiphyte upon trees and frequently in the tufts of *Astelia* which adhere to the stems of the larger timber, particularly *Kahikatea* (*Dacrydium*) in shaded woods [on the banks of the Kana Kana, and other rivers, Bay of Islands, etc., 1826], *A. Cunningham* 61, 616 (K); Waipoua Kauri forest, *Cockayne* 6421 (A); same locality, *Sledge* 74 (CU); Trounson Kauri forest, *Walker* 5280 (MO, US); Taranga (Hen) Island, *Moore & Cranwell s.n.* (AK); Poor Knights Islands, *Cranwell s.n.* (AK). AUCKLAND: Te Pahi, *Kirk s.n.* (A); Omaha, *Kirk s.n.* (AK, F, US); Leigh, *Buddle* 27204 (AK); same locality, *Turner s.n.* (AK); Kawau Island, *Matthews s.n.* (AK, MO); same locality, *Petrie s.n.* (CU); Birkdale, *Meebold* 5289 (BISH); Waitakere Ranges, *Cheeseman s.n.* (BISH, NSW, US); same locality, *Petrie s.n.* (NSW); epiphytic on *Metrosideros tomentosa*, Huia, *Wood s.n.*

(AK); Titirangi, *Cheeseman s.n.* (GH, NSW, US), 11 (K); Auckland, *Cranwell s.n.* (AK); Buckland, *Matthews s.n.* (AK, MO.) THAMES: Cape Colville, *Kirk s.n.* (MO); Coromandel Peninsula, *Adams s.n.* (AK); Shag Bay, Te Moechau, *Moore & Cranwell s.n.* (AK, K); Pakirarahi, *Adams s.n.* (AK); Tararu, *Kirk s.n.* (AK); Thames, *Adams s.n.* (US); in sylvis prope Tolaga [East Cape], Oporagi [Mercury Bay], *Banks & Solander s.n.* (BM). EAST CAPE: Lake Waikaremoana, *Sainsbury 15* (AK); Akatarawa Station, *Turner 162* (AK). WANGANUI: Parapara, Mangowhero, Waimarino, *Attwood s.n.* (AK); Turakina, *Allison s.n.* (A, NSW). WELLINGTON: epiphytic on *Podocarpus spicatus*, forest margin, Fielding, *Allan s.n.* (BH); Mungaroa, *Kirk 136* (BM); Orongorongo, *Kirk 130* (GH). MARLBOROUGH: terrestrial, Endeavour Inlet, Queen Charlotte Sound, *MacMahon s.n.* (AK); Tennyson Inlet, Pelorus Sound, *Turner 804* (AK). WITHOUT LOCALITY: *Banks & Solander s.n.* (AK, MO, US); *Bidwill s.n.* (K); *Colenso s.n.* (K); *A. Cunningham s.n.*, 616 (K); North Island, *A. Cunningham 616* (BM, K); ex Hort. Kew (figd. in Bot. Mag.) *s.n.* (K).

Inflorescences with up to 10 flowers appear to be male. The flowers have truncate to weakly capitate stigmas level with or shorter than the anthers, styles 3.5 - 4.0 mm. long, and ovaries 1.5 - 2.0 mm. long. I think that they are male as the ovaries are very thin, apparently abortive, and the anthers are elliptic-oblong, apparently functional. Inflorescences with only 1 or 2 flowers appear to be female. The flowers have capitate 2-lobed stigmas level with or exerted beyond the anthers, styles 2.0 - 2.5 mm. long and ovaries 3 - 4 mm. long. I think that they are female as the ovaries are plump, apparently functional, and the anthers are sagittiform and abortive. Kirk¹⁶⁷ and Petrie¹⁶⁸ described the flowers of *P. cornifolium* as unisexual, and Cheeseman¹⁶⁹ regarded the plants as polygamous or dioecious. Field studies are required to determine the significance of the morphological differences.

The species was described by W. J. Hooker from material grown at the Royal Botanical Gardens, Kew, and from Allan Cunningham's specimens and notes made by him in New Zealand in 1826. Two "type" sheets in the herbarium of the Royal Botanic Gardens, Kew, bear five labels, two sterile specimens, a fruiting specimen and fragments of flowers. One label is dated 1826, one 1833, two 1838, and one is undated. As the species was described in 1832 only part of the material can have been available to W. J. Hooker. Fortunately the species is distinct and the muddle of labels and specimens does not have serious consequences.

Vernacular name: Cornel-leaved Pittosporum.

23. PITTOSPORUM KIRKII Hook. f. ex Kirk, in N.Z. Inst. Trans. & Proc. 2: 92. 1869. (T.: *Kirk s.n.*!).

Shrubs 1 - 5 m. tall, epiphytic, occasionally terrestrial; branchlets reddish-purple, glabrous. Leaves subverticillate, linear-obovate to oblong-elliptic, acute or obtuse at the apex, acute at the base, entire, 4 - 11 cm. long, 0.7 - 3.2 cm. broad, pale green above, lighter beneath, glabrous, coriaceous, with thickened and slightly revolute margins, costa raised above, flattened beneath, secondary veins

¹⁶⁷ Students' Fl. N.Z. p. 49. 1899.

¹⁶⁸ N.Z. Inst. Trans. & Proc. 53:365. 1921.

¹⁶⁹ Manual N.Z. Fl. ed. 2 p. 495. 1925.

about 18 per side, anastomising, obscure; petioles 3 - 16 mm. long, 1 - 2 mm. broad, glabrous, purple. Inflorescences terminal, 3- to 10-flowered, umbelliform; pedicels 5 - 10 mm. long, contracted in fruit, glabrous, subtended by an approximate whorl of leaves and by numerous caducous glabrous bud scales 1 - 2 mm. long. Sepals imbricate at base, lanceolate, acuminate, 6 - 10 mm. long, 1.5 - 4.0 mm. broad, glabrous; petals oblanceolate, acuminate, 1.5 - 2.1 cm. long, 2.5 - 3.5 mm. broad, fused slightly above the base to the middle, sharply recurved above, yellow; stamens 6 - 7 mm. long, anthers elliptic-oblong, 2.5 - 3.0 mm. long. Pistil at anthesis equalling or slightly longer than the stamens; ovary 3 - 4 mm. long, 1.5 mm. broad, tomentulose; style about 3 mm. long, stout, stigma capitate. Capsules ellipsoid, 2-, rarely 3-, valved, apiculate, 2.6 - 3.9 cm. long, 1.1 - 1.7 cm. broad, green to yellow, glabrate; valves convex in transverse section, about 1.5 mm. thick, coriaceous, with a placenta bearing slender strap-like funicles up to 4 mm. long, from the base for three-fourths the length of the valve; seeds about 40, black, irregular.

Occasional from 250 to 1000 m. in North Auckland, Auckland, Thames, including Great Barrier Island, and Wanganui districts of New Zealand.

Flowers from November to January.

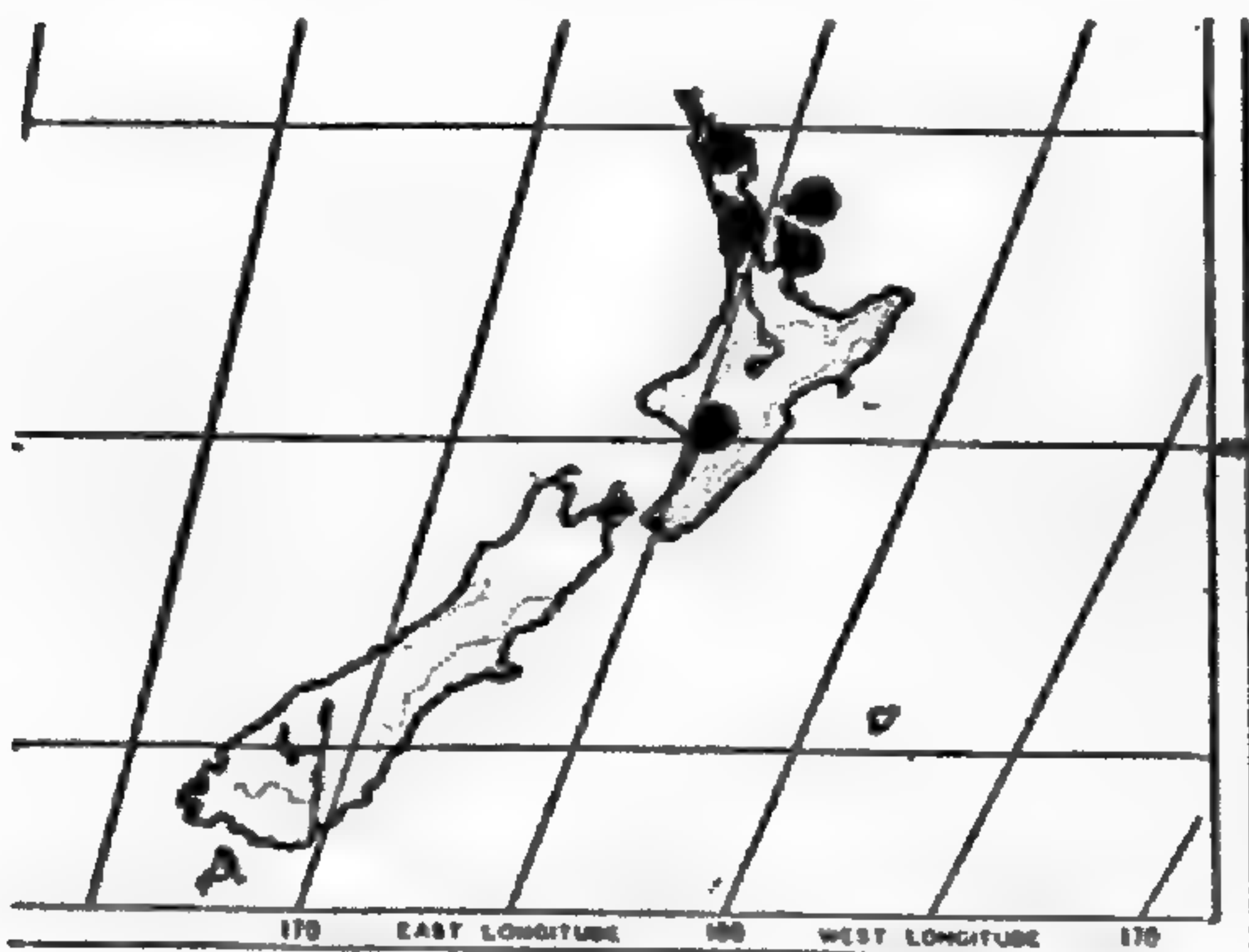


Fig. 28. *P. kirkii*.

NEW ZEALAND: NORTH AUCKLAND: 2000', Maungataniwha, Mangonui, *Cheeseman s.n.* (AK, K); epiphytic on a dead log, Warawara State Forest, North Hokianga, *Cooper 35572* (AK, MO); Hokianga, *Petrie s.n.* (K); same locality, Otatau, *Berggren s.n.* (BM); epiphytic on tall tree, Waipoua kauri forest, *Cockayne 6419* (A); same locality, *Turner 793* (AK); same locality, *Jessup 26640* (AK); Taheke, *Cheeseman s.n.* (AK); ridge near Puketutu, Takahue side, *Petrie s.n.* (AK, MO). AUCKLAND: Titirangi Ranges, *Cheeseman s.n.* (AK, GH, K, US), 12 (K); Huia, *Mackie s.n.* (AK); Huia dam, epiphytic in second-

growth *Agathis australis* forest, *Wood s.n.* (AK). THAMES: epiphytic, Kaeoruruwahine forest, Great Barrier Island, *Kirk s.n.* (F, GH, MO); 2000', Great Barrier Island, *Kirk 63* (K); Cape Colville, *Kirk s.n.* (AK); same locality, 2300', *Hector s.n.* (BM); same locality, *Adams s.n.* (AK); Thames and Thames Goldfield, 2500', *Kirk s.n.* (A, AK, K), 63 (K); same locality, *Adams s.n.* (AK); mixed forest, 1500', Wairongomai Mine, Te Aroha, *L. S. Gibbs, 1298* (BM); epiphytic, c. 2000', Te Mochau, *Moore & Cranwell s.n.* (AK, K). WANGANUI: Maungaturuturu, Maunganui-a-te-ao, *Attwood s.n.* (AK).

Vernacular name: Kirk's Pittosporum.

24. *PITTIOSPORUM REVOLUTUM* Aiton, Hort. Kew. ed. 2. 2: 27. 1811. (T.: *ex Hort. Kew.*!).

Pittosporum fulvum Rudge, in Trans. Linn. Soc. Lond. 10: 298. t. 20. 1811. (T.: *R. Brown s.n.*!—The type sheet at B.M. is marked "1. New Holland. Fleming").

Pittosporum tomentosum Bonpl. Descr. Pl. Rar. Malm. p.56. t.21. 1813. (T.: *Bonpland s.n.*!).

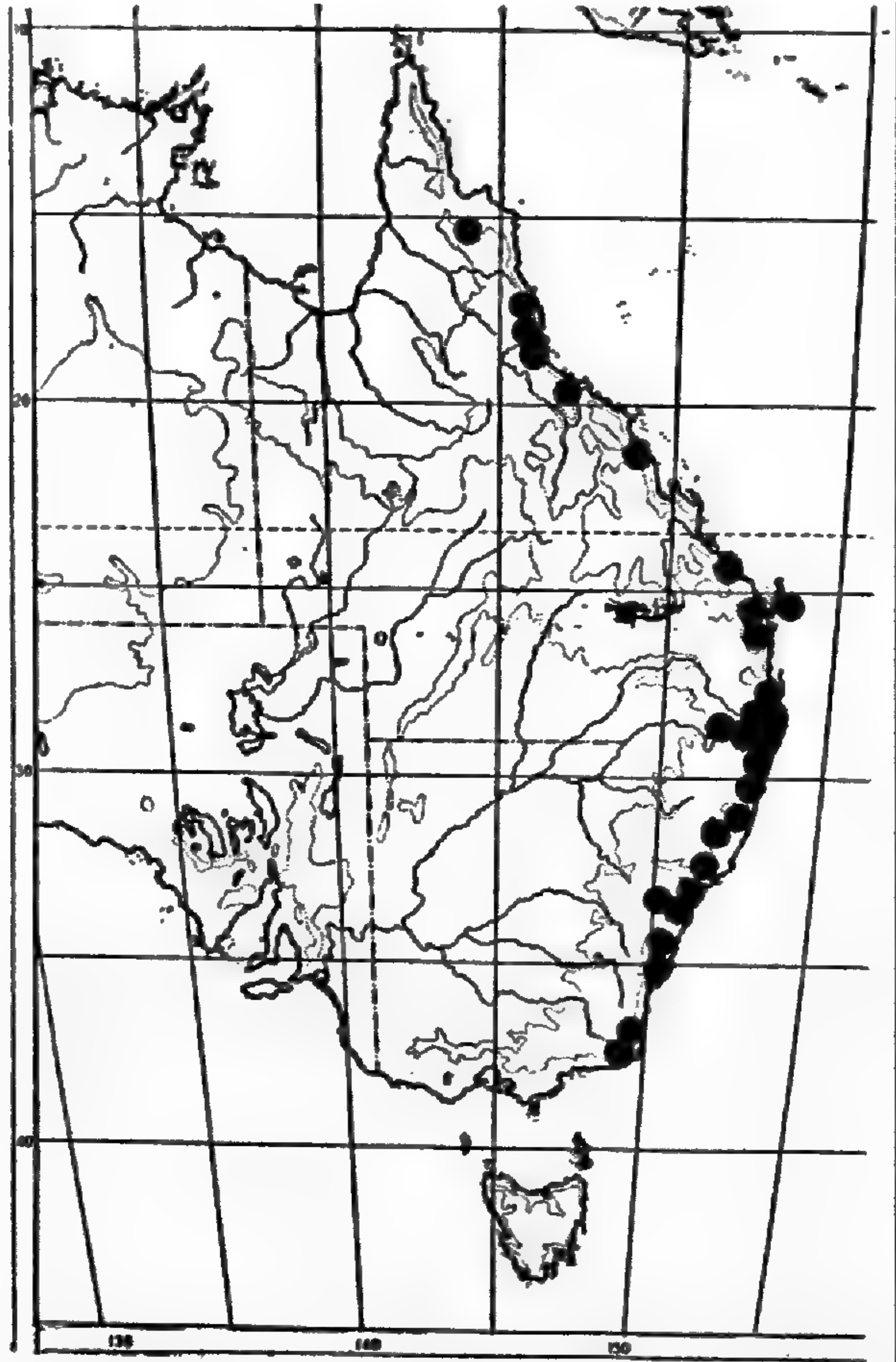
Pittosporum hirsutum Link, Enum. Hort. Berol. 1: 233. 1821, *ex char.* (T.: *ex Hort. Berol.*).

Pittosporum revolutum Aiton var. *tomentosum* (Bonpl.) Bailey in Queensland Agr. Jour. 28: 195. 1912.

Shrubs to 3 m. tall; branchlets grayish-brown, rusty-tomentose when young, glabrescent. Leaves alternate, usually crowded at the tips of the branchlets, elliptic-ovate to elliptic-oblong, acute to shortly acuminate at apex, attenuate at base, entire, 4 - 19 cm. long, 2 - 7 cm. broad, dull green above, glabrate or covered with fine appressed red hairs beneath, subcoriaceous, margins thickened and revolute, occasionally undulate, costa and side veins sunken above, raised beneath, side veins 4 - 10 per side, anastomosing; petioles 5 - 18 mm. long, 1 - 2 mm. broad, rusty-tomentose. Inflorescences terminal, rarely axillary, 1- to 11-flowered, cymose-umbelliform; peduncles brown-tomentose, subtended by several leaves and a whorl of persistent tomentose bud scales 2 - 5 mm. long. Sepals slightly imbricate at base, lanceolate, acuminate with recurved tips, 4 - 8 mm. long, 1.5 - 3.0 mm. broad, sparsely tomentulose and ciliolate, glabrate; petals linear-oblong to linear and pandurate, spreading to reflexed at the tips, obtuse to subacute at apex, clawed, 12.5 - 18 mm. long, 2.5 - 5.0 mm. broad, connivent from the base for two-thirds their length in a cylindrical or somewhat urceolate tube, yellow; stamens 6.4 - 12.0 mm. long, anthers sagittiform to oblong, 1.9 - 4.0 mm. long, 0.5 - 1.5 mm. broad. Pistil at anthesis equal to or slightly longer than the stamens; ovary 3.5 - 6.0 mm. long, 2 - 4 mm. broad, tomentose; style 3.5 - 7.0 mm. long; stigma capitate and obscurely 2- to 4-lobed. Capsules ellipsoid to subglobose, 4- to 6-lobed, 2- to 4-valved, apiculate, 1.5 - 2.8 cm. long, 1.1 - 2.1 cm. broad, green to brown, coarsely rugose, tomentose or glabrate; valves convex to sulcate in transverse section, 2 - 3 mm. thick, woody, with a placenta bearing peg-like funicles up to 4 mm. long from the base to near the apex; seeds 20 - 76, red to reddish-brown, round to irregular.

Occurs from northern Queensland to Victoria, Australia. Flowers from July to October, earlier in Queensland, later in New South Wales and Victoria.

AUSTRALIA: QUEENSLAND: Dalrymple Heights, South Kennedy District, *Clemens s.n.* (BRI); common in rain forest, 600 m., Scrubby Creek, Herberton Range, *White 1370* (A, BRI); Clump Point, via El-Arish, *Fenby s.n.* (BRI); Stony Creek, Rockingham Bay, *Dallachy s.n.* (F, MEL, MO); Herbert River, *Eaton s.n.* (BRI); Cleveland Bay, *Daintree s.n.* (MEL); Port Mackay, *Mueller s.n.* (MEL); creek alluvium, Rosedale, *Dovey 55* (BRI); Pinalba, *White s.n.* (A, BRI); in scrub in sandy valley, Fraser Island, *Hubbard 4466* (BRI, K); same locality, *Petrie 120* (BRI); Wide Bay, *Eaves s.n.* (MEL); same locality, *Bidwill s.n.*, 89 (K); Cootharaba, Wide Bay district, *Francis s.n.* (BRI); Lagoon Pocket, via Gympie, *Lowe 14* (BRI) Gympie, *Kenny s.n.* (BRI); Noosa Heads, *Longman s.n.* (K); Eumundi, *Bailey & Simmonds s.n.* (BRI); on bank of creek in cleared rain-forest country, Mudgeeraba, *Hubbard 4180* (K); Moreton Bay, *without collector s.n.* (GH, U); same locality, *Mueller s.n.* (K); Brisbane River, *Dietrich s.n.* (BM, BRI, ILL, MO); *Goodna* scrubs, *Longman s.n.* (K); in dense shade in "scrub" along banks of Pullen Creek, in alluvium, near Riverview, *Hubbard 4815* (K); in heavy soil, bank of Coomera River, Oxenford, S. of Brisbane, ca. 10', *Hubbard 3701* (A, BM, BRI, K); Curumbin, *Longman s.n.* (K); brown loam, rain forest, 3000', Springbrook, Macpherson

Fig. 29. *P. revolutum*.

Range, *Hubbard* 4278 (A, BM, BRI, K); at edge of rain forest, ca. 2000', Canungra Creek, Lamington National Park, *Goy & Smith* 142 (BRI); at edges of lower rain forest, 1800', Nixon's Creek Valley, Macpherson Range, *Johnson s.n.* (NSW); edges of scrub, ca. 2000', Macpherson Range, *Bailey s.n.* (BRI); Tambourine Mt., *Longman & White s.n.* (BRI); Point Danger, *Schneider s.n.* (BRI); Mt. Lindsay, border Queensland and New South Wales, *White s.n.* (A). NEW SOUTH WALES: Tweed, *Guilfoyle s.n.* (MEL); Brunswick River, *Maiden & Boorman s.n.* (NSW); Stanthorpe, *Davidson* 158 (BRI); Richmond River, *Prime s.n.* (MO); same locality, *Henderson* 20 (MEL); same locality, *Simmonds s.n.* (BRI); same locality, *Fawcett s.n.* (MEL); same locality, *Hodgkinson s.n.* (MEL); same locality, Goat Island, *Cheel s.n.* (NSW); Lismore, in scrub on river bank, *Tanner* 8 (NSW); Ballina, *Baeunton s.n.* (A); Clarence River, *Mueller s.n.* (BM); same locality, *Beckler s.n.* (MEL); same locality, Woodford Island, *Hadley s.n.* (NSW); New England, *Stuart s.n.* (MEL); Coffs Harbour, *Boorman s.n.* (BISH, NSW); MacLeay River, *Beckler s.n.* (MEL); Hastings River, *Mueller* (U); Gloucester Buckets, *Maiden s.n.* (NSW); same locality, bush at foot of Buckets, *Gregson s.n.* (NSW); Upper Williams River, *Fraser & Vickery s.n.* (NSW); same locality, undergrowth in brush forest, *White* 11474 (A, BRI); Bulahdelah District, *Forestry Officer* 20 (NSW); banks of Hunter's, William's and Paterson's rivers, *Brown* 5450 (BM); Hunter's River, *Brown* 5450 (BM, K); Box Point to Kangaroo River, *Maiden s.n.* (NSW); shaded woods on the coast, Illawarra District, Port Jackson, Cardunnee, *A. Cunningham* 18 (BM, K); Port Jackson, *R. Brown s.n.*, 5450 (BM, K, MO); same locality, *Canfield s.n.* (BISH, US); same locality, *Carey s.n.* (GH, K); prope Sydney, *Anderson* 21 (BM); Manly, *Helms s.n.* (NSW); Cronulla, *Steenbohm s.n.* (NSW); near Sydney, *Betche s.n.* (NSW); Paramatta, *Caley s.n.* (A); Nelson's Bay, *Boorman s.n.* (US); Hurstville, *Canfield s.n.* (US); Mt. Kembla, *Hamilton s.n.* (NSW); Blue Mountains, *Atkinson* 53 (MEL); same locality, Erskine Bend, *White*

695 (NSW); Nepean River, *without collector s.n.* (K); River Grose, *Brown 5450* (BM); Grose Vale, *Vickery s.n.* (NSW); Liverpool, *Moore s.n.* (BM); Bulli Pass Road, *Carne & Hudson s.n.* (NSW); Cambewarra, *Rodway 871* (K); near Nowra, *Barnard 109* (CANB); same locality, *Rodway 912* (K); Bomaderry, *Rodway 1294* (K); Comerong Island, Shoalhaven River, *Rodway 875* (BISH, K); Naval College Road, in wet hollow, Jervis Bay, *Rodway 1954* (K); Twofold Bay, *Mueller s.n.* (MEL). VICTORIA: Genoa River, *without collector s.n.* (MEL). WITHOUT LOCALITY: N. S. Wales, *Fraser s.n.* (A), 114, 115 (BM); N. S. Wales, *Caley s.n.* (A, BM); N. S. Wales, *A. Cunningham s.n.* (K); cote meridionale, *Baudin s.n.* (P); *A. Cunningham 248, 249, 265* (U); *Fleming 1* (BM); *Macarthur s.n.* (K). CULTIVATED: Jardin de la Malmaison, *Bonpland s.n.* (P), ex *Hort. Kew s.n.* (BM).

Pittosporum hirtum (Willd. Enum. Hort. Berol. p. 261. 1809) is sometimes cited as a synonym of *P. revolutum* Ait. but I have not seen specimens and the home of the plant is given by Willdenow as the Canary Islands.

Pittosporum revolutum is not common in cultivation but I have seen specimens from Italian, Californian, and Australian gardens. The leaves of specimens from New South Wales are frequently much smaller than those from Queensland, but the extremes are connected by numerous intermediates and I am unable to recognize distinct forms.

Vernacular names: Wild Yellow Jasmine (Lagoon Pocket, *Lowe 14*); Yellow-flowered Brisbane Laurel; Genoa Pittosporum (Victoria).

25. PITTOSPORUM RUBIGINOSUM A. Cunn. in Ann. Nat. Hist. 4: 108. 1839. (T.: *A. Cunningham s.n.*!).

Pittosporum wingii F. Muell. in South. Sci. Rec. n.s. 1: 49. March 1885. (T.: *Dallachy s.n.*!).

Shrubs 1.5 - 6.0 meters tall, branchlets brown and rusty-tomentose. Leaves basically alternate but rather irregularly subverticillate, elliptic to lanceolate or oblanceolate, acutely acuminate to cuspidate at apex, attenuate at base, entire, 6.0 - 33.5 cm. long, 2.5 - 13.0 cm. broad, dark green above, pale green to reddish-purple beneath, sparsely tomentose to glabrescent above, sparsely to densely tomentose beneath, especially on the veins, the hairs dark red and erect, membranous, margins flat or sometimes irregularly revolute, costa and secondary veins sunken above, raised beneath, rusty-tomentose, secondary veins 8 - 13 per side, anastomosing; petioles 2.5 - 12.0 mm. long, 1 - 2 mm. broad, tomentose. Inflorescences variable, consisting of a shoot 4.0 - 11.5 cm. long, red-tomentose, subtended by a whorl of leaves and bud scales and a sequence of cataphylls which become foliar above, sometimes producing 1 to several solitary flowers in the axils of the uppermost cataphylls and sometimes being terminal, 3- to 32-flowered, umbelliform; peduncles and pedicels red-tomentose, accrescent in fruit, subtended by numerous caducous foliar to scarious bracts. Sepals free or slightly imbricate at base, linear-lanceolate, acute to acuminate with recurved tips, sparsely ciliate with scattered hairs to densely ciliate, tomentose, 4.0 - 8.5 mm. long, 1 - 2 mm. broad; petals oblanceolate to linear-oblong, sometimes pandurate, obtuse to sub-acute, 11 - 17 mm. long, 2 - 4 mm. broad, coherent from the base to the middle in

a somewhat urceolate to spreading tube, or free and patent; stamens 4.5 - 11.5 mm. long; anthers sagittiform to ovate-elliptic, 1.0 - 3.5 mm. long, 0.5 - 1.0 mm. broad. Pistil at anthesis slightly shorter or longer than the stamens; ovary 2.0 - 5.5 mm. long, 1 - 3 mm. broad, villous; style 3.5 - 6.5 mm. long; stigma capitate and obscurely 2- or 4-lobed or truncate. Capsules ellipsoid to ovoid, 2-, or rarely 3-, valved, 1.3 - 2.1 cm. long, 6 - 15 mm. broad, with an evident stipe 0.5 - 4.0 mm. long, yellow to orange, densely to sparsely rusty-tomentose or glabrate, minutely rugose; valves convex to slightly sulcate in transverse section, less than 1 mm. thick, coriaceous, with a placenta thickened at the base and bearing peg-like flattened funicles up to 2.5 mm. long from the base to about the middle; seeds 3 - 14, dark rusty-red to red, irregular.

KEY TO THE SUBSPECIES

- Shrubs 1.5-2.5 m. tall; leaves sparsely rusty-tomentose to glabrate beneath; sepals sparsely ciliate with scattered hairs; petals coherent to the middle in a somewhat urceolate or cylindrical tube, linear-oblong, sometimes pandurate; stamens 6.0-11.5 mm. long; anthers 1-3 mm. long; capsules sparsely rusty-tomentose to glabrate. Queensland: Cooktown to south of Cairns.....25a. *P. r. rubiginosum*
- Shrubs to 6 m. tall; leaves densely rusty-tomentose beneath; sepals densely ciliate and rusty-tomentose; petals coherent to the middle in a spreading tube, linear-oblong to oblanceolate; stamens 4.5-11.0 mm. long; anthers 1.5-3.5 mm. long; capsules densely rusty-tomentose. Queensland: Atherton Tableland to Rockingham Bay.....25b. *P. r. wingii*

25a. *PITTIOSPORUM RUBIGINOSUM* ssp. *rubiginosum*

Known from Cooktown to south of Cairns, Queensland, from near sea-level to 1650 m. Flowers from July to September.

AUSTRALIA: QUEENSLAND: summit of Mt. Cook, Endeavour River, *A. Cunningham* 26 (BM, MO); shaded woods on the sides of Mt. Cook, *A. Cunningham* 26 (K); Cooktown, *Rose* 109 (MEL, NSW); Mossman River, *Sayer* 186 (MEL); same locality, *Lucas s.n.* (MEL); in hillside forest in the lowlands, Daintree River, *Brass & White* 279 (BRI); in rain forest, Daintree, Cook District, *Blake* 14996 (BRI); same locality, *Brass* 2220 (A, BRI); in rain forest, 2500', Mt. Dimi, *Brass* 2090 (A, BISH, BRI, K); very common in rain forest, about 4000', Thornton Peak, *White & Brass* 227 (A, BRI, K); very common in rain forest, Mt. Spurgeon, *White* 10618 (A, BM, BRI); Trinity Bay Range, *Bailey s.n.* (AK, BRI, K); same locality, *Fitzalan s.n.* (GH); Cairns, *Bailey s.n.* (NSW); same locality, *Fitzalan* 77 (MEL); in rocky soil, light scrub, creek bank, Clark's Creek, near Cairns, *Toogood* 9 (BRI); Freshwater Creek near Cairns, *Francis s.n.* (BRI, K); same locality, *Cowley* 56 (K); in rain forest, ca. 100', at The Intake, near Cairns, *Blake* 14982 (BRI); 2000'-3000', Mt. Bellendenker, *Cabbage* 3821 (NSW); 4000'-5000', same locality, *Sayer s.n.* (MEL); same locality, *White* 1255 (A, BRI, NSW, US); same locality, *Bailey* 20 (BRI, K); in rain forest and montane forest, 3000' - 5000', Mt. Bartle Frere, North Peak, W. and N.W. slope, *Blake* 15242 (BRI); Russell River, *Johnson s.n.* (MEL); Johnstone River, *Michael* 9, 30, 117 (BRI); same locality, *Bancroft s.n.* (BRI, K); State Forest Reserve 185, Danbulla, *Doggrell* A.5. (BRI); Mt. Alexandra, *Bailey* 13 (BRI).

Specimens collected near sea-level have leaves much longer than those from high elevations; e.g. *Brass & White* 279 from lowlands near the Daintree River has leaves 19 cm. long and 6.5 cm. broad, and *Blake* 14982 from 100' above sea-level at The Intake, near Cairns, has leaves up to 20 cm. long and 6.5 cm. broad. *Brass* 2090 from 2500' on Mt. Dimi has leaves up to 11.5 cm. long and 3 cm. broad, and *White & Brass* 227, from about 4000' on Thornton Peak, has leaves up

to 10 cm. long and 4 cm. broad. Changes in leaf size are gradual and I cannot define distinct forms.

The flower parts also vary in size. Flowers which may be female have capitate and obscurely 2-lobed stigmas, styles 4 - 5 mm. long, plump ovaries 4.0 - 5.5 mm. long, 3 - 4 mm. broad, short stout filaments 4 - 6 mm. long, probably abortive sagittiform anthers 1 - 2 mm. long, and an almost urceolate corolla-tube from which the stigma is exerted. Flowers which may be male have truncate stigmas, styles 5.0 - 6.5 mm. long, slender ovaries 2.0 - 4.5 mm. long, 1 - 2 mm. broad, slender filaments 6 - 9 mm. long, probably functional ovate-elliptic anthers 2.5 - 3.0 mm. long, and a tubular corolla in which the stigma is included. Flower color is described as "white tinged with cream" (Blake 14982), and "yellow, paler toward the base" (Blake 15242).

Vernacular name: Rusty Pittosporum.

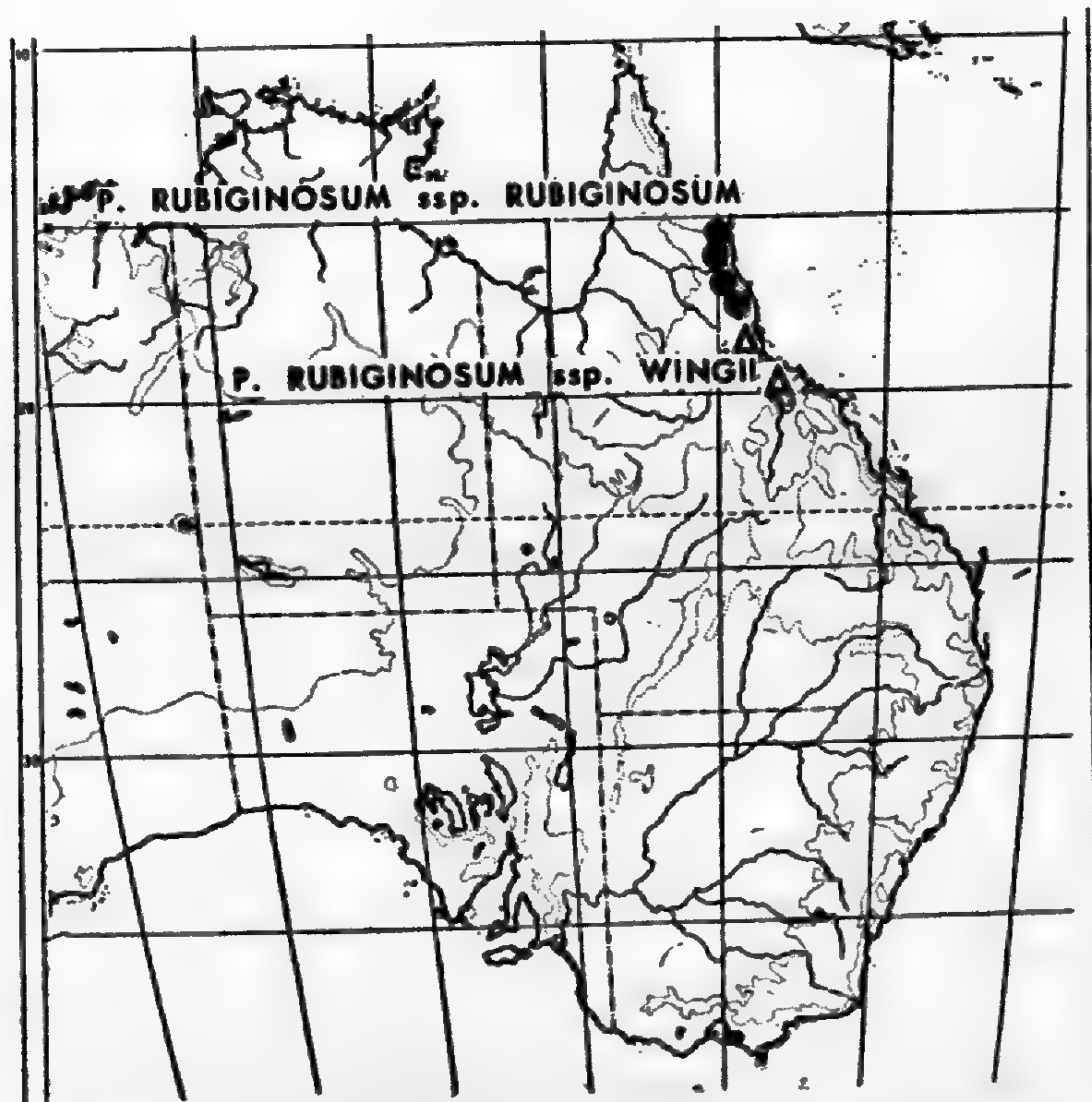


Fig. 30. *P. rubiginosum* ssp. *rubiginosum* and ssp. *wingii*.

25b. *PITOSPORUM RUBIGINOSUM* ssp. *wingii* (F. Muell.) R. C. Cooper, *stat. nov.*

Pittosporum wingii F. Muell. in South. Sci. Rec. n.s. 1: 49. March 1885. (T.:Dallachy s.n.!).

Known from the Atherton Tableland to Rockingham Bay, Queensland. Flowers in September.

AUSTRALIA: QUEENSLAND: top of the Coast Range, under the rocks, Rockingham Bay, *Dallachy s.n.* (GH, K, MEL MO); 800 m., Lake Barrine, Atherton Tableland, *Kajewski 1341* (A, BRI, K, MEL, NSW).

Variation in flower size and form has also been found in this variety. The Rockingham Bay flowers have truncate stigmas, styles 5 mm. long, ovaries 3 - 4 mm. long, 2.5 - 3.0 mm. broad, filaments 5 - 7 mm. long, and probably functional anthers 3.0 - 3.5 mm. long. The sepals are 7.5 - 9 mm. long, and the petals 13 mm. long. The Atherton Tableland flowers have 4-lobed stigmas, styles 3 - 4 mm. long, ovaries 3.5 - 4.0 mm. long, 2.5 - 3.5 mm. broad, filaments 3 - 4 mm. long, and apparently abortive anthers only 1.5 - 2.0 mm. long. In one flower two large functional anthers and three small aborted anthers were found. The sepals are 5 - 9 mm. long, and the petals 9 - 11 mm. long. It is possible that the Rockingham Bay flowers have been collected at a later stage in development than those from Atherton Tableland, but the slender ovaries, larger styles, truncate stigmas, and functional anthers of the former suggest that the flowers are male, while the plumper ovaries, shorter capitate stigmas, and apparently abortive anthers of the latter suggest that the flowers are female.

26. *PITTOSPORUM UNDULATUM* Vent. Descr. Pl. Nouv. Jard. Cels, t. 76. [1802]¹⁷⁰ *ex char. & icon.*

Shrubs or trees 5 - 13 m. tall; branchlets gray, the young parts tomentose, soon glabrate. Leaves alternate, elliptic-oblong to oblanceolate, acuminate at apex, attenuate at base, entire, 6 - 16 cm. long, 1.5 - 5.0 cm. broad, green above, paler beneath, tomentulose when young, glabrate, membranous, margins undulate or flat, sometimes recurved, costa sunken or raised above, raised below, secondary nerves about 12 per side, anastomosing, distinct; petioles 7 - 26 mm. long, 1 - 2 mm. broad, tomentulose when young, glabrate. Inflorescences terminal, 4- to 15-flowered, subumbelliform; peduncles and pedicels 1.9 - 3.1 cm. long, accrescent in fruit, tomentose; peduncles subtended by a whorl of leaves and numerous caducous, brown-tomentose, ciliolate bud scales 1 - 2 mm. long. Sepals frequently connate in a tube which splits into 2 parts, one 1- to 2-lobed, the other 3- to 4-lobed, lanceolate, acuminate, 6.5 - 10.5 mm. long, 1.2 - 2.5 mm. broad, tomentulose, falling before the petals; petals linear-oblanceolate to linear-oblong, obtuse, 11 - 17 mm. long, 3 - 4 mm. broad, coherent at the base, spreading to recurved above, white; stamens 5 - 11 mm. long, sometimes reduced to sterile rudiments 0.5 - 1.0 mm. long; anthers lanceolate-oblong to sagittiform, 2.5 - 5.0 mm. long, 1.0 - 1.5 mm. broad. Pistil at anthesis slightly shorter or longer than the stamens; ovary 4 - 6 mm. long, 1.8 - 4.0 mm. broad, tomentulose; style 2.0 - 4.5 mm. long; stigma capitate and obscurely 2- to 4-lobed or almost truncate. Capsules subglobose, 2-valved, 10 - 14 mm. in diameter, yellow to brown, smooth to slightly rugose, glabrous; valves convex in transverse section, less than 1 mm. thick,

¹⁷⁰ W. T. Stearn (Jour. Soc. Bibl. Nat. Hist. 1:199-201. 1939) gives the dates of publication of this work as 1800-1802, t.76 being published in 1802.

coriaceous, with a placenta thickened at the base and bearing 2 - 3 rows of short stout peg-like funicles from the base to just above the middle; seeds 12 - 22, red to dark red or black, irregular.

Occurs from the Macpherson Range, in southern Queensland, to the Victorian Alps, along the ranges of New South Wales. Flowers in August and September.

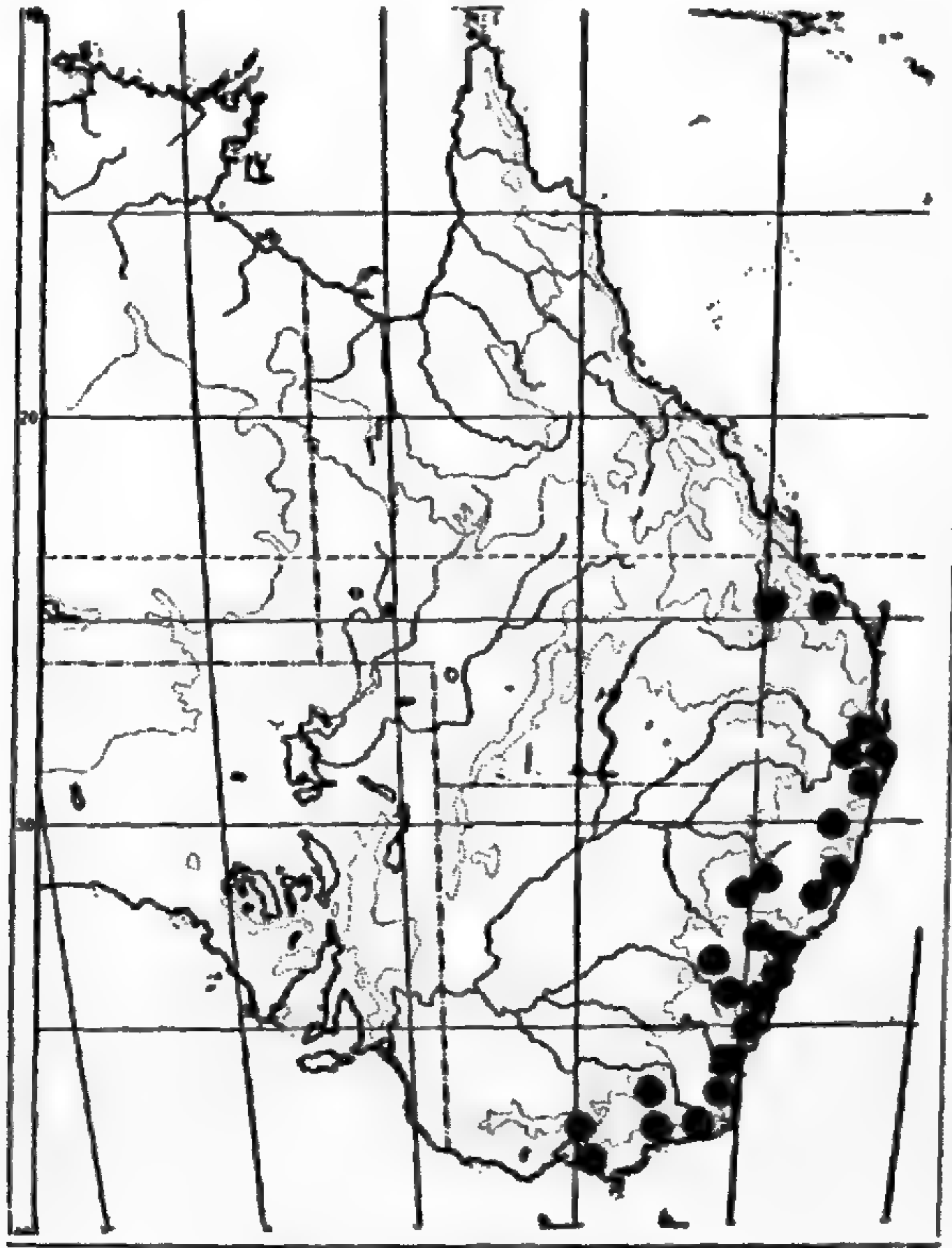


Fig. 31. *P. undulatum*.

AUSTRALIA: QUEENSLAND: Bunya Mts., *Bailey s.n.* (BRI, NSW); same locality, *White s.n.* (BRI); same locality, *Moulday s.n.* (BRI); 2800', at edge of scrub in partial shade, Mount Mistake, *Hubbard 5225* (A, K); same locality, *Shirley s.n.* (A); Eumundi, *Simmonds s.n.* (A); Moreton Bay, *without collector s.n.* (U); moderately common in light rain forest, sandy soil, Southport, *White 9206* (A, BH, BRI); Tambourine Mountain, *Shirley s.n.* (NSW); same locality, *Longman & White s.n.* (BRI); same locality, *White 3570* (BRI); same locality, *Simmonds s.n.* (A); near Canungra, *Brass s.n.* (NSW); Lamington N. Park, *Moore s.n.* (BRI); Beechmont, *White 6179* (BRI); Acacia Creek via Killarney, *Dunn 129* (NSW); near Emu Vale, Macpherson Range, *Francis s.n.* (BRI); Cunningham's Gap, *Bailey s.n.* (BRI); on Rhyolite at edge of rain forest in wet sclerophyll forest, ca. 2400', Nixon's Creek, Upper Falls, Macpherson Range, *Johnson 106* (NSW). NEW SOUTH WALES: 3000', in bush, Waterfall Creek, Mt. Wilson, *Johnson s.n.* (NSW); Tiba Tilba, *Bate 94* (MEL) near Tentfield, *Stuart s.n.* (K); Conjola, *Heron s.n.* (NSW); Lismore, *Maiden 17* (U); New England, *Stuart s.n.* (MEL); in bed of creek, ca. 20 miles N.N.E. of Boggabi, towards Nandewar Range, *Swain s.n.* (NSW); Barraba, *Kifford s.n.* (NSW); Hastings River, *Beckler s.n.* (MEL, U); Gloucester Buckets, *Maiden s.n.* (A, NSW); Rylstone, *Baker s.n.* (A); ca. 1000', Macquarie Pass, Robertson to Albion Park, *Johnson s.n.* (NSW); banks of River Grose, first branch, *Brown 5451* (BM); Kurrajong, adjacent to the River Grose, *Atkinson s.n.* (MEL); occasional in gullies on granite, 690 m., Ruby Creek, Mt. Werong, ca. 30 miles south of Oberon, *Johnson & Constable s.n.* (K, NSW); upper Chichester River, *Fraser & Vickery s.n.* (A, BISH, BH, MO, NSW, US); on old sand dunes, peninsula north of the entrance to Tuggerah, via

Wyong, *Helms* 582 (A); Box Point to Barber's Creek, *Maiden s.n.* (K, NSW); in shaded woods on the sea-coast, Illawarra, Port Jackson, *A. Cunningham s.n.* (K); shores of Port Jackson, *Brown* 5451 (BM); Port Jackson District, *Brown* 5451 (K, MO); same locality, *Siemssen* 97 (MEL); same locality, *Steel s.n.* (NSW); same locality, *Helms s.n.* (BRI); same locality, *Camfield s.n.* (MO); near Sydney, *Weber s.n.* (NSW); Cheltenham, *Johnson s.n.* (NSW); Petersham, *Steel s.n.* (AK); Sydney, *Haswell s.n.* (BRI); same locality, *Backhouse s.n.* (BM); same locality, *Wilkes s.n.* (K, US); same locality, *McWilliams s.n.* (K); same locality, *Verreaux* 406 (K); Illawarra, *Macarthur* 26 (K); Berry Mountain, *Maiden s.n.* (NSW); Sugar Loaf Mountain, Braidwood, *Baeunton s.n.* (MEL, NSW); Queanbeyan, *Breakwell s.n.* (NSW); 1200', between Nowra and Kangaroo Valley, Cambewarra Range, *Rodway* 1690 (A, K); Nowra, *Rodway* 361, 847 (K); Shoalhaven River, Wingello, *Murphy* 9 (NSW); Comerong Is., same locality, *Rodway* 874 (K); Candelo, *White s.n.* (MEL); Twofold Bay, *Father s.n.* (A); same locality, *Mueller s.n.* (MEL). VICTORIA: Genoa River, *Reader s.n.* (MEL); Broadrib, or Broadribb River, *Mueller s.n.* (K, MEL); in rupibus prope Buchan ad flumen Murrandale, *Mueller s.n.* (MEL); Snowy River, *Mueller s.n.* (K, MEL); Stony Creek, *Smith s.n.* (MEL); East Gippsland, *Mueller s.n.* (GH, MEL); Dead-Cock Creek, E. of Lindenow, *Green s.n.* (MEL); in small steep gully above sea cliff, Mt. Martha, E. Port Phillip, *Johnson s.n.* (NSW); in moist sandstone gully, Epping, *Ford s.n.* (NSW); Wilson's property, near Korumburra, Strzlecki Ranges, *without collector s.n.* (MEL). WITHOUT DEFINITE LOCALITY: Australia, *Verreaux* 48 (BM), 44P (P, US); East Australia, *Schomburgk s.n.* (MEL); South Australia, *Schomburgk s.n.* (NSW); Australia, *Lhotsky s.n.* (BM); Australia, *Sieber* 221 (A, BM, ILL, K, MEL, MO); N. S. Wales, *A. Cunningham* or *Anderson and others* 321 (U); N. S. Wales, *Caley s.n.* (BM).

Pittosporum undulatum is widely cultivated as an ornamental, hedge, or shelter plant, and I have seen specimens from New Zealand, Australia, Chile, Colombia, Bolivia, Jamaica, Bermuda, the United States (California and Florida), the Azores, the Canary Islands, France, Israel, India, Ceylon, China, and Hawaii. It has become naturalized in Bermuda, the Canary Islands and Hawaii. A form with variegated leaves is available in the trade in Australia,¹⁷¹ and a small-leaved plant, labelled "*Pittosporum* hybrid," and "a glabrous-leaved form of *P. bicolor*" have been collected from the Strzlecki Ranges, Victoria, (*without collector s.n.* MEL) and from South Australia (*Schomburgk s.n.* NSW). The last form is connected with the large-leaved plants by intermediates, and I am unable to recognize it as a distinct variety. According to Bentham,¹⁷² the height of *P. undulatum* is "about 40 feet, or according to M'Arthur 60 to 90 feet". Recent collectings are from smaller trees, but a plant at East Alameda Plaza, Santa Barbara, California, is stated to be about 60 feet tall and 50 feet in crown diameter (*Moran* 2349 BH), so it is possible that trees of 60 to 90 feet were found in the early days of Australian botany.

The variation in the morphology of the flower has been described and illustrated by Maiden,¹⁷³ Gowda,¹⁷⁴ and Cufodontis.¹⁷⁵ Flowers which may be female

¹⁷¹ *Pittosporum undulatum* "variegatum", commonly known as the Variegated Sweet Pittosporum (Lord, Shrubs and Trees for Australian Gardens. p.34. 1948).

¹⁷² Fl. Austr. 1:111. 1863.

¹⁷³ For. Fl. N.S.W. 7:124. 1920.

¹⁷⁴ Jour. Arnold Arb. 32:276. 1951.

¹⁷⁵ Österr. Bot. Zeitschr. 98:114. 1951.

have capitate obscurely lobed stigmas, styles 2 - 3 mm. long, and ovaries 4.0 - 4.5 mm. long and 2 - 3 mm. broad. The stamens are rudimentary, gland-like structures 0.6 - 1 mm. long. Flowers which may be male or bisexual have weakly capitate to truncate stigmas, styles 3.0 - 4.5 mm. long, ovaries 3.5 - 5.0 mm. long, 1.5 - 2.0 mm. broad, stamens 8.5 - 11.0 mm. long, and functional anthers 3.5 - 5.0 mm. long and 1.0 - 1.5 mm. broad. Intermediate forms occur in which the stamens are reduced, the most remarkable being *Ford s.n.* in which the stamens vary in length from 5 - 7 mm. in the same flower. Flowers also occur with 1 - 2 extra sepal lobes, and petals.

Vernacular names: Wave-leaved Pittosporum, Cheesewood, Engraver's wood, New South Wales Box Tree, New South Wales Mock Orange, Native Laurel, Victorian Laurel, Sweet Pittosporum (Victoria), *Wallundundeyren*, *Bart-Barb* (Aboriginal).

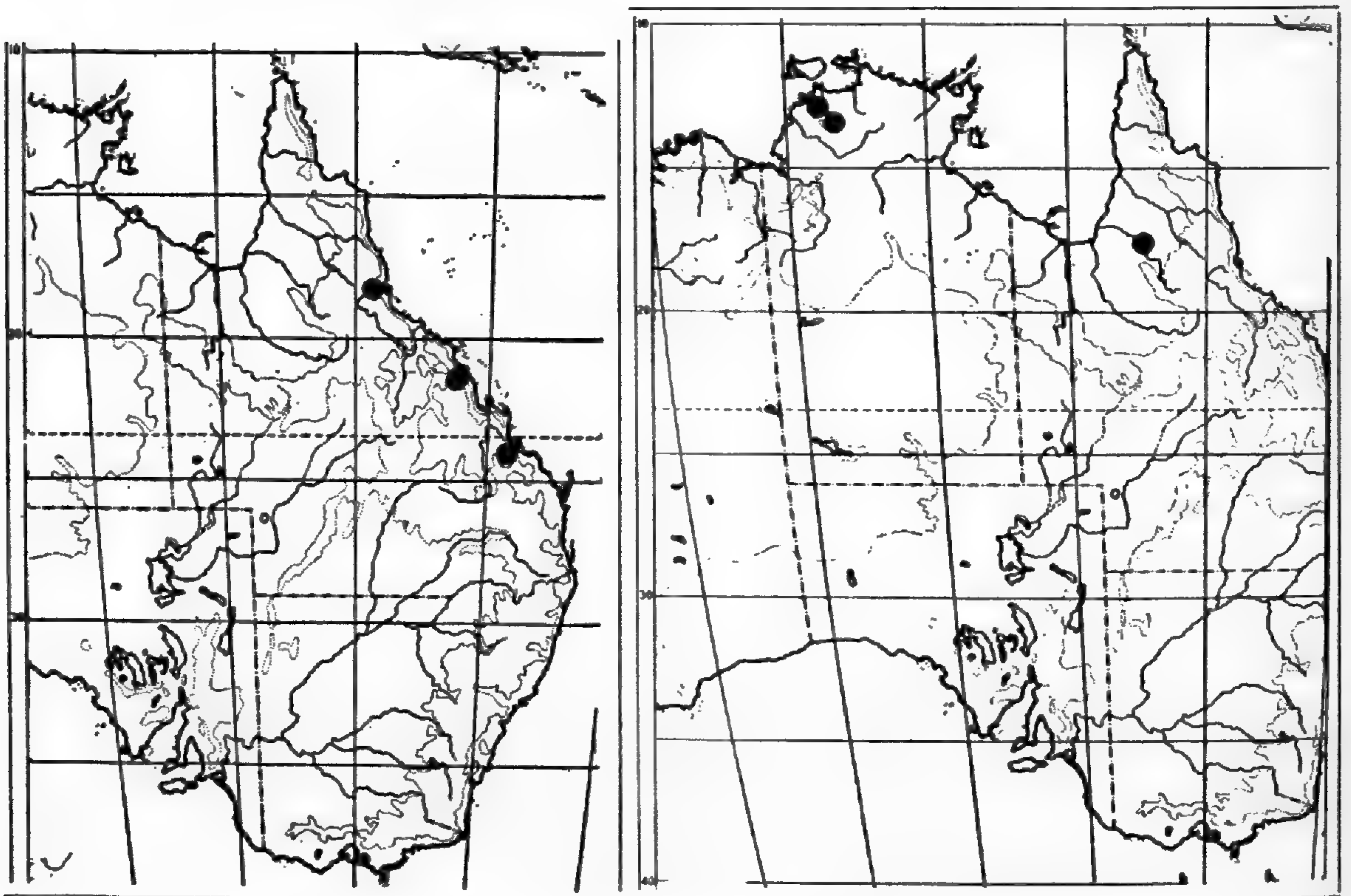
27. PITTOSPORUM VENULOSUM F. Muell. Frag. Phyt. Austr. 6: 186. 1868. (T.: *Dallachy s.n.*!).

Trees to 10 m. tall; branchlets gray, rusty-tomentose when young, soon glabrate. Leaves alternate to subverticillate, lanceolate to ovate-lanceolate, acute to acuminate at apex, attenuate at base, entire, 4.5 - 10.5 cm. long, 1.7 - 4.2 cm. broad, rusty-tomentose when young, especially on costa, glabrate, coriaceous, margins undulate, irregularly revolute, costa immersed or sunken above, raised below, secondary veins 8 - 12 per side, anastomosing, distinct; petioles 6 - 21 mm. long, 1 - 1.5 mm. broad, rusty-tomentose when young, soon glabrate. Flowers terminal, in umbelliform cymes; peduncles subtended by a loose whorl of leaves and by numerous caducous rusty-tomentose bud scales 2 - 6 mm. long; peduncles and pedicels accrescent in fruit, rusty-tomentose, soon glabrate. Sepals not imbricate, oblong, obtuse, 4.0 - 4.5 mm. long, 1.5 - 2.0 mm. broad, ciliate, rusty-tomentose without, glabrous within; petals oblong, obtuse, 8 - 11 mm. long, 1.5 - 2.0 mm. broad, free, spreading at the tips, white; stamens 4 - 5 mm. long, anthers sagittiform, 2.0 - 2.5 mm. long, 0.5 - 1.0 mm. broad. Pistil at anthesis longer than the stamens; ovary 4.0 - 4.5 mm. long, 2 mm. broad, rusty-tomentose; style 1.5 - 2.0 mm. long; stigma capitate, obscurely 4-lobed. Capsules subglobose to obovoid with an evident stipe, 2-, rarely 3-, valved, apiculate, 1 - 2 cm. long, 1.0 - 1.4 cm. broad, glabrate, rugose; valves convex in transverse section, 1 - 2 mm. thick, woody, with placentas much thickened and fused at the base, bearing 6 - 8 peg-like funicles up to 2 mm. long about the middle; seeds 6 - 14 per capsule, reddish-black to black, irregular.

Occurs in the coastal ranges of Queensland, between Rockingham Bay and Keppel Bay.

AUSTRALIA: QUEENSLAND: Coast Range, at edge of scrub, Rockingham Bay, *Dallachy s.n.* (BM, K, MEL, NSW); Eungella Range, *Francis s.n.* (BRI, MEL); rare, at edge of light rain forest on rather steep hillsides, Byfield near Keppel Bay, *White 8142* (A, BRI); Mt. Spec, *White 8974* (A, BH).

I have not seen adequate flowering material and have described the inflorescence from immature specimens.

Fig. 32. *P. venulosum*.Fig. 33. *P. melanospermum*.

28. *PITTIOSPORUM MELANOSPERMUM* F. Muell. Frag. Phyt. Austr. 1: 70. 1859.
(T.: Holt s.n. !)

Pittosporum setigerum Bailey, in Queensland Agr. Jour. 1: 451. 1897. (T.: Barclay-Millar s.n. !).

Pittosporum muticum Domin, in Bibliog. Bot. 22: 718. 1925. (T.: Schultz 758 !).

Shrubs or small trees to 6 m. tall; branchlets reddish-gray, glabrous. Leaves alternate, sometimes crowded, oblanceolate to oblong, rarely obovate, obtuse to acuminate or mucronate at apex, attenuate at base, entire, 4 - 14 cm. long, 1.1 - 4.5 cm. broad, glabrous, coriaceous, margins thick, flat to slightly undulate, costa immersed above, raised below, secondary veins 13 - 18 per side, anastomosing, raised on both surfaces; petioles 1.4 - 4.0 cm. long, 1 mm. broad, glabrous. Flowers terminal, very numerous, in spreading paniculiform cymes; peduncles subtended by an approximate whorl of 3 - 4 leaves and minute caducous bud scales, and bearing branches which are subtended by caducous cataphylls, and which are again divided, the ultimate divisions each bearing several pedicels; peduncles, branches, and pedicels accrescent in fruit, white-tomentulose, soon glabrate. Sepals slightly imbricate to coherent in a shallow cup, ovate, subacute to acute, 1.5 - 2.5 mm. long, 1 - 2 mm. broad, white-tomentulose becoming glabrate; petals obovate to lorate, obtuse, 7 - 9 mm. long, 2.0 - 3.5 mm. broad, free, patent, yellow; stamens 6.5 - 10.5 mm. long, anthers elliptic-ovate, 1.5 - 2.0 mm. long, up to 1 mm. broad. Pistil at anthesis slightly shorter than the stamens; ovary 2.5 - 3.5 mm. long, 0.5 - 2.0 mm. broad, white-tomentulose, on a glabrous stipe about 1 mm. long; style about 1.5 mm. long; stigma truncate. Capsules obovoid to subglobose, 2-

valved, apiculate, 6 - 15 mm. in diameter, frequently with a stipe 0.5 - 1.5 mm. long, glabrate, brownish-yellow; valves convex to sulcate in transverse section, less than 1 mm. thick at sides, coriaceous, with a placenta much thickened at base and apex, and occasionally fused to form 2 chambers, bearing several short stout peg-like funicles between the base and middle; seeds 2 - 6, black, irregular.

Known from northern Queensland and the Northern Territory.

AUSTRALIA: NORTHERN TERRITORY: Arnhem's Land, *Mueller s.n.* (K); north of Arnhem's Land and Port Darwin, *Mueller s.n.* (NSW); Port Darwin, *Holt s.n.* (MEL); same locality, *Schultz 626, 758* (K); McKinlay, North Arnhem's Land, *Jim Millar s.n.* (MEL). QUEENSLAND: Cape York Penins. Expedition, *Hann 98* (K); Walsh River, *Barclay-Millar s.n.* (A, BM, BRI, K); common in rain forest, 500 m., Lake Barrine, Atherton Tableland, *Kajewski 1352* (A, BRI, P).

29. PITTOSPORUM RHOMBIFOLIUM A. Cunn. ex Hook. Icon. Pl. 7: t. 621. 1844.
(T.: *A Cunningham 29!*).

Trees 13 - 30 m. tall; branchlets light brown, glabrous. Leaves alternate, sometimes crowded at the tips of the branchlets, rhombic to ovate, acuminate to obtuse at apex, attenuate at base, coarsely serrate to entire, 4 - 10 cm. long, 1.5 - 7.0 cm. broad, glabrous, coriaceous, margins frequently flat or revolute, costa sunken above, raised beneath, secondary veins about 12 - 14 per side, anastomosing, raised above and below; petioles 0.9 - 2.7 cm. long, 1 - 2 mm. broad, glabrous. Flowers terminal, many, in spreading umbelliform cymes; peduncles and pedicels up to 5 cm. long, accrescent in fruit, glabrous, peduncles subtended by a single leaf and 1 or 2 minute caducous bud scales. Sepals coherent at base, ovate, acute to subacute, 1.1 - 3.0 mm. long, 0.5 - 2.0 mm. broad, glabrous; petals elliptic to oblanceolate, obtuse to subacute, 5.5 - 8.5 mm. long, 1.5 - 3.0 mm. broad, free, patent, white, with short claws; stamens 5.5 - 8.0 mm. long, anthers lanceolate, 1.7 - 2.4 mm. long, about 1 mm. broad. Pistil at anthesis slightly shorter than the stamens; ovary 3.5 - 4.0 mm. long, 1 - 2 mm. broad, short-stipitate, tomentulose; style 0.5 - 1.0 mm. long; stigma truncate. Capsules subglobose to obovoid, 2-valved, obtuse to apiculate at apex, stipitate at base, 5 - 10 mm. long, 5 - 8 mm. broad, yellow, slightly rugose, glabrous; valves convex to sulcate in transverse section, less than 1 mm. thick, coriaceous, with a conspicuous placenta more or less fused to form 2 chambers and bearing 1 - 2 minute funicles near the base; seeds 1 - 3, black, irregular.

Occurs from northern Queensland to northern New South Wales, Australia. Flowers in November, December and January.

AUSTRALIA: QUEENSLAND: Canaan Valley, near Proserpine, *Michael 973* (BRI, NSW); Tooloom Range, *Maiden s.n.* (NSW); Rockhampton, *Tbozet s.n.* (MEL); same locality, *O'Shanesy 87/9* (MEL); in red, sandy loam, 12 miles east of Emerald, Leichardt District, *Everist 2522* (BRI); in mixed soft-wood forest, Guluguba, Leichardt District, *White 1146* (BRI); between Brisbane and Dawson, *Mueller s.n.* (K); Dawson River, *Mueller s.n.* (MEL); Gladstone, *Bailey s.n.* (NSW); Mt. Perry, *Keys s.n.* (BRI); Eidsvold, *Bancroft s.n.* (BRI); Wallaville, 30 miles s. of Bundaberg, *Bancroft s.n.* (BRI); parish of Woowooyang, Maryborough, *Simon 37* (BRI); Maryborough, *Young s.n.* (BRI, NSW); Wide Bay, *Bidwill 52* (K); in light sub-xerophytic mixed scrub, Roma, *White*

9522 (A, BRI); Yalebone Creek via Rome, *McKenzie s.n.* (BRI); in "ringed" brigalow scrub, Chinchilla, *Beasley 27* (BRI); Blackbutt Range, *Shirley s.n.* (A); Yarraman, *Clemens s.n.* (BRI); Crow's Nest, *Kenny s.n.* (BRI); same locality, *Clemens 43747* (A); Crystal Brook, Bowenville, *Fuller s.n.* (NSW); Moreton Bay, *A. Cunningham s.n.* (GH); Brisbane, *Bailey s.n.* (BRI, NSW); in shaded woods on the banks of the Brisbane River, *A. Cunningham 29* (BM, BRI, K); same locality, *A. Cunningham s.n.* (MEL); same locality, *White s.n.* (NSW); Enoggera, near Brisbane, *Boorman s.n.* (NSW); Ipswich, *Nernst 34* (MEL); Beau-desert, *Brass s.n.* (A); Roberts Plateau, Lamington National Park, *White 6045* (A); Milford, Fassifern District, *Michael 2024* (A, BRI); Beech Mountain, *White 1903* (A, BRI); Acacia Creek, via Killarney, *Dunn 136* (NSW); National Park, *Shirley s.n.* (NSW); in regrowth on rain-forest margin, ca. 3000', O'Reillys, Lamington National Park, *Smith & Webb 3612* (BRI); common in light rain forest, Unumgar, near Mt. Lindesay, NSW-Q border, *White 12507* (BRI). NEW SOUTH WALES: Tweed, *Guilfoyle s.n.* (MEL); Burringbar, *Betche s.n.* (NSW); same locality, *McLean s.n.* (NSW); Lismore, *Baeunton s.n.* (A); same locality, *Tanner s.n.* (NSW); same locality, *Maiden s.n.* (U); Richmond River, *Moore s.n.* (GH, K); Possum Shoot, Richmond River, *Watts s.n.* (NSW); Clarence River, *without collector s.n.* (NSW). WITHOUT LOCALITY: *Walter s.n.* (MEL).

The plant is useful as an ornamental tree, and I have seen cultivated specimens from California, Florida, Queensland, New South Wales, and South Australia.

Vernacular names: White Myrtle, Diamond-leaf Laurel, Rhombus-leaved Queensland Laurel, *Burrawingee*.

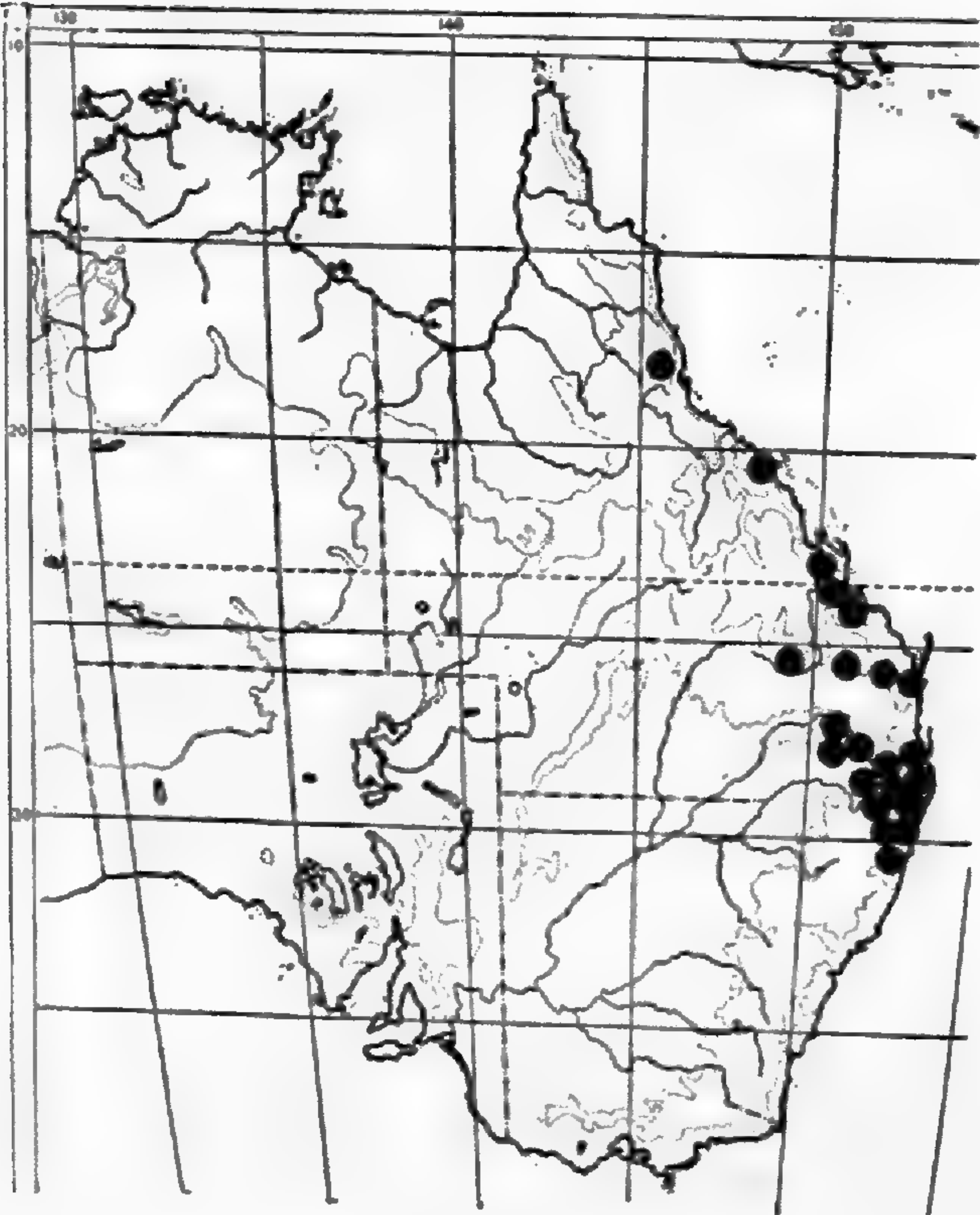


Fig. 34. *P. rhombifolium*.

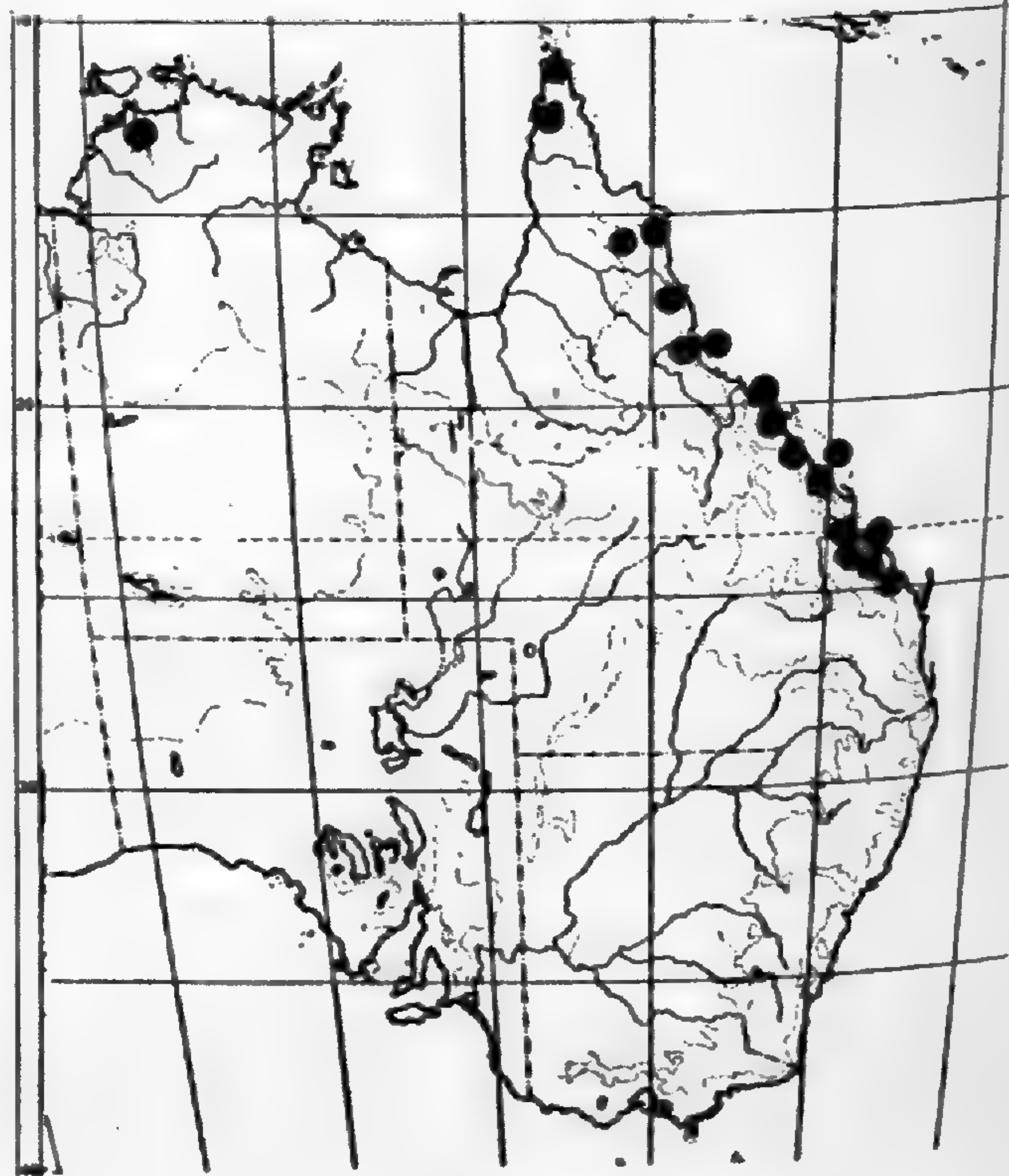


Fig. 35. *P. ferrugineum*.

30. *PITTOSPORUM FERRUGINEUM* Aiton, Hort. Kew. ed.2. 2: 27. 1811. (T.: *ex hort. Kew.*!).

Pittosporum linifolium A. Cunn. in Ann. Nat. Hist. 4: 109. 1839, as *tinifolium*. (T.: *A. Cunningham s.n.*!).

Pittosporum ovatifolium F. Muell. Frag. Phyt. Austr. 2: 78. 1860. (T.: *Dallachy s.n.*!).

Pittosporum queenslandicum Domin, in Fedde. Repert. Sp. Nov. 11: 201. 1912. (T.: *R. Brown 5449*!).

Trees or shrubs 8 - 20 m. tall; branchlets grayish-brown, rusty-tomentose when young, glabrate. Leaves alternate, frequently crowded at the tips of the branchlets, elliptic to elliptic-ovate or obovate, acute to acuminate or occasionally obtuse at apex, attenuate at base, entire, 4.8 - 11.5 cm. long, 2.0 - 5.5 cm. broad, green above, paler beneath, rusty-tomentose when young, soon glabrate except on costa, margins flat or recurved, costa sunken above, raised below, secondary nerves 4 - 8 per side, anastomosing, obscure above, raised beneath; petioles 1.2 - 2.2 cm. long, rusty-tomentose when young, glabrate. Flowers terminal or axillary, many, in subumbelliform cymes; peduncles and pedicels 1.5 - 4.0 cm. long, rusty-tomentose; peduncles subtended by 1 to several leaves and a whorl of ciliolate bud scales about 1 cm. long; pedicels subtended by 1 to several caducous bracts 2 - 4 mm. long. Sepals free or coherent at the base, linear to linear-lanceolate, acuminate, 2.5 - 3.5 mm. long, 0.6 - 1.2 mm. broad, sparsely tomentulose and ciliolate; petals linear to oblanceolate-linear, 7 - 9 mm. long, 1.2 - 1.5 mm. broad, coherent in a cylindrical tube with recurved tips, yellow; stamens 4.0 - 6.5 mm. long, anthers oblong, 0.5 - 2.0 mm. long, 0.3 - 0.6 mm. broad. Pistil at anthesis slightly shorter or longer than the stamens; ovary 3 - 4 mm. long, 0.8 - 2.0 mm. broad, tomentulose; style 1.2 - 2.0 mm. long; stigma capitate and 2-lobed to almost truncate. Capsules globose, 2-valved, about 7 - 10 mm. in diameter, slightly rugose, glabrous; valves convex in transverse section, less than 1 mm. thick, coriaceous, with a placenta thickened at the base, bearing 2 rows of short, stout, peg-like funicles from the base to just above the middle; seeds 15 - 16, black, irregular.

Occurs mainly on the coast, from Cape York to Rosedale, Queensland; also found in Malaysia from the Solomon to the Nicobar Islands. Flowers in Australia from June to August.

AUSTRALIA: NORTHERN TERRITORY: Adelaide River, *Lea s.n.* (BM); QUEENSLAND: Albany Island, *Hill 12, 13* (K); same locality, on dry ridges, *Mueller s.n.* (K); Cape York Peninsula Expedition, *Hann 366* (K); Cape York, *Ramsay s.n.* (NSW); same locality, *Daemel s.n.* (BM, GH, K, MEL, US); Vrilya Point, *J. F. Bailey s.n.* (BRI); on banks of the Endeavour River, *A. Cunningham 27, 117* (BM); Endeavour Ridge, at some distance from the sea, *A. Cunningham s.n.* (K), 27 (MO), 117 (BM, BRI, K); same locality, *Persich 4* (MEL); common along creek banks in rain forest, Mossman, *Blake 15014* (BRI, MEL); same locality, *Sayer s.n.* (BM); botanic reserve, Cairns, *White 10560* (BRI, MEL); Cape Grafton, *A. Cunningham 8* (K); sterile sands of Fitzroy Island, near Cape Grafton, *A. Cunningham 116* (K), *s.n.*, 116 (BM); Frankland Isles, *MacGillivray 1* (K); Rockingham Bay, *Dallachy s.n.* (BM, F, GH, MEL, MO, U); same locality, *Bailey s.n.* (BRI, K); Cardwell, *Bailey s.n.* (BRI, K); Palm Island, *J. B. [Banks & Solander] s.n.* (BM); same locality, *Simmonds s.n.* (BRI); same locality, *Bancroft s.n.* (BRI); Sandy Cape and Port Bowen, *MacGillivray 105* (BM); Palm Creek, Proserpine, *Michael 1484* (BRI), *s.n.* (K); Pioneer River, Mackay, *Griffiths s.n.* (MEL, NSW); Port Mackay, *Dietrich 370*,

1299 (MEL); scrub, Pilot Station, Mackay, *Griffiths s.n.* (BM, BRI); in rocky water-gullies, and in thickets on the hills, Percy Island, *A. Cunningham s.n.* (K); Shoalwater Bay, Broad Sound, *R. Brown 5449* (BM); sandhills on beach, growing thickly, Yeppoon, *Court s.n.* (BRI); Keppel Bay, *R. Brown 5449* (BM, K); Rockhampton, Fitzroy River, *Dallachy s.n.* (U); in remnants of light rain forest along Archer Creek, near Rockhampton, *White 12216* (BRI); rare, sides of sandstone ranges, Gracemere, *O'Shanesy 1824* (MEL); Crocodile Creek, Capricorn, *Bowman 96* (MEL); Curtis Island, *Mueller s.n.* (NSW); Gladstone, *Hedley 13* (BRI); Bustard Bay, *J. B. [Banks & Solander] s.n.* (BM); common on sandhills near beach, Rosedale, *Dovey 140, 153, 1010* (BRI). WITHOUT LOCALITY: New Holland, *Banks & Solander s.n.* (MO); East Coast, *R. Brown s.n.* (BM, K, MO); east coast of Queensland, *Mueller s.n.* (NSW). CULTIVATED: *ex hort. Kew s.n.* (BM).

Flowers which may be female have capitate and 2-lobed stigmas, ovaries about 2 mm. broad, and stamens about 4 mm. long with anthers only 0.5 mm. long and 0.3 mm. broad. Flowers which may be male have weakly capitate to truncate stigmas, ovaries about 1 mm. broad, and stamens about 6 mm. long with anthers about 2 mm. long and 0.5 - 0.6 mm. broad. Intermediate forms occur with weakly capitate stigmas, and stamens 4 - 6 mm. long.

Vernacular name: Rust-leaved Pittosporum.

31. PITTOSPORUM DALLII Cheesem. Man. N.Z. Fl. p. 1134. 1906. (T.: *Dall s.n.*!).

Small trees 4 - 6 m. tall; branchlets gray, the young parts brown and puberulent. Leaves alternate, lanceolate-elliptic to oblong-elliptic, rarely obovate, obtuse, acute or acuminate at apex, acute to attenuate at base, coarsely serrate to entire, 5 - 10 cm. long, 2 - 4 cm. broad, dark green above, paler beneath, glabrous, coriaceous, the margins thin, flat, and ciliolate when young, thickened, slightly revolute and glabrate when mature, costa raised above and beneath, the secondary veins 14 - 18 per side, anastomosing, distinct above and beneath; petioles sparsely puberulent when young, glabrate, 3 - 18 mm. long, 1 - 3 mm. broad. Flowers terminal, about 40, in condensed umbelliform cymes; peduncles subtended by an approximate whorl of leaves and by caducous glabrous ciliate bud scales 15 - 21 mm. long; peduncles and pedicels 4-angular, up to 2 cm. long, accrescent in fruit, white-tomentose, each peduncle bearing 1 to many pedicels subtended by caducous, glabrous, linear bracts up to 1 cm. long. Sepals not imbricate, linear, 5 - 6 mm. long, about 0.5 - 1 mm. broad, glabrous; petals obovate, obtuse, 8 - 9 mm. long, 3.0 - 3.5 mm. broad, free, spreading from the base, white with red veins; stamens 7 - 8 mm. long, anthers elliptic-oblong, reflexed, 2 - 3 mm. long, up to 1 mm. broad. Pistil at anthesis longer than the stamens; ovary glabrous, about 3 mm. long, 1 mm. broad; style about 2 mm. long; stigma truncate. Capsules ellipsoid, 2-valved, about 15 mm. long, 9 mm. broad, green to black, glabrate; valves convex in transverse section, less than 1 mm. thick, coriaceous, with a slightly thickened placenta bearing alternate flattened and peg-like funicles, up to 2 mm. long, from the base to near the apex, dividing longitudinally into a woody mesocarp, which is shed on dehiscence, and a persistent membranous endocarp covering a cone-shaped mass of viscid seeds; seeds about 25, dark red, somewhat trigonal.

NEW ZEALAND: NELSON: mountains, near Collingwood, *Dall s.n.* (AK); same locality, 3500', *Gibbs s.n.* (A, AK, BM), 1854 (K).

Eleven trees have been found at Specimen Creek and Snow's Valley, near Boulder Lake, northwest Nelson. Others are reputed to occur in the vicinity, but as the locality is isolated and difficult to visit, the size of the population is not known. I suspect from their appearance that the flowers of the material available are male and that female flowers have not been collected.

Cheeseman¹⁷⁶ described the foliage as sharply and coarsely serrate from the flowering and fruiting specimens available to him (*Dall s.n.*, *Gibbs s.n.*). At Duncan & Davis Nursery, New Plymouth, cultivated plants have serrate leaves on the lowermost branches and as the lower cataphylls on new shoots. At the crown of the trees and at the apex of new shoots the leaves are entire. The species is cultivated as a rarity in New Zealand and England.

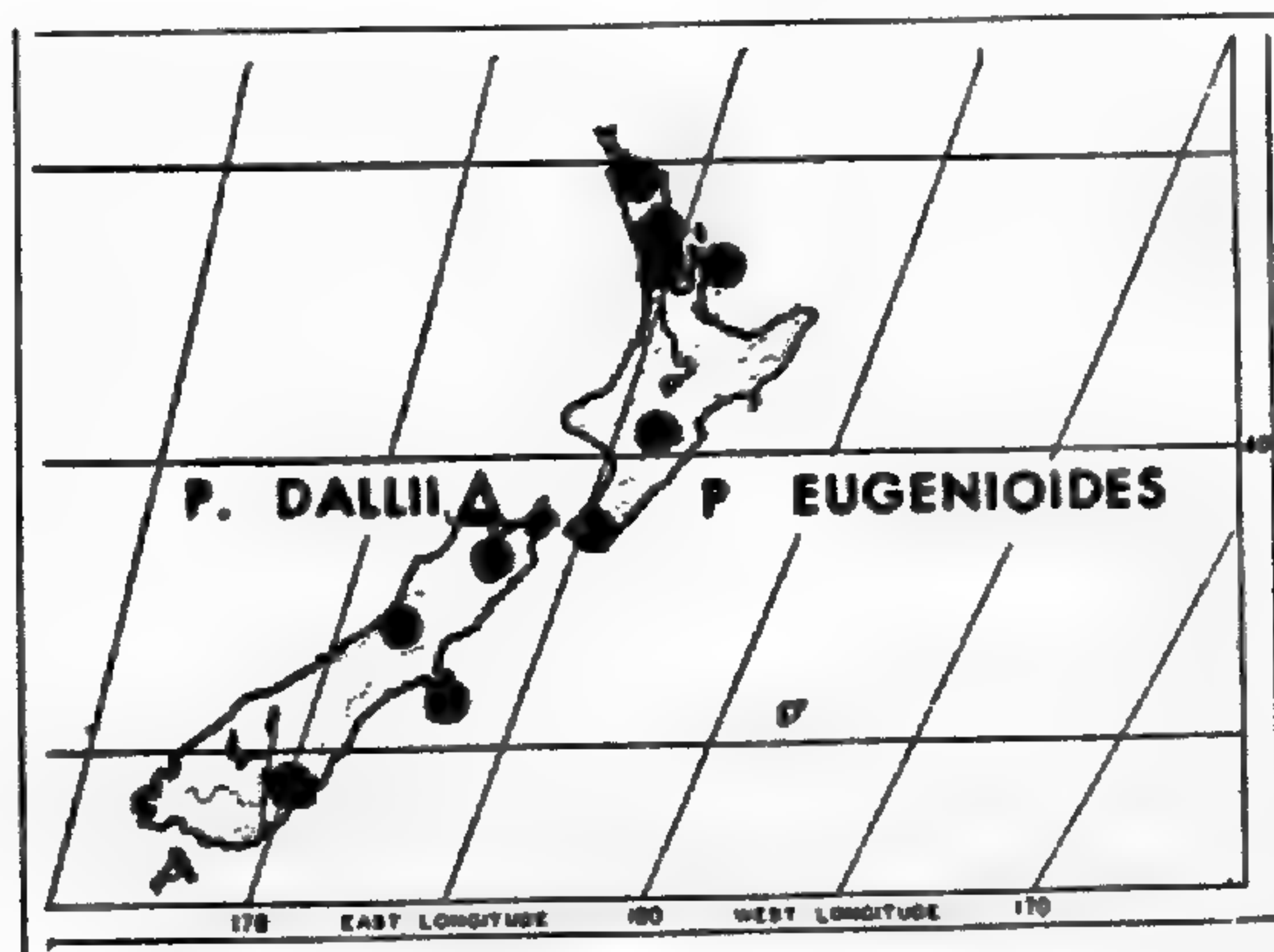


Fig. 36. *P. dallii* and *P. eugenoides*.

32. PITTOSPORUM EUGENIOIDES A. Cunn. in Ann. Nat. Hist. 4: 106. 1839.
(T.: *R. Cunningham s.n.* and 614!).

Pittosporum microcarpum Putterl. Syn. Pittosp. p. 15. 1839, *ex char.* (T.: *A. Cunningham s.n.*).

Pittosporum enkianthoides R. Cunn. & Hueg. in Putterl. *loc. cit.* p. 7. 1839, *nom. nud. in synon.*

Pittosporum umbellatum A. Cunn. in Putterl. *loc. cit.* 1839, *nom. nud. in synon.*

Pittosporum elegans Raoul, in Ann. Sci. Nat. III, 2:121. 1844. (T.: *Raoul s.n.*!).

Trees 6 - 13 m. tall; branchlets brown, glabrous. Leaves alternate, frequently crowded at the tips of the branchlets, oblong-elliptic to elliptic, subacute to acute at apex and base, entire, occasionally notched at base in juveniles, 5 - 15 cm. long, 2 - 4 cm. broad, glabrous, light green above, paler beneath, subcoriaceous, margins often undulate, the costa raised, the secondary veins 20 - 30 per side, anastomosing, obscure above, distinct beneath; petioles 0.8 - 1.8 cm. long, 1 - 2 mm. broad, glabrous. Flowers terminal or sometimes becoming lateral on development of a leading shoot from an axillary bud, 30 - 70, in spreading umbelliform cymes; peduncles subtended by an approximate whorl of leaves and by caducous, glabrous bud scales 1.0 - 1.7 cm. long; peduncles bearing branches which are again divided to bear 1 - 8 pedicels, branches and pedicels subtended

¹⁷⁶ Man. N.Z. Fl. ed.2. p.496. 1925.

by caducous, glabrous, linear bracts about 1.5 mm. long; peduncles, branches, and pedicels sparsely tomentose, accrescent in fruit. Sepals not imbricate, lanceolate, 1.5 - 3.0 mm. long, 0.5 - 1.0 mm. broad, glabrous; petals oblong, subacute to obtuse, 5 - 7 mm. long, 1.5 - 2.0 mm. broad, free, spreading from the base, yellow; stamens 3.0 - 5.5 mm. long; anthers sagittiform to elliptic-obovate, 1 - 2 mm. long, up to 1 mm. broad. Pistil at anthesis slightly shorter or longer than the stamens; ovary 1.5 - 3.0 mm. long, 1 - 2 mm. broad, tomentulose; style 1 - 3 mm. long; stigma capitate and obscurely 2-lobed or truncate. Capsules ellipsoid, 2-, rarely 3-, valved, acuminate, 9 - 10 mm. long, 5 - 6 mm. broad, green to black, glabrate; valves convex in transverse section, less than 1 mm. thick, coriaceous, with a slightly thickened placenta bearing near the middle 2 - 4 flattened and peg-like funicles up to 1 mm. long, dividing longitudinally into a coriaceous mesocarp, which is shed on dehiscence, and a membranous endocarp covering the seeds; seeds 1 - 8, reddish-black to black, irregular.

Known from the North and South Islands of New Zealand. Flowers from August to November.

NEW ZEALAND: NORTH AUCKLAND: Oruru, near Kaitaia, *Matthews s.n.* (AK); Kaitaia, *Matthews s.n.* (AK, MO); Onawero Bay, Wangaroa, R. *Cunningham s.n.*, 614 (K, as *P. microcarpum* R. Cunn.); in coastal forest remnants on Parua Bay Road, near Whangarei, *Carse s.n.* (AK). AUCKLAND: Paparoa, Kaipara, *Kirk s.n.* (AK); Henderson, *Cheeseman s.n.* (AK, GH, US); Waitakere, *Matthews s.n.* (AK); same locality, *Mackie s.n.* (AK); Anawhata, coast north of Piha, *Mackie s.n.* (AK) subtropical rain forest, Titirangi, *Chapman s.n.* (A); in second growth *Agathis australis* (Kauri) forest, Huia, Manukau Harbour, *Wood s.n.* (AK). THAMES: Kennedy Bay, *Matthews s.n.* (AK, MO); Coromandel, *Cheeseman s.n.* (AK, BISH, GH, NSW); Table Mountain, *Adams s.n.* (AK); Kaueranga, *Adams s.n.* (AK). VOLCANIC PLATEAU: 750 m., in mixed forest, Ohakune, *MacDaniels p.599* (CU); Ruapehu, *Attwood s.n.* (AK); Ohakune River, *Crompton s.n.* (K). WELLINGTON: York Bay, *Meebold 18278* (BISH). NELSON: Waimea woods, *Monro 66* (K); Nelson, *L. Travers s.n.* (K); Dun Mountain, *Mellor s.n.* (AK, MO); Foxhill, *Kirk 296* (BM). CANTERBURY: presqu'île de Banks, *Raoul s.n.* (GH, P, US); Akaroa, *Raoul 83* (K); same locality, *Belligny s.n.* (GH); Banks Peninsula, *Kirk 296* (GH, US); Lyttelton Hills, *Meebold 4745* (BISH). WESTLAND: Cobden Flat, Grey City, R. H. [*Helms*] *s.n.* (BM, MO). OTAGO: Dunedin, *Hector s.n.* (K); near Dunedin, *Thomson s.n.* (AK); bush, Dunedin Belt, *Watt s.n.* (K); Mokopeka, *Meebold 5497* (BISH); in mixed forest, Hunter Hills, *Anderson 210* (A, F, K, MO, US). WITHOUT LOCALITY: *A. Cunningham s.n.* (GH, U); *Bidwill s.n.* (K); *Brown 107* (BISH); *Colenso s.n.* (BM, K), 710, 768, 768b, 3789 (K); *Harvey s.n.* (GH); *Raoul s.n.* (A); *R.N.Z. Inst. Hort. s.n.* (NSW).

Flowers which are probably female have 2-lobed capitate stigmas slightly exserted, plump ovaries about 3 mm. long, 1.5 - 2.0 mm. broad, and sagittiform anthers which appear to be abortive. Flowers which are probably male have truncate stigmas slightly below the stamens, slender ovaries 1.5 - 2.0 mm. long, about 1 mm. broad, and elliptic obovoid anthers which appear to be functional. Godley has informed me (personal communication) that the species is dioecious.

I am indebted to Mr. W. T. Stearn of the British Museum of Natural History, London, for the following note on the priority of Cunningham's names over those of Putterlick.

That part of Allan Cunningham's paper "Florae Insularum Novae Zelandiae precursor" which deals with *Pittosporum* was published in Annals of Natural History Vol. 4, dated 1840, on the titlepage, whereas Aloys Putterlick's Synopsis Pittosporarum (Vienna) is dated 1839 and hence would appear to have priority. On this assumption J. do A. Franco in Bol. Soc. Broter ii. 25:227 (1951) has replaced the generally accepted name *Pittosporum eugenioides* A. Cunn. by *P. microcarpum* Putterl. This is not the only example of nomenclatural conflict between the two publications. Hence it has seemed desirable to investigate the matter further. Actually Cunningham's paper (pages 106-111) was published in Ann. Nat. Hist. no. 22, which is dated 'October 1839' both on its wrapper and on p. 74; a London publication, it was received by the Linnean Society of London on 2 October 1839, which can be confidently accepted as its date of issue. Putterlick's Synopsis, published at Vienna, was not received by the Linnean Society until 14 Jan. 1840; this suggests that it may have been issued towards the end of 1839. Unfortunately, the records of the Viennese publisher F. Beck were destroyed in the 1939-44 war, and no other Viennese source of information has been found. However, information about Austrian publications quickly became available in Leipzig, the well-organized centre of the German book trade. Thus the half-yearly catalogue of J. C. Hinrichs (Verzeich. neuer Bucher Juni-Dec. 1837 p. 182) lists Putterlick's Synopsis as published between June and December 1839. More precise evidence is given by the weekly Allgemeine Bibliographie für Deutschland 1839 (48):719 (29 Nov. 1839) where it is listed as a new publication. Even allowing as much as six weeks for the announcement of its publication to be sent to Leipzig by Friederich Beck, Putterlick's work would still be antedated by Cunningham's. No evidence has been found, despite extensive search, to suggest that Putterlick's came out earlier. Hence it can be accepted as published at the same time, in which event Cunningham's names are to be retained, having been adopted by J. D. Hooker who was the first to unite the species of Cunningham and Putterlick (cf. Int. Code Bot. Nom. 1952, art. 67), or Cunningham's paper issued on 2 October 1839 can be accepted as having priority over Putterlick's Synopsis, taking November 1839 as the date of issue for this in accordance with the only definite evidence available. Both procedures confirm the established nomenclature.

The type sheet at Kew bears three labels:

1. "*Pomaderris microcarpa*, Wangaroa, N. Zeal'd. R. Cunningham."
2. "*Pittosporum microcarpum*. R.C. (non. Putt.). (*P. eugenioides* A.C. Mss.). I gave it the Baron with this name. fl. non. vid. at Onewero Bay, Wangaroa, New Zealand, R. Cunningham. 1833."
3. "Taken from Herb. A. Cunningham, No. 614. *P. umbellatum* Gaert. (Putt.). *Pittosporum eugenioides* A. Cunn. Fl. N. Z. 1-22. Ann. Nat. Hist. V. iv. p.106. New Zealand. R. Cunningham 1833." The sheet is cited as "R. Cunningham s.n. and 614" to identify it. Presumably "the Baron" is Baron von Huegel whose collectings of *Pittosporum* were described by Putterlick.

Pittosporum eugenioides is commonly cultivated as a hedge-plant and ornamental tree in the United States, southern England, France and New Zealand, and I have seen specimens from Portugal (*Franco s.n.* K). The plant distributed by C. F. Baker of California as *P. undulatum*, "one of the most valuable species of the genus for garden and hedge planting" (Economic Plants of the World. No. 119.) is *P. eugenioides*. (A, CU, MASS, MO, NSW). A form with variegated leaves has been available in the trade for many years as var. *variegata*. Cheeseman¹⁷⁷ recorded that the abundant fragrant flowers were formerly used by the

¹⁷⁷ Man. N.Z. Fl. ed.2. p.496. 1925.

Maoris who mixed them with fat and applied them to their bodies, and the essential oil present might be suitable for the perfume trade.

Vernacular names: *Mapau*, *Tarata*, Lemon Matipo, Lemonwood, Lemon Tree. *Tarata* is the name preferred by modern writers.

EXCLUDED OR DOUBTFUL SPECIES

Pittosporum callicarpum Dom. in *Bibl. Bot.* 22: 713. 1925. I have not seen a specimen of this species.

Pittosporum nanum Hook. in *Comp. Bot. Mag.* 1: 275. 1835 = *Marianthus procumbens* (Hook.) Benth. *Fl. Austr.* 1: 117. 1863.

Pittosporum procumbens Hook. in *Comp. Bot. Mag.* 1: 275. 1835. = *Marianthus procumbens* (Hook.) Benth. *Fl. Austr.* 1: 117. 1863.

Pittosporum parviflorum Putterl. in *Lehm. Pl. Preiss.* 1: 189. 1844-5. I have not seen a specimen of this species but the drawings preserved at Vienna and generously lent by the Director of the Naturhistorisches Museum do not represent a species of *Pittosporum*.

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| <i>Marianthus procumbens</i> _____ | 182 | <i>crassifolium</i> _____ | 127 |
| <i>Pittosporoides</i> _____ | 121 | var. "album" _____ | 130 |
| <i>umbellata</i> _____ | 147 | var. <i>strictum</i> _____ | 127 |
| <i>Pittosporum</i> _____ | 121 | var. "variegatum" _____ | 130 |
| <i>acacioides</i> _____ | 140 | <i>crassifolium</i> _____ | 130 |
| <i>angustifolium</i> _____ | 140 | <i>crenulatum</i> _____ | 151 |
| <i>anomalum</i> _____ | 160 | <i>dallii</i> _____ | 178 |
| <i>bicolor</i> _____ | 144 | <i>discolor</i> _____ | 144 |
| BIVALVAE (Series II) _____ | 138 | <i>divaricatum</i> _____ | 159 |
| <i>bidwillianum</i> _____ | 134 | <i>divaricatum</i> _____ | 159 |
| <i>bracteolatum</i> _____ | 123 | <i>elegans</i> _____ | 179 |
| <i>buchanani</i> _____ | 136 | <i>ellipticum</i> _____ | 125 |
| <i>callicarpeum</i> _____ | 182 | ssp. <i>ellipticum</i> _____ | 125 |
| <i>colensoi</i> _____ | 135 | var. <i>decorum</i> _____ | 125 |
| var. <i>fasciculatum</i> _____ | 135 | ssp. <i>ovatum</i> _____ | 127 |
| <i>cornifolium</i> _____ | 162 | var. <i>ovatum</i> _____ | 127 |
| <i>crassicaule</i> _____ | 158 | <i>enderi</i> _____ | 134 |

<i>enkianthoides</i>	179	<i>procumbens</i>	182
<i>erioloma</i>	123	<i>queenslandicum</i>	177
<i>eugenioides</i>	179	<i>radicans</i>	151
"variegata"	181	<i>ralphii</i>	130
<i>fairchildii</i>	125	<i>reflexum</i>	151
<i>fasciculatum</i>	135	<i>revolutum</i>	164
<i>ferrugineum</i>	177	var. <i>tomentosum</i>	165
<i>fulvum</i>	164	<i>rhombofolium</i>	175
<i>gilliesianum</i>	151	<i>rigidium</i>	156
<i>hirsutum</i>	165	<i>rigidium</i>	159
<i>hirtum</i>	167	<i>roeanum</i>	140
<i>buegelianum</i>	144	<i>rubiginosum</i>	167
<i>huttonianum</i>	127, 132	ssp. <i>rubiginosum</i>	168
var. <i>fasciatum</i>	132	ssp. <i>wingii</i>	169
var. <i>viridifolium</i>	135	<i>salicinum</i>	140
<i>intermedium</i>	136	<i>setigerum</i>	174
<i>kirkii</i>	163	<i>tenuifolium</i>	133
<i>lanceolatum</i>	140	ssp. <i>colensoi</i>	135
<i>ligustrifolium</i>	140	var. <i>colensoi</i>	135
<i>lineare</i>	158, 159	var. <i>fasciculatum</i>	135
<i>linifolium</i>	177	sub. var. <i>cymosum</i>	135
<i>longifolium</i>	140	ssp. <i>fasciculatum</i>	135
<i>matthewsii</i>	149	ssp. <i>tenuifolium</i>	134
<i>mayi</i>	134, 137	"argenteum"	137
<i>melanospermum</i>	174	"garnettii"	137
<i>microcarpum</i>	179, 181	"purpureum"	137
<i>muticum</i>	174	"Silver Matipo"	137
<i>nanum</i>	182	"variegatum"	137
<i>nigra</i>	137	var. <i>tenuifolium</i>	134
<i>nigrescens</i>	137	<i>tomentosum</i>	164
<i>nigricans</i>	134	<i>translucens</i>	134
var. "Silver Queen"	137	TRIVALVAE (Series I)	122
<i>nigrum</i>	137	<i>turneri</i>	154
<i>obcordatum</i>	155	<i>umbellatum</i>	147
var. <i>kaitaiaensis</i>	156	var. <i>cordatum</i>	148
<i>oleaefolium</i>	140	<i>umbellatum</i>	137
<i>o'reillyanum</i>	146	<i>undulatum</i>	170
<i>ovatifolium</i>	177	"variegatum"	172
<i>parviflorum</i>	182	<i>uniflorum</i>	135
<i>patulum</i>	153	<i>venulosum</i>	173
<i>phillyraeoides</i>	140	<i>verticillata</i>	162
var. <i>microcarpa</i>	140	<i>virgatum</i>	149
<i>pimeleoides</i>	150	var. <i>crataegifolia</i>	149
var. <i>gilliesianum</i>	151	var. <i>seratum</i>	149
ssp. <i>major</i>	152	var. <i>sinuatum</i>	149
var. <i>major</i>	152	<i>viride</i>	135
ssp. <i>pimeleoides</i>	151	<i>wingii</i>	167, 169
ssp. <i>reflexum</i>	151	<i>Pomanderris microcarpa</i>	181
var. <i>reflexum</i>	151	<i>Trichilia monophylla</i>	134
<i>pimeleoides</i>	151		

THE CULTIVATED BEANS OF THE PREHISTORIC SOUTHWEST*

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Beans, corn, and squash were the basic cultivated plants of pre-Columbian North America. There is no monograph on prehistoric beans, and the history of their distribution and a description of their variations have not been published. Although prehistoric collections are few as compared with those of corn, a study of available material can contribute significantly to the history of agriculture in North America.

Apart from horticultural, agricultural, and other practices which create or modify ecological conditions so that domesticated plants and weeds might survive, man exercises conscious and unconscious varietal selection. Patterns of selection are set by culture-based criteria, and attitudes towards plants and selections are made within the limits of plants available and primary factors such as geography and climate.

The roles of plant geography, ecology, and of human culture in shaping the species composition and distribution of beans are taken up in the first part of this paper. The factors which determine the kinds of plant materials available for this sort of study are also discussed. Descriptions of the materials and their distributions in the Southwest are subsequently given, with discussions of the part they play in the history of cultivation and variation in beans.

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TAXONOMY AND DISTRIBUTION OF CULTIVATED BEANS

For purposes of this study beans are defined as the seeds of cultivated plants belonging to the genus *Phaseolus*. Bentham (1841) placed this genus with other trifoliolate genera in the papilionaceous tribe, PHASEOLINAE, sub-tribe EUPHASEOLEAE, but separated it from other genera of the sub-tribe by the coiled keel characteristic of *Phaseolus* flowers.

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The genus *Phaseolus* contains approximately 180 species (Ditmer *et al.*, 1937) distributed throughout the tropics and warm temperate regions of the World (Bailey, 1949). Distinctions between the Old and New World cultivated species are several, indicating long separation and independent evolution as cultigens (See Table I).

TABLE I
DISTINCTIONS BETWEEN OLD AND NEW WORLD CULTIVATED BEANS

	Old World	New World	Authority
Flower color	Usually yellow	Red, rose, violet, white (may be yellow-tinged)	Bailey, 1949, Piper, 1926
Seed size	Small	Large (teparies small)	
Testa pattern	Little variation	Highly varied	
Pods	Narrow	Broad	Hedrick, 1931
Flower morphology	Left keel petal with horn-like process	Left keel petal without horn-like process	Piper, 1926
Growth habit	Annual	Annual or perennial	Piper, 1926
Pathology			
<i>Cercospora cruenta</i>	Susceptible	Resistant	Piper, 1926
<i>Gloeosporium lindemuthianum</i>	Resistant	Susceptible	

Another distinguishing character which might be added is the geographical distribution of species included in the genus. According to Ditmer (Ditmer *et al.*, 1937) 126 species of *Phaseolus* occur in the Americas; 54 are natives of South Asia and East Africa; only two species are indigenous to Australia, and but one assigned to Europe.

As a result of the facile development of cool-temperature ecotypes and their acceptability as food, the range of the cultivated beans of the New World has been extended to the regions of Asia and Europe for which the Asiatic species have proven too thermophilic (Ditmer *et al.*, 1937). Photoperiodic adaptability (Allard and Zaumeyer, 1944) has apparently also contributed to the wide latitudes available to cultivation of the New World types. The Asiatic species, on the other hand, have not proved as successful for dry edible beans in the Americas as the highly productive and familiar common and lima beans. The mung bean, *Phaseolus aureus*, used in the sprouted form in oriental cookery, is the only Old World bean to have been grown in quantity in the United States. These beans were cultivated in Oklahoma to supply domestic needs for sprouting beans during the 1940's when Asiatic supplies were cut off.

Phaseolus vulgaris, the common garden bean, or kidney bean of Anglo-America, is frequently confused with the "cow pea" or "black-eyed bean," *Vigna sinensis* of Asiatic origin, which also provides green immature pods and dry seeds used for human food. The snap beans, both green and wax-podded, and field beans also

may usually be referred to *P. vulgaris*. In Mexico they are known as the *frijol*, in Colombia as the *frisol*, the names of Spanish origin having largely replaced the indigenous terms in these countries and elsewhere in Latin America. The numerous Spanish or English horticultural varieties are usually multinominal and are based upon seed characters such as color, color pattern, shape, supposed derivation of original seed (as Mexican Red, Hidatsa Red), use (as Navy Bean), productivity, growth habit, precocity, and the like.

CENTERS OF DOMESTICATION OF AMERICAN BEANS

The cultivated beans which were domesticated in the New World are represented by four species. A brief history of their origins is given below.

Phaseolus vulgaris L. (Sp. Pl. 723. 1753), Kidney or Common Bean: This highly variable species was considered by Linnaeus to be Asiatic in origin. De Candolle (1886) was convinced that the common beans are native to the New World but, because he was uncertain of the validity of archaeological evidence, placed them among plants of doubtful origin. The use of archaeological material in the demonstration of the New World origin of common beans is indicated below. Ivanov, according to Bukasov (1930), assigned the common beans to the Mexican-Guatemalan highlands region on the basis of varietal diversity.

McBryde (1945) and Burkart (1943) reported *Phaseolus* species which they considered were non-domesticated forms of the cultivated common bean. Collections of similar kinds from the Mexican plateau and Guatemala also exist, the descriptions of which have not as yet been published. The only such material which has been investigated experimentally is that of Burkart and Brücher (1953). They found beans from Honduras and Argentina to be sexually compatible with cultivated varieties of *P. vulgaris*, but not with those of *P. coccineus* or *P. lunatus*. The floral characters were similar to those of *P. vulgaris*. The Argentinian collections were from uninhabited (at the present time) high mountain valleys and were not thought to be escaped forms. The chromosome number in root tips of both the Central and South American material was 22, as in other members of the tribe. Burkart proposed the following nomenclature for *Phaseolus vulgaris* as now understood:

P. vulgaris L. *sensu amplissimo*

P. vulgaris subsp. *aborigineus* Burkart

P. vulgaris subsp. *cultigenus* Burkart (all cultivated varieties)

It would seem likely that a number of the so-called "wild *P. vulgaris*" types might have had an influence on what are known as the cultivated common beans by way of hybridization.

There is little doubt that the common beans were domesticated in the New World from a form or forms not yet specifically known, and it is probable that the highlands of Mexico and Central America which show the greatest diversity of cultivated forms (Ditmer *et al.*, 1937) were the center from which domesti-

cated varieties spread first throughout agricultural Indian-America, and later to the other continents.

Phaseolus lunatus L. (Sp. Pl. 724. 1753), Lima Bean:—Ames (1939) cited Bentham as having referred the origin of the lima bean to Brazil but stated that it is not known there in the wild state. Mackie (1943) concluded that Guatemala, as the center of varietal diversity and the region from which a wild bean (considered by him to be *P. lunatus*) has been collected, is the place in which lima beans were first domesticated.

Phaseolus coccineus L. (Sp. Pl. 724. 1753), Runner Bean or Scarlet Runner Bean:—Runner beans are not definitely known from any reliably dated archaeological site of pre-Hispanic America. The scarlet runners which have been found in the Southwest are cultivated on a small scale by the Hopi or have been found in caves and reported as viable. Whiting (1950) made reference to the oral traditions concerning these supposedly ancient beans; when planted, they were supposed to have sprouted and produced crops of the edible dry seeds. The author has heard from individuals in the Southwest that progeny of seeds taken from old cave habitations are of the large white type (R 1, Tables IV and V) and are said, when cooked, "to taste like mashed potatoes." It is more than probable that the limits of duration of viability would preclude any considerable age being assigned to these collections.

The reports of Ivanov (Bukasov, 1930) and of Ditmer (1937) of distribution of *P. coccineus* limited to southern Mexico and Guatemala, and other reports (cited below) of the occurrence of *P. coccineus* as a weed in fields of cultivated common beans in the same region indicate that this region is a center of domestication for this species.

Phaseolus acutifolius A. Gray (Pl. Wright. 1:43. 1852), Tepary Bean:—The cultivated forms of this species, described as *P. acutifolius* var. *latifolius* (Freeman, 1912), are known mainly from two centers: one is that of the Indian populations of southern Arizona (Freeman, *op. cit.*); the other, found by Russian botanists, is the Pacific Coast of Chiapas in southern Mexico (Bukasov, *op. cit.*). Although Freeman proposed the Sonoran Desert region as the probable center of domestication of the tepary bean, Bukasov stated only that Mexico is the center of origin. The question of origin of the tepary bean will be discussed again in this paper.

The greatest diversity among the cultivated beans was found by Russian investigators (Bukasov, *op. cit.*, p. 510) in southern Mexico and Guatemala. They thought that the highlands of these regions saw the earliest domestication among the Maya, with subsequent adoption by lowland peoples, along with corn and other cultigens. Bukasov, according to Ditmer (1937), maintained that contact between Mexico and Peru did not come until a relatively late date and that on the arid coast of Peru a second center of origin for large-seeded, cultivated *P. vulgaris* was established. Prehistoric common beans of the Ica valley (Table VII, collec-

tion numbers 225-231) are larger than those found in archaeological sites of other, non-Peruvian cultures; but so are the lima beans, and Cuzco maize (collections of Hugh C. Cutler) is larger-kerneled than any other race. It would seem at least possible that ancient Peruvians had a predilection for large-seeded crops and, through selection, developed large-seededness to the extent of the genetic potentiality of each variety.

Wild species of *Phaseolus* are abundant throughout the warmer regions of the Americas, especially North America (Piper, 1926). Coincident with this distribution may be found not only the greatest number of forms of the common bean, but also the ranges of species which have likely had influence in building the polymorphic character of *P. vulgaris*.

Bukasov (1930) and others reported the common occurrence of *Phaseolus coccineus* as a tolerated, useful weed in plantings of the common bean in Chiapas—a situation which may be expected to persist in Guatemala. This species, although observed by the author while in Mexico in 1954 in abundance in the markets of towns situated at higher elevations in Chiapas, is not seen in the lowland *tierra caliente*. The "tropical black complex," indicated by Freytag (unpublished thesis) to be the source of variability of the common bean in Central America, certainly extends its influence at least into the tropical lowlands of Mexico. In other regions of ancient bean cultivation, such as the arid Southwest, other hybridizing species probably have had little influence on the common bean because of the low rate of outbreeding in *P. vulgaris* under arid conditions.

For a review of the systematics and synonymy of the cultivated beans, as well as their recorded history and appearance in the herbals, the reader is referred to Van Eseltine's discussion in "The Vegetables of New York" (Hedrick, 1931, pp. 3-16) and to Burkart's (1943) diagrams of seed types of all cultivated bean species.

GEOGRAPHICAL LIMITS OF THE SOUTHWEST

Although of importance to the present problem, the precise geographical and ethnic limits of the Southwest region are not easily determined. The question of how to define the Southwest, whether in terms of distribution of subsistence patterns, geography, ecology, or other criteria remains a matter for open discussion among anthropologists and other specialists. This is evidenced by Kirchhoff's recent paper (1954) and the comments of Kroeber, Beals, and Sauer. Kirchhoff considers the "... Greater Southwest areally to include Central, Southern and Baja California, the Great Basin, Arizona, New Mexico, Southern Coastal Texas and Northern Mexico south to the Sinaloa and Panuco rivers." Ecologically and culturally he distinguishes arid America with a gathering population from coexisting Oasis America and farming peoples.

The difficulties in presenting a definitive boundary scheme for this region are discussed by C. Sauer following Kirchhoff's article. He reviews the vast areas of the Greater Southwest for which the archaeological record remains virtually unexamined and for which there is still little information on migrations of peoples,

diffusions of agricultural techniques and crops, and cultural data, including descriptive and analytic linguistic materials. He suggests that Kirchhoff's classification is essentially an ecological one, based upon geographic considerations, and that only more information will enable classification in cultural terms and reveal the relationships underlying the culture history of the region.

For purposes of this paper, the Southwest region includes the present states of Arizona and New Mexico, and parts of Utah, Colorado, Texas, Nevada, California, and northern Mexico.

SOUTHWESTERN CULTURE HISTORY AND ENVIRONMENT

Geology and archaeology give evidence of the presence of non-sedentary human cultures in the Southwest at least 15,000 years ago. Some time before 300 B. C. differentiations appear in the archaeological record which show that these hunting and gathering peoples had begun to develop along somewhat divergent cultural lines.

In southern Arizona, the most arid portion of the Southwest, the prehistoric cultural development has been termed the "Hohokam." It is not clear at what time agriculture became established in this region, nor is it known whether it was preceded or followed by pottery. However, agriculture was well established by 300 B. C., and irrigation reached a high development among the Hohokam. The contemporary Pima and Papago tribes live in the area once inhabited by the Hohokam.

Peoples living to the east and northeast of the Hohokam, in what is now New Mexico, have been called the "Mogollon," and their region included the best-watered and most mountainous sections of the Southwest. Corn and squash cultivation was established among the Mogollon as early as 2,000 B. C., and pottery did not appear until considerably later. The Indians now occupying the Mogollon area are of the Apache group.

In northern Arizona and the Four-Corners region of Arizona, Colorado, New Mexico, and Utah emerged the "Anasazi" culture. The Anasazi of pre-pottery times have been called the "Basketmakers," and their successors, who made fired pottery, have had their culture history divided into four "Pueblo" periods. Pottery came to the Anasazi later than to the other groups; corn and squash agriculture were pre-ceramic among the Basketmakers and appear not to have been derived directly from the Mogollon or Hohokam. The Hopi, the Zuni, and Rio Grande Pueblos continue the Anasazi Pueblo tradition. The Navajo, who, like the related Apaches, were late arrivals to the Southwest, also occupy much of the Anasazi area.

Entering the Pueblo Southwest in the 16th century, the Spaniards found a few concentrations of farming peoples inhabiting a large area which formerly supported a more disperse population. These concentrations probably began with the droughts of the 13th century and the destruction of agricultural land as a result of arroyo cutting when more reliable water sources, such as those of the seeps and springs of the Hopi mesas, were sought. Religious and political domination by the Spaniards

brought about rebellions and migrations of refugees which augmented the normal contact among native peoples and certainly led to the introduction and exchange of crop varieties.

Contemporary Southwest Indian peoples, who are to varying degrees the heirs and continuers of the cultures of pre-Hispanic and pre-Anglo-American times, continue the cultivation of many ancient crops in addition to relatively recent ones.

Use and Preparation of Beans:—It has been pointed out that, with the possible exception of the tepary, the centers of origin of American beans must be sought outside the area of prehistoric occupation with which this paper is concerned. It follows that beans entered this region as cultigens by diffusion and with the plants came modes of use and cultivation.

Carter has observed (1945) that boiling of dry beans without preliminary soaking is the common practice among native southwestern peoples in modern times. This practice has been similarly observed in many parts of Mexico by the author and is probably a very early form of preparation. Laborious preparation of foods is common in modern non-industrialized societies; witness the stone-grinding of corn in tortilla-making and the grating and leaching of mandioca. But these are basic starch crops. Were beans important or favored enough to warrant the protracted stone-boiling in woven baskets and high fuel consumption necessary in pre-pottery times?

Carter (1945, p. 75) thought it likely that, if bean culture did begin in pre-pottery times, the use was probably as a green vegetable. It is worth while here to consider the possible uses of beans by prehistoric Indian groups.

The green pods of common beans have been used among native peoples of Indian America; in Mexico they are called *ejote*, a word of Nahuatl origin (Santamaria, 1942). Pod beans as used by ancient Americans, however, were certainly not like the string or snap bean of today. The earliest string beans of low fiber to be cultivated were reintroductions to America of European selections in the 19th century (Hedrick, 1931). No stringless bean is known to have been contributed by Indian agriculture.

The use of the immature fruits of the common bean is described by Waugh (1906) for the Iroquois of Canada, in which the boiled pods were chewed and the fibrous remains ejected. That this pattern of consumption, or one like it, might have been expected among the southwestern peoples is evident from the finds of masticated vegetable fiber masses in many archaeological sites of the region. Most of these so-called quids have been described as agave or mescal quids, but for the most part they have been reported by persons unfamiliar with the identification of fragmentary plant remains. However, remains of this type have been examined by Cutler (Martin *et al.*, 1952) for Tularosa Cave and by Kaplan (unpublished) for Cordova Cave, two Mogollon sites with pre-pottery remains, and in Tularosa Cave, with beans associated with the pre-pottery remains. Only one of the hundreds of fibrous wads proved to have been a bean pod. There is no reason

to believe that masticated indigestible fibers from bean pods would not have been expectorated on the cave floor as were the wads of agave, yucca, cactus stems, and certain unidentified fruits, probably asclepiads. The conclusion that bean pods in the early levels of these sites were not extensively used is inescapable. The possibility of removal of the "strings" before cooking, however, cannot be excluded. Shelling and cooking of immature seeds would not be more difficult than the preparation of the immature pods in a pre-pottery technology.

That peoples of Indian America relied upon beans rather than animal foods as a source of protein is well known. Linton (1940) discussed the role of a balanced diet in culture history and pointed out that in Indian America starch and protein crops (beans) have been used, in contrast to other parts of the world where starch crops and animal food, or other kinds of legumes, have provided the balance. D. B. Jones *et al.* (1938) indicated the complementary nature of bean and corn amino acids in providing dietary protein needs.

The adequacy of beans as a protein source depends ultimately upon their utilization and preparation. The protein value of immature beans as given by Chatfield and Adams (1940) is highest for (almost mature) green-shell lima beans, 7.5 per cent of the total weight, while in green snap beans there is less than 3 per cent protein. For several commercial North American mature dry-shell varieties tested, protein was 22 per cent of the total. In addition, the green products are quite low in fuel value while the mature seeds are high. When mature and dried, beans are at the most useful stage, for then they can be employed by an otherwise protein-poor economy and also can be relatively easily stored.

Soils.—Tolerance of a wide variety of soils, if they are well-drained, is characteristic of cultivated American beans in general. The species differ, however, in response to alkali, acid, and saline soils, and these different responses have probably influenced the distribution of beans in the Southwest. Acid soils are not encountered in the arable Southwestern lands, while alkaline soils are more common in poorly drained alluvial lands of the southern and southwestern parts of the region (U. S. Dept. Agr. Yearbook, 1938, p. 110). The irrigation practices of the ancient Hohokam may well have contributed to alkalinity in these soils. Hendry (1918) indicated the low tolerance of commercial *P. vulgaris* varieties to alkalinity and considered *P. acutifolius* varieties as moderately tolerant.

Saline soils (.02 per cent NaCl) affect bean growth (Wadleigh *et al.*, 1943) by increasing the severity of drought conditions. The superior drought resistance of tepary beans is well known, while common beans are severely affected by a relatively few days of wilting. The small-seeded limas or sieva beans are characteristically more resistant to aridity and high-temperatures than are the large-seeded limas (Mackie, 1943). That salinity has been a factor in Indian agriculture, at least in the area of the Hohokam, is attested to by the Pima practice of tasting the soil preparatory to planting (Heintzelman in Emory, 1859, p. 112). If salt were detected, the soil was considered unfit for agriculture. It is probable that salinity

below the threshold of detection by human taste is sufficient to influence plant growth by altering water relations under drought. Many of the sites selected as acceptable could have been salty enough to intensify the effect of arid conditions.

Irrigation.—Emory (1859), in his survey of the Mexican-U. S. boundary, noted that little agriculture could be engaged in without water supplied in addition to the seasonal precipitation. To meet the water requirements the Pima and Papago (Castetter and Bell, 1942) have employed irrigation systems, drawing water from the Gila River as did the earlier Hohokam peoples. Halseth (1936), by aerial survey, found about 125 miles of ancient irrigation canals in the Salt River Valley and other canals about half that extent in the Gila Valley. Some of the canals are more than ten miles long, and all ruins associated with them were Hohokam in culture. The very high temperatures and high evaporation rates characteristic of southern Arizona may be supposed to have encouraged the cultivation of teparies rather than other beans despite irrigation and flood-water farming.

Extensive irrigation by canals has not been shown to be characteristic of farming among the Basketmaker and Pueblo peoples to the north, and the author is unaware of any irrigation in use in prehistoric Mogollon cultures. Some irrigation is practiced by the Hopi of Moencopi according to Whiting (1950, p. 10), who implies that this was learned from the Mormons. The terraced gardens observed by the author at the Hopi village of Hotevilla were irrigated by hand, and Whiting indicates that this is the general practice among the Hopi. According to him, neither corn nor bush-type beans planted in the same or separate fields in sandy washes and alluvial soils by the Hopi and the Navajo are irrigated except by occasional flood water.

Effect of Daylength.—Carter (1945) has stated that the majority of native Southwest beans are bush types, and the observations of Whiting (1950) and others that field-grown beans are planted apart from corn would substantiate this. Allard and Zaumeyer (1944) have studied the photoperiodic responses of many strains of cultivated species of *Phaseolus* and found that the bush types of *P. vulgaris* are mostly day-neutral in their flowering and vegetative responses. Daylengths used in their study were comparable in range to those of the latitudes of the Southwest. The semi-determinate or semi-pole types studied by them exhibited more positive reactions to photoperiod than the bush types. The twining habit of the semi-pole varieties was emphasized by long days and accompanied by a delay in flowering, while shorter-day treatment was correlated with earliness and the determinate habit. Thus varieties which were determinate at lower latitudes might well have taken on vining characters when introduced to the Southwest. It is apparently precisely this factor which prevents the semi-pole California Pink and Pinto varieties from entering the northern part of the western range where the delay in flowering would mean injury because of early frosts.

While many of the pole types were shown by Allard and Zaumeyer (1944) to be short-day, they proved to be mostly day-neutral for flowering. This type

remained twining at all daylengths so that the varieties would be expected to be twining even under conditions of short days when the semi-pole would be determinate. The lima beans tested were all day-neutral while runner beans were long-day. Allard and Zaumeyer did not include tepary beans in their work.

Planting dates to take advantage of the limited precipitation and of flood waters, or to avoid frost periods, might have been adjusted without difficulties arising from new photoperiodic relations. The diffusion of some bean varieties within the Southwest may have been impeded by photoperiodic reactions, but there is strong evidence from experimental and field studies that this environmental factor does not restrict bean distribution within this area.

Vegetal Remains of the Prehistoric Southwest.—Much of the Southwest region is arid, and many of the ancient peoples lived in caves, shelters, or houses which have remained relatively dry. For this reason perishable materials have been better preserved than in more humid areas such as in the Mississippi Valley and other parts of the eastern United States. Even in less-protected Southwestern ruins fires often occurred at or soon after the time of abandonment, frequently charring and preserving vegetal materials.

Collections of prehistoric vegetal materials have been studied and reported upon by various authors. Some of these studies have only provided descriptions of the materials found at particular sites; others have related their descriptions to other collections and other aspects of Southwestern culture. Among the latter, Carter's (1945) studies have been most comprehensive for remains of cultivated plants. He theorized that the division between Hohokam and Anasazi corn and a change in corn types is a result of Mexican and later Eastern (United States) influences. Some question exists as to the extent of the Eastern influences in the corn of the prehistoric Southwest. The steady reduction of the percentage of maize cobs with high row-numbers reported by Cutler (Martin *et al.*, 1952) for the more recent periods (especially 200–400 A. D.) of Tularosa Cave appears to be a pattern for the entire Southwest. Nickerson has recently (1954) provided evidence on the basis of anatomical characters to show the similarity of maize from widely distributed Southwestern sites.

Beans recovered from archaeological sites have received the attention of botanists and students of human culture. Earlier studies were directed toward demonstrating their place of origin by their presence in undisputed pre-Columbian ruins. Jones (1952) has adequately discussed the historical phase of prehistoric beans. He has shown that a mixed collection of charred seeds, later described as both *Phaseolus vulgaris* and *P. acutifolius*, found in Canyon de los Muertos, Arizona, was used by Ludwig Wittmack in 1888 to demonstrate conclusively the American origin of the garden or common bean, *P. vulgaris*. More recently beans dating from prehistoric times have been described from sites in the Southwestern United States in relation to migrations and diffusion of culture traits and other aspects of culture history. Most of this discussion has been of a highly general nature, and little attempt to classify bean types on a subspecific level has been made.

It is hypothesized that the distribution of beans in the prehistoric Southwest will show a relationship to the cultural subdivisions which have been recognized by archaeological studies. The distribution patterns can be expected to reveal something of the antiquity and history of beans as cultivated plants in this region.

MATERIALS AND METHODS

SOURCES AND COLLECTION OF MATERIALS

The data presented in this paper were collected from materials studied at or obtained on loan from museums and universities where they had been deposited by archaeologists and ethnologists active in the field of Southwestern prehistory. A trip¹ to the Southwest during the summer of 1953 enabled the author to study materials in museums of that region; the institutions visited are given in Table VII. In the course of this field work, observations were made of Hopi and Navajo cultivated lands. Further observations during field work² in rural Mexico in 1953 and 1954 contributed to the author's understanding of comparative native American farming and food habits.

Modern archaeological excavations are carried out with careful regard for the position of artifacts recovered and their relation to dates of occupation and culture change. Vegetal materials obtained from excavations are to a greater or lesser degree artifacts and can sometimes be dated reliably with respect to their associations with other material for which dates have been established. Cutler (Martin *et al.*, 1952) has pointed out the value of large samples of plant materials, such as corn cobs, in describing a specific class of vegetal remains occurring in a particular time level of a prehistoric site. One advantage of a large sample is that it minimizes the influence of extraneous material which may have been brought in from other levels by rodents or by human disturbance such as burials in the fill. Beans, unlike corn, seldom have a waste or by-product which can accumulate in the debris of a cave or dwelling over a period of years. Threshing of dry beans, as has been described in historic times among Indians in the Southwest (Whiting, 1950; Castetter and Bell, 1942), is carried out in flat cleared areas well removed from habitation. The bean seeds arrive at the habitation ready for the pot or storage with nothing to be discarded except, perhaps, the culls. The practice of threshing beans in the field from the dry picked pods or from piles of the harvested whole plants is widespread in Indian America. It is reported from coastal Peru (Gillin, 1945) as well as from the southwestern United States, and for representative climatic regions of Mexico (Brand and Nunez, 1951; Foster, 1946; Kelly and Palerm, 1950), where it was observed by the author in 1954. A clue as to why pods are occasionally encountered in some abundance in prehistoric occupied sites is pro-

¹ Supported in part by a Wychwood Fellowship in the Department of Botany, University of Chicago.

² Supported in part by a Chicago Natural History Museum Fellowship in the Department of Botany, University of Chicago.

vided by Kelly and Palerm (1950) referring to the hand shelling of beans during rainy weather when the pods cannot be rendered fragile by drying. Also, small amounts of beans may be brought in and shelled by hand for daily use before the main harvest or threshing. These practices, if carried on in the shelter of the dwelling, could account for the large numbers of pods described by V. H. Jones (Steen and Jones, 1941) and materials recently excavated from caves in Tamaulipas, Mexico, by R. S. MacNeish.

The uncharred bean seeds, fortunately for the archaeologist and botanist, have escaped being eaten or have been left after being used in connection with burials or ceremonial practices. The beans of Tularosa Cave, for example, were dispersed throughout the debris and were probably seeds which had been dropped accidentally. Some of these seeds may have been moved from their original positions by rodent or human activity, as mentioned above, but the collection as a whole can be said to characterize the period of occupancy of the site. Notwithstanding the fact that there are sites (see Table VII) where time sequence of bean collections has been fixed with some certainty, the emphasis in this paper is on the larger time and cultural units and their relation to the regional history of agriculture. Thus the individual collections which we have before us obtain greater significance as they are considered with related collections in the Southwest. Dates or cultural affiliation for each collection are taken from published or otherwise indicated data based on standard methods and nomenclature used in Southwestern archaeology.

Samples obtained have been generally small, or at least of smaller numbers than desirable. Samples always suffer in some degree from subjectivity in treatment. The vegetal materials were collected by persons who, through lack of specialized training in the recognition of plant materials and working under trying field conditions, often may have failed to recognize and obtain all the material available. Of the various classes of prehistoric cultivated plant materials, corn cobs, because of their size and durability, are most easily recognized, while squash and bean seeds are less noticeable. This is particularly true with scattered charred materials: squash seeds become frustratingly fragile, and beans, losing their seed coats, occur as elusive, single cotyledons. Beans are most readily collected when observed in conjunction with larger artifacts, such as ceramic vessels or fragments of more immediate interest to the archaeologist or his hired diggers. Laborious screening of the fine debris which usually fills long-abandoned ruins is the most effective technique for the recovery of seeds. Flotation also is useful in the separation of charred materials from less buoyant debris.

CLASSIFICATION OF MATERIALS

As each collection was received it was first examined for state of preservation; that is, was it desiccated and in good condition, partially decayed, charred? Then all bean material was separated from contaminants. The state of preservation determined the number of characters which could be used for diagnosis, and accordingly a classification was made using as many as possible of the characters

discussed below. The divisions were made first on the basis of species and then into types of the species. The latter were the smallest divisions, and each putative type was treated as a population which was described in its entirety or from a random sample of its best-preserved units.

The term "type" is used here in a sense which is coordinate with "variety" as used in such publications on bean classification as "Garden Beans" (Irish, 1901), "American Varieties of Garden Beans" (Tracy, 1907) or "The Vegetables of New York: Beans" (Hedrick, 1931). "Variety" in these works, although not specifically defined, is taken to mean sexually propagated generations of plants which retain characteristics enabling the separation of one such continuum from another of the same species. Thus the characteristics used would be subspecific and, in a cultivated plant, are those which affect its usefulness or recognition. An example of the first kind of character might be precocity or disease resistance, and of the second, seed-coat pattern. Since only a relatively few of the cultivated beans are recorded to have been developed under recent cultivation, the term "horticultural variety" is not much used. In agricultural practice bean-seed characters, along with agronomic characteristics, are much used in classifying the varieties. The nature of the present study precludes the use of agronomic characteristics; seed characteristics are relied upon. This makes it uncertain, at best, to include the materials treated here with the named varieties used in the above-mentioned works or as listed in seed catalogues. For this reason the series of types described for Southwestern beans cannot have formal taxonomic standing but are presented as entities with which new materials may be compared.

Cardenas (unpublished thesis), Freytag (unpublished thesis), and others have presented certain correlations between seed and vegetative characters, but these are largely of a general nature not always useful in determining the nature of the parent plant if only the seed is available. Pending further studies which will enable more certainty in correlations of this sort, one can state similarities between the seed types and the named varieties.

Diagnostic Characters.—Because of their large size and frequently distinctive colors and markings, the seeds have been extensively used in the classification of bean species and varieties. Hedrick (1931) and Bukasov (1930) have dealt sufficiently with the synonymy and history of bean classification.

Diagnostic characters of bean seeds have been studied individually from the standpoints of their genetics, physiology, and anatomy. The genetics of seed-coat coloration and variegation has been shown by Lamprecht (1939b), Smith (1939), and others to be quite complex. Smith found that six color genes plus modifiers were responsible for the red testa color of the common bean variety Red Kidney and that in other varieties no linkage was found among ground color, variegation color, and extent of eye color. Glossiness of seed coat was reported by Prakken (1937) as appearing to be genetically independent of factors for color and variegation of seed coat and pod and vegetative characters in crosses of *P. vulgaris*

varieties. However, as far as I am aware, no one has studied the dull testas of *P. acutifolius* seeds which is a diagnostic character of that species.

Shaw and Norton, according to Kooiman (1931), distinguished two classes of color in bean-seed coats, a red-and-purple, and a yellow-black. The pigments of the second were only slightly soluble in alcohol and alkali.

Use of the character of color quality introduces the problem of dealing with color change over time. Hedrick (1931) recognized this problem and chose to describe seed-coat color as it appeared in the first year subsequent to harvest. It is common to find dark brown specimens in old collections labeled "yellow beans," or to find familiar varieties of quite a different (dark) color than the fresh seed of the same variety. Skalinska (cited by Kooiman, 1931) showed that yellow and yellowish pigments oxidize to brown *in vitro*.

It is possible to divide color change into two physiological periods, that of ripening and during dry dormancy. Very young seeds are green and may remain so or may be tinged with green through maturity, as in French horticultural and certain greenish-white tepary beans. Loss of the chlorophyll may be accompanied by whiteness or lack of color which may persist or be quickly replaced by light tints of what would probably be the color at maturity. Coloring is first noticeable in the eye ring and then appears in the other parts of the testa, but darkening earlier with proximity to the placenta. Where there is patterning, it occurs as a sort of "developing out" process, reminding one of the development of a latent image on photographic paper. Streaks, spots, or other forms of variegation appear as islands of coloration on a light ground which itself may become colored subsequently. The color change which occurs during this period is largely quantitative, as indicated previously, but may proceed to a point where it appears to be qualitative. In the tropical black *P. vulgaris* the young rose-colored testa changes by the time of maturity to a purple so deep as to give the effect of black.

Subsequent to ripening, the rate of color change in the dry bean is slower but may be accelerated under certain conditions. The darkening of the light pink ground color of the seed coats of "Mexican pinto" (Type C13) beans has been observed to occur at a differential rate when the seeds were exposed to strong sunlight for several months. The sides of the seeds exposed to sunlight were much darker than the sides not so exposed. Samples of seeds which had been stored at room temperature for fifty to sixty-five years failed to show any color change when maintained at a temperature of 60° C. for thirty days, suggesting that limits of normal change had been reached at some time during this period.

It is sometimes difficult to distinguish what the color of the seed coat might be were it not for opacity. Thus, among black beans it is difficult to determine the nature of the blackness. The Hopi "Blue Dye" beans (Type C29), for example, are very dark blue while other "blacks" may be dark purples. In this study the use of color in the classification of seed types has been made with a realization of the changes in color which have undoubtedly occurred; nevertheless, all designations are based upon color quality at the time of examination. The larger color

TABLE II

DISTRIBUTION OF COMMON BEANS ON THE BASIS OF SEED-COAT COLOR PATTERNS

	Indian Southwest				Mexico*	Peru*	U. S. Commercial**
	All periods	Prehist. only	Contemp. only	Prehist. and Contemp.			
Self							
Number of types	19	6	7	6	162	43	117
Per cent	65	55	70	65	67	56	50
Variegated							
Number of types	11	5	3	3	84	34	118
Per cent	37	45	30	35	33	44	50

* Ditmer, *et al.* (1937).

** Hedrick (1931).

categories have been used rather than an exact description which would be subjective and not too meaningful.

Seed size in beans has been estimated (Kooiman, 1931) to be the result of the action of many genes which apparently affect the various dimensions equally. Thus within a population of seeds which have been selected for uniformity, the ratios between the dimensions of the larger seeds and those of the smaller seeds may be expected to vary little, providing all have reached normal maturity at the time of harvest and were grown under similar conditions. Within a given pod the largest seeds usually occupy a medial position and the smaller seeds are at either extremity. It would be well, then, to obtain seed samples for measurement from the entire contents of fully matured pods. Seed measurements, considered as reflections of the size and shape of seeds, represent the most useful set of criteria for the quantification of variation in these organs. But it should be recognized that seed dimensions may be differently affected by environmental conditions. Bean growers in humid eastern lands who plant disease-free seed from western arid lands note that the beans that they harvest are shorter and less flat than those which they planted (Hardenburg, 1942).

Prominence of the radicle and plumule located on the ventral (adaxial) margin of the seed, just anterior to the hilum, lends an apiculate appearance which is more frequent in some varieties than others. The extremes or ends of the seed are rounded in the lateral view, or one or both extremes of the seed may be truncate or appear to be flattened. If only one end is truncate, it is the posterior end and the apiculation may still be seen at the other extreme. In the pod, seeds are borne on the placenta along the ventral surface, with the growing parts of the embryo toward the apex. The scar, formed by abscission of the placenta and seed, is oriented longitudinally on the ventral margin of the seed, with the micropyle at

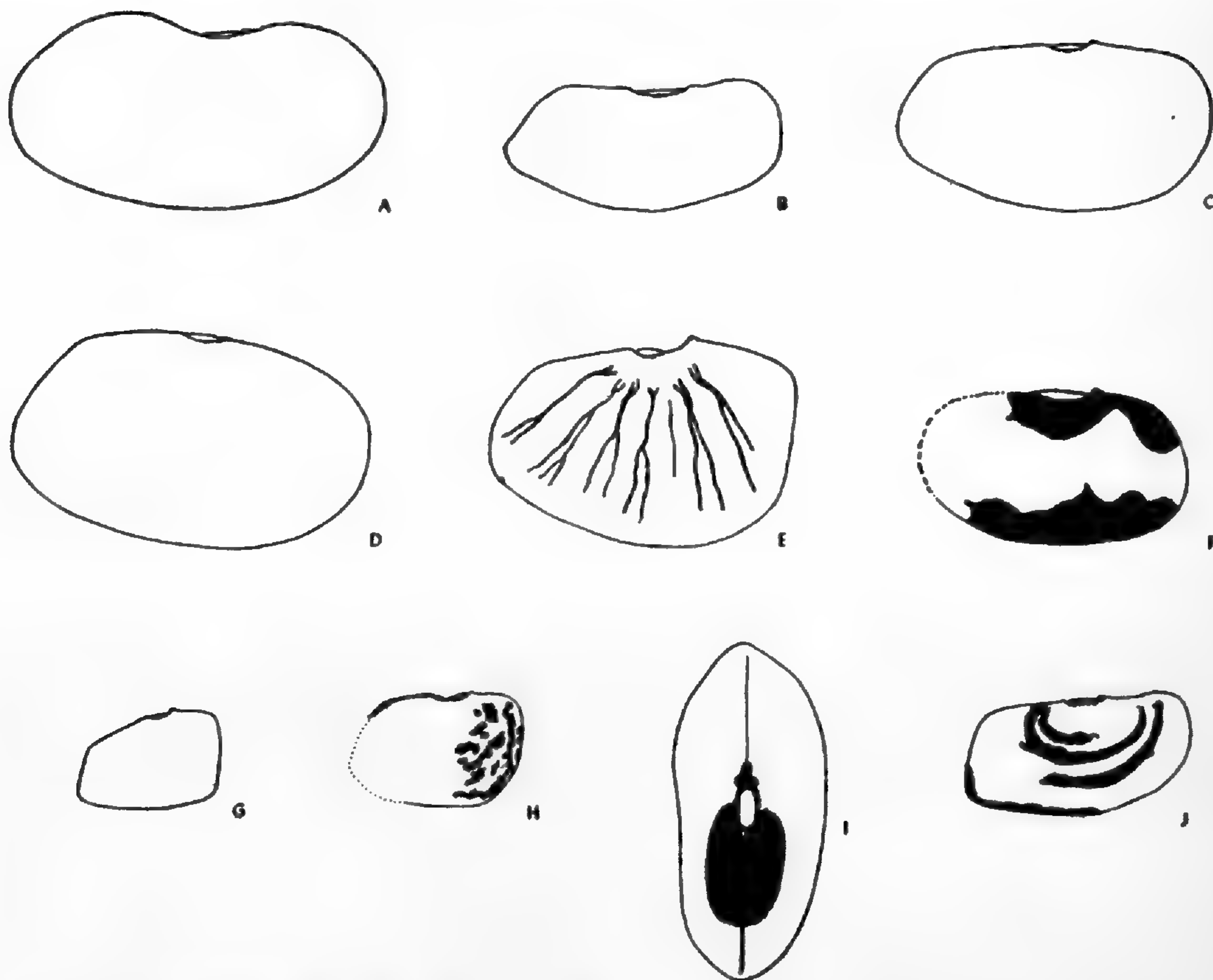


Fig. 1. Morphological characters of seeds: A, reniform; B, apiculate anterior end; C, rounded ends; D, entire; E, testa venation radiating from hilum of lima bean; F, mottled; G, truncate ends; H, flecked pattern; I, eyed; J, longitudinally striped.

the anterior end closest to the growing parts, and the paired elevated peaks of the testa, the caruncle, at the posterior end. It has been suggested that truncate seeds in *Phaseolus* are the results of: (a) interference by intralocular parenchyma tissue; (b) abutment of the seeds themselves. The first explanation assumes that mechanical pressure of the parenchyma is sufficient to limit the growth of a maturing seed and that it exerts its influence in some varieties but not others. In the second, truncate seeds are characteristic of some of the tepary beans the seeds of which are not at all appressed in the pod.

Technique.—All measurements of seed dimensions were taken with a vernier caliper and are given in the metric system. Each dimension was measured to give the maximum result so as to standardize the method and make repetition easier. In the actual measuring of length, for example, the apical anterior end was placed against the stationary jaw of the caliper and the sliding jaw closed until the posterior end was contacted. The jaws were then tightened to the extent that, when rotated on the apical end of the seed, the basal end would just slip by, neither sticking nor passing freely the surface of the movable jaw. An adequate degree of precision is obtained in this manner. Each seed was measured in its length from anterior to posterior extreme, in width from ventral to dorsal margin, and in thickness from one lateral surface to the other.

TABLE III
EXTERNAL SEED CHARACTERS OF FOUR SPECIES OF *PHASEOLUS*
WITH PARTICULAR REFERENCE TO SOUTHWESTERN VARIETIES

	<i>P. vulgaris</i>	<i>P. acutifolius</i>	<i>P. lunatus</i>	<i>P. coccineus</i>
Dimensions (cm.)				
Length	1.85-.74	1.20-.66	1.80-1.14	2.39-1.46
Width	1.08-.49	.78-.44	1.29-.85	1.48-1.13
Thickness	.85-.34	.56-.27	.60-.35	1.21-.72
Form	Various but seldom cuboid	Semi-spherical or flat, often cuboid with sharply truncate ends	Reniform, especially in larger-seeded groups; flat, smaller-seeded forms with posterior end broad and truncate, anterior end attenuate in dorso-ventral plane	Various, usually semi-round in cross-section, ends round
Seed coat Venation	Reticulate or not apparent	Not apparent	Parallel and branching radially from hilum	Not apparent
Glossiness after polishing	Very glossy to moderately dull	Dull	Glossy to dull	Highly glossy
Hilum				
Caruncle*	Two prominences separate	Same as <i>P. vulgaris</i>	Prominences joined anteriorly	Same as <i>P. vulgaris</i>
Ring**	Elevated	Little elevated	Elevated	Elevated
Size	Roughly proportional to seed size	Not proportional to seed size, remains small in large-seeded types	Same as <i>P. vulgaris</i>	Same as <i>P. vulgaris</i>

* See fig. 2.

** Margin of testa encircling hilum.

In many cases among the archaeological collections it was possible, owing to the fragmentary or charred nature of the material, to measure only a few of the seeds in a collection.

It is possible to obtain a surface impression of the bean seed using any one of several acetone or ethyl acetate soluble plastics or Duco cement. Microscopic examination of a number of such impressions from seed coats of varieties of the four species dealt with here failed to show consistent differences which could be used in the classification of seeds.

DESCRIPTION OF BEAN TYPES

The use of scatter diagrams was adopted for graphic presentation of the data, as this method (Anderson, 1949, pp. 81–101) facilitates the comparison of several classes of data simultaneously. The source and size of each collection and its measurements are given in Table VII, as well as the number with reference to the typing system discussed previously. In Table IV the qualitative data—color, variegation, and form—are listed for each type. Table V includes the maximal, minimal, and median dimensions for each and the numbers of all collections represented by each type. Tables IV and V, along with figs. 1 and 2, provide all the characteristics of each type. A summation of species characteristics for Southwestern beans is found in Table III.

Association of Seed Characters.—The scatter diagrams (figs. 3–13) show that in the collections studied greater size in either seed length or width is associated with larger size in the other dimension. The degree of seed thickness has a less regular association with either of the other two dimensions than they have with one another. It may also be noted that variegated seed-coat patterns in the common bean also tend to accompany large seeds.

Seeds of the two principal species of *Phaseolus* dealt with here, *Phaseolus vulgaris* and *Phaseolus acutifolius* var. *latifolius*, form a discontinuous distribution readily seen in the scatter diagrams. Although this discontinuity is a reflection of seed dimensions, except for the patternless, or phenotypically patternless, white seeds common to both species, the color patterns are discontinuous also. It is the symbols mainly of the small white (Type C 6) seeds of *P. vulgaris* which cluster below the dimensional modes of this species and are found within the range of *P. acutifolius*, in the lower left-hand portion of the diagrams.

In addition to the small white type, the two curious small red (Type C20) and small flecked red (Type C12) *P. vulgaris* types overlap the teparies in size range. These were classed with *Phaseolus vulgaris* with some misgivings. However, should further study prove them to be variants of *P. acutifolius* rather than *P. vulgaris*, two interesting aspects will remain. First, the Murder House (Collection Number 195d) beans are from an area of tepary importance and common beans as well as lima occurrence; the other (Collection Number 206) are from the "Northern Periphery," an area of which the cultural and agricultural affinities are not yet well defined. Second, the seed characters show similarities to those of both

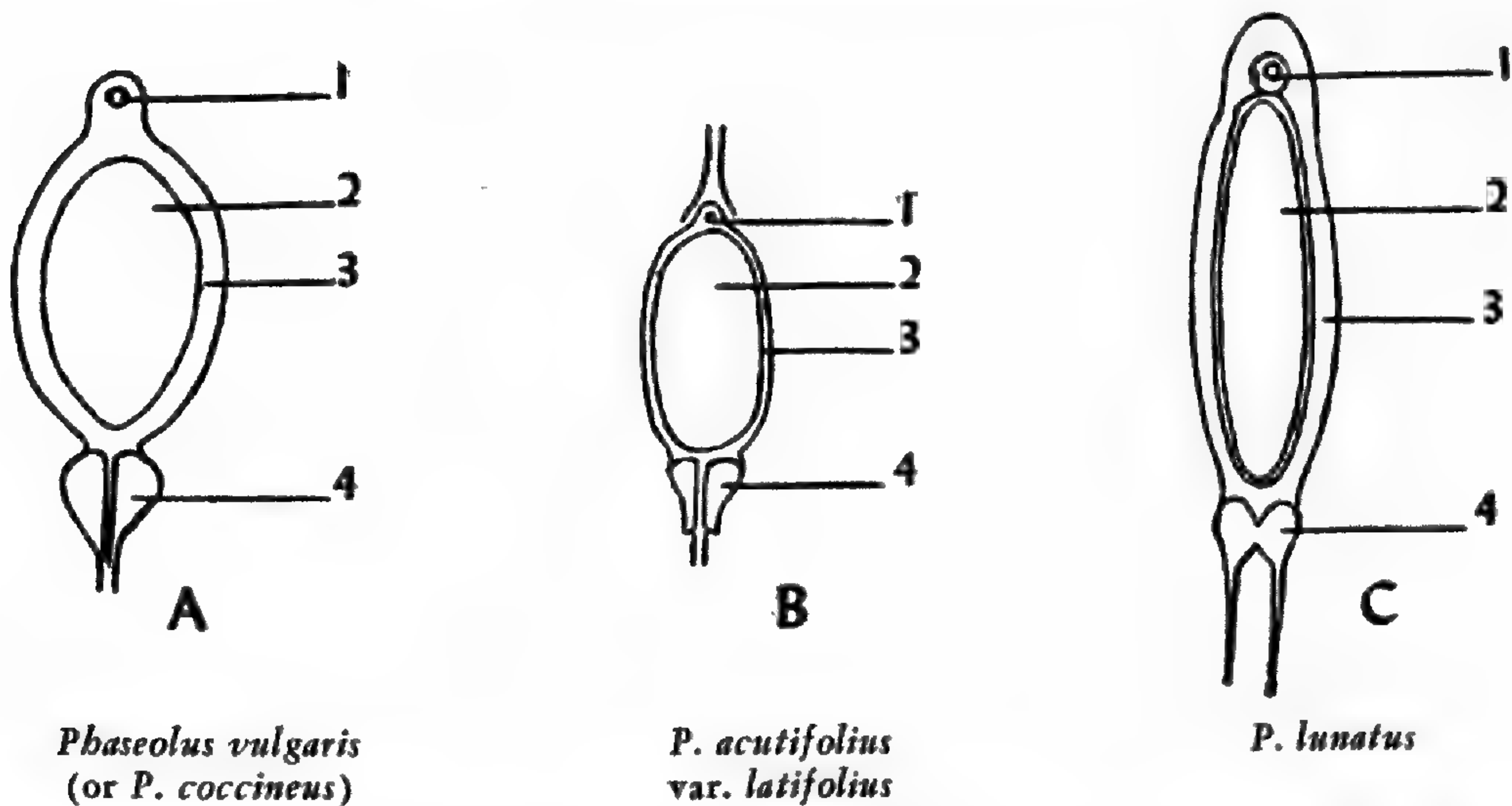


Fig. 2. Variation in hilum form: 1, micropyle; 2, placental scar; 3, hilum ring; 4, caruncle. Note incomplete separation of caruncle ridges in *P. lunatus*.

species to a greater extent than is usual. It is true that among white-seeded varieties it may be quite difficult to distinguish between *P. vulgaris* and *P. acutifolius* seeds, but this is not the case with the darker-colored and patterned seeds. It would be most interesting if viable seed of these types could be obtained and sown, to examine the vegetative characters of the plant.

The Earliest Bean Remains.—The earliest well-dated beans reported from Southwestern sites are those of the Mogollon in the pre-pottery or prior to 1 A. D. occupation level of Tularosa Cave (Martin *et al.*, 1952). This singular discovery offers sharp contrast to pre-pottery cultures of the Anasazi and Hohokam. In the Anasazi and Hohokam areas beans have not been found in cultures reliably dated as prior to Basketmaker III (ca. 500 A. D.) and from early Hohokam sites. In Tsegi Canyon in Northern Arizona, a prepottery Basketmaker site (Kidder and Guernsey, 1919), investigators failed to find beans, but they reported corn and other vegetal remains which evidence good preservation of artifacts of this sort. Beans, as well as squash and corn, were found in Tsegi Canyon sites subsequent to the introduction of pottery. Jones and Fonner reported fully on the vegetal remains of a number of Basketmaker II sites near Durango, Colorado (Morris, 1954), but they did not describe any beans. Gladwin's (1937) excavations at Snaketown, a Hohokam ruin now the site of a Pima Indian settlement, uncovered carbonized corn in houses dated at about 500 A. D. at the earliest. The only beans from this site were charred tepary and common beans dated at about 1000 A. D., which would correspond to Pueblo II in the Anasazi. The identification of these remains was made by Volney Jones (Castetter and Bell, 1942).

As has been indicated previously, in the quest for bean remains we are looking primarily for the very materials which the prehistoric Indians would have least wanted to leave behind. In times of food scarcity, single beans dropped on the floor of the dwelling may have been carefully retrieved. The most that can be said then of the occurrence of beans in the early periods is that, if present, they were not plentiful.

TABLE IV
MORPHOLOGY OF TYPES

Type	Color pattern	Ground color	Gloss**	Eye ring	Anterior end	Posterior end	Three-dimensional shape	Varietal similarity
*C1	Self	Orange-red to dark orange-red	+++	Dark	Truncate	Truncate	Cylindrical, entire	
C2	Self	White	++	Indistinct	Round	Round	Subreniform, semi-round	
C3	Self	Dark red-brown	++	Indistinct	Subapiculate to round	Round	Reniform, flat	Large Red Kidney
C5	Faint mottle	Dark red-brown	++	Dark	Apiculate	Round	Entire	
C6	Self	White	++	Indistinct	Subapiculate	Round	Entire	
C7	Self	Cream to yellow	+++	Indistinct	Subapiculate	Round	Entire, flat	
C8	Self	Dark red	++	Indistinct	Subapiculate	Round	Entire, flat	
C9	Self	White	++	Indistinct	Subapiculate	Round	Entire, semi-round	
C10	Self	Dark red-brown	++	Indistinct	Subapiculate	Round	Subreniform, cylindrical	

* C refers to common bean (*Phaseolus vulgaris*) types.

** +++ Highly glossy seed coat.

++ Moderately glossy seed coat.

+ Dull seed coat.

C11	Faint longitudinal stripe	Pale violet to violet-brown	++	Dark	Subapiculate	Round	Entire, semi-round	
C11a	Distinct longitudinal stripe	Brown-violet	++	Dark	Subapiculate	Round	Entire, semi-round	
C12	Fleck	Dark red-brown	++	Dark	Round, tapered	Round to flattened	Entire, semi-round	
C13	Brown fleck and stripe	Pink	++	Dark	Subapiculate to apiculate	Round	Reniform, flat	<i>Garrapata</i> or Pinto
C14	Red or tan mottle	White to cream	++	Indistinct	Round	Round	Entire, semi-round	Jacob's cattle bean; Vaquita
C14a	Red or tan mottle	White to cream	++	Indistinct	Round to apiculate	Round	Reniform, flat	
C15	Self	Dark red	++	Dark	Subapiculate to apiculate	Round	Entire, flat	Red Mexican
C16	Red-brown eye	White	++	Indistinct	Round	Round	Entire, semi-round	China Red Eye; Golden Wax
C17	Self	Yellow-brown	+++	Dark	Subapiculate	Round	Subreniform to reniform	<i>Vayo (Bayo)</i>
C18	Self	Violet-brown	+++	Indistinct	Round			
C19	Self or dark fleck	Dark red	++	Indistinct	Round	Round	Subreniform	
C19a	Dark fleck	Dark red-brown	++	Indistinct	Round to truncate	Round to truncate	Reniform	
C20	Self	Red-brown	++	Dark	Round	Round	Entire, semi-cylindrical	

TABLE IV (Continued)

Type	Color pattern	Ground color	Gloss**	Eye ring	Anterior end	Posterior end	Three-dimensional shape	Varietal similarity
C21	Self	Dark red	+++	Indistinct	Round	Round	Entire, semi-round	<i>Bolitas</i>
C22	Self	Yellow, brown, brown-red	+++	Dark	Round	Round	Entire, semi-round	
C23	Self	Brown	+++	Dark	Round	Round	Entire, semi-round	
C24	Brown eye-pattern superimposed on stripes	White	+++	Indistinct	Subapiculate	Round	Entire, semi-round	Dwarf Golden Wax
C25	Violet stripes	Pale violet	+++	Indistinct	Subapiculate	Round	Entire, semi-round	
C26	Dark red stripe	Red	++	Indistinct	Round	Round	Entire, flat	
C27	Self	White	+++	Indistinct	Round	Round	Entire, semi-cylindrical	
C28	Self	Pink	+++	Dark	Subapiculate	Round	Entire, flat	
C29	Self	Black (dark blue)	++	Indistinct	Round	Round to flat	Entire, flat	
C30	Self	Black	+++	Indistinct	Apiculate	Round to truncate	Entire, cylindrical	
*L1	Self	Dark purple	++	Indistinct	Round to subapiculate	Truncate	Entire	
L2	Self	White	++	Indistinct	Round	Round	Entire	

*L refers to lima bean (*Phaseolus lunatus*) types.

L3	Dark fleck	Brown	++	Indistinct	Subapiculate to round	Round	Entire	
L4	Dark fleck and stripe	Dark red	++	Indistinct	Round	Round	Entire	Jackson's Wonder
L5	Light tan eye pattern suffused	Dark brown	++	Indistinct	Subapiculate to round	Truncate	Entire	
*T1	Self	Red-brown	+	Indistinct	Subapiculate	Round	Entire, semi-round	
T2	Black fleck	Tan	+	Black	Round	Truncate	Entire, flat	
T3	Self	White	+	Indistinct	Round	Round	Semi-round	
T4	Self or brown fleck	Orange-brown	+	Indistinct	Truncate	Truncate to round	Entire, flat	
T5	Self	Brown	+	Dark	Truncate	Truncate	Entire	
T6	Self	White	+	Indistinct	Round	Round	Entire, semi-round	
T7	Black flecks almost completely cover ground	Tan	+	Indistinct	Truncate	Truncate	Entire, flat, cuboid	
T8	Dark fleck	Red-brown	+	Indistinct		Round	Semi-round	
*R1	Self	White	+++	Indistinct	Round	Round	Semi-round	
R2	Purple mottle and fleck	White, violet	+++	Indistinct	Round	Round	Semi-round	

*T refers to tepary bean (*Phaseolus acutifolius*) types.

*R refers to runner bean (*Phaseolus coccineus*) types.

The Mogollon furnishes a situation which may help to explain both the spotty occurrence of early beans in other areas and the clear regional differentiation of varieties in later times. The peoples of Cordova and Tularosa Caves (Martin *et al.*, 1952) were contemporaries living in the Reserve, New Mexico, region. They shared many basic cultural traits, but the people of the Cordova Cave site relied more upon hunting than did those of Tularosa Cave. Bean remains were relatively abundant in the latter site, but only a single bean and one pod fragment were found in Cordova Cave, and vegetal materials from other pre-1200 Mogollon sites indicate non-importance of bean cultivation. If the same kind of distribution—few bean-growing and many non-bean growing communities contemporaneous in the same region—occurred in the Basketmaker Anasazi region, it may be said that early Basketmaker beans have not yet been found but that they do exist. With greater attention on the part of persons trained to recognize and identify charred seeds and other remains, more Basketmaker beans and those of other pre-pottery peoples might be recovered.

Varietal Change.—On the basis of seed characters the earliest beans of Tularosa Cave do not differ in any way which could be interpreted as part of an evolutionary sequence from the most recent beans of Tularosa Cave, despite the difference of over 1,000 years. This is generally true of Southwestern bean remains. Changes in cultivated prehistoric beans of the Southwest which are correlated with time changes are those which show the introduction of new species or varieties from an older to a newer region or culture. The question of evolutionary change in beans under domestication may be reopened with the anatomical study of bean-pod remains. However, it can be said that the apparent lack of change of beans under domestication in the Southwest is further indication that development from the wild kinds occurred elsewhere or outside of the Southwest, and at an earlier date.

Bean Preparation.—Among the beans collected from contemporary Indian peoples there is in the Museum of Anthropology of the University of California at Berkeley a sample (Collection No. 117a) of parched beans labeled “parched small white *P. vulgaris*” obtained from Yuma Indians.³ A collection of more than one quart of common beans from Kiet Siel, a Pueblo III ruin in Tsegi Canyon, northern Arizona, was examined at the Museum of Northern Arizona and found to have been lightly toasted. This sample, as well as the preceding one, emits a characteristic odor; seeds which obviously were originally white are tanned irregularly, and cotyledons of the white seeds which have the most tanned testas are browner than those of less tanned lighter seeds. Seeds of this collection are described in Table VII Nos. 188, 189, 190, 191, 192, 193, 194a, 194b.

³ These, however, are teparies (Type T 3) rather than common beans.

TABLE V. DIMENSIONS OF SEED TYPES

Type	Range of Measurements (cm.)						Median of Measurements		
	Maximum			Minimum					
	Length	Width	Thickness	Length	Width	Thickness	Length	Width	Thickness
C1	1.69	.94	.67	1.05	.61	.48	1.30	.71	.57
C2	1.49	.87	.66	1.10	.64	.44	1.25	.73	.55
C3	1.67	.92	.66	1.07	.68	.42	1.43	.80	.57
C5	1.63	.95	.70	1.13	.76	.47	1.35	.85	.57
C6	1.28	.75	.55	.79	.50	.37	.99	.60	.48
C7	1.35	.90	.68	1.15	.73	.50	1.29	.87	.51
C8	1.61	1.03	.56	1.43	.91	.49	1.49	.99	.54
C9	1.50	.91	.68	1.05	.66	.36	1.34	.83	.57
C10	1.69	.80	.70	1.61	.79	.65	2 seeds sep. coll.	2 seeds sep. coll.	2 seeds sep. coll.
C11	1.73	.97	.73	1.20	.66	.45	1.42	.81	.61
C11a	1.16	.78	.60	1.09	.71	.44	2 seeds sep. coll.	2 seeds sep. coll.	2 seeds sep. coll.
C12	.89	.63	.50	.74	.52	.34	.84	.62	.48
C13	1.71	.89	.68	1.08	.67	.41	1.26	.78	.54
C14	1.76	.95	.68	1.04	.65	.39	1.32	.81	.56
C14a	1.26	.92	.74	1.03	.66	.55	1.16	.78	.64
C15	1.38	.84	.59	1.07	.65	.42	1.08	.65	.43
C16	1.22	.70	.59	1.00	.68	.57	2 seeds	2 seeds	2 seeds
C17	1.65	.92	.64	1.11	.64	.43	1.41	.81	.56
C18	1.70	.87	.67	1.36	.68	.47	1.46	.76	.54
C19	1.65	.90	.59	1.33	.70	.44	1.50	.72	.51
C19a	1.85	.94	.67	1.39	.63	.49	1.58	.85	.58
C20	.94	.62	.45	.87	.56	.40	.93	.59	.43
C21	1.22	.86	.76	1.19	.80	.62	1.20	.82	.69
C22	1.38	.83	.66	1.03	.63	.46	1.22	.74	.55
C23	1.38	.78	.57	.95	.60	.42	1.08	.68	.47
C24	1.51	1.08	.85	1.26	.75	.63	1.44	.93	.73
C25	1 seed						1.14	.86	.68
C26	1.54	.84	.63	1.28	.74	.41	1.38	.80	.48
C27	.86	.58	.42	.77	.49	.36	.79	.53	.39
C28	1.41	.86	.78	1.00	.66	.43	1.18	.74	.50
C29	1.54	.87	.60	1.10	.70	.41	1.26	.76	.52
C30	1.34	.62	.69	1.34	.60	.58	2 seeds	2 seeds	2 seeds
L1	1.64	1.16	.60	1.29	.90	.40	1.47	1.03	.53
L2	1.58	1.11	.58	1.18	.85	.41	1.37	.93	.52
L3	1.80	1.20	.62	1.37	.95	.42	1.58	1.08	.55
L4	1.76	1.29	.55	1.51	1.05	.49	1.62	1.14	.52
L5	1.48	1.04	.49	1.14	.91	.35	1.37	.91	.44
T1	1 seed						.67	.52	.37
T2	1 seed						.70	.54	.27
T3	1.19	.70	.50	.87	.57	.37	1.00	.65	.43
T4	1.20	.78	.45	.81	.50	.31	1.03	.67	.41
T5	1.05	.69	.47	.66	.44	.28	.89	.60	.39
T6	.98	.69	.56	.73	.46	.30	.84	.55	.41
T7	1.11	.76	.49	.85	.61	.35	1.02	.68	.42
T8	1 seed						.82	.55	.36
R1	2.15	1.48	1.20	1.46	1.20	.94	1.90	1.28	1.13
R2	2.39	1.47	1.21	1.71	1.13	.72	1.99	1.32	.98

West (1947) reports an interesting practice of certain Tarascan Indians which may be related to this problem. A variety of *P. coccineus*, grown only by the more conservative people and tended mainly by the women in their house gardens, is used in special dishes, among which is a *pinole* made with a special "black maize." The corn is said to be toasted, but the preparation of the beans prior to grinding is not indicated. This practice was not found among non-Indian (Ladinoized) residents of the area.

Whiting (1950) reported that the Hopi parch white and mottled teparies before cooking. This treatment of the white tepary (or in its absence, "other white beans") is noted in connection with the breaking of a ritual fast by priests.

Although the material from Kiet Siel, which, according to tree-rings dates back to as early as 1106 A. D. and as late as 1221 A. D. (McGregor, 1934), contains the oldest sample of parched beans yet seen, parching may be supposed to have been practiced earlier and may well have formed the basis of dry-bean use for protein in pre-pottery times.

Parching of dry mature beans for use in such foods as *pinole* may have once been important and widespread, but now parching has been all but superseded by boiling. Ritual food preparations, such as those referred to above, may be the most likely conditions under which an ancient manner of food use might be retained although reinterpreted.

DISTRIBUTION OF BEAN TYPES

Tepary Beans.—The greater importance of tepary bean cultivation in the most arid region of the Southwest, that of the Pima and Papago (Hohokam), has been shown among the contemporary Indians by Freeman (1912), and Castetter and Bell (1942). Fewer tepary varieties than the forty described by Freeman were encountered in the collections available for this study. However, collections from the Pima and Papago and the Colorado River tribes (Table VII and figs 3–13) substantiate the extensive use of teparies by these tribes in recent historic times.

Efforts by the author to obtain teparies in 1953 and 1954 on the Pima and Papago Reservation at Sells and Ajo, Arizona, and from trading posts on the Cocopa Reservation were unsuccessful. Local residents said that droughts of recent years and availability of the popular pink beans (Type C26) may explain the general decline of old bean varieties among the Indians.

As the agronomic, botanic, and ethnologic writings on the tepary invariably refer to the drought and heat resistance of this species, some of the problems relating to the history of its domestication should be discussed.

Freeman (1912) first reported the superiority of yield of teparies over common bean varieties under dry-land and irrigated conditions in Arizona. Good yields under dry-land conditions have been obtained as far north as Colorado, where the Redfield tepary out-yielded the high-producing Pinto common bean (Brandon, 1943). The paucity of prehistoric tepary bean remains outside of the southern

Arizona-New Mexico region is not to be explained by any unsuitability of varieties of this species to the northern, Anasazi, region.

If the tepary bean is a domesticate of the Hohokam or other peoples of the Sonoran Desert region, then its involvement with the history of these people may help to account for its importance among them, while the restricted occurrence in the Anasazi and Mogollon may be attributed to partial unacceptability of teparies to peoples long accustomed to common beans. If, on the other hand, tepary beans were domesticated far in the south of Mexico, they must have found acceptance among many peoples who were familiar with common beans, and probably lima and runner beans as well, before reaching the Southwest. Although early Hohokam archaeological sites are not good ones for the preservation of vegetal materials, distribution patterns of teparies (Table VI) suggest their late introduction and diffusion in the Southwest.

The question of origin of the tepary bean will be solved neither by De Candolle's criterion of the location of related forms in the wild state nor by Vavilov's "center of varietal diversity" hypothesis nor will studies of archaeological materials supply all the needed information to elucidate the role of the tepary bean in Southwestern prehistory. It is necessary to know the source of variability and the history of domestication of this plant.

Freeman (1912) supposed that the tepary bean was domesticated from very small, angular-seeded, broad-leafed indigenous forms (*P. acutifolius* var. *latifolius*) growing in the watered canyons of the Sonoran Desert and that selections from these types yielded the many varieties which he recognized among contemporary cultigens. Freeman made no estimate of the time period necessary for the great increase in seed size and change in form from the wild to the domesticated forms nor were the mechanics of the change indicated. Carter (1945) accepted Freeman's hypothesis, and used the element of time as an argument for greater antiquity of man in the Southwest. Castetter and Bell (1942) rejected Freeman's conclusion on the basis of the great difference in size and form between the cultivated and the non-cultivated *P. acutifolius* var. *latifolius*, and on the fact that the earliest prehistoric beans which they had seen in no way resemble any of the non-cultivated beans but can be equated with modern cultivated varieties. The latter view concerning the identity of the prehistoric and modern materials is supported by data presented in this paper (Table VII). It would be strange indeed if beans of the already-high agricultural cultures which supply the earliest material of this sort were to be of a primitive type. Cultivation under irrigation of the small, angular-seeded wild teparies (Castetter and Bell, 1942) did not change the seed characters.

Selection and cultivation without accompanying or preceding changes in the germ-plasm could hardly account for the differences between Southwestern cultivated and indigenous teparies. A source of change might be mutation, but seed size is not a single-gene character; rather it appears, as indicated previously, to be the result of interaction among several genes directly, while many other characters are involved indirectly. The rates of mutation at these loci are not known, but extremely careful selection and breeding, as well as a very long time, would

TABLE VI. OCCURRENCE OF TYPES

Type	Prehistoric					Contemporary					
	Mogollon	San Juan Anasazi Mesa Verde	Northern Arizona Anasazi	Verde Valley Hohokam-Anasazi	Northern Periphery	Rio Grande Pueblos	Hopi	Zuni	Navajo	Arizona Piman	Colorado River Yuman
*C1	X	X	X	X		X	X				
C2	X		X	X			X				
C3	X			X			X	X			
C4	X			X	X						
C5	X			X				X			
C6	X								X		X
C7	X										
C8	X										
C9	X						X		X		
C10	X										
C11		X	X	X	X		X	X			X
C11a			X	X	X						
C12				X	X	X					
C13				X		X	X		X	X	
C14			X	X		X	X	X	X		
C14a			X	X		X	X				
C15	X			X	X	X					
C16	X			X		X					
C17				X		X	X				
C18				X		X	X	X		X	X
C19	X		X								
C19a			X		X						
C20				X							
C21				X							
C22				X		X					
C23						X			X		
C24								X			
C25											
C26						X	X				
C27							X				X
C28							X			X	
C29							X				
C30							X				
*L1				X			X				
L2							X				
L3							X				X
L4							X				
L5							X				
L6							X				
*T1				X							
T2						X					
T3						X					
T4						X		X			
T5						X					
T6				X					X		X
T7				X					X		X
T8				X					X		X
*R1							X				
R2							X				

* C refers to common bean (*Phaseolus vulgaris*) types; L, to lima bean (*Phaseolus lunatus*) types; T, to tepary bean (*Phaseolus acutifolius*) types; R, to runner bean (*Phaseolus coccineus*) types.

probably be necessary for the effect of any such mutations to be expressed phenotypically. A more likely source of variability in tepary beans is hybridization with some other related species. This process is certainly suggested by Freytag's demonstration (unpublished thesis) of the effect of introgressive hybridization in common beans.

Unfortunately, very little genetic or even breeding work has been done on teparies, and no interspecific crosses have been reported. Teparies in the Southwest, and probably common and lima beans as well under arid conditions, are almost entirely self-fertilizing owing to very early pollination in the unopened flower bud. A thorough study of cultivated and non-cultivated *P. acutifolius* and *P. acutifolius* var. *latifolius* and suspected hybridizing species is necessary to indicate what the source or sources of variability in this species might be. Also of importance would be the determination of the geography and ecology of hybridization in this species.

Southwestern and Other Bean Assemblages Compared.—The grouping of bean types presented in Table II suggested that large geographic areas have characteristic bean assemblages. At present, it is not possible to give more significance to the distributional patterns other than to indicate that they exist. Whether the cultural or natural agencies shaping the distribution are selective or non-selective is likewise obscure; however, some of the selective factors which might be worthy of further investigation are discussed below. Data are drawn from Southwestern materials examined by the author, from the reports of the Russian investigators (Ditmer *et al.*, 1937), and from Hedrick's study (1931) of the United States commercial beans.

It will be noted that never does the percentage of variegated-seeded forms exceed that of the corresponding self-colored forms. The highest percentage of variegated forms, 50 per cent in the United States, reaches that figure largely because of the great diversity and number of variegated forms among the bush snap beans. Many of these are introductions from Europe, and the needs of the canning industry and available year-round markets have stimulated the use of many varieties with differing horticultural characteristics. Diversity in seed characteristics here is incidental. Among the bush snap beans described by Hedrick (about 127 named varieties), 55 per cent have variegated seed coats. In all other varieties there are considerably fewer variegated forms than there are self-colored ones. The percentage of strictly prehistoric types of the Southwest most closely approximates Peruvian distribution, while the totals for the Southwest, including prehistoric, contemporary, or both periods combined, are most like the Mexican distribution and very little like the 1:1 ratio for the United States. The high percentage of self-colored beans, which occurs only in contemporary Southwestern Indian cultures, and the fact that few of these are found as field beans in other more humid parts of the United States, indicate an influx during historic times of self-colored beans. The trend in the Southwest thus has been toward absolute and percentage reductions in the numbers of variegated bean types and a corresponding increase

in self-colored types which are dry shell beans, except for the Hopi "Black" string bean (Type C30). The importance of the Pinto or *Garrapata* bean (Type C13), a variegated dry shell bean, is also recent.

Freytag (unpublished thesis) states that Latin American beans used in the dry-shell stage over a wide area are likely to be self-colored and not of an unusual shape, while variegated or odd-shaped dry-shell types are of restricted distribution. These selective factors are apparently not operative in snap beans as such beans are consumed before seed maturity. This seems to be true in the United States, as variegated dry beans, with the exception of the pinto varieties which are used for Mexican or Texas style dishes, are of quite restricted distribution.

Interpretations of Bean Distribution:—

Three fairly distinct regions can be outlined in the prehistoric Southwest for the cultivation of beans. So far as is possible, the source of beans, the dates of their introduction, cultural affinities, and movements within the Southwest will be indicated.

It was hypothesized that the distribution of cultivated beans in the prehistoric Southwest would show a diversity resulting from differing climatic and ecological conditions and from differences in culture history. The influence of the environment and some ethnobotanical factors such as food preparation have already been discussed. A division of the Southwest following three main cultural groupings was adopted for the organization of bean distributions into regions. These regions can be compared with those of other plant materials and culture traits.

I. Mogollon:—

Although beans are known only from a few sites in a limited area of the Mogollon, it is evident that the cultivation of the common bean in this area preceded the introduction of pottery. The number of pre-pottery beans from Tularosa Cave is small but the prepottery context is clear, and it may be stated that by 300 B. C. common beans, along with maize and pepo squash, were being cultivated by Mogollon Peoples. The number of communities or settlements cultivating beans at this time cannot be estimated, but it is probable that it was not large, as none of the Mimbres River sites nor Cordova Cave, which is even closer to Tularosa Cave, show any evidence of important bean cultivation. The open sites of Higgins Flat and Hinkle Park, which appear to be immediately subsequent to and in the same cultural tradition as the Tularosa Cave, indicate that bean culture continued with common types similar to those of Tularosa Cave and may indicate a greater extent of bean growing. Since tepary beans do not occur in the Mogollon before 1100 A. D. (Higgins Flat), they may be regarded as introductions from the Hohokam; there seems to be no prior association of *P. acutifolius* in the Mogollon with *Cucurbita pepo* of which abundant remains were found in Tularosa Cave.

2. *Hohokam*:—

As noted previously, vegetal materials are absent in most early Hohokam sites. While this lack may be due to poor conditions of preservation, beans first appear in the Sacaton phase, or about 1,000 A. D. at Snaketown. The charred tepary and common beans identified by Volney Jones are said by Castetter and Bell (1942, p. 32) to constitute these remains, and may be the earliest record of tepary beans in the whole Southwest as well as in the Hohokam. Not enough evidence is available at present to warrant conclusions as to approximate dates for the introduction of cultivated beans to the Hohokam, nor is it possible to say whether beans were utilized in pre-pottery times in this region. Since the distinguishing feature in Hohokam beans seems to be that they are tepary varieties, which may represent a response to climatic rather than cultural factors, a long history of selection for varietal preference need not be hypothesized. The climatic conditions of southern and southwestern Arizona would quickly encourage the cultivation of tepary beans after their introduction. If domestication of the tepary occurred in the region of the Hohokam, it is not now possible to estimate when the cultivated varieties emerged as different enough from the indigenous forms to be differentiated from them. The Hohokam ruins which have provided the best bean material are later than 1,000 A. D., and usually they show the influence of the Anasazi in several aspects of culture. Montezuma's Castle (1300 A. D., Collection Nos. 201–205a), located in the Verde Valley, central Arizona, is listed by Carter (1945, p. 24) as a Pueblo III, Little Colorado River site, among those sites demonstrating the advance of *Curcubita moschata* from the Mesa Verde region to the south and west into the area of the Hohokam. In this site only have been found uncharred, definitely identifiable bean remains representing the three species known to occur in the prehistoric Southwest. A mixture of bean assemblages of the Hohokam and Anasazi are evident in the teparies, and limas from the Hohokam and the characteristic striped violet common bean (Type C11) of the Anasazi. Other sites of the Verde Valley evidence the influence of the Anasazi bean types rather than those of Mogollon.

The lima bean appears to be characteristic of the Hohokam. Mackie (1943) has the theory that lima beans entered the Southwest by way of western Mexico and the Colorado River tribes into the Hohokam area. He discounts the likelihood of the eastern Mexico-Sierra Madre Oriental corridor as unsuitable because of excessively humid conditions. Mackie also finds that the Hopi lima beans and the beans of eastern United States Indian groups are identical and suggests that the eastern limas are an extension across the Mississippi Valley of the Hopi varieties. Carter considers that the absence of native archaeological lima beans east of the Hopi mesas until Pine Bluffs, Arkansas, necessitates an eastern Mexico-Texas corridor to the east. I have found, in undated excavated material from Sunny Glen Cave, Texas (Anonymous, 1932), and in sites from Tamaulipas, Mexico, (specimens and personal correspondence from McNeish, in 1955), extensive remains of common bean pods and a few seeds. The lima bean pods found among

the vegetal remains from Tamaulipas strengthen the eastern Mexico corridor hypothesis.

Lima beans are known from relatively few prehistoric Southwestern sites; these are discussed by Steen and Jones (1941) and mapped by Carter (1945).⁴ The sites from which these beans are known are in the Verde Valley which shows an admixture of Hohokam with other cultures. However, since the lima beans are found neither in the Mogollon nor northern Anasazi sites, their relationship to the Hohokam seems clear.

3. *Anasazi*:—

In the scatter diagrams the bean remains of the Mesa Verde pueblos are separated from those of the northern Arizona Anasazi to emphasize varietal diversity. In this study only two types are recognized as present among the Mesa Verde pueblos, and the larger number of types found in the ruins of northern Arizona. The frequency of occurrence of the striped, violet common bean, type C11, in both the northern Arizona and Mesa Verde Anasazi, and its rarity elsewhere unifies these two regions with regard to bean distribution.

Collections of beans from Zion National Monument in southeastern Utah examined at the Museum of Anthropology, University of Michigan, provide evidence which helps to clarify the relationship of Northern Periphery beans to those of the Anasazi. Although the stratigraphy has been disturbed, habitation of the site probably extended from Basketmaker II times until about 1150 A. D. (correspondence from A. H. Schroeder to Volney H. Jones). Among these well-preserved beans are to be found: types C11, C15, C12, C19a, and possibly C1—collection numbers 232–236 respectively.

Jones' description (Brew, 1946) of charred beans (limas, common beans, and others whose dimensions fell within those for Southwestern teparies) from the Alkali Ridge site in southeastern Utah may indicate early agricultural influence from the south. Since the beans of Mesa Verde in southwestern Colorado—an occupied area showing many cultural affinities with Alkali Ridge (Brew, 1946)—are all common beans, none of which even in the charred condition could be mistaken for lima beans or teparies, Northern Periphery and Anasazi beans do not correspond completely. The presence of the small red, flecked bean, type C12 in the Zion material (the small charred seeds found by Jones in the Alkali Ridge collection may be of this type), links the Verde Valley (collection no. 162a) with southeastern Nevada Virgin River sites (collection nos. 206, 206a), said by Reed (1954) to be Pueblo II outliers of Anasazi culture, and with southeastern Utah.

The Verde Valley and Anasazi, then, appear to have had beans in common with those of the Northern Periphery. Although Northern Periphery materials discussed in this paper are probably earlier than the Anasazi beans, which are mostly

⁴ The charred seeds cited by Carter as those of lima beans from the Hodges site in south-central Arizona are actually *Canavalia ensiformis*, as evidenced by the broad hilums which are about half the length of the entire seed.

from Pueblo III, there is little to indicate a direct movement of agricultural complexes to the Anasazi from the south by way of Nevada and Utah. However, it does seem evident that the characteristic bean—C11—of the Anasazi did derive from the Northern Periphery or, at least, although rare in the Anasazi, was common to both regions in pre-pottery times.

In Basketmaker III times (Wormington, 1955) and later culture periods, many traits point to a close relationship between the Northern Periphery and the San Juan Anasazi. Among such evidence is the Central Mexican type of corn found in prehistoric sites of southeastern Utah (Wormington, *op. cit.*). This type of corn was described from the vegetal remains of Alkali Ridge by Anderson (1944) and, with other artifacts, strongly suggest Mexican influence. However, neither Nickerson (Wormington, 1955) nor Carter (1945) believed the corn to have come directly through the Arizona Pueblo, Mogollon, or Hohokam areas, but both authors consider a plains route as a likely alternative. The high row-number corn of many early Southwestern sites, however, may indicate an early widespread distribution of the Central Mexican corn. Evidence provided by bean remains supports early southern rather than eastern agricultural influence.

The Existence of Bean Areas.—Two theories may be advanced for the existence of bean areas and their coincidence with culture areas in the Southwest.

One theory would involve an early introduction of beans to the Mogollon and a later introduction to the Anasazi of varieties distinct from those found in the Mogollon and unlike those found in the Hohokam. Thus the late introduction to the Anasazi would not have come by way of either of these two regions and therefore hardly could have come from Mexico directly except by way of eastern Mexico and Texas. There are no dated remains to support this. An indirect route from the Mexican-Central American center by way of the Caribbean, the Gulf Coast, and eastern United States cannot yet be properly evaluated, but in the opinion of the author this remains an unlikely route for reasons of cultural affinities and plant geography.

A more likely theory would assume the early entrance and widespread distribution of beans throughout the Southwest but their adoption and culture by a relatively small number of communities. This might explain both their presence and their rarity in Basketmaker sites. The early beans thus could have been both widespread and varieties more uniform than indicated by the later materials. These later materials, as yet the only ones available to us, would have come from a time postdating an intensification of bean culture, a time more likely to have left bean remains simply because more people were growing them. During the period between the introduction or introductions of beans to the Southwest and the beginning of their more general cultivation, differentiation of types on the basis of local or regional cultural preferences and regional climatic and edaphic conditions would have occurred.

CONTEMPORARY BEANS

Early Spanish and later Anglo-American contacts brought new plants to the Indian farmers, some of which became important and sometimes basic crops. During the historic period contact among Pueblo peoples has been of more than a casual or even trading nature, and introductions of Peruvian beans by way of California and United States commercial varieties have occurred.

1. *Hopi Beans*:—

The assemblage of Hopi bean types (Table VI and fig. 9) appears to be most closely related to that of the Verde Valley among the prehistoric groups. Beans of the Verde Valley are the most diverse of the prehistoric groups and seem to be composed of types which had come from the northern Anasazi, the Hohokam, and the Reserve, New Mexico, Mogollon area. The mixture of types and species found in the Verde Valley is not to be found in any one of the three great culture groupings discussed in this paper.

In addition to the "old" beans which appear to have come down to the Hopi from Verde Valley peoples, newer varieties which do not appear in the archaeological record have been adopted by the Hopi. These new varieties have had several sources. The Pinto beans (Type C13) as known in the United States are only a few variants of the *Garrapata* or tick bean group, which is highly diverse and well distributed in northern Mexico (Collections of Oficina de Estudios Especiales, Secretaria de Agricultura y Ganaderia, Chapingo, Mexico). The occurrence in the Verde Valley (Collection number 164) of the only prehistoric collection of Pinto beans indicates a distribution limited to a single variety of the *Garrapata* group as well as a rather restricted range of cultivation. The highly important and widespread Pinto bean varieties now in use among most Southwest Indians probably represent historic introduction of *Garrapata* varieties from Mexico as well as a possible expansion of cultivation of the Verde Valley type. The arrival of these beans among the Hopi and other Indians may have been early, with the Spanish missionaries, or with later Mexican contacts.

Two other types which have become important in the contemporary Southwest but which are absent in prehistoric collections are the Pink and Bayo types (Types C28 and C17, respectively) both of which are found among the Hopi. Hendry (1918) states that the Pink bean is Chilean in origin, and that a translation of its northern Mexican name is "White man's bean." The date of introduction of the Pink bean is not known, and whether it arrived overland by way of Mexico, or sailing vessel by way of California, is equally obscure. The Bayo types which are found among the Zuni and the Hopi are said by Hendry to have come to California prior to 1850 in sailing vessels from Chile and to have become well established in the Southwest. These also have become widespread in western Mexico.

2. *Zuni Beans*:—

It is probable that the collections of Zuni beans studied are less complete than those of the Hopi, and the same may be said for other contemporary Southwestern

groups. The Zuni types, without important exception, may be the same as the Hopi types (See Table VI) of common beans. The fact that only one tepary type and no lima beans occurred among the Zuni indicates less influence of the Verde Valley, and ultimately Hohokam bean assemblage, upon the Zuni than on the Hopi.

3. *Rio Grande Pueblo Beans*:—

From the scatter-diagrams it may be seen that the common beans of the Rio Grande Pueblos are, as a group, smaller and less-variegated than the other common bean groups (figs. 3-13). There is no information concerning prehistoric beans of the Rio Grande peoples, but it may be that during the long Spanish rule of the Rio Grande Pueblos these beans were introduced from Mexico.

4. *Navajo Beans*:—

It has been often said that Navajo agriculture was derived from the Pueblos, particularly from the Hopi. There is nothing in the Navajo bean assemblage to indicate that Navajo beans were not derived from the Hopi or, in the case of the newer beans (*e.g.* the Pinto), from the same source as that of the Hopi.

5. *Piman and Yuman Beans*:—

Beans of the Arizona Piman and Colorado River Yuman peoples are most like those of that part of the Verde Valley which was probably most influenced by the Hohokam. There can be little doubt that the tepary beans of the Piman and Yuman groups are directly related to beans of the ancient Hohokam. If lima beans were a prehistoric Hohokam crop, as is believed by the author, one would expect them to have persisted at least among the Pima. However, little remains of the traditional crop varieties. It is extremely difficult to obtain corn of older non-commercial types from the Pima, and beans other than the commercial types are even harder to find. In addition to the difficult farming conditions of recent drought years, it is probable that the importance of cash-cropping among these people since the mid-nineteenth century has operated against retention of the older crops, especially the poorly marketable tepary bean and dark-colored lima beans.

CONCLUSIONS

A complex assortment of varieties of *Phaseolus vulgaris* began to enter the Southwest at least 2,000 years ago. Their appearance in the archaeological record of the Mogollon in west-central New Mexico was prior to the introduction of pottery, while in the Anasazi area of northern Arizona the bean record begins at about the same time as the introduction of pottery, and in the Hohokam of southern Arizona, subsequent to pottery. The existence of well-defined prehistoric bean areas and the probability that beans were prepared for eating by parching and grinding in early non-pottery times suggest that beans were cultivated in the Southwest for a longer time than indicated by the now available archaeological

materials. The parching and grinding of mature bean seeds may have been practiced by relatively few communities in a given area for a long time before culture changes which are not now precisely known stimulated the general adoption of beans. The early but restricted use would have afforded ample time for the differentiation and selection of varieties characteristic of particular areas.

Lima beans probably entered the Southwest by way of both the Sonoran and eastern Mexican corridors but at a later date than the common beans; their earliest record is found in 13th or 14th century ruins. Lima beans remained restricted to the central and north-central parts of Arizona and nowhere became as important as common beans.

Phaseolus acutifolius appeared as an important bean only in extremely arid southern Arizona, having come into use by the Indians of that region sometime prior to 900 A. D. There is insufficient evidence as yet to locate the center of domestication of the tepary bean; it may have been a domesticate of Sonoran Desert Indians or of peoples in the southern part of Mexico.

The presence of *P. coccineus* in prehistoric Southwest cultures has not been established, and its contemporary cultivation, limited to the Hopi, does not indicate a position of importance for these beans.

The absence of change indicative of evolution under domestication in prehistoric beans is attributed in part to the fact that the center of origin of the cultigens represented is far removed from the Southwest, and in part that beans were cultivated previous to the period for which archaeological material is available.

Among the prehistoric cultures, large, variegated common beans with a high frequency of a violet bean (Types C11 and C11a, which is distinctly or indistinctly longitudinally striped) are characteristic of the prehistoric Anasazi cultural division. The tepary bean is of greatest importance in the Hohokam region, while the Mogollon culture division is characterized by large-seeded non-variegated common beans and the absence of the striped violet bean of the Anasazi. Central Arizona, including the Verde Valley, shows evidence of the bean influence of the Hohokam and Anasazi and has the most varied assortment of beans, with common, lima, and tepary beans present.

The prehistoric source of the contemporary Hopi beans appears to have been the Verde Valley while the beans of the Pima and Papago tribes came from southern Arizona. In addition to the prehistoric bean types, contemporary Southwestern Indians have acquired beans from Mexico, Peru, and from commercial seed sources in historic times.

SUMMARY

1. Collections of cultivated beans from contemporary Southwest Indian peoples and bean remains from prehistoric sites in the same area were studied.
2. On the basis of external seed morphology and anatomy a series of cultivated bean types is described in tabular and graphic forms. The types have about the same taxonomic significance as named horticultural varieties. Thirty-two common

bean (*P. vulgaris*) types are recognized and described for the Southwest. Of these, thirteen have been found only among prehistoric remains, ten occur only in contemporary collections and nine have been found among both prehistoric and contemporary collections. Eight tepary bean (*P. acutifolius* var. *latifolius*) types are recognized from prehistoric and contemporary collections, and five lima bean (*P. lunatus*), and two runner bean (*P. coccineus*) types are recognized and described from contemporary collections only.

3. Using the criteria for classification of bean types as presented in this paper, new materials may be compared to the existing Southwestern types. With this basis for comparison bean collections from different cultural and temporal contexts can be related and the history of bean domestication, variation, and use patterns may come to be better understood.

4. Bean areas are defined on the basis of distribution of the types; prehistoric and contemporary divisions are made according to temporal distribution. The areas outlined correspond to Indian cultural divisions and to climatic conditions.

5. It is suggested that parching and grinding of mature bean seeds was an early method of preparation for food and that the role of beans in the diet was as a source of protein to supplement animal and complement maize protein.

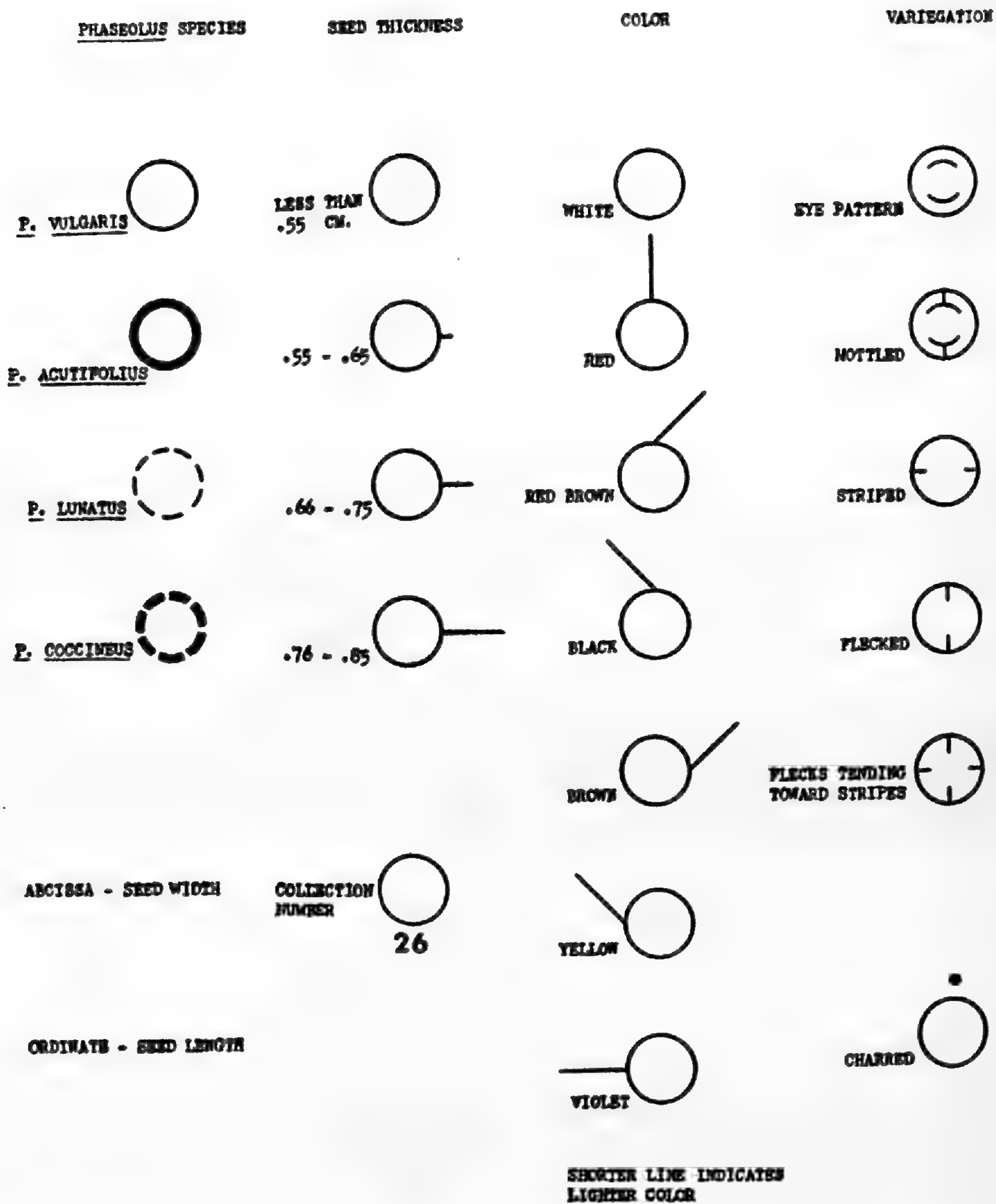
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KEY TO SCATTER DIAGRAMS, FIGS. 3-13



EXPLANATION OF SCATTER DIAGRAM COLLECTION NUMBERS, TABLE VII

Fig. 3, Mogollon

a, 215; b, 219; c, 224; d, 208; e, 209; f, 212; g, 210; h, 218; i, 214; j, 220; k, 222; l, 216; m, 211; n, 223; o, 221; p, 217; q, 213.

Fig. 4, Verde Valley, Arizona (Anasazi-Hohokam)

a, 205a; b, 195a; c, 195, 196; d, 195c; e, 195b; f, 185; g, 162; h, 201; i, 164; j, 185; k, 162d; l, 186; m, 204; n, 203; o, 138.

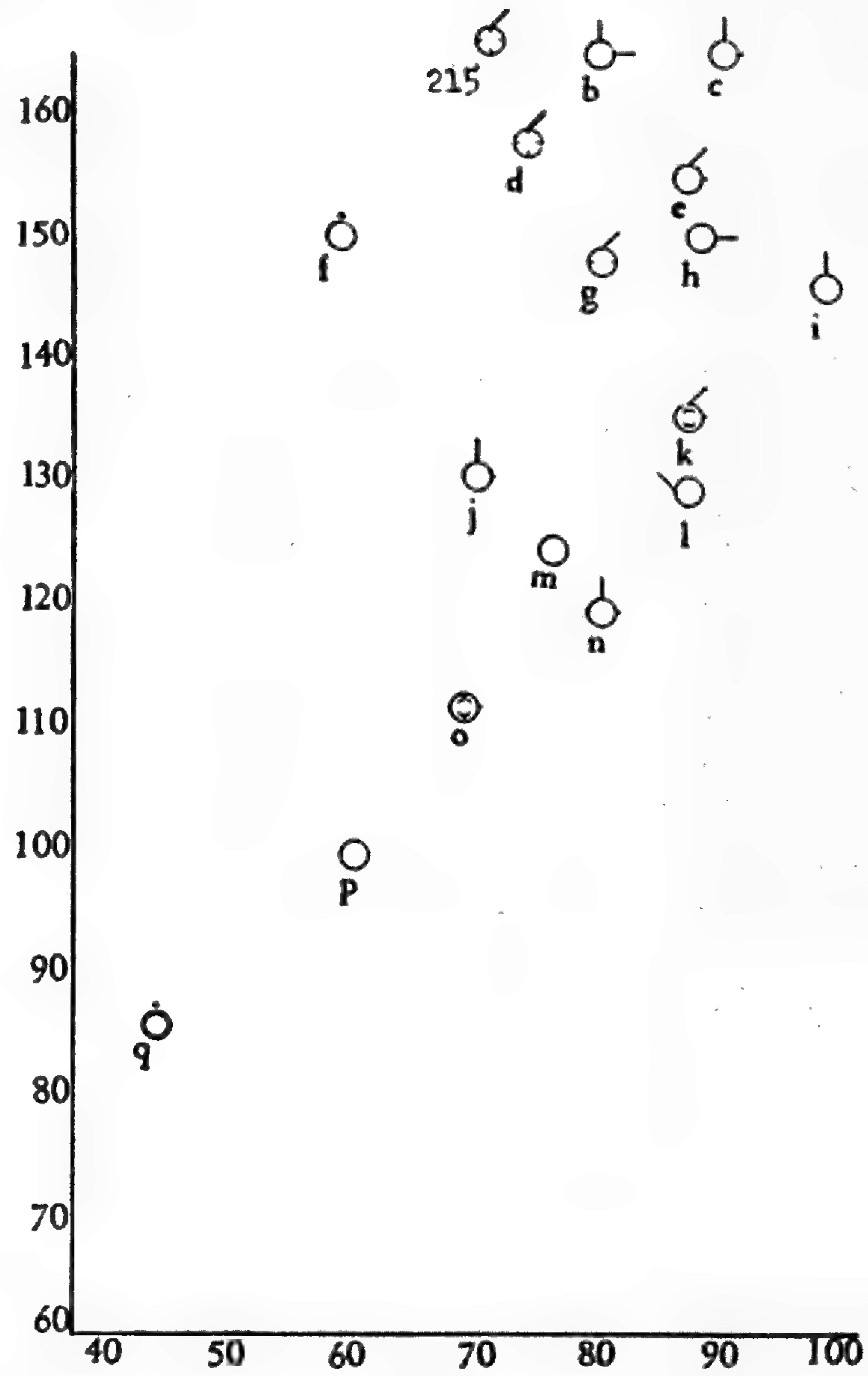


Fig. 3

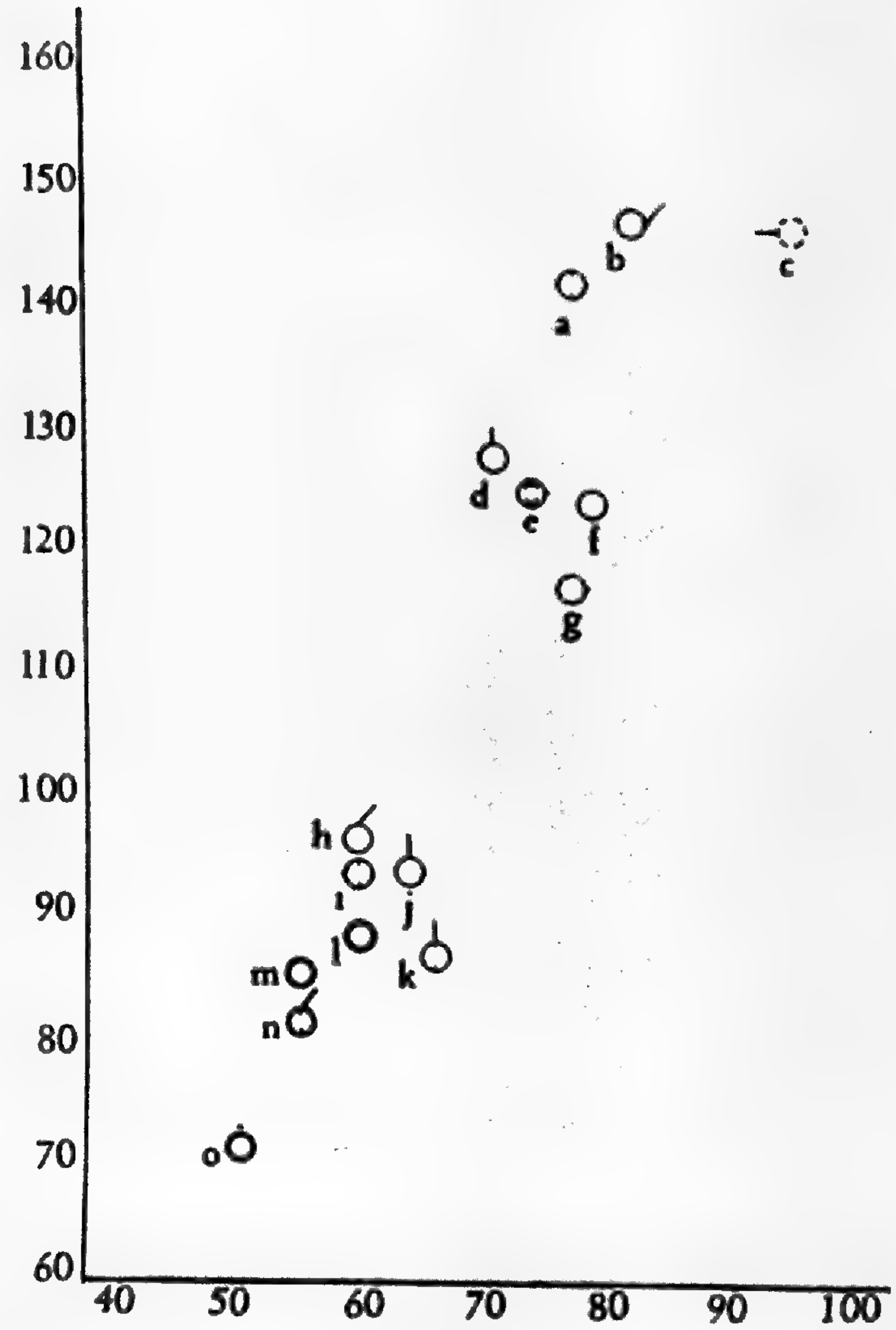


Fig. 4

Fig. 5. Northern Periphery

a—207; b—206a; c—206.

Fig. 6. Northern Arizona Anasazi

a—189; b—193; c—199, 194b; d—88, 161, 188, 190, 198; e—12, 160, 192; f—81, 202;
g—191.

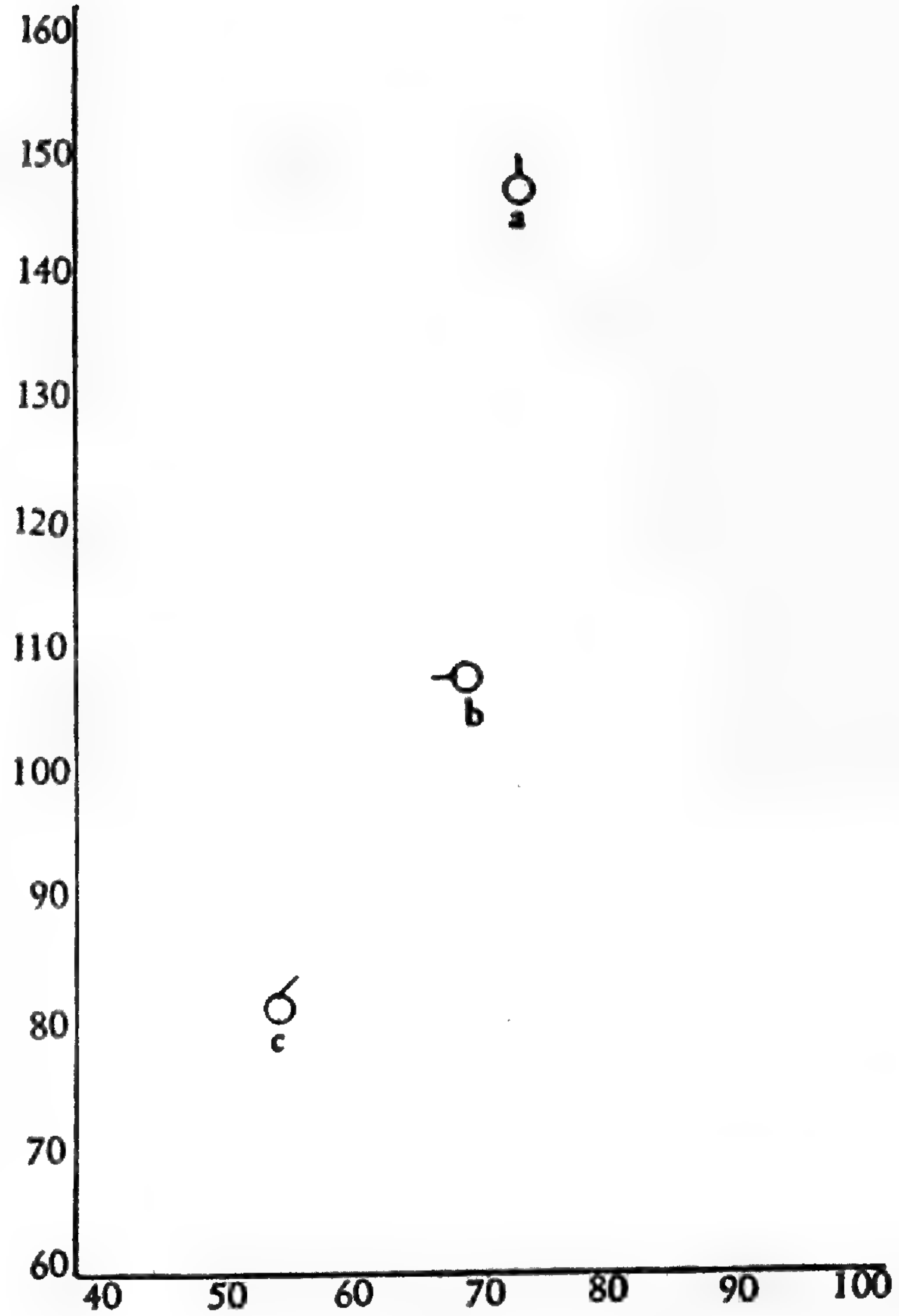


Fig. 5

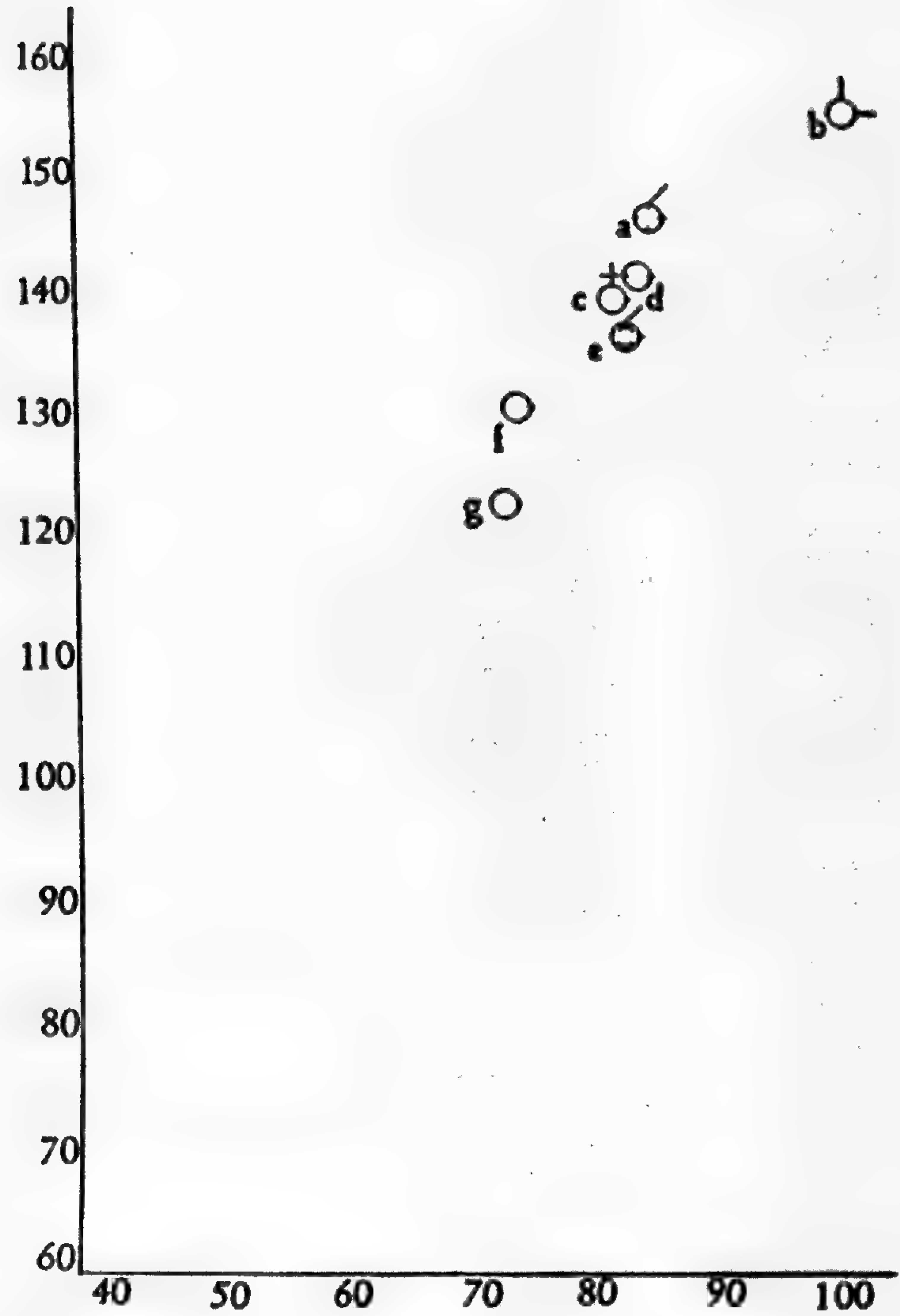


Fig. 6

Fig. 7. San Juan Anasazi, Mesa Verde

a—63, 65, 66, 67; b—64.

Fig. 8. Rio Grande Pueblos

a—9; b—106, 139; c—97a; d—103, 107, 157; e—105, 114, f—97b; g—98, 112; h—8;
i—109.

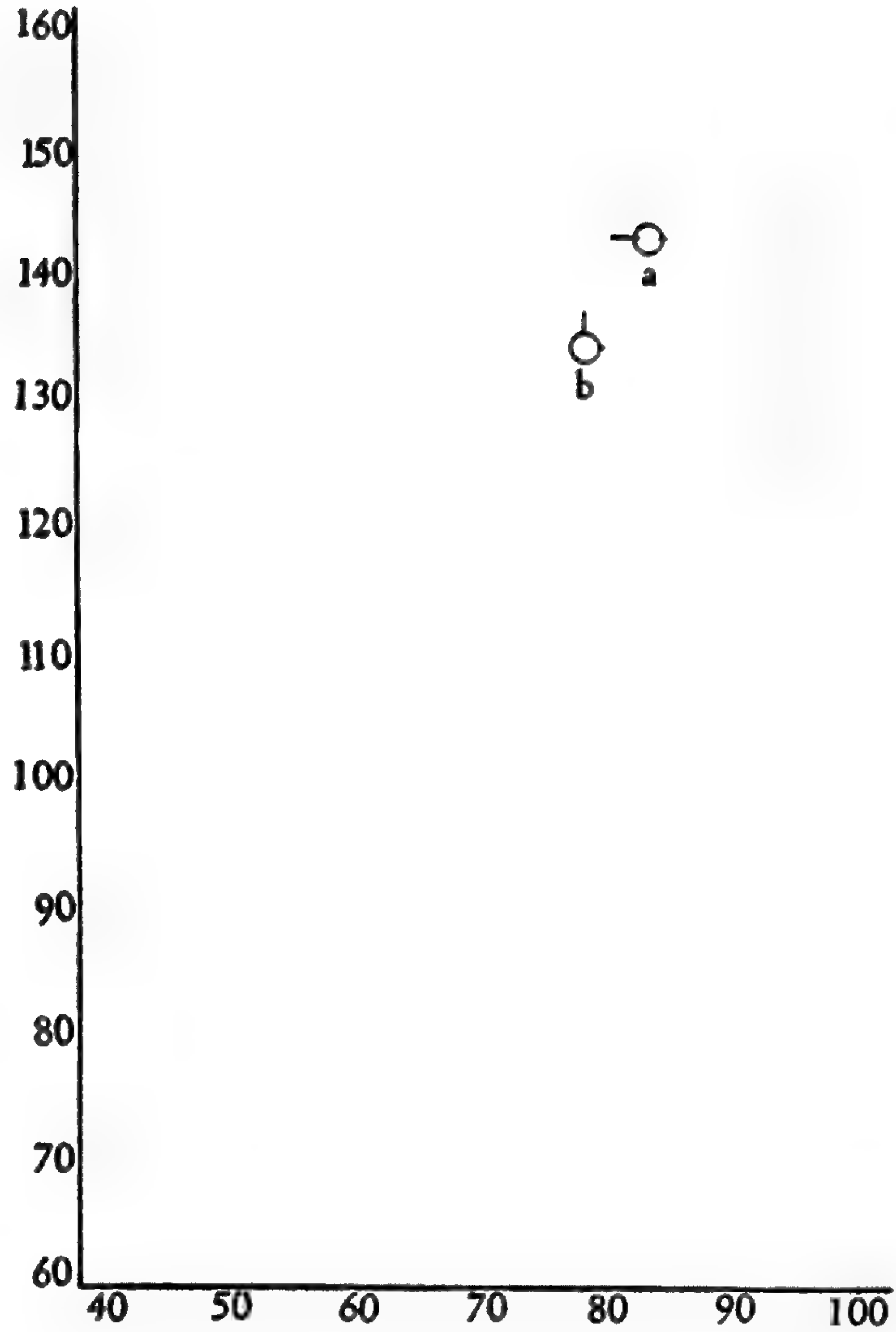


Fig. 7

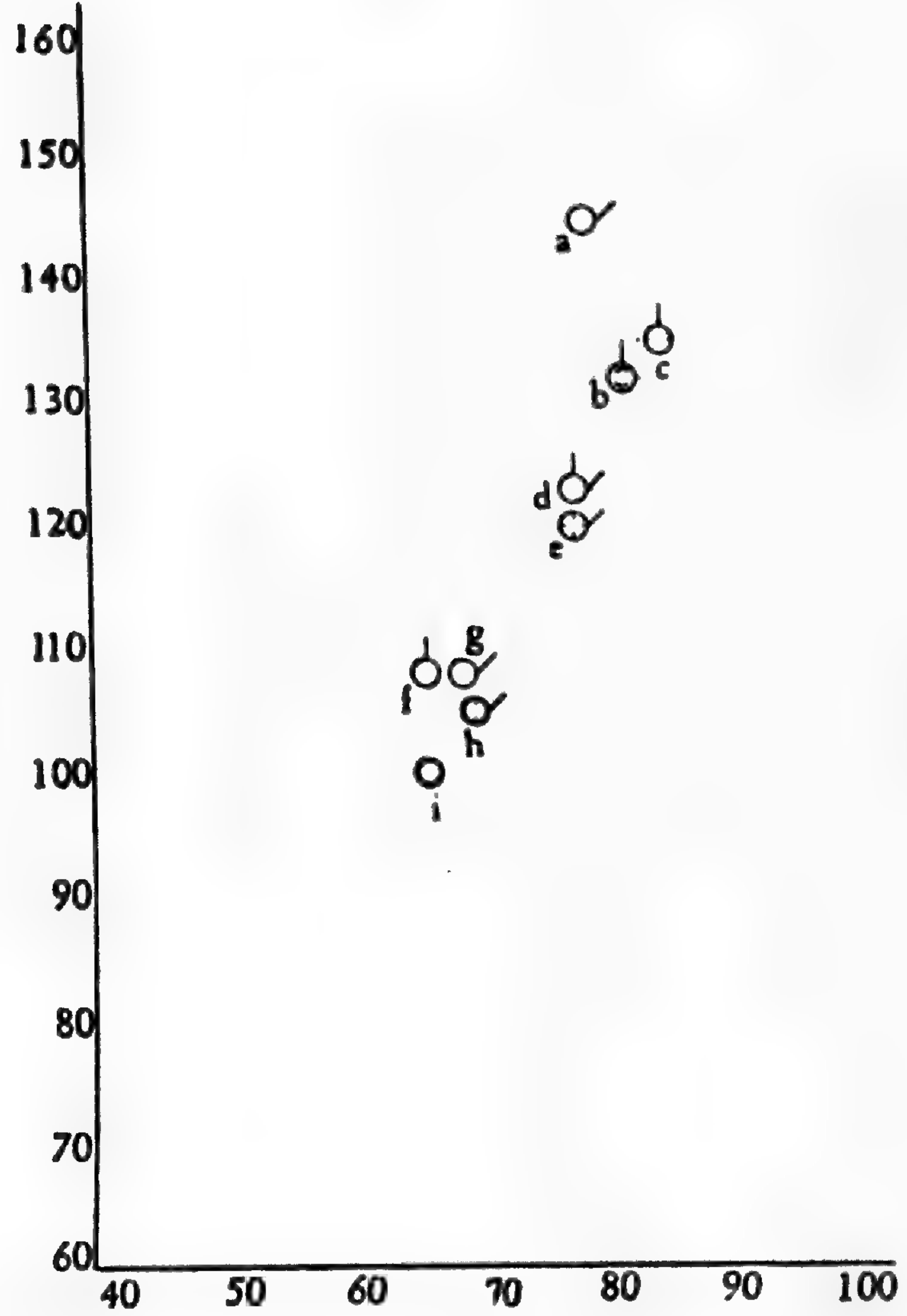


Fig. 8

Fig. 9. Hopi

a—43b; b—17a; c—42; d—16, 24, 29; e—31a; f—35; g—35a; h—31, 32, 34; i—54; j—45, 46, 55; k—49c; l—17b; m—19; n—57; o—14, 56, 58, 59; p—50; q—26; r—27, 28; s—33; t—18, 43, 44; u—22; v—23; w—37, 38; x—36; y—40, 41; z—39.

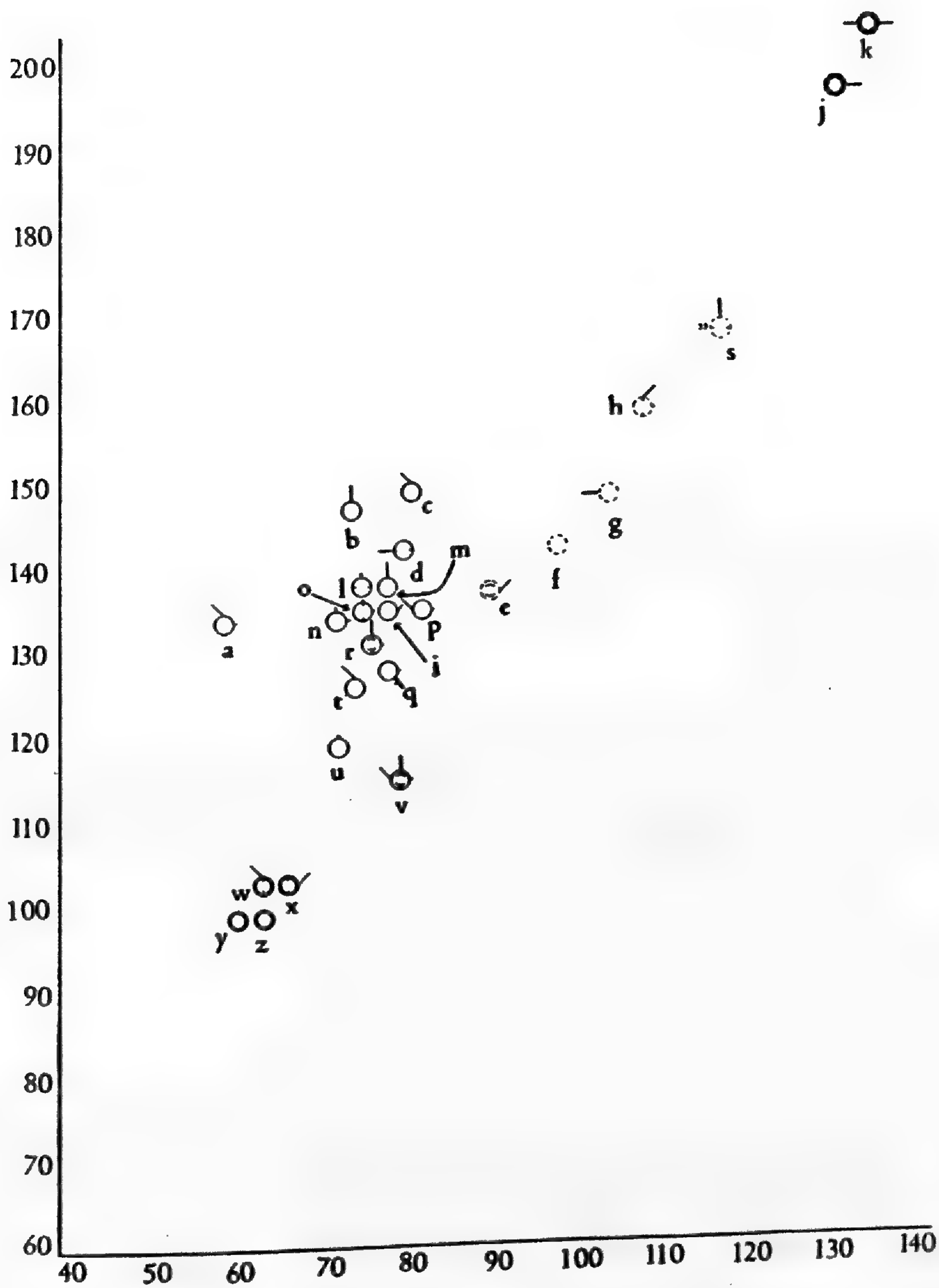


Fig. 9

Fig. 10. Zuni

a—153, 154; b—146; c—125; d—90; e—151; f—120; g—152; h—161; i—111; j—62; k—83.

Fig. 11. Navajo

a—86, 118; b—91, 104, 140; c—93, 123; d—119; e—124; f—128; g—85.

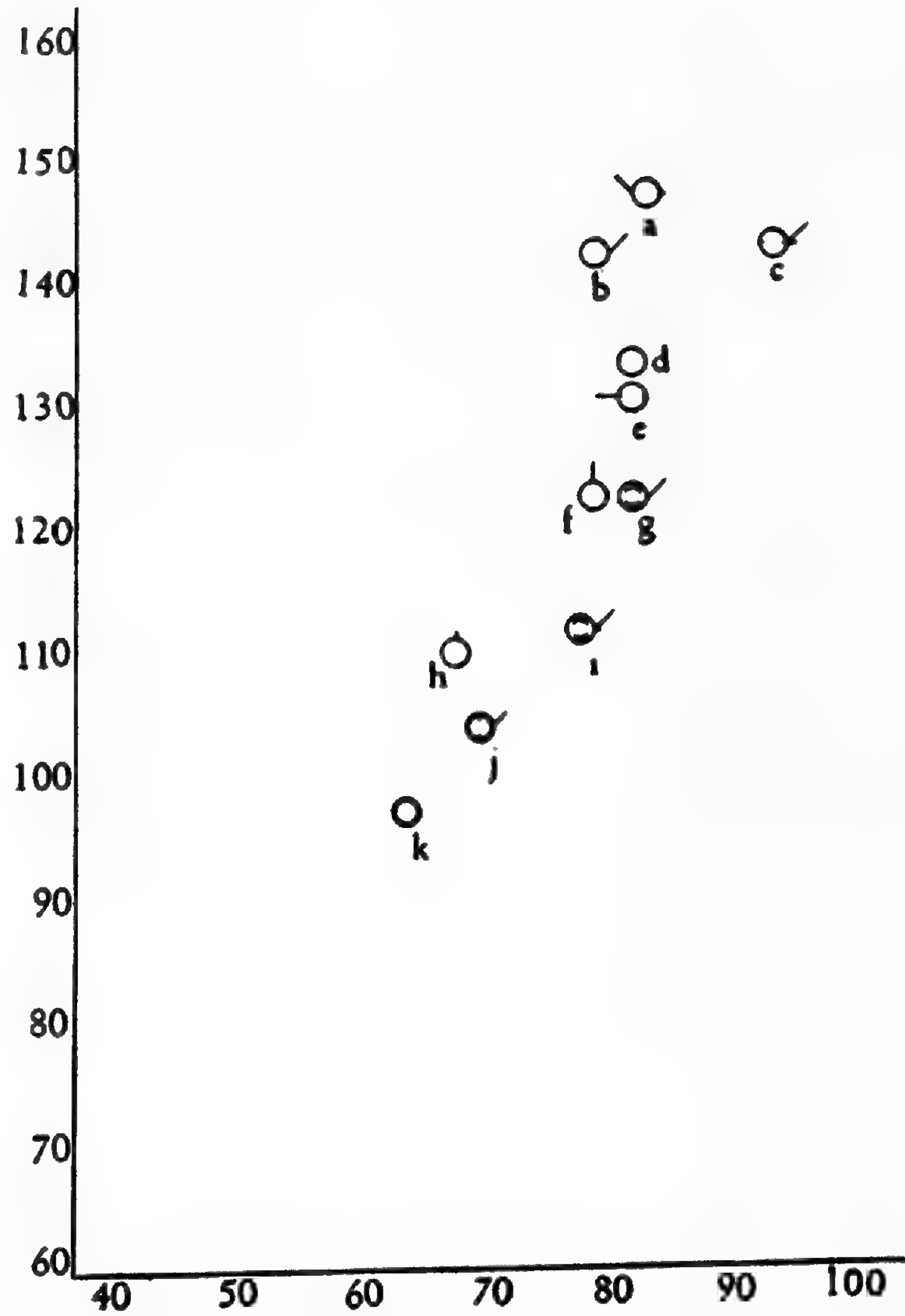


Fig. 10

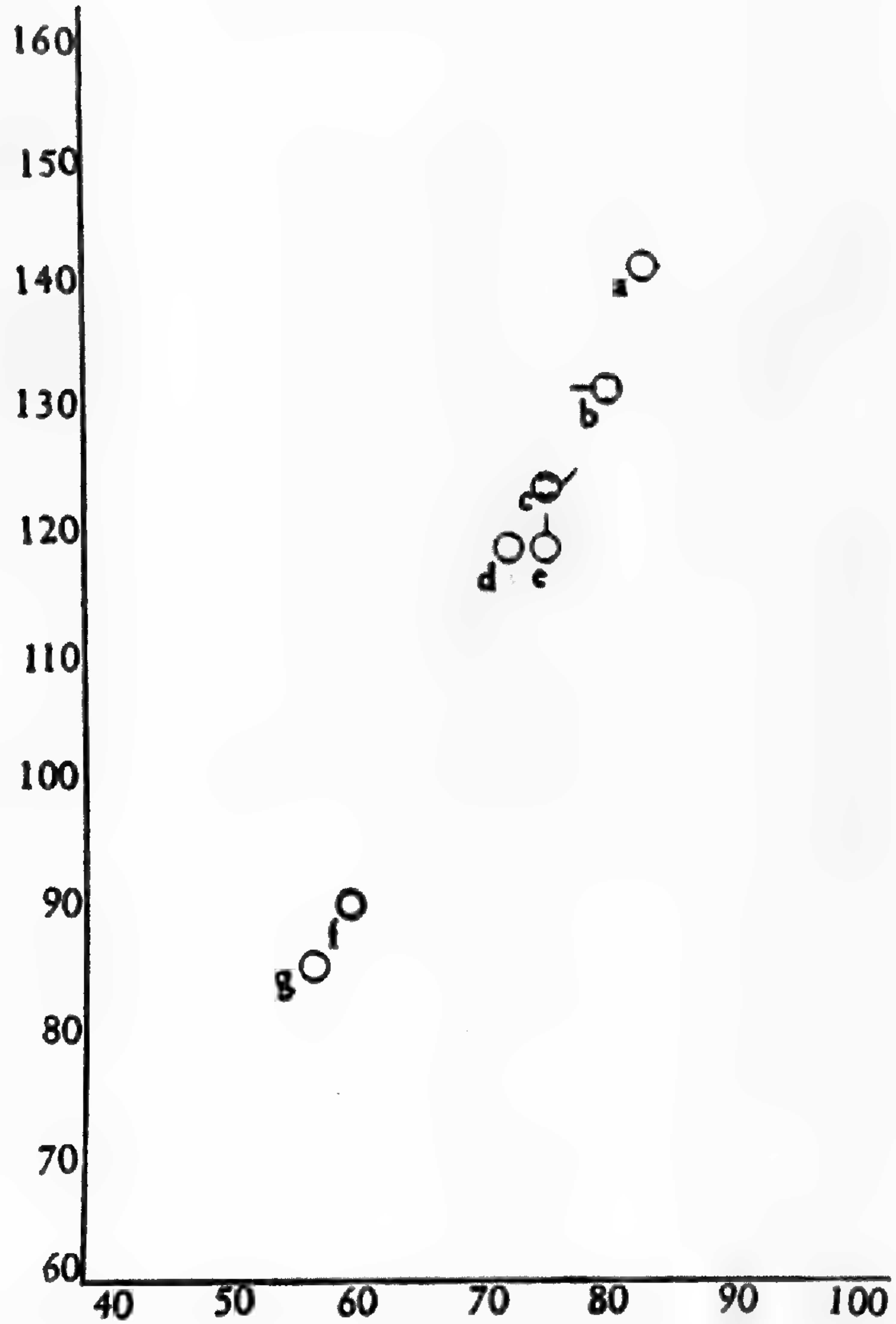


Fig. 11

Fig. 12. Arizona Piman

a—142, 156; b—11, 94; c—11a, 87, 108, 137; d—10, 82, 116, 130; e—110.

Fig. 13. Colorado River Yunan

a—127; b—15a; c—126; d—149; e—143, 144, 145, 148, 150; f—134, 135, 136; g—5, 121, 122, 132, 133, 147, 158; h—117.

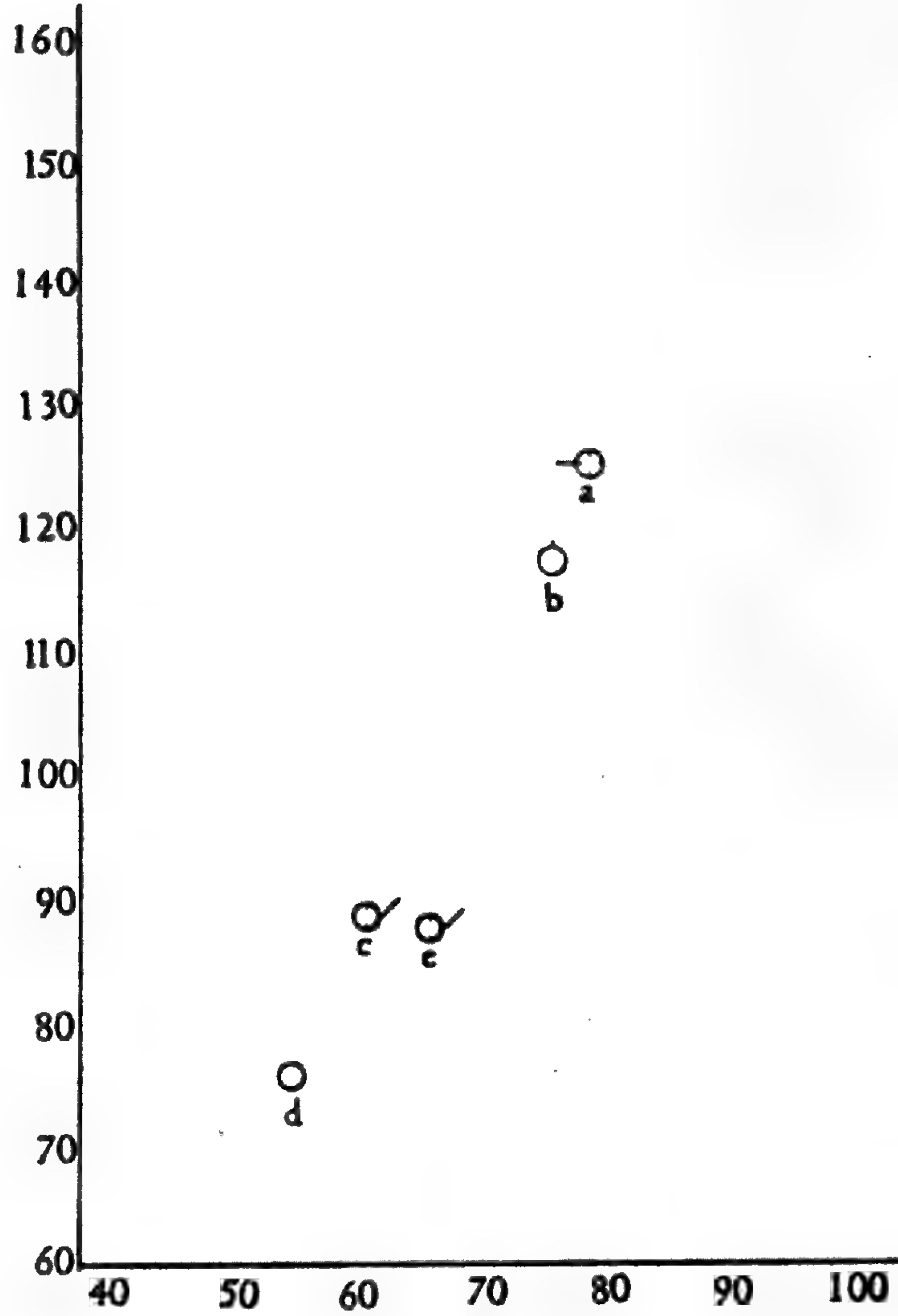


Fig. 12

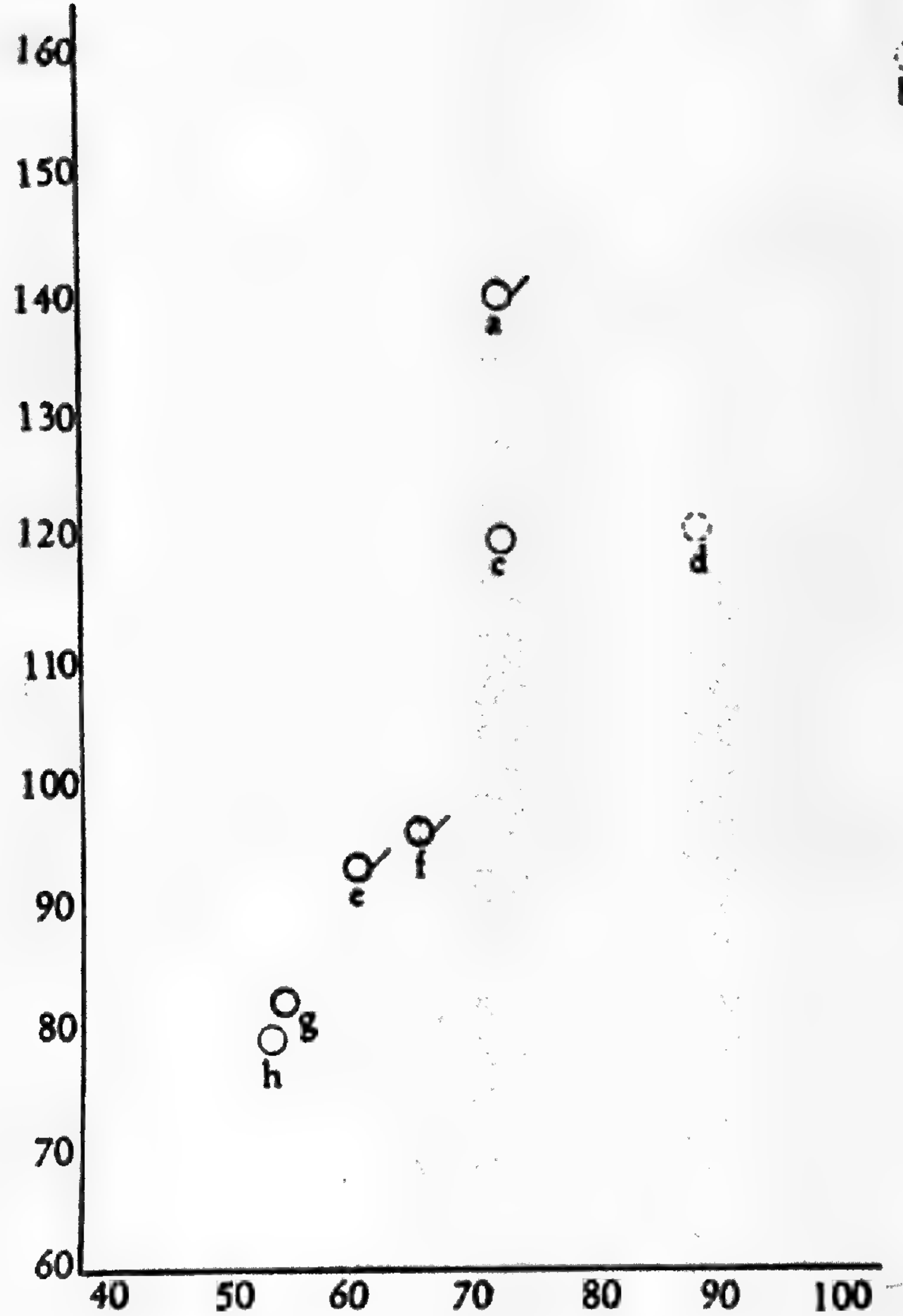


Fig. 13

EXPLANATION OF TABLE VII

The following abbreviations are used:

Amerind — Amerind Foundation, Dragoon, Ariz.

Berke. — Museum of Anthropology, University of California, Berkeley, Calif.

C.N.H.M. — Chicago Natural History Museum, Chicago, Ill.

Denver — Denver Museum of Natural History, Denver, Colo.

Lab. of Anth. — Laboratory of Anthropology, Santa Fe, N. M.

Mesa Verde — Mesa Verde Museum, Mesa Verde National Park, Colo.

Mich. — Ethnobotanical Laboratory, Museum of Anthropology, University of Michigan, Ann Arbor, Mich.

M.N.A. — Museum of Northern Arizona, Tucson, Ariz.

Tucson — Arizona State Museum, Tucson, Ariz.

Univ. Ariz. — Department of Anthropology, University of Arizona, Tucson, Ariz.

Commonly accepted abbreviations are used for names of states. P. and B.M. refer to Pueblo and Basketmaker periods of the Pecos Archaeological classification under "Site, culture, and date."

Collection numbers followed by an asterisk are collections included in the scatter diagrams. The number of seeds measured, if less than the entire collection, is given in parenthesis under "Number and quantity of seeds." Pertinent notes on museum labels are included with the collection.

TABLE VII
LIST OF COLLECTIONS

Number	Collection source and number	Site, culture and date	Number or quantity of seed	Medial dimensions of seed (cm.)			Species or type
				Length	Width	Thickness	
3	M.N.A.	Havasupai, 1940	6	1.31	.78	.57	C 11
5	" 1047/4559	" Havasu Canyon, Ariz. Contemp.	3	.89	.58	.44	T 6
6a	Berke. 3-7867	Cocopa, Lower Colorado River. Contemp.	1	.78	.55	.43	<i>P. acutifolius</i>
6b	" 3-2976	Same as 6a	1	.94	.56	.40	"
6c	" 3-2982	" " "	1	.90	.61	.25	"
6d	" 3-2983	" " "	1	.82	.60	.38	"
6e	" 3-2984	" " "	1	.91	.61	.37	"
6f	" 1-62242	Cave near Jacumba, San Diego Co., Calif. Date unknown.	(1)	.82	.58	.35	"
6g	" 1-62241	Same as 6f	(1)	.88	.69	.37	"
6h	" 1-62240	" " "	(1)	.91	.61	.37	"
6i	" 1-62243	" " "	(1)	.80	.55	.40	"
7	" 2-17461	Sia Pueblo, N. M. Contemp. Escaped from cult.	(5)	.70	.53	.27	T 2
8	" 2-17537	Isleta Pueblo, N. M. Contemp.	2	1.06	.69	.43	T 4
9	" 2-17419	Acomita Pueblo, N. M. Contemp.	(5)	1.47	.78	.50	C 18
10*	" 2-17281	Pima, Santan, Ariz. Contemp.	(5)	.75	.52	.39	T 6
11*	" 2-17330	Papago, Ariz. Contemp.	(5)	1.22	.77	.55	C 28
11a*	" 2-17288	Pima, Ariz. Contemp.	(5)	.94	.64	.45	T 5

12*	Berke.	2-17765	Gourd Cave, Nitair, Tsegi Canyon, n. Ariz. P. III ?	3	1.44	.82	.64	C 14
13	"	2-17763	Same as 12	4	1.34	.74	.54	<i>P. vulgaris</i>
14*	M.N.A.	771/1744	Hopi Crop Surv. 1935	(10)	1.38	.83	.56	C 13
15a*	"	From Mus. display case	Havasupai. Contemp.	4	1.56	1.10	.62	L 4
16*	M.N.A.	771/1730	Hopi Crop Surv. 1935	(10)	1.42	.81	.61	C 11
17	"	771/1751	" " " "	(10)	1.14	.86	.68	C 25
17a*	Berke.	2-17694	Hopi	4	1.47	.76	.57	C 1
17b*	"	2-17577	"	5	1.38	.79	.48	C 26
18*	M.N.A.	1046/3935	" Contemp.	(10)	1.26	.76	.52	C 29
19*	"	771/1810B	Hopi Crop Surv.	(10)	1.38	.80	.60	C 3
20	"	725/2744	Hopi. Moencopi, Ariz. Contemp.	6	1.44	.66	.48	<i>P. vulgaris</i>
21	"	725/2745	Hopi Crop Surv. Moencopi, Ariz.	3	1.60	.82	.75	"
22*	"	771/1806	Hopi Crop Surv. 1935. "Similar to robust"	(10)	1.1	.74	.50	C 28
23*	"	771/1809a	Hopi Crop Surv. "Jacob's cattle"	(10)	1.16	.81	.65	C 14a
24*	"	756/745	Hopi Crop Surv. First Mesa, Ariz.	8	1.37	.80	.63	C 11
25	"	771/1741	Hopi Crop Surv. "string bean"	4	1.23	.77	.72	<i>P. vulgaris</i>
26*	"	771/1809B	Hopi Crop Surv. 1935 "Jacob's cattle"	9	1.32	.78	.56	C 14
27*	"	771/1771	Hopi Crop Surv.	5	1.22	.72	.55	C 2
28*	"	771/1823B	" " "	(5)	1.28	.80	.55	C 2
29*	"	1046/3939	Hopi, Hotevilla, Ariz.	(10)	1.48	.79	.59	C 11
30	"	771/1827	Hopi Crop Surv. "red string bean"	(10)	1.38	.74	.54	<i>P. vulgaris</i>
31*	"	771/1781	Hopi Crop Surv. "brown yellow lima"	(10)	1.60	1.08	.54	L 3
31a*	Berke.	2-17591	Hopi	3	1.37	.92	.44	L 5
32*	M.N.A.	756/B.729	Hopi Crop Surv.	(10)	1.58	1.08	.55	L 3
33*	"	771/1835	" " "	(10)	1.61	1.14	.52	L 4
34*	"	771/1768A	"red lima" Hopi Crop Surv.	10	1.57	1.02	.56	L 3
35*	"	771/1825	"brown lima" Hopi Crop Surv.	(10)	1.42	1.00	.53	L 2
35a	Berke.	2-17592	"white lima" Hopi Crop Surv.	4	1.47	1.03	.54	L 1
36*	M.N.A.	771/1727	Hopi Crop Surv. "mottled tepary"	(10)	1.03	.68	.39	T 4
37*	"	771/1808	Hopi Crop Surv. "black tepary"	(10)	1.01	.65	.38	T 7
38*	"	756/B727	Hopi Crop Surv.	(10)	1.04	.68	.39	T 7
39*	"	771/1807	" " "	(10)	1.02	.66	.48	T 3
40*	"	771/1758	" " "	(10)	1.00	.66	.42	T 3
41*	"	756/728	" " "	(10)	.99	.64	.42	T 3
42*	"	771/1742	" " "	(5)	1.49	.83	.47	C 29
43*	"	771/1838	"dark blue bean" Hopi Crop Surv.	(10)	1.22	.76	.54	C 29
43b*	Berke.	2-17635	"Hopi blue dye bean" Hopi Crop Surv.	2	1.34	.61	.55	C 30
44*	M.N.A.	771/1769	" " "	(10)	1.30	.76	.50	C 29
45*	"	1046/3940	" " "	(5)	1.90	1.33	1.13	R 1
46*	"	906/E250A	" " "	4	1.87	1.18	.94	R 1
46a	"	771/1772	" " "	2	1.62	.80	.59	C 18
49a	"	725/B2740	" " "	3	1.97	1.21	.77	R 2
49b	"	854/2845	" " "	4	2.20	1.40	1.07	R 2
49c*	"	906/E250B	" " "	5	1.99	1.32	.98	R 2

TABLE VII (Continued)

Number	Collection source and number	Site, culture and date	Number or quantity of seed	Medial dimensions of seed (cm.)			Species or type
				Length	Width	Thickness	
50*	M.N.A. 771/1801A	Hopi Crop Surv. "yellow beans"	(10)	1.40	.82	.60	C 17
51	" 1046/3936	" " "	(10)	1.34	.74	.56	C 28
52	" 1046/4670	" " "	(10)	1.42	.82	.50	C 17
53	" 771/1809D	" " "	(10)	1.41	.82	.54	<i>P. vulgaris</i>
54*	" 771/1770	" " "	(10)	1.41	.80	.51	C 17
55*	" 906/E250A	" " "	3	2.05	1.28	1.14	R 1
56*	" 1046/3934	" " "	8	1.38	.78	.54	C 13
57*	" 771/B1730	" " "	13	1.38	.76	.56	C 11
58*	" 771/B1731	"purple string bean" Hopi Crop Surv.	(15)	1.31	.71	.57	C 13
59*	" 771/1731	" " "	(15)	1.45	.82	.64	C 13
60	" 771/1837	" " "	(15)	1.45	.82	.58	C 17
61*	Berke. 2-17407	Zuni. Ojo Caliente, N. M. Contemp.	2	1.10	.69	.46	C 28
62*	" 2-17388	Zuni. N. M. Contemp.	(5)	1.04	.67	.38	T 4
63*	Mesa Verde 417/345	Cliff Palace, Mesa Verde. P. III	5	1.42	.74	.58	C 11
64*	" 3324/275	Cliff Canyon, Mesa Verde. P. III	2	1.35	.77	.63	C 1
64a	" 3441/298	Square Tower House, Mesa Verde. P. III	3	1.27	.76	.58	C 1
65*	" "	Same as 64a	5	1.45	.78	.63	C 11
66*	" 2848/171	Step House, Mesa Verde. P. III	10 (8)	1.37	.75	.57	C 11
67*	" 2488/86	Same as 66	1/2 pint (250)	1.42	.82	.59	C 11
68a	Amerind 992K	Kukendahl, s.e. Ariz. near Nogales. 1200- 1450 A. D.	30 cc. 4 char. frag.	1.20	.64	—	<i>P. vulgaris</i> , subreniform subapiculate, single cotyle- dons; testas destroyed by charring
68b	" "	Same as 68a	4 frag.	.89	.62	.43	<i>P. vulgaris</i> , possibly C12 20 or 27, testas affected by charring
69	" 1049	" " "	1 frag. charred	1.31	.72	—	Similar to 68a
70a	" P/501B(2)	S. Ariz. 16th cent.	2 charred	1.36	.97	.53	<i>P. lunatus</i>
70b	" "	" " " "	5 charred	.80	.50	.38	Probably a small-seeded <i>P. vulgaris</i>
70c	" "	" " " "	1 charred	1.55	.87	.55	<i>P. vulgaris</i> , entire, ends rounded

71	M.N.A.	N.A.862	Site unknown	Ca. 100 charred incl. frags. Nos. 71 -75	.94	.63	.58	Probably C 6
72	"	N.A.862	" "	(6)	1.20	.66	.47	Like C 19a, but smaller
73	"	"	" "	(10)	.91	.60	.46	Entire, rounded ends
74	"	"	" "	(5)	.67	.48	—	<i>P. vulgaris</i>
75	"	"	" "	(1)	.90	.61	—	Ends flat
76	"	508/NA1764B.2	Dead Man's Fort, Ariz. P. II	Ca. 50 frag., charred (9)	1.14	.62	—	<i>P. vulgaris</i> , round ends, some much curved, similar to 72
80	Berke.	2-17417	Acomita, N. M. Contemp.	5	1.23	.66	.11	C 1
81*	"	2-17764	Gourd Cave, Nitair, Tsegi Canyon, n. Ariz. P. III	4	1.31	.75	.59	C 2
82*	"	2-17291	Pima. Santan, Ariz. Contemp.	(5)	.84	.57	.44	T 6
83*	"	2-17384	Zuni, N. M. Contemp.	4	.97	.64	.42	T 3
84	"	2-17731	Cave, S. Francisco R., N. M. Undated	(5) parched	.86	.55	.42	T 6
85*	"	2-17347	Navajo, Jeddito, Ariz. Contemp.	(5)	.85	.56	.43	C 6
86*	"	"	Same as 85	4	1.42	.83	.58	C 9
87*	"	2-17290	Pima. Santan, Ariz. Contemp.	(4)	.91	.60	.42	T 5
88*	"	2-17766	Gourd Cave, Nitair, Tsegi Canyon, n. Ariz. P. III	(5)	1.30	.82	.64	C 11
89*	"	2-17720	Near Isleta, N. M. Contemp.	(5)	1.29	.76	.52	C 14
90*	"	2-17408	Zuni. Ojo Caliente, N. M. Contemp.	(5)	1.34	.82	.53	C 9
91*	"	2-17347	Navajo. Jeddito, Ariz. Contemp.	4	1.36	.82	.56	C 13
92	"	"	" " "	2	1.32	.77	.56	C 23
93*	"	"	Same as 92	2	1.26	.80	.57	C 14
94*	"	2-17316	Papago, Ariz. Contemp.	(5)	1.18	.75	.52	C 28
96	"	2-17480	Cochiti Pueblo, N. M. Contemp.	(5)	1.22	.78	.50	C 13 ?
97	"	"	Same as 96	(5)	1.10	.73	.43	C 9
97a*	"	2-17556	Picuris, N. M. Contemp.	4	1.35	.82	.47	C 26
97b*	"	2-17560	Taos, N. M. Contemp.	(5)	1.08	.65	.43	C 15
98*	"	2-17480	Cochiti Pueblo, N. M. Contemp.	(5)	1.10	.68	.45	C 23
99	"	2-17771 #1A	Turkey House, Casa Grande, Ariz. Hoho- kam-Anasazi	8	1.33	.80	.62	C 11
100	"	" #2	Same as 99	4	1.20	.82	.67	C 21
101	"	" #3	" " "	5	1.42	.81	.53	C 11
102	"	" #4	" " "	2	1.42	.78	.59	C 1
103*	"	2-17412	Acomita Pueblo, N. M. Contemp.	(5)	1.27	.77	.54	C 22
104*	"	2-17343	Navajo. Jeddito, Ariz. Contemp.	(5)	1.32	.80	.56	C 13
105*	"	2-17709	Truchas, N. M. Contemp.	(5)	1.21	.73	.51	C 13

TABLE VII (Continued)

Number	Collection source and number	Site, culture and date	Number or quantity of seed	Medial dimensions of seed (cm.)			Species or type
				Length	Width	Thickness	
106*	Berke. 2-17434	Acomita Pueblo, N. M. Contemp.	(5)	1.32	.81	.62	C 14
107*	" 2-17701	Chimayo, N. M. Contemp.	(5)	1.22	.78	.60	C 22
108*	" 2-17326	Papago, Ariz., near Mex. bord. Contemp.	(5)	.80	.55	.39	T 5
109*	" 2-17443	Laguna Pueblo, N. M. Contemp.	(5)	1.00	.65	.46	T 3
110*	" 2-17327	Papago. Big Fields, Ariz. Contemp.	(5)	.88	.65	.43	T 4
111*	" 2-17389	Zuni, N. M. Contemp.	(5)	1.12	.78	.64	C 14a
112*	" 2-17479	Cochi Pueblo, N. M. Contemp.	(5)	1.08	.69	.51	C 23
114*	" 2-17703	Cordola, N. M. Contemp.	(5)	1.28	.80	.60	C 13
115	" "	" " "	(5)	1.11	.72	.53	<i>P. vulgaris</i>
116*	" 2-17332	Papago, Ariz. Contemp.	(5)	.84	.54	.41	T 6
117*	" 2-17230	Yuma, Ariz. Contemp.	4	.78	.52	.42	C 27
117a	" 2-17728	" " " "parched small white <i>P. vulgaris</i> eaten thus or ground"	frags. parched				T 6
118*	" 2-17344	Navajo, Jeddito, Ariz. Contemp.	(5)	1.34	.83	.57	C 9
119*	" 2-17341	Same as 118	(5)	1.20	.73	.50	C 2
120*	" 2-17390	Zuni, Ojo Caliente, N. M. Contemp.	(5)	1.27	.82	.50	C 3
121*	" 2-17262	Cocopa, Somerton, Ariz. Contemp.	(5)	.86	.60	.46	T 6
122*	" 2-17249	Mohave, Parker, Ariz. Contemp.	(5)	.84	.61	.47	T 6
123*	" 2-17345	Navajo, Jeddito, Ariz. Contemp.	(5)	1.24	.75	.51	C 14
124*	" 2-17778	Navajo, Two Gray Hills, N. M. Contemp.	(5)	1.16	.74	.53	C 22
125*	" 2-17387	Zuni, Ojo Caliente, N. M. Contemp.	(5)	1.44	.93	.73	C 24
126*	" 2-17272	Havasupai, Ariz. Contemp.	3	1.20	.68	.51	C 6
127*	" 2-17232	Yuma, Ariz. Contemp.	(5)	1.41	.72	.53	C 18
128	" 2-17346	Navajo, Jeddito, Ariz. Contemp.	(5)	.88	.60	.45	T 6
129	" 2-17259	Same as 128	(5)	1.34	.77	.58	<i>P. vulgaris</i>
130*	" 2-17310	Pima, Sacaton, Ariz. Contemp.	(5)	.76	.56	.41	T 6
131	" 2-17754	Kiet Siel, Tsegi Canyon, n. Ariz. P. III	4 charred	1.43	.97	.62	<i>P. vulgaris</i> (?) frags. of dark red testa
131a	" "	Same as 131	1 charred	.85	.45	.43	<i>P. acutifolius</i> ?
132*	" 2-17248	Mohave, Parker, Ariz. Contemp.	(10)	.89	.60	.46	T 6
133*	" 2-17235	Yuma Indians, Ariz. Contemp.	(10)	.86	.57	.41	T 6
134*	" 2-17261	Cocopa, Somerton, Ariz. Contemp.	(5)	.89	.62	.41	T 4

135*	Berke.	2-17261	Same as 134	(5)	1.03	.71	.42	T 4
136*	"	"	" " "	(5)	.96	.65	.38	T 4
137*	"	2-17337	Papago, Ariz. Contemp.	(10)	.89	.60	.38	T 5
138*	"	2-17756	Tusigoot, near Clarksdale, Ariz., Verde Valley. Hohokam, 1100- 1400 A. D.	5 charred	.70	.45	.32	<i>P. acutifolius</i>
139*	"	2-17414	Acomita Pueblo, N. M. Contemp.	(5)	1.45	.90	.56	C 14
140*	"	2-17342	Navajo, Jeddito, Ariz. Contemp.	(5)	1.31	.83	.55	C 13
141	"	"	Same as 140	(5)	1.20	.81	.53	C 22 ?
142*	"	2-17318	Papago, Ariz., near Mex. bord. Contemp.	(5)	1.32	.80	.59	C 13
143*	"	2-17271	Havasupai, Ariz. Contemp	(10)	.90	.60	.38	T 5
144*	"	2-17247	Mohave, Parker, Ariz. Contemp.	(5)	.97	.58	.35	T 5
145*	"	2-17250	Same as 144	(5)	.96	.60	.40	T 5
146*	"	2-17401	Zuni, Ojo Caliente, N. M. Contemp.	(5)	1.43	.76	.54	C 18
147*	"	2-17267	Walapai, Peach Springs, Ariz. Contemp.	(5)	.84	.58	.45	T 6
148*	"	"	Same as 147	(5)	.83	.59	.45	T 5
149	"	2-17233	Yuma Indians, Ariz. Contemp.	(5)	1.21	.87	.45	L 2
150*	"	2-17260	Cocopa, Somerton, Ariz. Contemp.	(5)	.93	.65	.41	T 5
151*	"	2-17405	Zuni, Ojo Caliente, N. M. Contemp.	(5)	1.32	.81	.60	C 11
152*	"	2-17409	Same as 152	(5)	1.23	.82	.54	C 14
153*	"	2-17406	" " "	(5)	1.52	.88	.56	C 17
154*	"	2-17410	" " "	(5)	1.48	.83	.57	C 17
155	"	2-17704	Cordola, N. M. Contemp. "bolitas"	(9)	1.10	.71	.55	C 22
156*	"	2-17324	Papago, Big Fields, Ariz. Contemp.	(5)	1.26	.78	.54	C 13
157*	"	2-17418	Acomita Pueblo, N. M. Contemp.	(5)	1.23	.71	.61	C 22
158*	"	2-17231	Yuma Indians, Ariz. Contemp.	(5)	.82	.56	.41	T 6
159	M.N.A.	695/NA2519 M96C	Kiet Siel, Tsegi Canyon, n. Ariz. P. III	1 charred	1.51	.85	.64	<i>P. vulgaris</i>
160*	"	621/405 M18	Wupatki Pueblo, Little Colo. R., 1000-1200 A. D.	1	1.14	.72	.61	C 14
161	"	712/NA2520.32	Turkey Cave, Tsegi Canyon n. Ariz. P. III	6 (3 im- mature)	1.42	.82	.61	C 1 or C 11
162*	"	692/A86b	Hidden House, Verde Valley, Ariz. 1100- 1300 A. D.	1	1.16	.78	.60	C 11a
162a*	"	"	Same as 162	1	.84	.62	.48	C 12
164*	"	514/1814A. 231R6	Juniper Terrace, n.e. of Flagstaff, Ariz. 1000- 1200 A. D.	4	.91	.58	.34	C 13
165	"	561/NA739.18	Walnut Canyon, Cliff Dwellings, Ariz. Sinagua, P. III	3	1.39	.82	.58	C 3 ?
166	"	583/117-U-26 #579	No information	2	2.67	1.66	1.09	<i>Canavalia ensiformis</i>
167a	Lab. Anth.	30/1343	Cave on S. Francisco R., undated	8 (5 parched)	.87	.63	.43	T 6
167b	"	"	Same as 167a	1 parched	.98	.60	.43	C 20 ?

TABLE VII (Continued)

Number	Collection source and number	Site, culture and date	Number or quantity of seed	Medial dimensions of seed (cm.)			Species or type
				Length	Width	Thickness	
168	365131. Vial 2	Sunny Glen Cave, Big Bend, Tex. Undated prehist.	12	1.38	.81	.61	C 9
169	" " 1	Same as 168	20 (10)	1.38	.80	.51	C 5
170	" " 1	" " "	1	1.07	.70	.58	C 14a
171	Tucson Rm. 70, Ariz. W. 10, 50	Pt. of Pines. Ca. 1280 A. D.	Ca. 1 qt. (15) charred	1.05	.64	.54	<i>P. vulgaris</i>
172	" " "	Same as 171	Ca. 30 & frag. charred (10)	1.50	.80	.60	"
173	" " "	" " "	3 charred	1.47	.72	.68	"
174	" G.P.11071	Gila Pueblo excavations	3	1.28	.74	.58	"
175	" "	Same as 174	4	1.33	.80	.63	"
176	" G.P.16962	" " "	2	1.20	.72	.57	"
177	" "	" " "	2	.87	.61	.48	C 12
177a	" "	" " "	1	1.37	.90	.56	<i>P. lunatus</i> , L1?
178	" "	" " "	1	1.11	.78	.35	<i>P. vulgaris</i>
179	" G.P.11084	" " "	4	1.46	.78	.67	"
181	" G.P.11055	" " "	2	1.54	.82	.64	"
182	" "	" " "	1	1.14	.75	.47	"
183	" G.P.11032	" " "	2	1.51	.82	.68	"
184	" G.P.11046	" " "	1	1.48	.82	.61	"
185*	" G.P.19691	" " "	1	1.23	.80	.47	C 9
186*	" "	" " "	2	.88	.60	.45	T 6
187	" H.899 H.959 H.111 H.1115	Hodges #793, s.e. Ariz. Pre 1300. Hohokam	6 charred	1.70	1.10	.71	<i>Canavalia ensiformis</i> (Called "lima beans" by Carter, 1945)
188*	M.N.A. 695/NA2519 M223	Kiet Siel, Tsegi Canyon, n. Ariz. P. III, 1274- 1286 A. D.	4 parched	1.38	.88	.62	C 11
189*	" "	Same as 188	(10) parched	1.47	.84	.57	C 19 or 19a
190*	" "	" " "	(11) parched	1.55	.81	.61	C 11
191*	" "	" " "	(15) parched	1.25	.71	.55	C 2
192*	" "	" " "	1 parched	1.35	.83	.55	C 14
193*	" "	" " "	5 parched	1.58	1.02	.54	C 8
194a	" "	" " "	16 parched	1.58	.85	.58	C 19a
194b*	" "	" " "	15 parched	1.40	.81	.57	C 1
195a*	" 692/A85	Murder House, Lay Can- yon, Verde Valley, Ariz. P. III	2 parched	1.46	.84	.58	C 18

195b*	M.N.A. 692/A85	Same as 195a	1	1.24	.72	.55	C 14a
195c*	" "	" " "	1	1.27	.71	.57	C 1
195d*	" "	" " "	1	.95	.61	.39	C 20
196*	" "	" " "	2	1.45	.97	.48	L 1
197	" 712/NA2730.4	Dry cave, Tsegi-ot-sosi. B.M.I.	1 frag.	1.24	.67	.54	C 3 ?
198*	" 909/NA2520.13	Turkey Cave, Tsegi Canyon, Ariz. P. I-III	1	1.49	.78	.65	C 11
199*	" 712/NA2519M97	Kiet Siel, Tsegi Canyon. P. III	2 parched	1.36	.76	.55	C 1
200	" " M97b	Same as 199	1 charred	1.48	.82	.55	<i>P. vulgaris</i>
200a*	" " M97c	" " "	2	1.28	.72	.57	C 2
201	Tucson	Montezuma's Castle, Verde Valley, cent. Ariz., ca. 1300 A. D.	4	.94	.59	.42	C 20
202	"	Same as 201	1	.67	.52	.37	T 1
203*	"	" " "	1	.82	.55	.36	T 8
204*	"	" " "	3	.85	.54	.40	T 6
205*	"	" " "	8	1.47	.95	.55	L 1
205a*	"	" " "	1	1.41	.79	.61	C 11
206*	Univ. Ariz. B.P.6004 4590	Rock Shelter, Overton, Nev. P. II	ca. 100 (15 parched)	.81	.55	.39	C 12
206a*	Univ. Ariz. B.P.5990	Rock Shelter, Virgin R., Nev. P. II	1	1.09	.71	.44	C 11a
207*	Denver 7146	Fremont, s.e. Utah. B.M.	1	1.51	.75	.49	C 3
208*	C.N.H.M.	Hinkle Park, w. cent. N. M. Mogollon	3	1.58	.74	.51	C 19
209*	"	Same as 208	2	1.55	.87	.59	C 3
210*	"	" " "	2	1.48	.80	.56	C 5
211*	"	" " "	1	1.24	.76	.47	C 15
212*	"	Higgins Flat, near Reserve, N. M. After 1100 A. D.	6 frags. charred	1.50	.59	—	C 19
213*	"	Same as 212	60 (frags. charred) (4)	.85	.44	—	<i>P. acutifolius</i>
214*	"	Tularosa Cave, near Reserve, N. M. Mogollon. 300 B. C.—1100 A. D.	2	1.46	.98	.52	C 8
215*	"	Same as 214	2	1.66	.71	.54	C 19
216*	"	" " "	4	1.29	.87	.51	C 7
217*	"	" " "	4	.99	.60	.48	C 6
218*	"	" " "	1	1.50	.88	.60	C 9
219*	"	" " "	2	1.65	.80	.78	C 10
220*	"	" " "	1	1.30	.70	.58	C 1
221*	"	" " "	2	1.11	.69	.58	C 16
222*	"	" " "	19	1.35	.87	.59	C 5
223*	"	" " "	11	1.19	.80	.55	C 15
224*	"	" " "	1	1.65	.90	.59	C 3
225	Berke. 4-4821	Ica Valley, Peru. Early Nazca. 200 A. D.	20 lbs. (5)	2.47	1.37	.61	<i>P. lunatus</i> Yellow-tan to red-brown. Black-eyed, striped, spotted, or self
226	" 4-7255B	San Nicolas, near Supe, Peru. Middle Supe. 1100-1200 A. D.	150 total (5)	1.56	.85	.64	<i>P. vulgaris</i> Dark purple
227	" "	Same as 226	(5)	1.18	.92	.76	<i>P. vulgaris</i> Dark purple

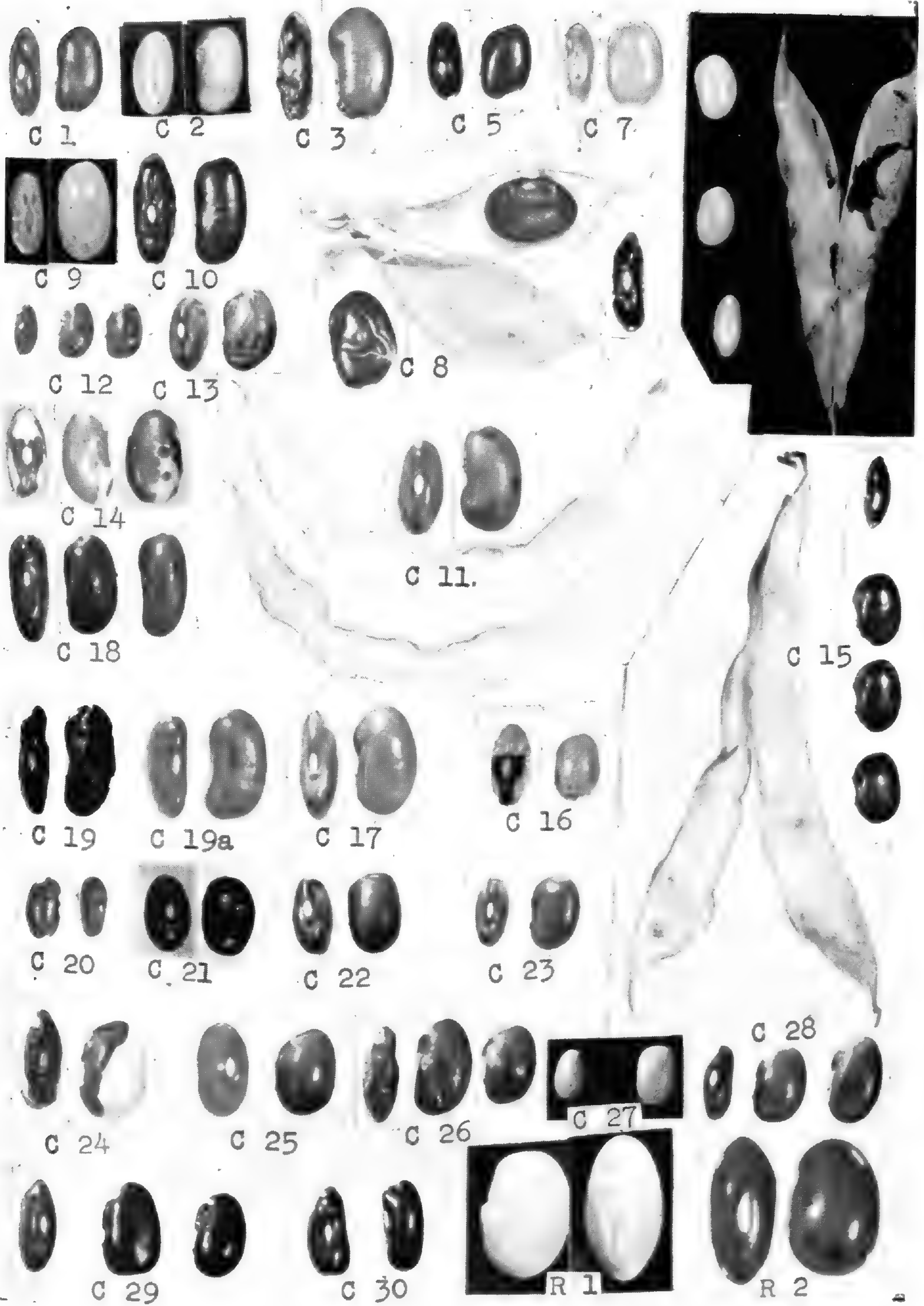
TABLE VII (Continued)

Number	Collection source and number	Site, culture and date	Number or quantity of seed	Medial dimensions of seed (cm.)			Species or type
				Length	Width	Thickness	
228	Berke. 4-7255B	" " "	(5)	1.50	.80	.62	<i>P. vulgaris</i> Red-brown with black eye extending ant. end
229	" "	" " "	(5)	1.51	.95	.64	<i>P. vulgaris</i> Red ground, ca. $\frac{2}{3}$ covered by solid black and ant. mottle
230	" "	" " "	Several hundred (5)	2.83	1.53	.75	<i>P. lunatus</i> Yellow-brown self, some with black ant. mottle
231	" 4-7269	" " "	1	1.80	1.26	.93	<i>P. lunatus</i> Black
232	Mich. 4445 c-3, c-4 4452 c-1, c-2 c-6	Zion Natl. Mon., s.e. Utah	(19)	1.25	.72	.56	C 11
233	" 4452c, c-5, 6	Same as 232	(14)	1.18	.77	.50	C 15
234	" 4445 b 4452 b	" " "	(12)	.88	.57	.38	C 12
235	" 4445 c-2, 4	" " "	5 (3)	1.39	.63	.63	C 19a
236	" 4452c, 5, 6	" " "	(2)	1.34 1.49	.70 .72	.60 —	C 1 ?

EXPLANATION OF PLATE

PLATE 1

Common and runner bean types. Slightly less than natural size.



KAPLAN—PREHISTORIC SOUTHWESTERN BEANS



KAPLAN—PREHISTORIC SOUTHWESTERN BEANS

EXPLANATION OF PLATE

PLATE 2

T 1–T 8. Tepary types; L 1–L 5. lima bean types. Seeds slightly less than natural size.

A. Dried pods and beans, type C11, Mesa Verde, Colorado. Pueblo III.

B. Charred beans, *in situ*. Point of Pines, Arizona.

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No. 3

A REVISION OF RAUVOLFIA WITH PARTICULAR REFERENCE TO THE AMERICAN SPECIES*

ARAGULA SATHYANARAYANA RAO**

Rauvolfia is one of the apocynaceous genera that long has awaited a taxonomic revision. Since the inception of the genus by Plumier¹ in 1703 with two species, the literature has accumulated an abundance of novel specific epithets, based frequently on insufficient material and often due to misconceived synonymy. The 'Kew Index', including all the supplements, lists about 175 names for the world, while the Kew and the Gray Indices together account for about 90 names for the New World alone. An inadequate comprehension of the generic characteristics also has led to the proposal of new genera, such as *Ophioxylon*, *Cyrtosiphonia*, *Dissolaena* and *Heurckia*, to include the Asian and New Caledonian *Rauvolfias*. Bentham and Hooker correctly recognized the synonymy of these genera with *Rauvolfia*. Plants belonging to other genera, and even other families, in the past have been described as *Rauvolfias*. Thus Ruiz and Pavon² described several species of *Citharexylum*, a genus of Verbenaceae, as species of *Rauvolfia*.

Alphonse de Candolle,³ in his treatment of Apocynaceae for the 'Prodromus', included 23 species of *Rauvolfia* and, for the first time, provided lists of dubious and excluded species, even though he maintained *Ophioxylon* as a distinct genus. Schumann's⁴ much later account for the 'Pflanzenfamilien' recognized about 45 species for the world, but the taxonomic treatment necessarily was brief and sketchy. Pichon⁵ estimated about 110 species for the world in a brief synopsis of

¹ Plumier, C. *Plant. Am. Gen.*, p. 19. 1703.

² Ruiz & Pavon, *Fl. Peruv. et Chil.* 2:26. 1799.

³ A. DC. in DC. *Prod.* 8:336-342. 1844.

⁴ K. Schum. in Engl. & Prantl, *Nat. Pflanzenfam.* 4¹⁻²:153-154. 1897.

⁵ Pichon, M., in *Bull. Soc. Bot. Fr.* 94:32-39. 1947.

* An investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University, and submitted as a thesis in partial fulfillment of the requirements for the degree of doctor of philosophy.

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the genus, and included an analytical key and brief Latin diagnosis of the fourteen sections. Pichon's treatment has badly suffered from the fact that he had not examined more than half the species which he listed. Apart from these, no comprehensive monograph of the genus for the world exists.

As far as the New World species are concerned, the most outstanding account is that of Mueller-Argoviensis.⁶ This, however, was limited to about 11 species of Brazil. Markgraf's⁷ essay on the relationships of the American Rauvolfias was more comprehensive and included a discussion of the geography and taxonomy of the tropical American species and provided a key to distinguish the species. He recognized 34 species, including 7 new of his own.

Like several other related members of the subfamily Plumeroideae, several species of *Rauvolfia* contain alkaloids of considerable pharmacological importance. The Asian *Rauvolfia serpentina* recently has attained phenomenal publicity in this regard. This naturally has resulted in the extension of interest in these plants to a far wider informed public.

The present revision of the genus in the New World was begun in September of 1954. It is based on a critical study of more than 2,000 herbarium specimens, and also a handful of plants grown in the greenhouse of the Missouri Botanical Garden. Even though the living plants did not yield any statistically significant data, they played a very important role in suggesting the growth and variation pattern of the species concerned.

Fully realizing that the American Rauvolfias are only a small cluster of the world species and cannot therefore be studied entirely by themselves I have given some time to a critical evaluation of Pichon's fourteen sections. I have examined all the specimens which he had for study, and more, although it must be confessed that I too have not been able to examine material for all the species. Any authoritative and detailed presentation of the taxonomy of the extra-American Rauvolfias will have to await more extensive study.

I have reduced the fourteen sections of Pichon to nine, the American Rauvolfias comprising two of these sections and including 34 species, grouped under four series and three subseries.

HISTORY OF THE GENUS

The Minim monk and pioneer Caribbean botanist, Charles Plumier, founded the genus *Rauvolfia* in 1703 to commemorate Leonhart Rauwolf, a German drug-plant collector who had widely traveled in the eastern countries. Plumier briefly diagnosed two species: *Rauvolfia tetraphylla angustifolia* and *Rauvolfia tetraphylla latifolia*.

Linnaeus,⁸ in adopting the genus, described one species and held another simply as a variety. Thus originated a confusion concerning the identity of the two

⁶ Muell.-Arg., J., in Mart. Fl. Bras. 6¹:30-34. 1860.

⁷ Markgraf, F., in Fedde, Rep. Spec. Nov. 20:111-122. 1924.

⁸ Linn. Hort. Cliff. p. 75. 1737.

original species of Plumier. Rendle,⁹ who was fortunate in having all the relevant original material at the British Museum, has related the entire story and has ably untangled the complex question of synonymy. The description of *Rauvolfia tetraphylla* in the 'Hortus Cliffortianus' was based on Ehret's drawing of a plant that Linnaeus had seen growing in the Chelsea Garden (pl. 3, fig. 3). Linnaeus wrongly equated this with *Rauvolfia tetraphylla angustifolia* of Plumier and considered Plumier's second species merely a variety. He repeated this error in the first edition of the 'Species Plantarum'. This must have been due evidently to the very brief diagnosis of Plumier on which Linnaeus had to depend in deciding synonymy of his *Rauvolfia tetraphylla*. In 1775 Burmann's edition of Plumier's 'Plantarum Americanarum Genera', containing illustrations of both of Plumier's species, was published (pl. 3, fig. 1). Jacquin, apparently unaware of Burmann's work, published in 1760 three names: *R. nitida*, *R. hirsuta*, and *R. tomentosa*, and later, in 1763, gave descriptions for them with an illustration for *R. tomentosa* (pl. 3, fig. 2). His *R. nitida* was synonymous with *Rauvolfia tetraphylla angustifolia* of Plumier, and *R. hirsuta* and *R. tomentosa* were conspecific and identical with *Rauvolfia tetraphylla latifolia* of Plumier and *Rauvolfia tetraphylla* of Linnaeus. Apart from Jacquin's illustration of *R. tomentosa*, I have studied a specimen from Jacquin's herbarium at Vienna, annotated in his own handwriting as *Rauvolfia tomentosa*, which proves the correctness of the above dispositions.

The fact that Linnaeus had become aware of his earlier mistake and that he had also seen the descriptions and illustrations of the two species in Burmann's edition of Plumier is indicated in the second edition of the 'Species Plantarum'. In this Linnaeus described *two* species: *Rauvolfia nitida* and *Rauvolfia canescens*. Linnaeus was correct in citing *Rauvolfia tetraphylla angustifolia* of Plumier in synonymy with *Rauvolfia nitida*, and *Rauvolfia tetraphylla latifolia* of Plumier with *Rauvolfia canescens*. In establishing this new name he did not realize that it was conspecific with his earlier *Rauvolfia tetraphylla*.

Jacquin's *Rauvolfia hirsuta* was allegedly based on the reference to the same specimen of Patrick Browne on which Linnaeus based his *R. canescens*. Hence it is a just cause for surprise as to why Linnaeus should have ignored Jacquin's prior name, even if he had considered the Patrick Browne specimen (pl. 3, fig. 4) distinct from the one of Ehret's drawing on which his *R. tetraphylla* was founded. The Linnaean name *R. tetraphylla* has priority over Linnaeus' later name of *R. canescens*, and is the equivalent of Plumier's second species *Rauvolfia tetraphylla latifolia*. *R. nitida* of Jacquin is equivalent to Plumier's first species *Rauvolfia tetraphylla angustifolia*.

Another question of some concern is that of orthography. Plumier used the Latin version of Rauwolf's name and called the genus *Rauvolfia*. The fact that Rauwolf himself was inconsistent about the spelling of his name, once spelling it Leonhardt Rauwolff and at another time Leonhard Rauwolf, should not concern us

⁹ Rendle, A. B., in Proc. Linn. Soc. Lond. 149:106. 1937. This contains references to all the pertinent literature.

very much here. Linnaeus himself was faithful to the original spelling in all his editions of the 'Genera' and the 'Species Plantarum'. However, Burmann¹⁰ had used three different spellings in quick succession, even in the same page, thus: *Rawolfia*, *Rauwolffia*, and *Rauwolfia*. In the seventh edition of Linnaeus' 'Genera Plantarum' under Reichard, the name was spelled *Ravwolfia* in the text and *Rauwolfia* in the index. The eighth edition under Schreber used *Rauwolfia* and thereafter Willdenow, Alphonse de Candolle, Bentham and Hooker, and Schumann have all used the altered spelling.

Woodson,¹¹ who at first used the original spelling and later came to prefer the "corrected" spelling of *Rauwolfia*, recently has recounted the story of inconsistency in the spelling.¹² In that account, however, he has clearly indicated that though the spelling *Rauwolfia* is contrary to the requirement of the International Code of Nomenclature, yet he preferred the altered spelling in view of popular usage in that form and particularly because the publication was meant for non-botanical readers.

As mentioned earlier, the spelling *Rauwolfia* transgresses Article 82 of the International Code of Botanical Nomenclature.¹³ In this work the original spelling of Plumier, *Rauwolfia* has been consistently used.

MORPHOLOGY AND ANATOMY

Habit: Plants of *Rauwolfia*, except *R. purpurascens* of Panama, which Standley has described rather incredibly as a vine, are undershrubs, shrubs, or trees. Most of them are moderately good-sized shrubs, only a few being either puny undershrubs or big trees. The smallest one, appropriately named *R. nana*, of northern Rhodesia in Africa, attains a height of only 15 cm.

Amongst the American species, almost all species belonging to section RAUVOLFIA are shrubs scarcely exceeding a height of about 2 m. The majority of species of section MACROVOLFIA, on the other hand, are sturdier and more robust shrubs or trees. *R. linearifolia* is the smallest, hardly reaching a height of 5 dm. Amongst the arboreal species, *R. praecox* is the tallest, reaching a height of about 30 m. Most of the other species have an intermediate habit that can be described at times as shrubs, and at other times as trees.

All the plants are lactescent, particularly in the aerial parts. In *R. tetraphylla*, *R. littoralis*, and *R. serpentina*, roots at any stage of their growth have failed, in my experience, to show latex exudation, when cut. But all the other parts above the hypocotyl exude a milky latex on wounding.

Branches: Branching is usually whorled, often rather densely so. The branches are usually terete, rarely angular or even winged to some extent, as in the African

¹⁰ Burmann, J., Plum. Plant. Am. Gen. p. 252. 1755.

¹¹ Woodson, R. E., in Ann. Mo. Bot. Gard. 17:3. 1930; in N. Amer. Flora 29²:134-138. 1938.

¹² Woodson et al. *Rauwolfia: Botany, Chemistry and Pharmacology*. Little, Brown & Co., Boston. In press.

¹³ Int. Code Bot. Nomencl. p. 43. 1952.

R. macrophylla. Except in several species of section RAUVOLFIA, where the young twigs are variously pubescent, the branches are glabrous, and in most species lenticellate to varying degrees.

Nodes: The nodes are emphatically marked by the pectinate glands that usually are present in the leaf axils, as well as by leaf scars. Except in members of series LATIFOLIAE of section MACROVOLFIA, where the terminal nodes are very short and condensed, unlike the more distantly spaced nodes further down, the nodes of all the species are fairly evenly and distantly spaced. However, a condensation of the terminal nodes is evident also in *R. sellowii*, a member of series ANGUSTIFOLIAE. A similar situation exists in the Hawaiian species and in the African *R. macrophylla* and *R. caffra*. This condensation of the terminal nodes, often accompanied by foliage only at the tips of twigs, gives a characteristic appearance to these species.

Leaves: The leaves are whorled, the number in a whorl being variable in different species and sometimes even in the same species. There is also an inconsistency in the shape, size, and indument of the leaves, even in the same species. In spite of this, leaves offer some fairly reliable characteristics for the taxonomic diagnosis of the different species.

The leaves of a given whorl are more or less anisophyllous. They are petiolate or sessile, simple, entire, and ovate, elliptic, lanceolate, obovate, or oblanceolate in outline. The venation is pinnately reticulate, the secondary veins and the vein network extremely variable in clarity on the two surfaces. The secondary veins are mostly arcuate and often unite at the margins to form a marginal vein. However, in species such as *R. nitida*, *R. sarapiquensis*, and *R. pentaphylla* the secondary veins are transverse or almost so.

The leaves are either membranaceous or coriaceous. All the species included in section RAUVOLFIA have membranaceous leaves, whereas the species in the other sections have leaves of variable texture, from membranaceous to coriaceous. The two surfaces usually are opaque, but in species such as *R. cubana*, *R. salicifolia*, *R. praecox*, and *R. nitida*, the upper surface is lustrous and the lower opaque. Though there is a certain amount of difference in the emphasis of the green color on the two surfaces, the upper being usually dark and the lower varying shades of light green, and although Markgraf¹⁴ has used this as a key character, my experience with fresh and dry leaves of identical species has shown that no reliance can be placed on this character. The leaves are glabrous except for some species of section RAUVOLFIA, where one or both surfaces exhibit pubescence to varying degree.

The leaves are variable in size. Like certain species of Asia and New Caledonia, the three Cuban species, *R. cubana*, *R. salicifolia*, and *R. linearifolia*, have rather narrow leaves, the last having the narrowest leaves of all the species. With the exception of a few species which may possess rather narrow leaves at times, most of the species have comparatively broad leaves.

¹⁴ Markgraf, F., in Fedde, Rep. Spec. Nov. 20:113-118. 1924.

The petiole varies considerably in length. In most of the species it is short and becomes obscured by the gradual decurrence of the lamina. In *R. praecox* and *R. sellowii*, however, the leaves have fairly long and quite distinct petioles. The petiole usually is entirely glabrous, but in species of section *RAUVOLFIA* it has also either a sparse or dense glandular covering.

Stipules and Glands: As in other members of Apocynaceae, the nodal region in *Rauvolfia* is marked by a distinctive ring, and the leaf axil is provided with a number of pectinate glands. There has been some difference of interpretation of the nature of these glands. The two observers holding diverse opinions on this score, Woodson and Pichon, have based their conclusions on an observation of more extensive material than was possible for me. Woodson¹⁵ has held, following Gluck's original interpretation, that these appendages are "doubtless in the category of stipules". Pichon,¹⁶ in a lengthy discussion of the stipules and glands of

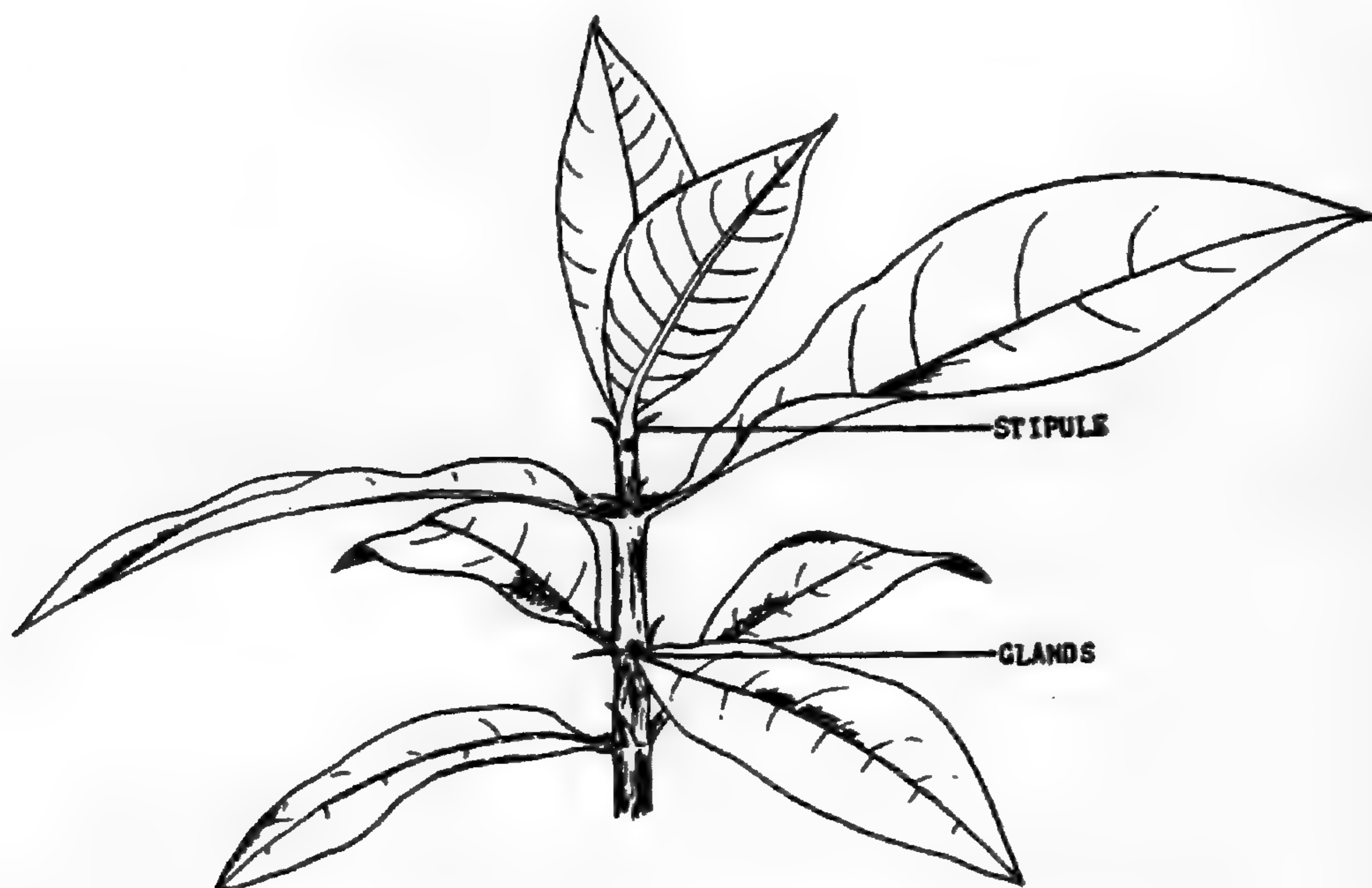


Fig. A. *Rauvolfia littoralis*. Twig showing stipules and glands.

Apocynaceae, has concluded that the glands are in the nature of foliar appendages "*sui generis*" and are distinct from the stipules. There is an obvious lacuna in our knowledge of the morphology and physiology of these glandular appendages.

I have studied the nodal region in living plants of *R. tetraphylla*, *R. littoralis*, and *R. serpentina* with special interest. In the first two species, in addition to the numerous pectinate glands in the leaf axils as well as on the petioles, there are distinct stipules at each node. These stipules are interpetiolar in position, subulate or linear, and are about 2 mm. long. They are deciduous and leave a minute scar on the node (text-fig. A). In *R. serpentina*, the leaf axil does not exhibit many glands, but lateral to the petiole minute subulate structures are clearly observable which are obviously stipules. I have noted similar interpetiolar stipular structures,

¹⁵ Woodson & Moore, in Bull. Torr. Bot. Club 65:148. 1938.

¹⁶ Pichon, M., in Bull. Mus. Nat. d'Hist. Nat. II Ser. 1:467-473. 1949.

in addition to the ubiquitous glands, in young shoots of *R. cubana* preserved in alcohol. Furthermore, in all members of series LATIFOLIAE, there are prominent, deciduous bud-scales which obviously are stipular structures. In *Rauvolfia* at least, examination of both the glands and the stipules leads to the conclusion that the two appendages, although associated, are distinct.

Inflorescence: The inflorescence is terminal. There is no recent discussion in the literature on the position of the inflorescence either in *Rauvolfia* or any of its close relatives in the family. However, some observations and interpretations have been made in certain genera of the allied family Asclepiadaceae. Bugnon,¹⁷ in a study of the inflorescence in *Gomphocarpus fruticosus*, summarized the three principal views on the position of the inflorescence. The three views are: (1) The inflorescence is a sympodium. (2) The inflorescence is an axillary branch. (3)



Fig. B. *Rauvolfia tetraphylla*. Inflorescence as it appears (left), and as it is interpreted (right).

The inflorescence is one branch of a dichotomy. On the basis of his studies, Bugnon has rejected all three views and has put forward a rather ambiguous interpretation of his own. Holm,¹⁸ on the other hand, in his studies on the inflorescence of species of *Sarcostemma*, has preferred the classical interpretation of Payer and others, and has held the inflorescence to be a sympodium.

I have studied carefully the development of the inflorescence in living plants of *R. tetraphylla*. The vegetative shoot sooner or later ends in a simple dichasium. By the time the terminal flower-bud is ready to blossom, one of the axillary buds in the subjacent leaf whorl becomes active and soon develops a vigorous shoot. In this process the originally terminal cyme is gradually pushed to one side and the axillary shoot increasingly veers to assume a terminal position (text-fig. B). The inflorescence thus becomes interpetiolar in position after this spatial transposition. Holm has pointed out that the lateral sliding of the inflorescence of *Sarcostemma*

¹⁷ Bugnon, F., in Bull. Soc. Bot. Fr. 102:105-114. 1955.

¹⁸ Holm, R., in Ann. Mo. Bot. Gard. 37:485-486. 1950.

occurs alternately at successive nodes and as the result the inflorescences appear to be in two rows. In *R. tetraphylla*, however, the situation is further complicated by the leaves being in whorls of four. There is no constancy or visible pattern in the order in which axillary buds at any given node develop, or the relationship of the inflorescence to any one axillary bud in the whorl. Commonly, however, only one of the axillary buds in the whorl is developed, be it associated with a smaller or a larger leaf. Yet occasionally two, three, or even all four axillary buds develop, in which case the terminal nature of the inflorescence is left in no doubt whatever. Although these observations have been made in only the living plants of one species, a careful study even of herbarium material of the rest of the species confirms the view that the inflorescence is primarily terminal.

The most generalized type of inflorescence in *Rauvolfia* is the dichasium. Woodson,¹⁹ in a discussion of the inflorescences of Apocynaceae and their phylogenetic significance, concluded that a reduction has taken place in the originally complex inflorescence. This trend is also evident in the inflorescence of *Rauvolfia*. The most complex type of inflorescence is the "aggregate dichasium". A wide range of variation is exhibited within this type alone, in numerous species, by differences in the degree of branching of the peduncle and the relative proportions of the branches. A further contributing factor is the nature of the ultimate cymule, which may be umbelliform or corymbiform.

The reduction trend is perhaps best exemplified by the species of section RAUVOLFIA. A species such as *R. littoralis* has much-branched, multiflorous inflorescences. On the other hand, a closely related species, *R. tetraphylla*, possesses few-flowered, mostly unbranched inflorescences. The fact that even within a single species such as *R. tetraphylla* or *R. ligustrina* the two extremes from a much-branched, multiflorous, to an unbranched, pauciflorous condition is not uncommon contributes further to the idea of reduction in the evolution of the inflorescence. Incidentally, much value was formerly attached to the inflorescence patterns as key characters, but the variation noticed in this study renders them valueless. A pauciflorous inflorescence is also present in species such as *R. macrantha* and *R. paucifolia*, both belonging to the essentially pluriflorous section MACROVOLFIA.

The peduncle in different species is variable in length and in degree of branching. It is usually glabrous, but in the species of section RAUVOLFIA, it may be variously pubescent.

The pedicel is usually distinct and of varied length. In some of the African and Asian species, however, it is much reduced or often even wanting.

Flower: As in the other genera of Apocynaceae, the flower in *Rauvolfia* is regular, bisexual, tetracyclic, and pentamerous, usually pedicellate, rarely sessile as in some African and Asian species. It is relatively small, except in several species of sections MACROVOLFIA, OPHIOXYLON, and OPHIOXYLANTHUS. In several species the flowers often exude a pleasant odor.

¹⁹ Woodson, R. E., in Ann. Mo. Bot. Gard. 22:1-42. 1935.

Calyx: The calyx is usually green, synsepalous, and mostly campanulate with the lobes usually imbricate in aestivation. The lobes vary considerably in size, shape and texture. In all the American species they are considerably shorter than the corolla. They are ovate to lanceolate in shape, with the apex varying from acute to obtuse or rounded. They are eglandular within and usually glabrous without, except in section RAUVOLFIA where the calyx is variously pubescent without. In some species of section MACROVOLFIA, they are either ciliate or glandular-dentate at the margin.

Corolla: The corolla is sympetalous and of varied shapes: urceolate, campanulate, salverform, or infundibuliform. It is usually white, but some of the species show either lilac or rosy hues or are even variously spotted.

The corolla-tube is generally cylindrical, sometimes constricted at the throat, and sometimes dilated. It is usually glabrous without and variously pubescent within. The extent of pubescence in the tube, the relative proportion of the tube to the corolla-lobes, on the one hand, and to the calyx-lobes, on the other, and the region of constriction and dilatation, all offer fairly reliable taxonomic criteria.

The corolla-lobes are sinistrorsely contorted in aestivation. They are ovate, obovate, elliptic or oblong in outline with acute or obtuse apices. In species of section ENDOLOBUS, the apices are inflexed in the bud.

Stamens: The stamens are epipetalous, five in number and fairly uniform in all the species. The anthers are ovate, acute or apiculate, and slightly varying in size in different species. They are free from each other and the stigma. The thecae are fully fertile and enclose free spherical or subspherical, triculcate pollen grains. The connective in species of sections MACROVOLFIA, OPHIOXYLON and OPHIOXYLANTHUS appears to be projecting in the form of a conical hump on the dorsal surface of the anther, just at the point of attachment with the filament. There is a distinct filament in all the species, though it may vary in length from species to species.

Pistil: The pistil is superior, bicarpellary, the ovary being variously syncarpous or apocarpous. The ovary is of various shapes: globose, cylindrical, ovoid or obovoid. Each locule encloses one or two anatropous ovules, on an axile or ventral placenta.

The style is simple, linear or columnar, glabrous except in the African *R. vomitoria*, where it is villous at the base.

The stigma-head is prominent and variously shaped: depressed-capitate, calyptriform, tympaniform or sub-mitriform. Miers²⁰ was the first to use the term "clavuncle" to describe the stigma-head of Apocynaceae. The stigma-head possesses a basal ring or collar, a contracted or expanded median region, and a distal indusium encircling the biapiculate apex. Pichon has used the term "strophium" to indicate the median region of the stigma-head. Much of the variation in the shape of the stigma-head in the several species is brought about by a difference in the relative de-

²⁰ Miers, J. Apoc. S. Am. p. 2. 1878.

velopment of the three regions and the presence or absence of hairy induments on them. I have noticed in *R. tetraphylla* a frequent clustering of masses of pollen grains around the base of the apiculate tip and in the depression formed by the distal indusium, an observation in consonance with that of Miers. However, it is not possible to conclude from this observation whether the depression itself is truly receptive or if it is the apiculate tip that is so. As there is some confusion in the precise use of the term "clavuncle", I have preferred to use the simpler term stigma-head.

The shape of the stigma-head differs with the age of the flower and becomes distorted in the pressed herbarium specimens. This renders the use of the stigma-head valueless as a taxonomic character.

The disc is annular or cupuliform, usually shorter than the ovary which it encircles. It is usually entire.

Woodson,²¹ in an elaborate study of the floral anatomy of 39 genera and 60 species of Apocynaceae, commented on the inconsistency in the vascular pattern, particularly in the calyx of *R. nitida* (referred to as *R. tetraphylla* in that paper). He also pointed out the carpelloid nature of the disc or nectary.

In a taxonomic treatment it is not my intention to digress in an account of the floral anatomy. However, I was able to make a few observations concerning flower-buds of *R. tetraphylla* and *R. cubana* which Dr. Woodson had kindly preserved for me. After a study of whole cleared mounts, hand and microtome sections of flower-buds of these two species, no inconsistency in the vascular pattern of the calyx was observed. In both there is a ring of five sepal traces, each of which gives off two lateral traces just prior to entering the calyx-lobe. The corolla and the stamens each have a typical and consistent vascular pattern. The traces to the disc emerge as branches of traces going up to the two carpels, bearing out the carpelloid nature of the disc. Also, I could find no evidence for Boke's²² interpretation of the corolla-tube as being partly receptacular in origin.

Fruit: The fruit of *Rauvolfia* is a drupe. It is variously syncarpous or apocarpous. The calyx is persistent on the fruit in all the species and the pedicel tends to become stouter in the fruit. The fruit is comparatively small, syncarpous and globose in all species of section RAUVOLFIA. In the species of other sections, however, it is rather large and variously syncarpous or apocarpous. The biggest fruit is that of the Amazonian *R. paraensis*, about 40 mm. in diameter, while the smallest perhaps is that of the Bahian *R. blanchetii*, about 6 mm. in diameter.

The fruit is either rounded or somewhat flattened. The two lobes in hemisyncarpous fruits or the drupelets in the apocarpous fruits differ considerably in their mutual relationship as well as in shape. They may either be parallel or divergent to differing degrees. These characters offer trustworthy taxonomic criteria for specific diagnosis. With the gradual ripening of the fruit there is a change in the color of the pericarp from green to red and black. This is true for almost all the species. The exocarp is usually thin and membranaceous. The

²¹ Woodson & Moore, in Bull. Torr. Bot. Club 65:147. 1938.

²² Boke, N. H., in Am. Jour. Bot. 35:422-423. 1948.

mesocarp is fleshy, rarely slightly fibrous, and the endocarp stony. *R. linearifolia*, the dwarf undershrub of eastern Cuba, has fruits with unusually thin pericarps resembling superficially a follicle more than a drupe. The stone is usually sclerotic, with a smooth or rugose outer surface and a smooth inner surface. It is generally ovoid, with a stout basal region and a rather flattened distal region. The stone also offers some reliable key characters. In all the species there is a tendency towards the abortion of one of the carpels during development. Although a considerable number of extra-American species possess apocarpous fruits, *R. sellowii* is the only American species on which they occur.

Seed: The seed is albuminous and is usually symmetrically ovoid. In *R. nitida* of section MACROVOLFIA and in all the species of section RAUVOLFIA the seed is slightly gibbous. This is true also in several African and Asian species. The seed-coat is membranaceous and easily separable from the endocarp, on the one hand, and the albumen, on the other. The albumen is carnose, entire, and fairly abundant.

The embryo is typically dicotyledonous, either erect or slightly to strikingly arcuate. Usually it is about as long as the seed, with the terete hypocotyl about equal to the usually ovate, obtuse cotyledons.

Seedling: I have observed germination in the seeds of *R. tetraphylla*, *R. littoralis*, and *R. serpentina*. Owing to the sclerotic endocarp, they require from ten to thirty days for the first signs of germination. The radicle emerges first, and three to four days later the crook of the plumule appears and soon becomes erect and disentangles the cotyledons from the still-persisting endocarp and seed-coat. The cotyledons expand and serve as the first pair of green leaves for the seedling. In *R. tetraphylla* and *R. littoralis* the cotyledonary leaves are ovate and obtuse, but in *R. serpentina* they are orbicular, rounded, or slightly emarginate. Only pairs of decussate leaves are produced in the subsequent two or three nodes of the actively growing seedlings. The fourth node, however, almost invariably exhibits the characteristically whorled phyllotaxy of the adult plant. The plants of *R. tetraphylla* appear to be precocious and flower when they are about four months old.

Anatomy: The literature contains very little reference to the anatomy of *Rauvolfia*. Metcalfe and Chalk²³ have remarked briefly on the anatomy of Apocynaceae. The recent importance of the roots of *Rauvolfia*, from the point of view of the pharmacognosists, has required a precise knowledge of their anatomy for accurate determination of the species and for detection of adulterants.

Woodson²⁴ has recently reported on the anatomy of about twenty *Rauvolfia* species, of which nine are American. At least in one example there is no verifiable herbarium material available, resulting in a certain amount of doubt. Even as the cytologists are increasingly depositing specimens of plants which they investigated in an herbarium, it is strongly recommended that anatomists and biochemists

²³ Metcalfe, C. R. & Chalk, L. *Anatomy of the Dicotyledons* 2:914. 1950. Oxford.

²⁴ Woodson et al. *Rauvolfia: Botany, Chemistry and Pharmacology*. Little, Brown & Co., Boston. In print.

too realize the advantage of preparing herbarium specimens for resolving future questions of identity.

In a genus characterized by copious latex, surprisingly, no laticiferous tubes have been observed in *Rauvolfia* roots even though artifacts simulating latex tubes have been noticed in the Asian *R. serpentina* and *R. cambodiana*. This is in keeping with the observation of excised roots of living plants.

The roots are tetrarch and in the mature state have metaxylem to the exclusion of the pith. The outer bark is of varying thickness and consists of phloem and phellem. The bark may be flaky or indefinitely ribbed. The color of the bark also varies in relation to the color of the soil in which the roots grow. The secondary phloem is characterized by the presence of sclerotic cells, either in the form of prominent bands or of scattered nests of few to many cells. The xylem consists of vessels, tracheids, and xylem parenchyma. Growth rings are not present in many of the species. The diameter of the vessels varies considerably, offering a reliable guide for species determination.

The phloem and xylem characteristics show a trend—possibly phylogenetic—indicative of a transition from the arboreal to the sub-herbaceous habit. The phloem exhibits a change from strongly radially arranged sieve cells collapsible on desiccation in the arboreal species, to weakly radial, non-collapsible sieve cells in the shrubby species. There is a parallel change in the prominence of the sclerotic nests of the phloem. An associated change has been noticed in the xylem, the tracheary wedges consisting roughly of about 50 per cent of the volume in the arboreal species and 25 per cent or less in the shrubs. The vessels in the arboreal species are wide, as much as 250μ in diameter, while those of the least ligneous shrubs are as narrow as 20μ . To what degree phylogenetic value can be attached to these trends is an open question. Based as the study was on only about 20 species for the world, it is not surprising that Woodson has "failed to associate definite anatomical characteristics with Pichon's fourteen sections".

VARIATION AND HYBRIDIZATION

The multiplicity of specific names for essentially similar plant populations of *Rauvolfia* has been due to an inadequate awareness of the range of variability. Many of the species, particularly in the New World, show variation in leaf and inflorescence characters which has led astray earlier students of the genus. *R. mollis*, from Mato Grosso, and *R. paraensis* and *R. pentaphylla*, from the Amazon area, offer examples for such variation to a limited degree. *R. macrophylla*, *R. caffra* of Africa, and *R. verticillata* of Asia, also have caused much taxonomic confusion by their variability.

Two of the American species that have been the cause of vexatious problems of synonymy are *R. tetraphylla* and *R. ligustrina*. Fairly abundant material of these two species has afforded me an opportunity for a statistical analysis of variation in some measureable characters. A perusal of the literature provided me with a list of characters that had attracted the attention of the earlier students. These

characters are: leaf number per whorl, leaf shape and size, degree of anisophylly, degree of clarity of the vein network, leaf indument; peduncle length and degree of branching; flower number per peduncle; corolla-tube length and fruit size. Of these, the characters that I have measured are indicated by their mean values in the following chart (p. 266).

At first I obtained data for small populations restricted to narrow areas. As these data did not reveal any pattern of variation, as a matter of convenience I divided the populations into three major areas: Antilles, Central America, and South America. The variability in leaf shape in *R. tetraphylla* is erratic and cannot be correlated with any other character. The ideograph and the accompanying mean values (fig. 1 of chart) show to what extent the measured characters of these populations are alike. An evident variable character is the pubescence of the leaf. The Central American populations have an overwhelmingly large number of glabrous plants; the Antillean are the most pubescent; while the South American populations are intermediate with puberulent leaves. This is true in spite of the disparity in the sample size from the three areas. However, in each of these regions it is not unusual to encounter plants exhibiting the extreme conditions of pubescence. Because of inconsistency in the variability of these populations, I would not consider according even subspecific rank to them.

The second species analyzed, *R. ligustrina*, indicates a quantitative variation in leaf size in the three areas (fig. 2 of chart). Here again a disparity in the sample size makes the conclusion somewhat uncertain.

In *R. tetraphylla*, I was able to note the trend in variation and to compare my data from herbarium material with data from plants growing in the greenhouse. I have observed one plant each from Costa Rica, Cuba, and the Dominican Republic, and about twenty plants from Lucknow and the Anamalai hills, both introduced in India²⁵ from the Antilles.

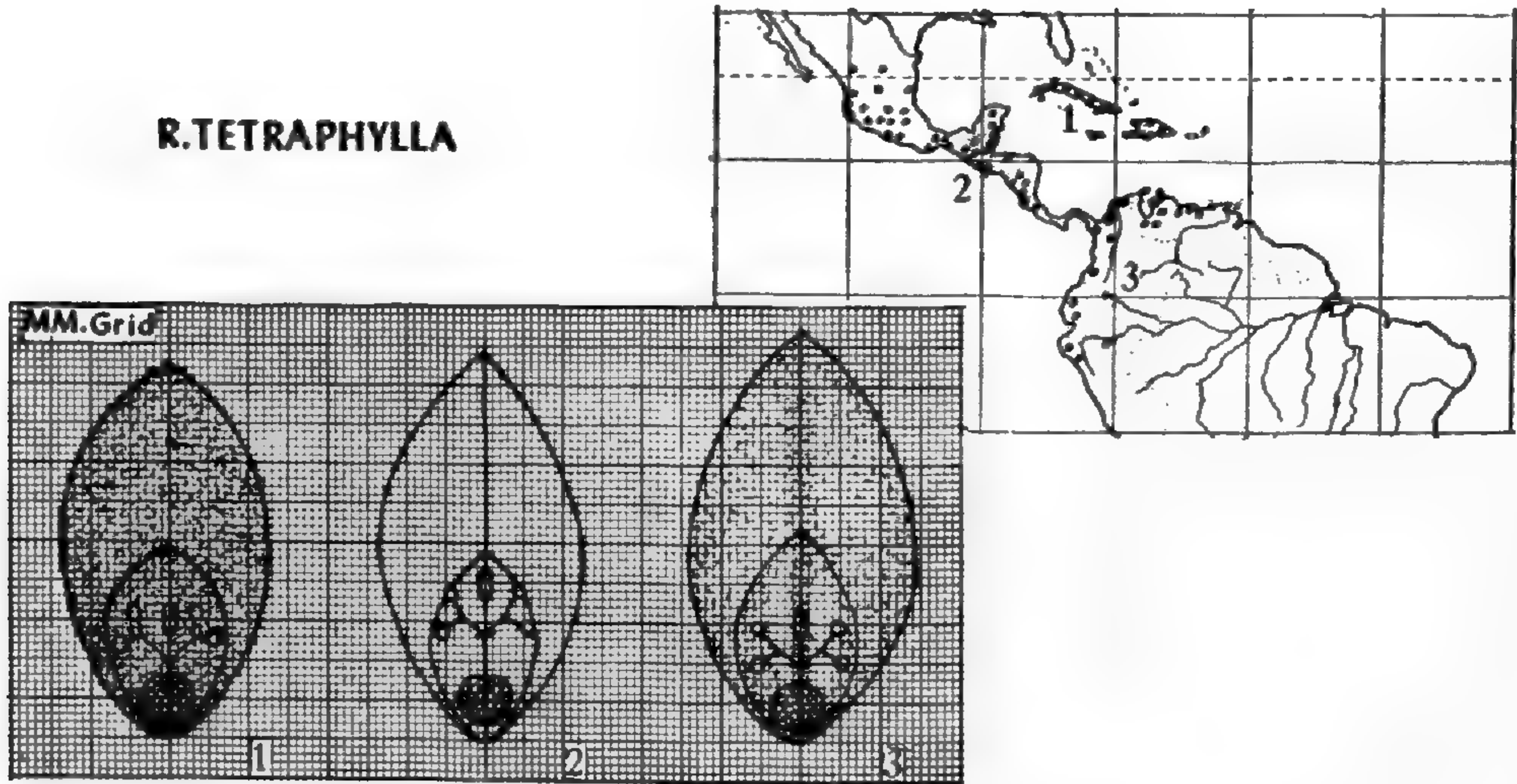
A study based only on herbarium material cannot be expected to provide an explanation for this variability in these two species. However, it may be significant that these two species are widespread and have been well known to man and associated with his environment. As to what extent variability is inherent in these species and to what extent it may be due to extraneous agents can only be resolved by carefully planned cytogenetic experiments. The large-scale cultivation of *R. tetraphylla* plants in some areas, and their spreading as weeds in India, and more recently in Australia, should also afford ideal opportunity for a detailed field study of variation in this species.

Hybridization: Herbarium material is not ideal for providing conclusive data regarding hybridization. However, often specimens which could not be referred with certainty to one of two sympatric species pointed to the possibility of introgression. Several such specimens were encountered, particularly of *R. tetraphylla* populations. *R. tetraphylla* is sympatric, in the range of its distribution, with three closely related species: *R. ligustrina*, *R. littoralis*, and *R. viridis*. The fre-

²⁵ Voigt, J. O. Hort. Suburb. Calcut. Cat. Pl. p. 202. 1845.

Region	Sample size	Largest leaf l'gth × b'dth	Smallest leaf l'gth × b'dth	Leaf indument			Length of peduncle	Number of flowers per peduncle	Fruit	
				Glabr.	Puber.	Pubes.			Height	Breadth
1. Antilles	77	(cm.) 5.9 × 2.6	(cm.) 3.0 × 1.8	9	17	51	(cm.) 1.2	5	(mm.) 6.4	(mm.) 7.2
2. Cent. America	255	6.2 × 2.9	3.0 × 1.8	220	35	0	1.3	5	6.2	7.1
3. So. America	47	6.6 × 2.8	3.4 × 1.4	4	39	4	1.3	5	6.4	7.5

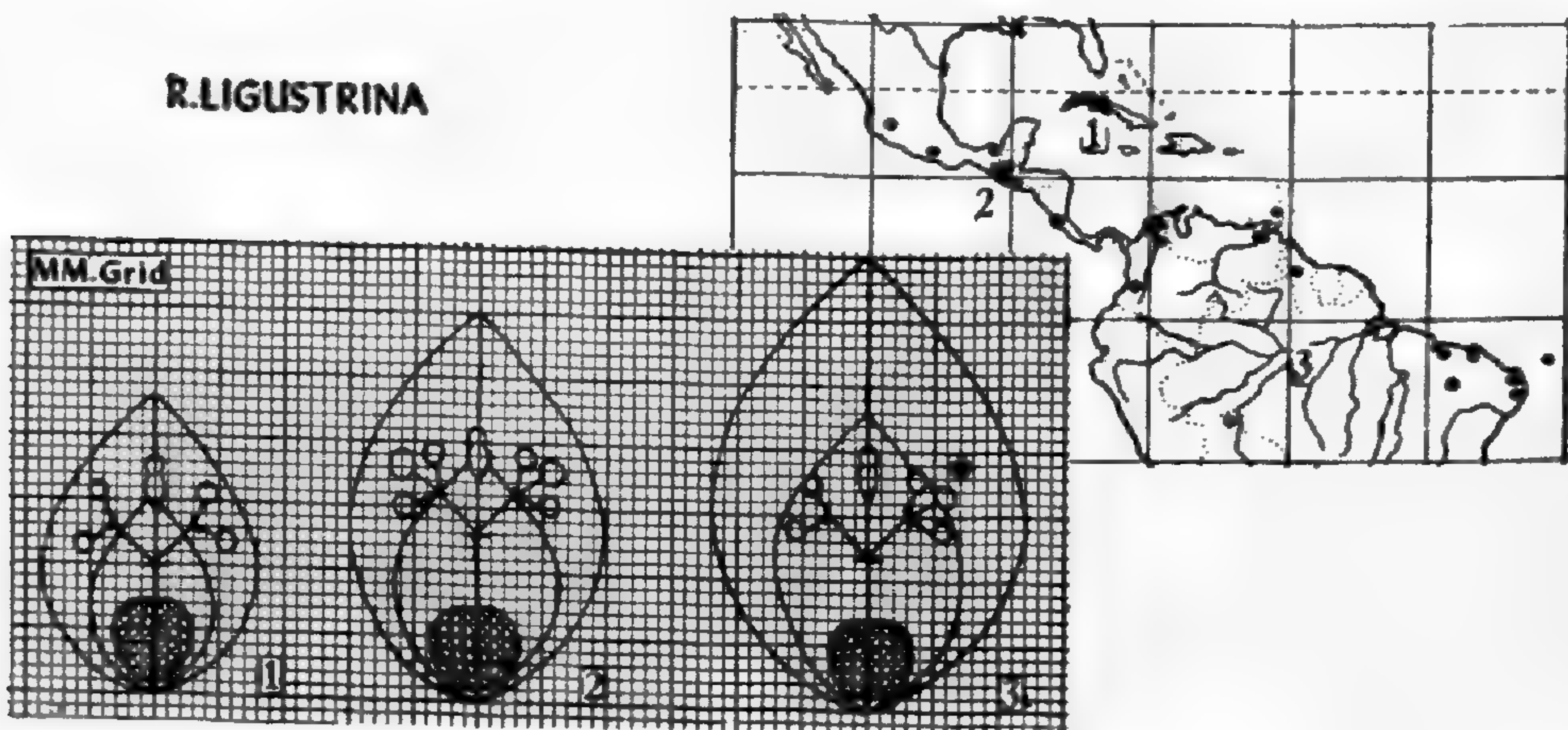
Rauvolfia tetraphylla



1

Region	Sample size	Largest leaf l'gth × b'dth	Smallest leaf l'gth × b'dth	Length of peduncle	Number of flowers per peduncle	Length of corolla tube	Fruit	
							Height	Breadth
1. Cuba	21	(cm.) 2.3 × 1.6	(cm.) 1.5 × 1.1	(cm.) 1.0	5	(mm.) 3.0	(mm.) 5.6	(mm.) 6.5
2. Cent. America	15	3.0 × 2.0	1.8 × 1.3	1.3	7	3.0	5.6	6.7
3. So. America	39	3.5 × 2.4	2.2 × 1.2	1.2	6	3.0	5.5	6.4

Rauvolfia ligustrina



2

Chart showing variation in two species of *Rauvolfia*

quency of fruits with abortive embryos in many of these examples indicates a genetic abnormality and lends further support to the possibility of hybridization.

An instance of what, in my opinion, is very possibly a complex hybrid has been described as a distinct species, *R. mollissima* Mfg. The original description of this species is based on two specimens: *Tonduz 13940* from Costa Rica, and *Karsten 17b* from Colombia. I have examined both specimens. Of the two, the *Tonduz* specimen inclines more toward *R. littoralis* in leaf shape and size, inflorescence branching, and flower number, though to a large extent, particularly in leaf indument, it resembles the other suspected parent, *R. tetraphylla*. Similarly, the *Karsten* specimen, while resembling *R. tetraphylla*, still indicates a close approach in those characters to *R. viridis*. I have treated *R. mollissima* as a synonym of *R. tetraphylla*. The situation is obviously complicated by a complex, interbreeding involving several back-crosses. Also, I have strongly suspected hybridization in *R. paraensis* and *R. sprucei*. I am recording these opinions with the hope that they will stimulate further observations in the field.

ECONOMIC USES

The many names existing for several *Rauvolfia* species throughout the world testify to man's familiarity with these plants. I have listed the known common names separately under each species.

The most significant use of *Rauvolfia* plants has been in the healing of certain chronic human ailments. The raw roots of the Asian *Rauvolfia serpentina* have been used for several centuries in treating intestinal disorders and in heart and nervous conditions. Recent biochemical and clinical investigations have amply proved the efficacy of the chemical contents of the roots in alleviating high blood pressure and in calming excitable subjects. The invaluable nature of the chemical contents naturally has led to an extensive investigation of the substances involved, not only in the famed Asian species but also in many of the related ones.

Much information on the botany and chemistry of *Rauvolfia serpentina* is available and I do not propose to duplicate it here. Monachino²⁶ has a detailed contribution on the botany of the species, while the New York Academy of Sciences²⁷ has published a symposium on the chemistry, pharmacology, and clinical nature of the active alkaloid, reserpine, the most valuable of about 30 alkaloids so far isolated from the roots of *R. serpentina*. Furthermore, Feuell²⁸ has a more general account of several important *Rauvolfia* species which is particularly valuable for its exhaustive bibliography.

With the recent pharmacological vindication of the early claims from folk-lore of the curative properties of *serpentina* roots, attention has now been directed to some related species. Several additional species have been found to contain the reserpine in exploitable quantities. Almost all commercially extracted reserpine is

²⁶ Monachino, J., in *Econ. Bot.* 8:349-365. 1954.

²⁷ Miner, R. W. (editor). *Ann. N. Y. Acad. Sci.* 59:1-140. 1954.

²⁸ Feuell, A. J., in *Colon. Pl. & An. Prod.* 5:1-33. 1955.

now obtained from the African *R. vomitoria* and the circum-Caribbean *R. tetraphylla*. A detailed account by Schittler²⁹ of the chemistry of the several species so far investigated is expected in a forthcoming publication.

In America *R. tetraphylla* and *R. nitida* have been much used in indigenous medicine. The decoction of the bark and leaves has been used as a gargle and internally administered in intestinal disorders and in syphilitic infections. The bark has been further used as an unguent on skin eruptions. The fruits are reputedly poisonous. In Nicaragua the fruits of *R. tetraphylla* have been used as a source of ink and a black dye.

Standley³⁰ and Roig y Mesa³¹ have recounted these numerous uses for the two species in Central America and in Cuba respectively, while Descourtilz³² has given a picturesque account of the deleterious properties of *R. nitida*, which he refers to as *R. canescens*. An accurately colored illustration of the plant in the text leaves no doubt regarding the identity of the species. A confusion on this count has led Feuill to attribute all properties of *R. nitida*, described by Descourtilz, to *R. canescens*, which is identical with *R. tetraphylla* of Linnaeus.

Apart from the medicinal importance, some of the arboreal species are useful as sources of timber. Record and Hess,³³ however, do not attach much importance to the value of *Rauwolfia* as a source of timber. They describe the wood as of fine texture, easily worked, but perishable in contact with the ground. Monteiro da Costa mentions the use of *R. pentaphylla* wood for "furniture and turnery work." *R. nitida* has been introduced into Florida and has been recommended as an efficient wind-break on the seashore.

R. salicifolia and *R. cubana* bushes, with their glistening coriaceous leaves and fragrant flowers, invite serious consideration as ornamental plants in tropical and subtropical gardens and parks.

GEOGRAPHY

I will confine myself here to a general discussion of the geography of the genus. Data concerning the ecology and distribution of individual species have been included with the descriptions, while the accompanying maps indicate areas which could be accurately plotted on the outline maps with the help of the 'Lippincott's Gazetteer of the World' and an assortment of large-scale maps published by the National Geographic Society and other such agencies.

Rauwolfia is a pantropical genus, with a distribution extending to the 30th parallel in the north as well as the south. In addition to tropical America, there are numerous species in Africa, Asia, and in several of the Oceanic islands. How-

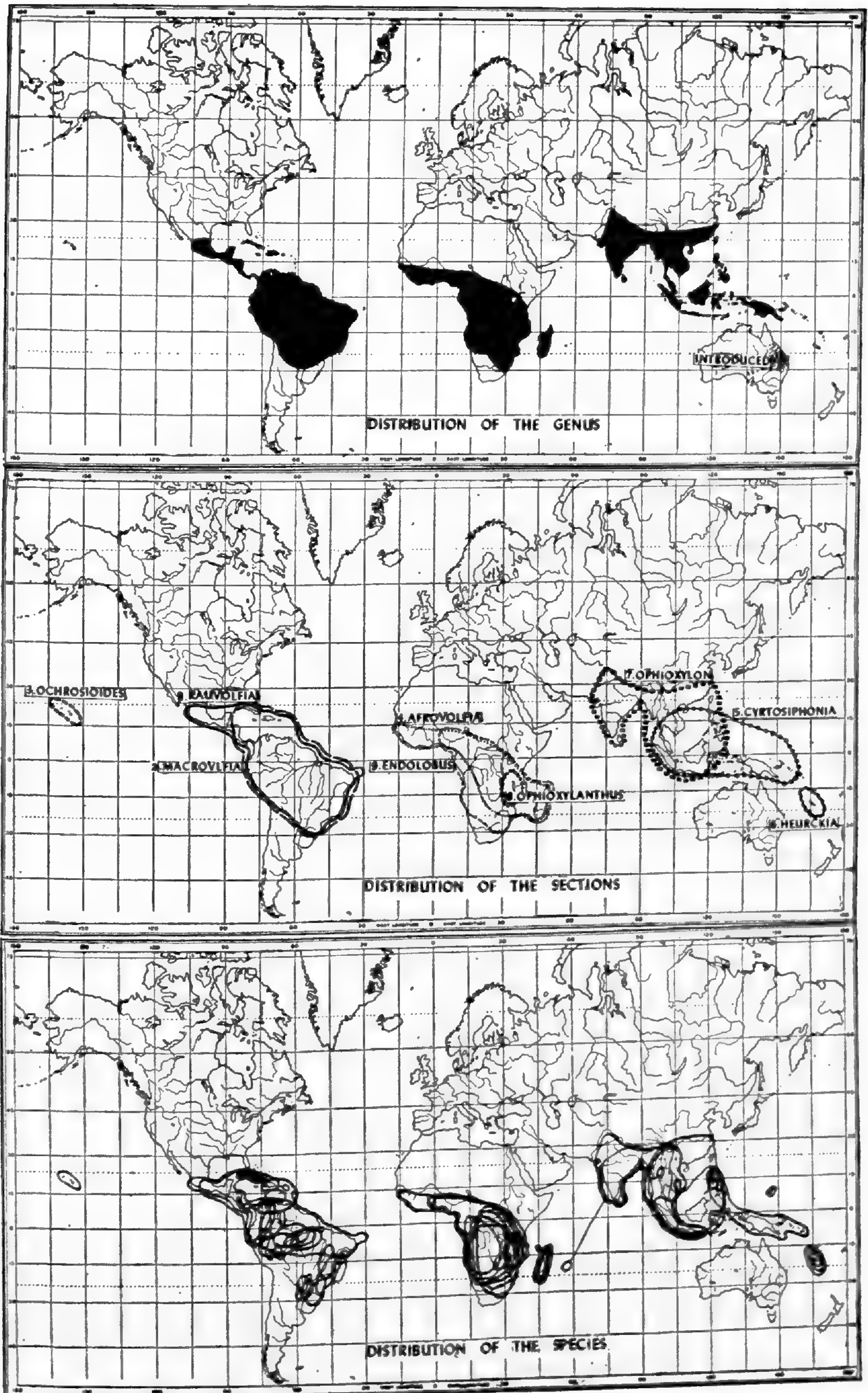
²⁹ Schittler, H., in Woodson et al., *Rauwolfia: Botany, Chemistry and Pharmacology*. Little, Brown & Co. Boston. In press.

³⁰ Standley, P. C. Trees and shrubs of Mexico. In Contr. Smithsonian Inst. 23:1153. 1924.

³¹ Roig y Mesa, J. T. Plant. Medicin. Aromat. Venen. de Cuba. p. 631. 1945. Havana.

³² Descourtilz, M. E. Fl. Med. Ant. 3:151. 1827.

³³ Record, S. J. & Hess, R. W. Timbers of the World. p. 66. Yale Univ. Press. 1943.



MAP 1

Distribution of *Rauvolfia* throughout the world. (All outline maps used in this paper are from Goode's Series of Base Maps, University of Chicago Press.)

ever, it is not native to Australia where *R. tetraphylla*, the American species, has been introduced and has now become naturalized in a small area in Queensland (Map 1). The distribution pattern of the sections and the species suggests three or four centers of differentiation. In each of the major land areas there are one or two widely distributed species. Significantly, these are also widely variable and have broad tolerances to varied environment. In America, *R. tetraphylla* and *R. ligustrina* are the two "wide" species. In Africa, *R. caffra*, *R. macrophylla* and *R. vomitoria* are fairly widespread, while in Asia *R. densiflora* and *R. verticillata*, closely followed by *R. serpentina*, have a wide distribution.

The American *R. tetraphylla* flourishes equally well in much-exposed, sunny, sandy soils near the seashore and in wet and marshy, shady grasslands at elevations of about 2000 m. The Asian *R. serpentina* is similarly characterized by a wide ecological range. Such traits should make these two commercially useful species easy for domestication and large scale cultivation.

The distribution of the sections and the world species can also be obtained by a reference to Map 1. The large number of species that are endemic is rather unusual. Willis³⁴ has stated that he has no doubt whatever that in the great majority of cases endemics are simply the early stages of dispersal of species which as yet have not had the time nor the opportunity to spread far. In *Rauvolfia*, however, evidences of comparative morphology, and to some extent of anatomy, points to the contrary. It is the widespread species that are relatively the most advanced, while the endemics are relatively primitive from the standpoint of comparative morphology.

The problem of plant distribution is an ever-present challenge to the botanist. Particularly in a genus such as *Rauvolfia*, with no fossil history for the genus nor for almost the entire family, an attempt to solve the problem is fraught with disillusion and disappointment. It is perhaps for this reason that both Pichon and Woodson, though they have included considerable information on the geography of many genera, have not attempted to integrate the information and present ideas on the origin and area of the family.

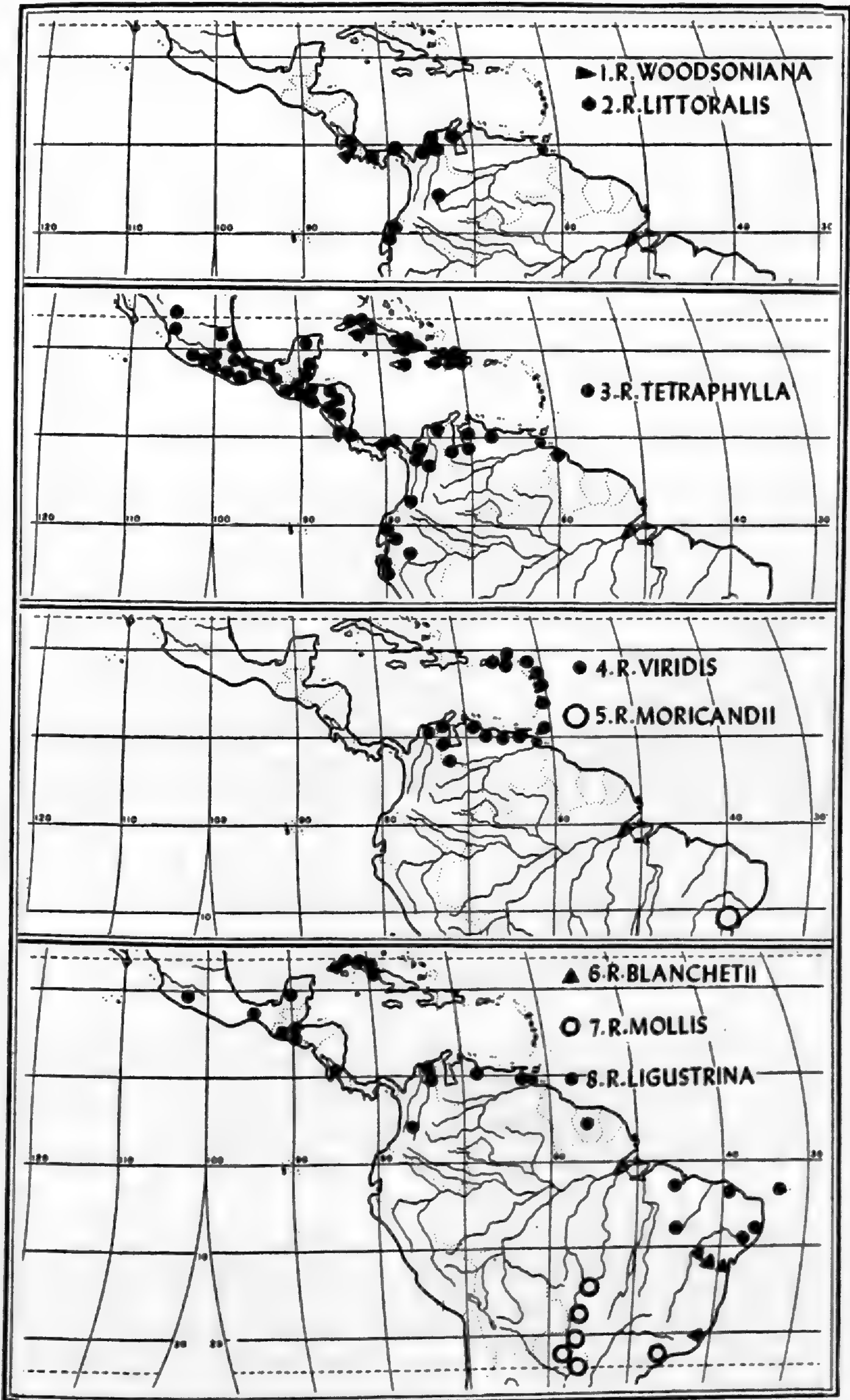
In the past, with an innocent belief in the existence of innumerable convenient land bridges or in the drifting apart of the originally concentrated land masses, it was fairly easy to advance hypotheses concerning various problems of plant dispersal. Thus Macfarlane,³⁵ with an unquestioned belief in land bridges, had no further difficulty in believing that many of the apocynaceous genera had their origin in West Africa, from where they migrated to America, on the one hand, and to Asia, on the other. Both Good³⁶ and Schmidt³⁷ have recently reviewed such ideas in plant and animal geography respectively. Schmidt has pointed out

³⁴ Willis, J. C. The birth and spread of plants. In *Boissiera* 8:509. 1949.

³⁵ Macfarlane, John M. *The Evolution and Distribution of Flowering Plants*. Philadelphia. 1933.

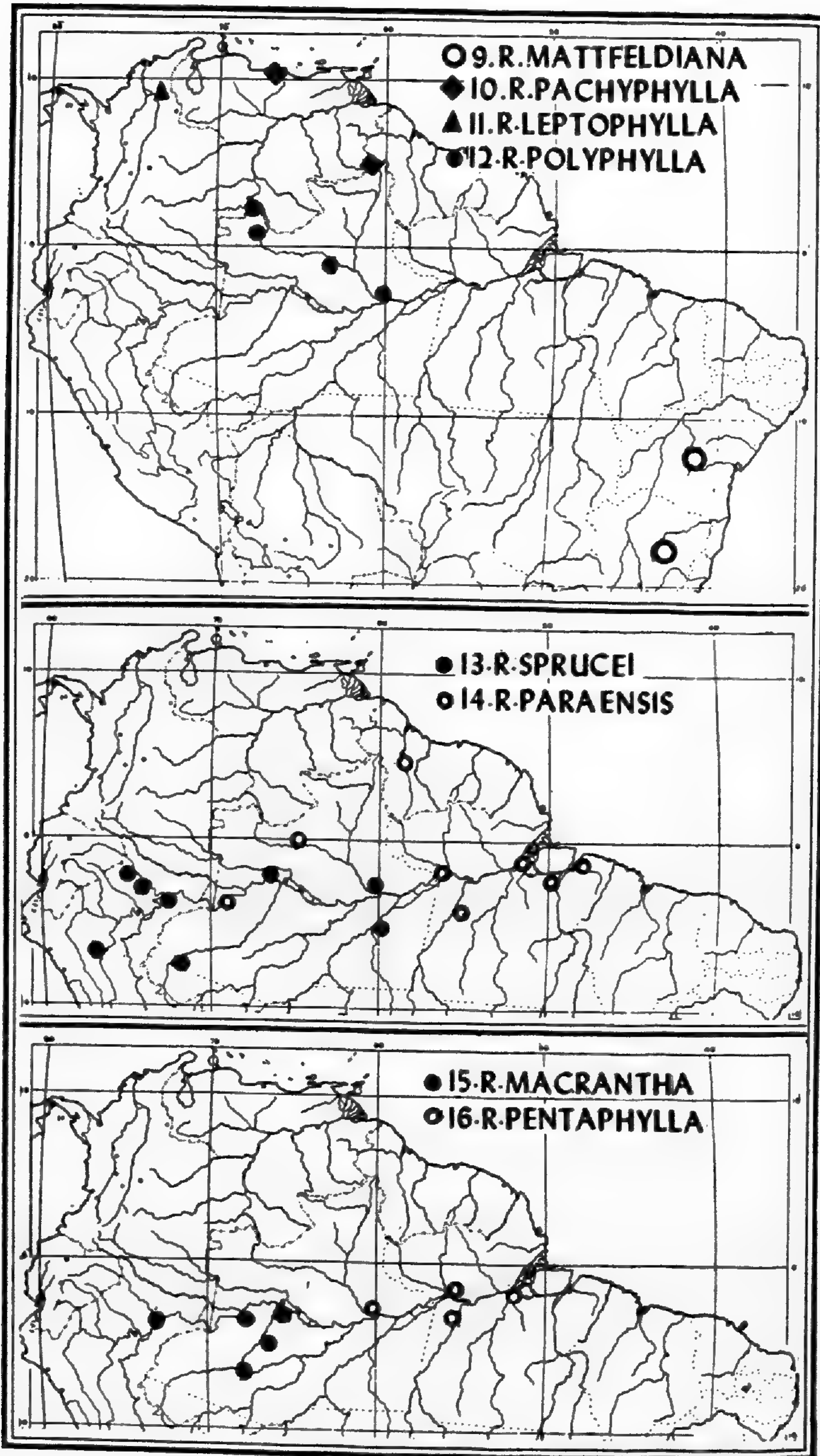
³⁶ Good, Ronald, in "A Century of Progress in the Natural Sciences." *Calif. Acad. Sci.* p. 747. 1955.

³⁷ Schmidt, Karl P. *ibid.* p. 767. 1955.



MAP 2

Distribution of eight species of the section RAUVOLFIA



MAP 3

Distribution of eight species of series *LATIFOLIA* of the section *MACROVOLFIA*

that there is no evidence from geology to support the past existence of land bridges other than what are present today, and he gives evidence from geodesic studies to disprove the idea of continental drift.

It cannot therefore be either through land bridges or drifting continents that the spread of *Rauvolfia* from the place of its birth can be explained. Plant dispersal commonly is effected by animals and birds. Here again there is very little information available concerning *Rauvolfia*. Biswas³⁸ has noted that fruits of *R. serpentina* are eaten by birds and scattered by them. The brightly colored fruits of the other species may similarly be attractive to birds. Many species, not only in America but also in Africa and Asia, have a distribution following rivers and streams. The stones of *Rauvolfia* are hard and can withstand considerable buffeting in water currents. It may well be that birds and water currents together are responsible for the wide dispersal of the genus.

Another tempting problem is that of the center of origin of the genus. Cain³⁹ has recently made a critical evaluation of the several criteria, first used by Adams,⁴⁰ as indicators of the center of origin of a genus or species. In the absence of evidence from several sources such as Paleontology, Cytology and Zoogeography, the only recourse is to appeal to the present distribution and comparative morphology of the species. Some supporting evidence may be obtained from the distribution data of related genera, for example, *Aspidosperma*, *Plumeria*, *Tabernaemontana*, *Thevetia*, and *Vallesia*. Of these, only *Tabernaemontana* has a pantropical distribution, while the others are almost exclusively New World genera.

I have estimated about 80 species of *Rauvolfia* for the world, with 34 species in the western hemisphere and the remaining 46 species distributed fairly equally in Africa and Asia in the eastern hemisphere. Species concentration and the maximum number of endemics are evident in tropical America. The eight species of section RAUVOLFIA are the most advanced while the species constituting section MACROVOLFIA include an assemblage variously primitive and advanced. Thus species concentration, species differentiation, and distribution pattern of related genera all indicate the possibility of tropical America being the birthplace of the genus.

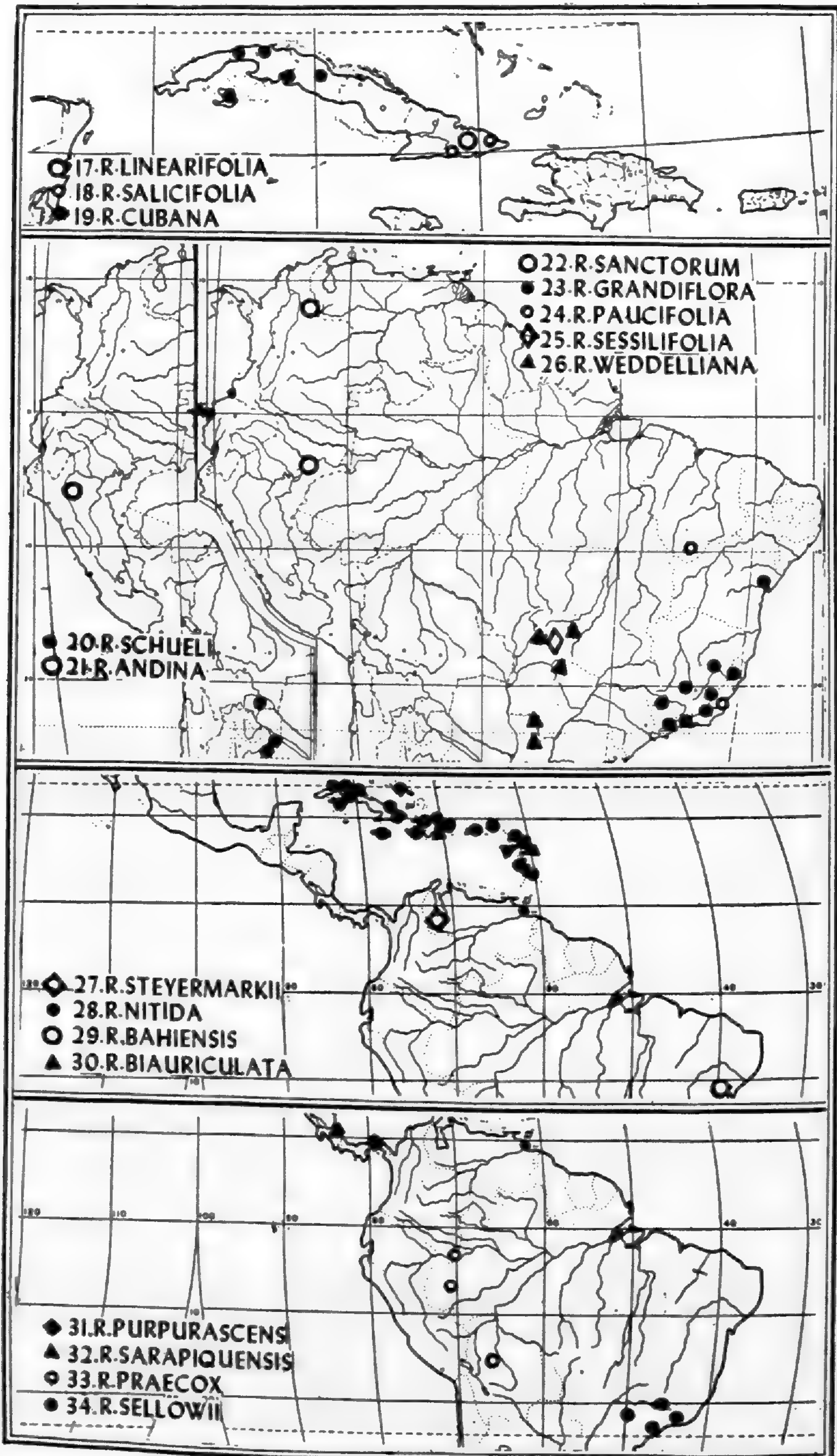
RELATIONSHIPS

Rauvolfia is generically distinct, with its whorled leaves, terminal cymose inflorescences, relatively small flowers with eglandular calyx and esquamellate corolla, and the ovary with one or two ovules developing into one-seeded variously connate or free drupelets. However, within the genus, the frequent morphological parallelism in the several species of the major land areas makes a clear-cut classification of the sections slightly difficult. A comparison of the flowers of *R. serpentina* and *R. vomitoria* (figs. C and D), with those of *R. grandiflora* (fig. 23) and *R. praecox* (fig. 32) respectively will best exemplify this situation.

³⁸ Biswas, K., in *Sci. & Cult.* 18:579. 1953.

³⁹ Cain, Stanley A. *Foundations of Plant Geography*. Chap. 14. New York. 1944.

⁴⁰ Adams, Charles G., in *Biol. Bull.* 3:115-131. 1902.



MAP 4

Distribution of eighteen species of series *ANGUSTIFOLIAE* of section *MACROVOLVIA*

Comparative morphology, combined with the geography of the species, serves to produce a reasonably satisfactory key reflecting the natural relationships amongst the species. Some of the characters that provide necessary taxonomic criteria are: shape and size of the corolla and the extent of pubescence within, the position and proportion of the anthers in the corolla tube, the dorsal surface of the anthers, and the extent of carpellary cohesion in the ovary and in the fruit. None of these characters solely can be used in delimiting a section.

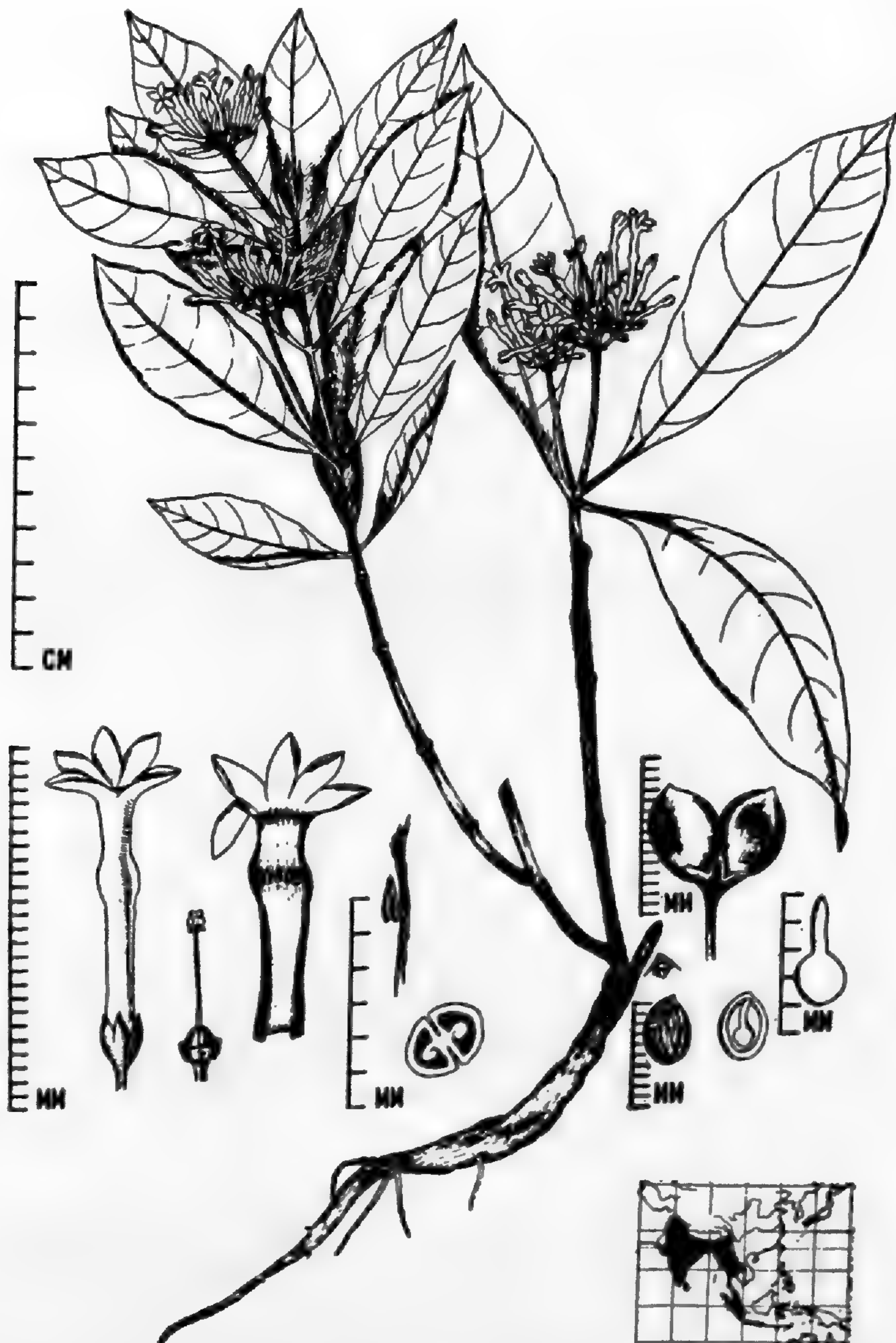


Fig. C. *Rauvolfia serpentina* Benth.

A survey of the above-mentioned and other features in all the species lead to the conclusion that advance in the genus has taken a path of simplification by reduction. Section *MACROVOLFFIA*, with 26 species, exhibits these various characters at different stages of development. Species of series *LATIFOLIAE*, most of them confined to the Amazon valley, are prominent by their comparatively broad, terminally clustered leaves and fairly large flowers. The fruit, however, is very variable. It is large and fully fused in *R. paraensis* and *R. pentaphylla*, while it is half-fused in the closely related *R. sprucei* and *R. macrantha*. In series *ANGUSTIFOLIAE* again, *R. grandiflora*, with its large flowers and deeply inserted anthers and hemisyncarpous fruits, is at one end of the scale, while *R. sellowii*, with its short

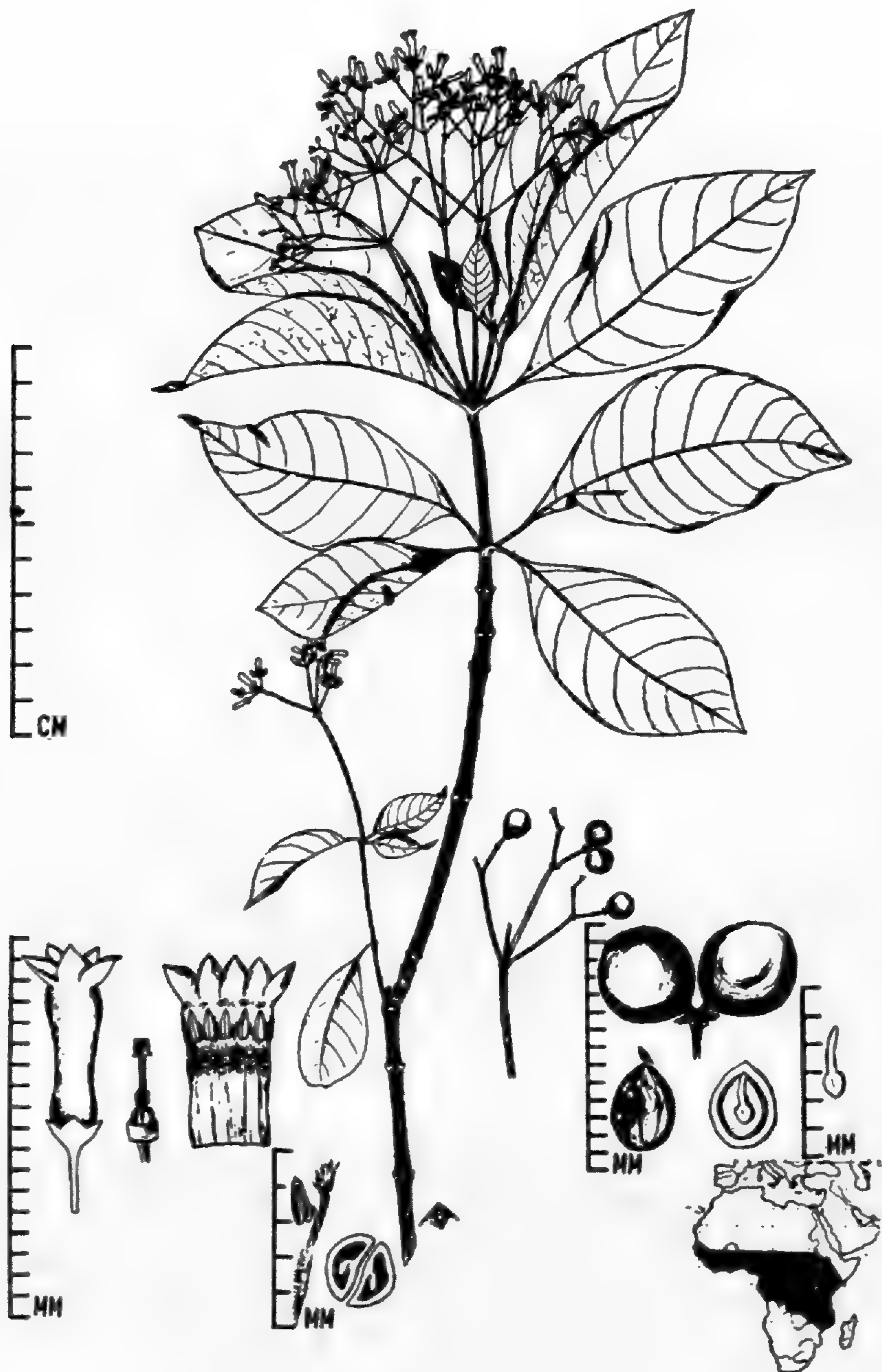


Fig. D. *Rauvolfia vomitoria* Afzel.

flowers and free drupelets, occupies the other end. All the other species can be appropriately placed between these two extremes. *R. nitida*, with its short flowers and syncarpous fruits and slightly arcuate embryos, represents a further step in the evolutionary progress of the genus. In all the other species of section MACROVOLFFIA and in most of the species of the other sections, except CYRTOSIPHONIA, the embryo is straight. In several species in each of the sections this tendency for a curved embryo is noticeable. What advantage this imparts to the species is a matter of speculation.

Section RAUVOLFIA, containing mostly undershrubs with variously pubescent or glabrous, membranaceous leaves, tiny flowers in comparatively poorly branched inflorescences, and syncarpous fruits with convolute embryos, represents the most advanced group.

The African species forming section AFROVOLFFIA, the Malaysian species forming section CYRTOSIPHONIA, and the Hawaiian species forming section OCHROSIODES, all show morphological features extraordinarily similar to the species of section MACROVOLFFIA. Likewise, species of section ENDOLOBUS of Africa and Madagascar show close relationship with AFROVOLFFIA as well as with MACROVOLFFIA, except that in species of section ENDOLOBUS the corolla-lobes are inflexed in the bud. Also the two African species, *R. oreogiton* and *R. volkensii*, constituting section OPHIOXYLANTHUS, with large flowers and the anthers inserted almost halfway down the tube, are in proximity with species of the Asian section OPHIOXYLON.

The species of Hawaii and New Caledonia appear to be evolving in their own fashion. They are less related to the species from the major land masses. Sherff,⁴¹ in a provisional classification of the Hawaiian Rauvolfias, recognized seven species, mainly based on variation in leaf characters but to some extent on calyx and corolla size. Obviously, some factor is influencing a reduction in the size of calyx and corolla. My own experience with the other *Rauvolfia* species makes me cautious in attaching much taxonomic value to leaf characters in founding new species.

The Hawaiian species show some relationship with the species of section MACROVOLFFIA of America. They appear to be intermediate between species of series LATIFOLIAE and series ANGUSTIFOLIAE, having generally broad leaves with a strong tendency to persist only at the terminal nodes, fairly large flowers with characteristic foliaceous calyx-lobes, and a rather large corolla. Unlike MACROVOLFFIA, the Hawaiian species, constituting the section OCHROSIODES, have anthers with smooth backs. In this they resemble the African species of section AFROVOLFFIA.

The New Caledonian species, constituting the section HEURCKIA, are distinct. They have strikingly coriaceous leaves 4–6 in a whorl, and the flower with leathery calyx-lobes and twisted corolla. The stigma-head has no distinct collar, but the two apiculate lobes are very prominent. The fruit is apocarpous in all the species and the drupelets are strongly divergent.

⁴¹ Sherff, Earl E., in *Field Mus. Nat. Hist. Bot.* 23:321–331. 1947.

My proposed classification of the sections is based on that of Pichon.⁴² As I have indicated above, no one character can be given undue weight in delimiting the sections. In my opinion, Pichon's classification suffers from this defect. He has given much importance individually to the extent of fusion of the fruits, the size of the leaves, and the size of the disc around the ovary.

As I have shown above, even in very closely related species the fruit may remain in different degrees of fusion. For example, of the three Cuban species, *R. linearifolia* shows fruits fused only at the base and the lobes divergent, while *R. cubana* and *R. salicifolia* have fruits more than two thirds fused and lobes parallel. Furthermore, all three species have narrow leaves, but they have very close relationships with the rest of the American species.

Referring to the Asian *Rauvolfias*, Pichon⁴³ himself has stated that his section OPHIOXYLON differs from DISSOLAENA only in having slightly fused fruits. Consequently, I have merged DISSOLAENA with OPHIOXYLON. On the same basis, I have merged RHOPALANTHUS with ENDOLOBUS and DILOBOCARPUS with CYRTOSIPHONIA, and amongst the American sections HESPEROVOLFIA and MACROVOLFIA. Another section which disappears is CRYPTOGYNE, characterized by species with broad discs concealing the ovary. Except for this, the two species of this section, *R. amsoniaefolia* and *R. chaudocensis*, have many characters in common with the species of section CYRTOSIPHONIA. Hence, I have included CRYPTOGYNE with CYRTOSIPHONIA. While I have examined representative specimens for most of the species, I have not been able to study any specimens for species of section OPHIOXYLANTHUS, nor at least three of the species included in section OPHIOXYLON. I would therefore not claim any finality for this proposed classification of the sections. A further examination of the material for the species I have mentioned may very likely lead to a recasting of the system.

ACKNOWLEDGEMENTS

I am grateful to the people and the government of the United States of America for the award of a Fulbright Fellowship during 1953-54, which enabled me to visit this country and to spend a year of graduate study at Cornell University, Ithaca, New York. I am greatly indebted to Dr. Robert E. Woodson, Jr., of the Missouri Botanical Garden, for much understanding kindness and generosity and considerable guidance in the course of this investigation. My thanks are due to the Ciba Pharmaceutical Products Inc., for the grant of a fellowship during the tenure of which this work was completed. It is also a pleasure to acknowledge the various privileges and facilities accorded to me by Dr. Edgar Anderson, the director, and other authorities of the Missouri Botanical Garden where this research has been carried out. My fellow students have rendered me much help by testing and discussing the taxonomic keys. I should like to express my thanks to the curators of the various herbaria who have lent specimens for my study, and to

⁴² Pichon, M., in Bull. Soc. Bot. Fr. 94:31-39. 1947.

⁴³ Pichon, in Mem. Mus. Nat. d'Hist. Nat. 27:235. 1948.

Dr. K. N. Kaul, director of the National Botanic Garden, Lucknow, India, and Dr. Jorge León of Instituto Interamericano de Ciencias Agrícolas, Turrialba, Costa Rica, for seeds of *R. tetraphylla* from those areas. Finally, I appreciate very much the editorial assistance of Miss Nell Horner in the preparation of the manuscript.

MATERIALS

This study is based on herbarium specimens from the following herbaria. The abbreviations for them are taken from Lanjouw & Stafleu's 'Index Herbariorum' part I (Regnum Vegetabile, vol. 2, 2nd. ed., 1954).

- A —Arnold Arboretum, Harvard University, Cambridge, Massachusetts.
 EAP —Escuela Agrícola Panamericana, Tegucigalpa, Honduras
 F —Chicago Natural History Museum, Chicago, Illinois
 G —Conservatoire et Jardin Botanique, Genève, Switzerland.
 GH —Gray Herbarium of Harvard University, Cambridge, Massachusetts.
 K —Herbarium, Royal Botanic Gardens, Kew, England.
 L —Rijksherbarium, Leiden, Netherlands.
 M —Botanische Staatssammlung, München, Germany.
 MO —Missouri Botanical Garden, St. Louis, Missouri.
 NY —New York Botanical Garden, New York, New York.
 P —Muséum National d'Histoire Naturelle, Laboratoire de Phanérogamie, Paris, France.
 RB —Jardim Botânico Rio de Janeiro, Rio de Janeiro, Brazil.
 S —Naturhistoriska Riksmuseet, Botanical Department, Stockholm, Sweden.
 UC —Herbarium of the University of California, Berkeley, California.
 UPS —Institute of Systematic Botany, Botanical Garden and Botanical Museum of the University of Uppsala, Uppsala, Sweden.
 US —National Museum, Smithsonian Institution, Washington, D. C.
 W —Naturhistorisches Museum, Wien, Austria.

TAXONOMY

RAUVOLFIA [Plum.] L. Sp. Pl. ed. 1. 208. 1753; Gen. Pl. ed. 5. 98. 1754; Pichon, in Bull. Soc. Bot. Fr. 94:32. 1947. L. Gen. Pl. ed. 7 (Reichard). 118. 1778 (as **RAUWOLFIA**). L. Gen. Pl. ed. 8 (Schreber). 160. 1789; L. Sp. Pl. ed. 4 (Willdenow). 1217. 1798; A. DC. in DC. Prod. 8:336. 1844; Benth. & Hook. Gen. Pl. 2:637. 1876; K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4²:153. 1895 (as **RAUWOLFIA**).

Ophioxylon L. Sp. Pl. ed. 1. 1043. 1753.

Dissolaena Lour. Fl. Cochinch. 137. 1790.

Cyrtosiphonia Miq. Fl. Ind. Bat. 2:401. 1856.

Heurckia Muell.-Arg. in Flora 53:168. 1870.

Lactescent shrubs or trees with dichotomous or verticillate branches, the nodes with small interpetiolar deciduous stipules and persistent glands confined to the leaf-axils or ascending the petiole. LEAVES whorled, 3–5 at each node (opposite in seedlings), petiolate or sessile, simple, entire, penninerved, membranaceous or coriaceous, glabrous or pubescent, often anisophyllous. INFLORESCENCES terminal or lateral and interpetiolar, often geminate, 2-, 3- or 4-chotomously branched, bracteate, few- to many-flowered dichasia. FLOWERS pedicellate or sessile; calyx cam-

panulate, 5-lobed, the lobes eglandular within; corolla salverform, infundibuliform, urceolate or campanulate, usually white, glabrous externally and variously villous internally, the lobes 5, equal, sinistrorsely contorted, the apices usually just overlapping in the bud, rarely inflexed; stamens 5, epipetalous, the anthers free from each other and the stigma, included, fully fertile, the filament slender, short, the pollen-grain spherical or subspherical, triculate; pistil 2-carpellary, superior, the ovary apocarpous or variously syncarpous and bilocular, with 1-2 ovules on a ventral or axile placenta, the disc annular or cupuliform, entire or dentate, the style single, slender, usually glabrous, rarely villous at the base, the clavuncle or the stigma-head conspicuous, cylindrical, calyptriform or sub-mitriform, obscurely bi-apiculate. FRUITS apocarpous or variously syncarpous drupes, often only one carpel developing, 1-seeded, the seeds stout or flat, with a membranaceous testa and a linear hilum, albuminous, the albumen carnose, entire, easily separable from the testa, the embryos nearly as long as the seeds, or half as long, straight or slightly to deeply arcuate, the cotyledons 2, flat, fleshy, ovate, obtuse, the hypocotyl terete, about as long as the cotyledons.

TYPE SPECIES: *Rauvolfia tetraphylla* L.

KEY TO THE SECTIONS

- A. Leaves with glands in the axil and on the petiole. Corolla-tube urceolate. Fruits fully syncarpous, globose; embryo U-shaped. Antilles, Central America, and South America.
.....Sect. I. RAUVOLFIA
- AA. Leaves with glands in the axil only. Corolla-tube salverform, infundibuliform, or campanulate. Fruits apocarpous or variously syncarpous, globose or bilobed; embryo straight or slightly curved.
- B. Corolla-lobes not inflexed in the bud.
- C. Throat of the corolla-tube very narrowly pilose within (a ring of less than 1 mm.), above the anther-tips.
- D. Anthers clearly dorsifixed. Stigma-head with distinct collar. Fruits apocarpous or variously syncarpous, the drupelets slightly divergent.
- E. Anthers with a callosity at the back; filaments short and indistinct. Antilles, Central America, and South America.....Sect. II. MACROVOLFIA
- EE. Anthers with a smooth back; filaments slender and distinct.
- F. Anthers 6 to 8 times shorter than the corolla-tube.
- G. Corolla-tube 7-12 mm. long. Hawaii.....Sect. III. OCHROSIODES
- GG. Corolla-tube 2-6 mm. long. Tropical Africa and Madagascar.
.....Sect. IV. AFROVOLFIA
- FF. Anthers 2 to 4 times shorter than the corolla-tube. Southeast Asia and Malaysia.....Sect. V. CYRTOSIPHONIA
- DD. Anthers seemingly basifixed. Stigma-head with indistinct collar or none. Fruits apocarpous, the drupelets divaricate. New Caledonia.....Sect. VI. HEURCKIA
- CC. Throat of the corolla-tube pilose in a fairly broad band within (from 2 to 6 mm.), above the anther-tips.
- H. Ovary apocarpous or syncarpous only at the base. Fruits apocarpous or syncarpous only at the base, the drupelets divergent. Southeast Asia and Malaysia.....Sect. VII. OPHIOXYLON
- HH. Ovary syncarpous almost to its middle. Fruits syncarpous almost to the tip, the drupelets parallel. East Africa.....Sect. VIII. OPHIOXYLANTHUS
- BB. Corolla-lobes deeply inflexed in the bud. Tropical Africa and Madagascar.
.....Sect. IX. ENDOLOBUS

RAUVOLFIA IN AMERICA: KEY TO SECTIONS AND SERIES

- A. Leaves with intrapetiolar glands in the axil and on the petiole, membranaceous, glabrous or pubescent. Flowers small, corolla-tube 2–3 mm. long (4–5 mm. in *R. moricandii*). Fruits fully syncarpous, 5–8 mm. wide (rarely 18 mm. in *R. littoralis*), globose. Embryo U-shaped.....Sect. I. RAUVOLFIA
- B. Leaves 4 at each node, rarely 3 or 5, the largest leaf at each node 5–16 cm. long. Inflorescences 2–4 times shorter than the associated large leaf.....Ser. 1. TETRAPHYLLAE
- BB. Leaves 3 at each node, rarely 4, the largest leaf at each node 3–5 cm. long. Inflorescences about as long as the associated large leaf.....Ser. 2. TERNIFOLIAE
- AA. Leaves with intrapetiolar glands confined to the axil, membranaceous or coriaceous, glabrous. Flowers large, corolla-tube 4–24 mm. long. Fruits apocarpous or variously syncarpous, 9–30 mm. wide, bilobed (globose in *R. paraensis* and *R. pentaphylla*). Embryo straight.....Sect. II. MACROVOLFIA
- C. Flowering twigs leafy only at the tips; bud-scales or their scars present immediately above each node, the current growth consisting of but one verticillate node. Leaves about twice as long as broad (up to 3 times in *R. polyphylla*), obtuse to rounded at the base. Inflorescences terminal.....Ser. 3. LATIFOLIAE
- CC. Flowering twigs leafy throughout; bud-scales or their scars usually absent above the nodes, the current growth consisting of several verticillate nodes. Leaves 3–4 times as long as broad (about twice as long in *R. steyermarkii*), gradually attenuate at both ends or at least at the base. Inflorescence terminal or lateral.Ser. 4. ANGUSTIFOLIAE

SECTION I. RAUVOLFIA

§ ANISOPHYLLAE Mgf., in Fedde, Rep. Spec. Nov. 20:113. 1924.

§ AMEROVOLFIA Pichon, in Bull. Soc. Bot. Fr. 94:32, 38. 1947.

SERIES 1. TETRAPHYLLAE A. S. Rao, ser. nov.

Folia quaternata rarius ternata vel quinata in quoque nodo, folio majore 5–16 mm. longo. Inflorescentiae folio majore 2- vel 4-plo breviores. Species typica: *R. tetraphylla* L.

KEY TO THE SPECIES

- A. Leaves strikingly anisophyllous, the smallest leaf of each node about half as long as the largest. Inflorescences mostly lateral. Calyx-lobes acute, obtuse, or rounded.
- B. Largest leaves at the node narrow, 3 to 4 times as long as broad, lanceolate, glabrous, distinctly petiolate. Inflorescences lax, with elongate peduncles. Costa Rica.1. *R. woodsoniana*
- BB. Largest leaves at the node broad, about twice as long as broad, ovate, ovate-elliptic, or obovate, glabrous or pubescent, indistinctly petiolate. Inflorescences condensed, with short peduncles. Calyx-lobes acute, obtuse, or rounded.
- C. Leaves obovate, acuminate, gradually tapering at the base, glabrous or minutely puberulent. Inflorescences much-branched, 16- to many-flowered. Calyx-lobes obtuse or rounded. Costa Rica to Colombia, Ecuador, and Venezuela.2. *R. littoralis*
- CC. Leaves ovate or ovate-elliptic, acute or obtuse, abruptly tapering at the base, glabrous or pubescent. Inflorescences unbranched, or rarely 1- or 2-branched, 3- to 15-flowered. Calyx-lobes acute. Mexico to Colombia, Ecuador, Peru and Venezuela; Greater Antilles.....3. *R. tetraphylla*
- AA. Leaves slightly anisophyllous, the smallest leaf of each node usually more than half as long as the largest leaf. Inflorescences mostly terminal. Calyx-lobes acuminate or cuspidate.
- C. Leaves ovate or ovate-elliptic, 2–3 times as long as broad, secondary veins arcuate. Corolla-tube 2–3 mm. long. Colombia, Venezuela, and Lesser Antilles.....4. *R. viridis*
- CC. Leaves narrowly elliptic, 4–5 times as long as broad, secondary veins transverse. Corolla-tube 3–5 mm. long. Northeastern Brazil.....5. *R. moricandii*

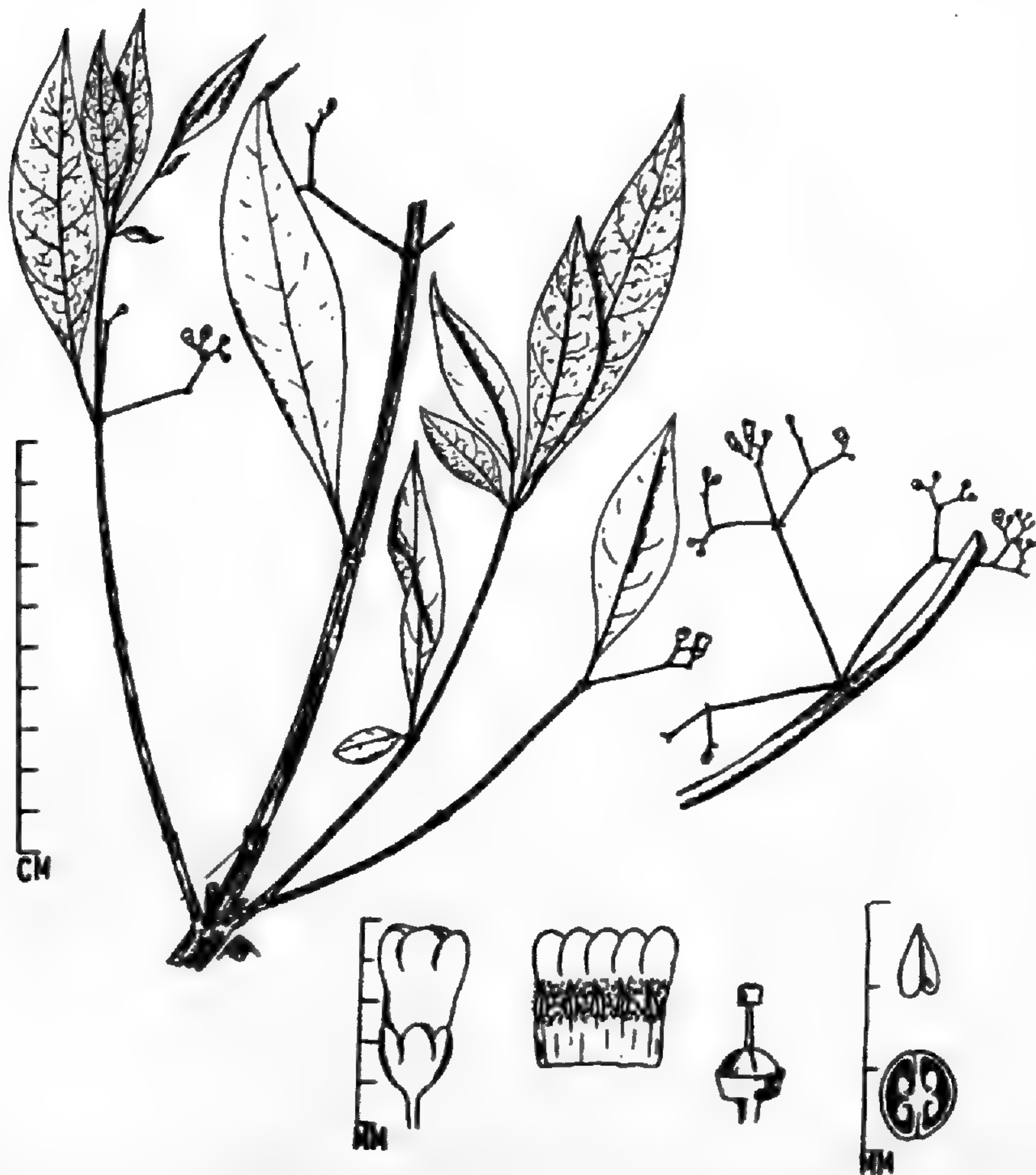


Fig. 1. *Rauvolfia woodsoniana* Standl. (Brenes 6801)

1. *RAUVOLFIA WOODSONIANA* Standl. in Field Mus. Nat. Hist.—Bot. 18:942. 1938. (T.: A. M. Brenes 6801!)

Plants with 2-, 3-, or 4-chotomous branches. Twigs slender, faintly angular, glabrous, the nodes with pectinate glands in the leaf-axils and the base of petioles. LEAVES strikingly anisophyllous, in whorls of 4 or sometimes 3 at each node, shortly petiolate, the larger leaves lanceolate, gradually tapering at both ends, 7–12 cm. long, 2–3 cm. broad, the smaller leaves narrowly ovate-elliptic to lanceolate, 1.5–4.0 cm. long, 1.0–1.5 cm. broad, membranaceous, glabrous, the secondary veins delicate, indistinct on the upper surface, but distinct on the under surface, 7–10 pairs, arcuate; petioles distinct, 4–8 mm. long. INFLORESCENCES lateral, interpetiolar, 1, or 2–3 at the nodes, several-flowered; peduncles relatively slender, 2–4 cm. long, 2-, 3-, or 4-chotomously branched, the branches divergent, minutely bracteate; pedicels slender, 2–3 mm. long. FLOWERS small; calyx deeply 5-lobed, the lobes ovate, rounded, minutely ciliolate, about 1.5 mm. long, glabrous; corolla broadly urceolate, the tube 2–3 mm. long, about 1.5 mm. in diameter at the base, glabrous without, but pilose within near the throat and around the stamens, the lobes rotund, about 1.5 mm. long; stamens 5, inserted near the throat, the anthers ovate, acute, about 1 mm. long, the filament distinct, about 0.5 mm. long; ovary

bi-carpellary, syncarpous, subspherical, about 1.5 mm. high, about 1.5 mm. in diameter, glabrous, the ovules 2 in each locule on an axile placenta, the disc annular, about 1 mm. high, the style slender, about 1.5 mm. long, glabrous, the stigma-head subcapitate, about 0.5 mm. high, faintly biapiculate. FRUITS not seen.

Flowering in April. La Calera de San Ramon, Costa Rica.

This species is easily separated from its related species by its lanceolate leaves and the loose inflorescences with slender, elongated peduncles.

COSTA RICA. ALAJUELA: San Ramon, *Brenes 6801* (EAP, F).

2. *RAUVOLFIA LITTORALIS* Rusby, *Descr. New Sp. S. Am. Pl.* 84. 1920. (T.: *H. H. Smith 1905!*)

R. multiflora Riley, in *Kew Bull.* 1927:124. 1927. (T.: *L.A.M. Riley 125!*)

R. macrocarpa Standl. in *Trop. Woods* 16:11. 1928, *nomen*; in *Publ. Field Mus.—Bot.* 4:254. 1929. (T.: *Cooper & Slater 200!*)

Shrubs and trees with milky latex, up to 9 m. tall. Branches dichotomous, terete, glabrous, sparingly lenticellate, the nodes with slender, interpetiolar deciduous stipules and glands in the leaf axils and on petioles. LEAVES whorled, strikingly anisophyllous, 4 or rarely 5 at the nodes, shortly petiolate, usually obovate, rarely ovate-elliptic or broadly elliptic, acute to acuminate, gradually tapering at the base, rarely abruptly so, the largest leaves 6–16 cm. long, 3–6 cm. broad, the smallest leaves 1–4 cm. long, 0.5–2.0 cm. broad, membranaceous, glabrous or rarely minutely puberulent, the secondary veins distinct on both surfaces, arcuate, 10–12 pairs; petioles 2–8 mm. long. INFLORESCENCES terminal or lateral, interpetiolar, paired at the nodes, several- to many-flowered; peduncles relatively stout, 1.5–4.0 cm. long, 2-, 3- or 4-chotomously branched, minutely bracteate; pedicels slender, 2–4 mm. long. FLOWERS small; calyx deeply 5-lobed, the lobes ovate, obtuse or rounded, about 1 mm. long, glabrous; corolla broadly urceolate or almost campanulate, white, the tube stout, 2–3 mm. long, 1.5–2.0 mm. in diameter at the base, glabrous without, villous within almost to the base, throat densely pilose, the lobes orbicular, 1.0–1.5 mm. long, glabrous or rarely ciliate at the margin; stamens 5, inserted near the throat, the anthers ovate, acute, about 1 mm. long, the filament distinct, about 0.5 mm. long; ovary bicarpellary, syncarpous, subspherical, about 1.5 mm. high, 2.0 mm. in diameter, glabrous, the ovule 1 in each locule on an axile placenta, the disc annular, about 0.5 mm. high, the style columnar, about 2 mm. long, glabrous, the stigma-head depressed-capitate, about 0.5 mm. high, faintly biapiculate. FRUITS spherical or subspherical, 8–15 mm. in diameter, green at first but changing as they ripen from pale red to deep red and black, 2-seeded, the stones ovate, stout and prominently ridged at the base, flattened and smooth above; seeds ovate, albuminous, with a membranaceous testa, the albumen copious, carnose, the embryo strongly arcuate, the cotyledons ovate, obtuse, 2–3 mm. long, the hypocotyl terete, about equal to the cotyledons in length.

Chiefly near sea-shore from 10 to 100 m. altitude. In thickets and somewhat

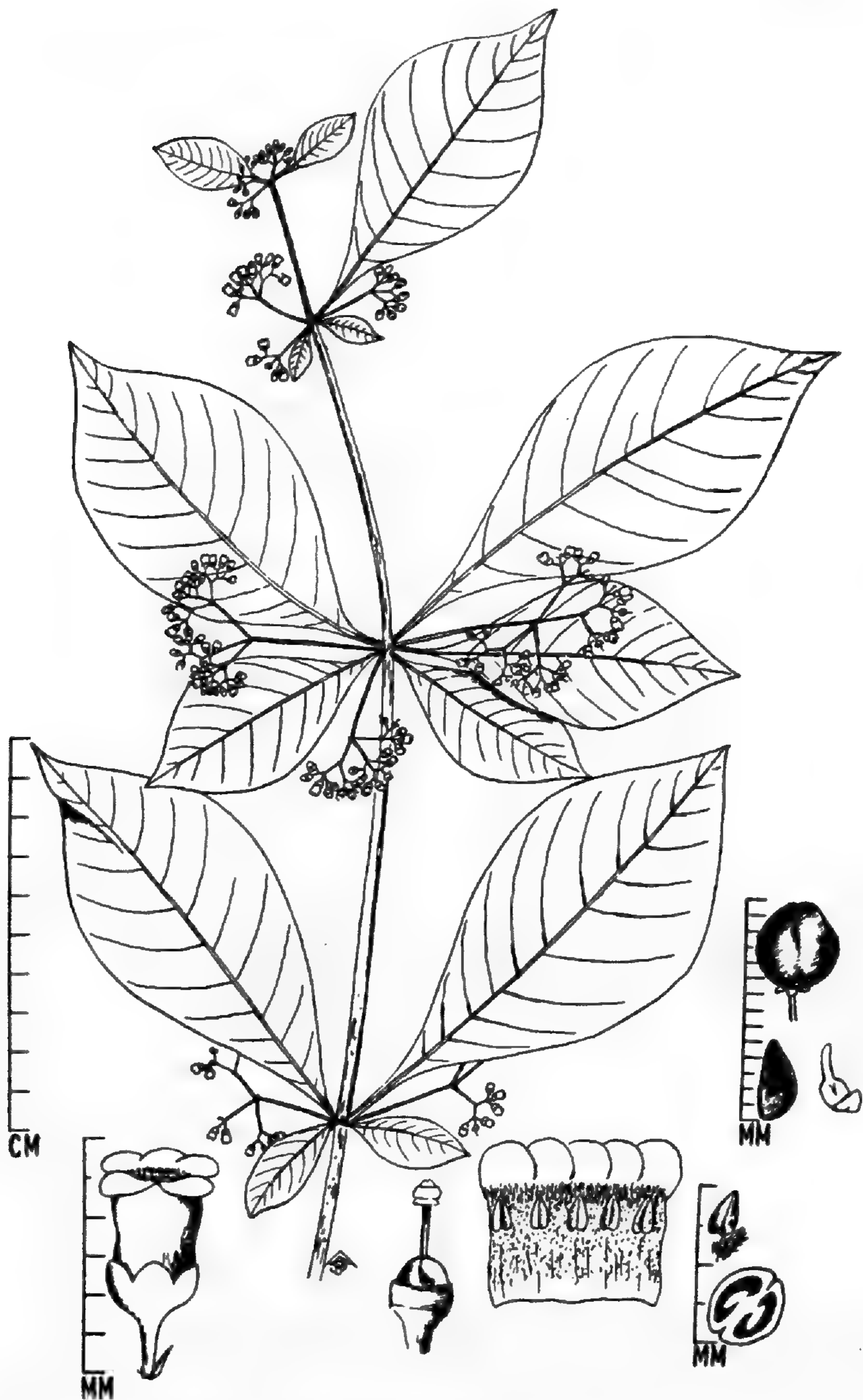


Fig. 2. *R. littoralis* Rusby (H. H. Smith 1905)

swampy areas. Flowering and fruiting from June to September. Costa Rica to Colombia, Ecuador and Venezuela.

COMMON NAMES: Colombia—*Anguito*, *Contra Solita*, and *Cruceto*. Panama—*Fruta del Diablo*.

This species is obviously closely related to *R. tetraphylla* L. It can easily be distinguished by the usually glabrous, obovate leaves with acuminate apex and the very distinct, strongly arcuate secondary veins, and by the usually geminate, many-flowered inflorescences.

Riley, in describing *R. multiflora*, mentions that it is distinct from all other Central American species. He may not have seen either Rusby's description or representative specimens of *R. littoralis*. Except that the leaves are slightly smaller, *R. multiflora* does not show any other significant difference from the type of Rusby's *R. littoralis*. Standley has described *R. macrocarpa* only on fruiting material. I have obtained material from the type locality, through the kindness of Mr. A. M. Bouché, and have given particular attention to the fruits. *R. littoralis* fruits profusely, and occasionally giant fruits have been noticed. It may also be significant that seeds of *R. macrocarpa* which I have dissected were found sterile. I am convinced, therefore, that the type specimen of *R. macrocarpa* is only an abnormal specimen of *R. littoralis*. I am accordingly putting it in synonymy.

COLOMBIA: ATLANTICO: Baranoa, *Dugand 4549* (US); Barranquilla, vicinity of Las Pendales, *Elias 1543* (F, MO, US). BOLIVAR: Manati, *Dugand 591* (F). MAGDALENA: Magdalena, *Dugand & Peten 398-842* (F); Santa Marta, *Smith 1905* (A, F, G, GH, L, MO, P, S, US), *1906* (A, F, G, GH, L, NY, P, S, US). VALLEE DEL CAUCA: Coli Soto Herrera *941* (US).

COSTA RICA. PUNTARENAS: San Rafael de Esparta, *León 4499* (MO).

ECUADOR. MANABI: El Recreo, *Eggers 15531 = 15568* (F, K, M, MO, S, US).

PANAMA. CANAL ZONE: Cocoli, *Riley 125* (MO, US); *G. White 120* (MO); Miraflores, Gorgas Memorial Lab., *P. White 130* (MO, US), west end of island, vicinity of lake, *137* (MO). CHIRIQUI: Progreso, *Cooper & Slater 200* (A, F, US).

3. RAUVOLFIA TETRAPHYLLA L. Sp. Pl. 208. 1753. (T.: *Linn. Hb.*, photo 293.4!)

R. hirsuta Jacq. Enum. Pl. Carrib. 14. 1760; Select. Stirp. Am. Hist. 47. 1763, *ex char.*

R. tomentosa Jacq. *l.c. ex char. et icon.*

R. canescens L. Sp. Pl. ed. 2. 303. 1762, *ex char.*, non *R. canescens* Descourt. Fl. Ant. 3:151. 1827.

R. subpubescens L. Mant. 2:345. 1771, *ex char.*

R. heterophylla R. & S. Syst. Veg. 4:805. 1819, *ex char.*

R. canescens var. *glabra* Muell.-Arg. in Linnaea 30:395. 1860. (T.: *Bertero s. n.*!)

R. canescens var. *tomentosa* Muell.-Arg. *l.c.* (T.: *Goudot 2!*).

R. latifolia var. *minor* Muell.-Arg. *l.c.* 396 (in part as to *Jameson 514!*)

R. heterophylla var. *puberula* A. Gray, in Proc. Am. Acad. 5:187. 1861, *nom. nud.*

R. odontophora Heurck & Muell.-Arg. in Heurck, Obs. Bot. 150. 1870. (T.: *Spruce 6302!*)

R. canescens var. *intermedia* Mgf. in Fedde, Rep. Spec. Nov. 20:115. 1924, *in clave.*

R. canescens var. *typica* Mgf. *l.c.*, *in clave.*

R. mollissima Mgf. *l.c.* 119. (T.: *Tonduz 13940!*)

R. hirsuta var. *glabra* (Muell.-Arg.) Woodson, in Ann. Mo. Bot. Gard. 26:299. 1939.

Sub-shrubs and shrubs with milky latex, 0.5–1.5 m. tall; branches 2-, 3- or 4-chotomous, terete, softly pubescent to glabrous, the nodes with interpetiolar, linear, deciduous stipules and pectinate glands in the axil and on the petiole. LEAVES in whorls of 4, rarely 3 or 5, strikingly anisophyllous, shortly petiolate, very variable in shape, ovate, ovate-elliptic, or oblong-elliptic to obovate-elliptic, acute to obtuse and broadly acute to obtuse at the base, the largest leaves at the node 5–15 cm. long, 2–4 cm. broad, the smallest 1–4 cm. long, 0.8–3.0 cm. broad,

membranaceous, glabrous to tomentulose on both surfaces, secondary veins distinct to obscure, arcuate, 5–12 pairs, the vein network distinct or obscure, extremely close-knit when distinct; petiole 2–5 mm. long. INFLORESCENCES terminal and lateral, few- to rarely many-flowered; peduncles slender, 1–4 cm. long, rarely 2- to 3-branched, glabrous to puberulent, minutely bracteate, the pedicels slender, 2–5 mm. long, glabrous to puberulent. Flowers small; calyx deeply 5-lobed, the lobes ovate, acute, about 1 mm. long, glabrous to puberulent without and glabrous within, corolla urceolate, white, the tube slender, 2–3 mm. long, glabrous to puberulent without and rather densely villous within near the throat, the throat slightly constricted, the lobes obovate to subrotund, rounded, about 1 mm. long; stamens



Fig. 3. *Rauvolfia tetraphylla* L. From living plant at the Missouri Botanical Garden.

5, included, inserted near the throat, the anthers ovate, acute, about 1 mm. long, the filament about 0.5 mm. long; ovary 2-carpellary, syncarpous, subspherical, about 1.5 mm. high and 2 mm. in diameter, the ovules 1–2 in each locule on an axile placenta, the disc annular, 0.5 mm. broad, the style slender, 1.5–2.0 mm. long, glabrous, the stigma-head subcapitate, about 1 mm. high, obscurely bi-apiculate. FRUITS spherical to subspherical, 5–8 mm. in diameter, glabrous, gradually turning from green to red and black as they ripen, 2-seeded, the stones ovoid, flattened ventrally, convex dorsally, distinctly rugose; seeds ovate, slightly curved, albuminous, testa membranaceous, the albumen carnose, the embryo deeply arcuate, the cotyledons cordate-ovate, obtuse, 2.0–2.5 mm. long, the hypocotyl terete, about as long as the cotyledons.

Plants of extremely varied habitat, near road-sites, in waste places, on hills, on lake banks, on rocky cliffs, in dry fields and in hedges, in moist rich soil in full sun or under shade of trees; at altitudes from sea-level to about 2,000 meters. Flowering and fruiting practically throughout the year. I have noticed in the greenhouse, young plants scarcely 3–4 months old bearing flowers. Greater Antilles, Mexico to Colombia, Ecuador, Peru and Venezuela.

COMMON NAMES: Colombia—*Anguito*, *Cruceto*, *Venenito*. Costa Rica—*Chalchupa*, *Cobataco*, *Guataco*. El Salvador, Nicaragua, and Panama—*Amatillo*, *Comida de Culebra*, *Guataco*, *Hierba de San Jose*, and *Señorita*. Mexico—*Coralilla*, *Corazillo*, and *Corralio*. Venezuela—*Boboro*.

R. tetraphylla can be distinguished from its related species by its very unequal leaves with usually obscure secondary nerves, the mostly lateral few-flowered inflorescences much shorter than the leaves, and the small flowers with acute calyx-lobes. It has been often confused with *R. nitida* Jacq., particularly in the Antilles, but differs from it in having dull leaves with few arcuate secondary veins, the inflorescences with slender, rarely branched peduncles, and the flowers with acute calyx-lobes.

The confusing nomenclatorial history of *R. tetraphylla* and its clarification by Rendle have already been discussed. The extremely variable leaf characters have occasioned the publication of several specific names for this polymorphic species. I have made a statistical analysis of variation in this species. Any study based on the herbarium material alone or a few plants from the greenhouse cannot be conclusive. *R. tetraphylla* offers a very interesting example for extensive observation in the field and in the botanical garden. This species has been known to have been introduced to India⁴⁴ in the last 150 years, and to Australia in the last 50 years or less, and in both countries it has become naturalized. Considering the paucity of information on the behavior of introduced plants in their new homes, a detailed botanical study of this species in these regions should be of great interest.

ANTILLES.—

BARBADOS: St. George, Jordan's estate, *Barrow 154* (NY); *Goodding 380* (NY).

⁴⁴ Voigt, l. c.

CUBA. CAMAGUEY: Camaguey to Santayana, *Britton 2401* (NY), *N. L. & E. G. Britton & Powell 13271* (MO, US); Cayo Guajaba, *Schafer 2847, 2853* (NY, US); vicinity of Tiffin, *2886* (NY, US). HAVANA: Havana, *Baker 5130* (NY, US); vicinity of Cojimar, *Britton, Earl & Wilson 6234* (NY), *Britton, Earle & Gager 6276* (NY), *Palmer & Riley 840* (US), *Ekman 348, 825, 944, 13419, 16892* (S), *Leon 1337, 5201* (NY), *Schafer 173* (NY), *Van Hermann 908* (NY, US), *Wilson 1369* (NY); Santiago de las Vegas, *Cook 91* (US). ISLE OF PINES: Nueva Gerona, *Curtiss 517* (A, G, GH, L, M, MO, NY, P, S, US). MATANZAS: Matanzas, near mouth of the Bueyoaca, *Britton & Wilson 32* (NY), *N. L. & E. G. Britton & Schafer 549* (NY). ORIENTE: Cupey, *Ekman 6301* (P); vicinity of Daiquiri, *Britton & Cowell 12688* (NY); Iguabo, *Eggers 5411* (P); Santiago de Cuba, *Havard 68* (NY), *Leon 138, 12366* (NY), *Gonzalez de Moya s.n.* (MO); Pico Turquino, south slopes, *Seifrizz 1010* (US); Yara to Manzanillo, *Schafer 12330, 12386*, along Río Canto, *1647* (NY, US), *Underwood & Earle 130* (NY); precise locality not known, *Ekman 5679, 7963, 9760* (S). PINAR DEL RIO: Bay of Mariel, *Britton & Earle 7582* (NY); Corrientes Bay, *Britton & Cowell 9976, 9976A* (NY); vicinity of Guane, *N. L. & E. G. Britton & Cowell 9749* (NY), *Schafer 10381* (MO, NY, US); Herradura, *N. L. & E. G. Britton, Earle & Gager 6323* (NY, US), *Van Hermann 706* (NY, US); Los Acostos, *Zanna Gutia 5272* (NY); vicinity of Sumidero, *Schafer 13410* (NY, P, US). SANTA CLARA (LAS VILLAS): Cienfuegos, *Combs 81* (GH, MO, NY, P, US), *Hodge & Howard 4139* (GH), *Jack 4661* (A, US), *5232, 5555* (A, P), *7297* (A); Jagua, *Howard, Briggs, et al. 253, 392* (UC); Bahía de Cochinos, *Leon 9563* (NY). PRECISE LOCALITY NOT KNOWN: *Rugel 389* (L, MO, NY), *Sagra s.n.* (W), *Sessé, Moçino, Castillo & Maldonado 5066, 5067* (F), *Wright 2942* (A, G, GH, MO, P, S, W).

DOMINICAN REPUBLIC: Barahona, *Miguel Fuertes 238* (GH, L, P, NY, S, US, W); Llano Castero, in thickets, *Ekman 12465* (S); precise locality not specified, *Bertero s.n.* (P), *Ehrenberg s.n.* (NY), *Poiteau s.n.* (G, P), *Von Jacquemont s.n.* (P).

HAITI: Artibonite, *Ekman 8535* (S, US); Dame-Marie, *Ekman 10452* (S, US); Ennery, *E. C. Leonard 8914* (NY, US); Fond Parisien, *E. C. Leonard 4145* (GH, NY, US); Gauthier, *E. C. Leonard 872* (NY, US); Gros Morne, *E. C. Leonard 9912* (GH, UC, US); Jacmel, *Favrat 38* (G); Jean Rabel, *E. C. & G. M. Leonard 13705* (US); Massif de la Hotte, *Ekman 8575* (S); Miragoane & vicinity, *Eyerdam 434* (GH, P, US); Plaisance to Gonaives, *Nash & Taylor 1522* (NY); Tortue Island, La Vallée, *E. C. & G. M. Leonard s.n.* (A, GH, US); precise locality unknown, *Jaeger s.n.* (GH, M, P, S, UPS, W).

JAMAICA: precise locality unknown, *Boos s.n.* (W); *Swartz s.n.* (M, S, W).

SAINT THOMAS: precise locality not known, *Perrin s.n.* (NY).

TRINIDAD: *Trinidad Botanic Garden Herbarium 3570* (US); road to Galera Point, *Broadway 2746* (S); St. Anne's, *Broadway 9229* (A, MO), *Fendler 636* (P), *Freeman 8879* (MO). TOBAGO: *Thiebaut 1223* (P).

CENTRAL AMERICA.—

BRITISH HONDURAS: Belize, *Gentle 36* (F); Corozal, *Gentle 495* (MO); El Cayo and vicinity, *Chanek 120* (F).

COSTA RICA. GUANACASTE: camino de Concepción, *Echeverria 4166* (UC); El Coyolar, *Standley s.n.* (US); Filadelfia, *Echeverria 284* (UC); Guachipelin, *Kupper 1424* (M); Isla de Cabello, *Brenes 15695* (F); Isla de San Lucas, *Quinos 789* (F); La Cruz, *Morley 761* (MO, UC, US); Las Cañas, *Standley & Valerio 46663* (US), *466689* (US); Los Loros, *Brenes 21467* (F). PUNTARENAS: Puntarenas, *Beetle 26225* (UC, US), *Brenes 12365* (F), *Howell 10155* (US), *León 502* (F), *Maxon & Harvey 7857* (US), *W. W. & H. E. Rowlee 123, 124* (US); *Stork 528* (US), *3397* (F); San José, *Tonduz 13916* (P, US); precise locality not known, *Krukoff s.n.* (MO); Canton de Osa, vicinity of La Presa, *Allen 5287* (P, UC, US), vertiente del Pacífico, *P. Birlley fil. 17342* (US).

GUATEMALA. ALTA VERAPAZ: La Libertad, *Lundell 2493* (MO), *3399* (MO, S), *Mercedes Aguilar 138* (A, MO). CHIMALTENANGO: Patzún, *Heyde & Lux 6417* (G, F, M, MO, US). ESCUINTLA: Anubis, near Obispo, *Muenschler 12371, 12601* (F), Escuintla, *Pacheco s.n.* (F), *Pedro Pirales 2046* (US), *Morales Ruano 544* (US); Chichipin, *Morales Ruano 551* (US); San José, *Standley 64227* (F); Las Fianzas, *Salas 363* (US). GUATEMALA: *Ruehl s.n.* (MO, US), *Merck & Co. s.n.* (MO). HUEHUETENANGO: Agua

Caliente (Quezaltenango), J. M. & M. T. Greenman 5958 (MO); vicinity of Cuilco, Steyermark 50757 (F); Nentón, Sierra de los Cuchumatanes, Steyermark 51431 (F, MO). JALAPA: Jalapa, Kellerman 8059 (F). JUTIAPA: Jutiapa, Standley 75129 (F, MO), 75990 (F). RETALHULEU: Ayutla, Standley 68829 (F); Retalhuleu, Bernoulli & Cario 1835 (S), Standley 66786. SAN MARCOS: Ocos, Steyermark 37825 (F), Río Naranjo, Rojas 175 (US). SANTA ROSA: Chicquimulilla, southeast, Standley 78858 (F, MO); Guazacapán, Standley 78703 (F, MO); vicinity of Taxisco, Standley 79011 (F, MO). SUCHITEPEQUEZ: vicinity of Tiquisate, Steyermark 47717 (F). ZACAPA: Gualan, Blake 7684 (US), Deam 6287 (A, F, MO, US, W); trail between Río Hondo and waterfall, Steyermark 29489 (F, MO); Zacapa, Standley 72027 (F), 73654 (F, MO).

HONDURAS. COMAYAGUA: Comayagua, Williams & Molina 14680 (F), Standley & Chacon 5351 (F); El Bano, J. Valerio Rodriguez 2320, 2399 (F). CORTES: Barbara, Molina 3866, 3867 (F); La Lima, Johansen 37 (F, MO, US), Williams & Molina 12470 (F); Progreso, near San Pedro Sula, Hottle 69 (F); San Pedro Sula, Bangham 333 (A); FRANCISCO MORAZAN: between Suyapa & Tegucigalpa, Standley 14200 (F); Tegucigalpa, Fogg 21751 (MO); Río Yeguaré, Galsman 1600 (F), Williams & Molina 13266 (F, MO, US); Zamorano, Molina 30 (F), J. Valerio Rodriguez 230 (F), 1241 (F), Standley 1304, 3896 (F), Williams 14070 (F). OLANCHO: vicinity of Catacamas, Standley 18186, 18374 (F). VALLE: Amapala, J. Valerio Rodriguez 3353 (F, MO); vicinity of Amapala, Standley 20765 (US). YORO: Aguan River valley, Yuncker et al. 8078, 8655 (F, MO, P, S, US).

EL SALVADOR. AHUACHAPAN: vicinity of Ahuachapan, Standley 20219 (US). LA LIBERTAD: vicinity of Ateos, Standley 23332 (US); near Comasagua, Carlson 260 (F, UC), 552 (F). LA UNION: Acajutla, Stork, Eyerdam & Beetle 8732 (A, P, UC), Standley 21935 (S, US); vicinity of La Union, Beetle 26262 (A, MO, P, UC, US), Standley 20783 (S, US); Laguna de Maquigue, Standley 20981 (US). SAN SALVADOR: Apulo, Williams & Molina 16760 (F, US); along the road from San Martín to Laguna de Ilopango, Standley 22558 (US); vicinity of Tonacatepeque, Standley 19529 (US); Cerro de San Jacinto, near San Salvador, Standley 20601 (US), Velasco 9006 (US), Salvador Calderón 348 (US). SANTA ANA: vicinity of Metapán, Standley & Padilla Y 3033 (F). SAN VICENTE: vicinity of San Vicente, Standley 21309 (US). SONSONATE: Acajutla, Standley 21935 (S, US), Stork, Eyerdam & Beetle 8732 (A, P, UC), vicinity of Armenia, Standley 23440 (US); Nahuizalco, Hartman 20, 63 (S); Sonsonate, Standley 21761 (US). PRECISE LOCALITY UNKNOWN: Renson s. n. (US).

NICARAGUA. CARAZO: vicinity of Jinotepe, Standley 8490 (F). CHINANDEGA: Ameyer, Maxon, Harvey & Valentine 7104 (US) Maxon et al. 7156 (US); Chichigalpa, Standley 11306, 11396 (F). CHONTALES: Juigalpa, Standley 9376 (F). GRANADA: Granada, Baker 173 (MO, UC), 608, 846, (US), Levy 214 (P, W), Maxon et al. 7613 (US); Momotombo, Baker 215 (MO), 667 (US), C. L. Smith 127 (MO, UC, US). ESTELÍ: vicinity of Condega, Standley 20402 (F). MANAGUA: Managua, Chaves 88 (A), Garnier 328 (MO), J. M. & M. T. Greenman 5687 (MO), Maxon et al. 7221 (US), 7282, 7545 (US); Laguna de Masaya, Maxon et al. 7740 (US); Cosiguina Volcano, Howell 10257 (F); Ometepe Island, Lake Nicaragua, Shimek & Smith 73 (US), C. L. Smith s. n. (UC). PRECISE LOCALITY UNKNOWN: Wright s. n. (P).

PANAMA. PANAMA: Canal Zone, Bouché s. n. (MO), Celestine 57 (US), Standley 25546 (A, US); Juan Díaz, Standley 30471 (US); Panama City, J. M. & M. T. Greenman 5145 (MO); Panama Vieja, Asplund s. n. (UPS), Panama Vieja to Bella Vista, Allen 831 (F, MO, P, US); Taboga Island, Standley 27100, 27851 (US), Woodson, Allen & Seibert 1530 (A, MO).

MEXICO. CAMPECHE: Campeche, Fogg 21759 (MO); Hopelchen, Fogg 21760 (MO). CHIAPAS: Acapetahua, Matuda 16506 (F); Acacoyagua, Escuintla, Matuda 16423 (F); Paderón, Matuda 16896 (F); southeast of Puerto Arista, Morley 716 (MO, UC). COLIMA: Armeria, Jones 342 (MO), Palmer 86 (A, F, MO, P, UC, US); Colima, Palmer 106 (US); Manzanillo, Eyerdam & Beetle 8711 (A, MO, P, UC), Palmer 1030 (US), West 3515 (UC); Paso del Río, Emrick 186 (F). GUERRERO: Acapulco, Palmer s. n. (US); Aca-

pulco, sea cliffs, *Clark* 7172 (MO); Guerrero, *C. L. Smith* 6018 (A, MO, P); Iguala, *J. N. & J. S. Rose & Painter* 9305 (MO, US); Mazatlán, *Stork & Horton* 8606 (MO, P, UC); San Luis, *Hinton* 10874 (A, MO, P); Pungarabato, Coyuca, *Hinton et al.* 5799 (F); south of Taxco, *Clark* 7105 (MO). JALISCO: La Palma, *Jones* 66 (MO, US). MEXICO: Amatepec, *Matuda* 31291 (MO); Tamacaltepec, *Hinton* 724 (F, MO, US), *Hinton et al.* 3582 (US), *Hinton* 3826 (P); San Luis de Turrubales, *S. Jimenez Canossa* 2 (F); Maria Madre Island, *Octavis Solis* 89 (US), *Mason* 1839 (US); Mexico, *Wawra* 89 (W). MICHOACAN: Apatzingan, *Hinton* 12028 (US), *Leavenworth* 475 (F, MO), *Leavenworth & Hoogstraal* 1352 (F, MO). NAYARIT: Acaponeta, *Rose, Standley & Russell* 14280 (US); vicinity of San Blas, *Roxana S. Ferris* 5324 (A, US). SAN LUIS POTOSI: Rascon, *Purpus* 5309 (F, MO, UC, US); Tamasopo, *Pringle* 5068 (G); Tamazunchale, *Kenoyer s. n.* (MO), *Stanford* 6938 (UC); Valles, *Kenoyer* A641 (MO), *Vines* 3326 (US). SINALOA: Culiacán, *Brandegees s. n.* (UC, US); Copradia, *Brandegees s. n.* (UC); Guadalupe, *Rose* 14680 (US); Labrados, *Ferris & Mexia* 5208 (A, F), *Mexia* 940 (A, UC, US); Imala, *Gentry* 4955 (MO), *Palmer* 1437 (US), 1439 (F, UC), *Ortega* 4167 (US); Mazatlán, *MacDaniels* 39 (F), *Ortega* 7013 (F, P), 7210 (F, MO, P), 7360 (F), 7482 (MO), *Rose* 14032, *s. n.* (US); Rosario, *Rose* 1575, 14622 (US); San Juan, *Ortega* 4023, 4126 (US); Santa Fe, *Ortega* 4678 (US). PUEBLA: Tlaxcoapan, *Hahn s. n.* (P); Xochiltepec, *Lyonnet* 2185, 2655 (US). VERA CRUZ: Antigua, *Purpus* 6143 (F, MO, UC, US); Ojapa, *Orcutt* 5193 (MO, US); Papantla, *Liebmann* 15135 (MO, UC, US); Pueblo Viejo, *Palmer* 421 (F, MO, US); Río de Santa Maria, *Purpus* 2016 (UC, US); Rinconada, *Ross s. n.* (MO); San Francisco, *C. L. Smith* 1336 (UC); Vera Cruz, *Galleotti* 7114 (P); Wartenberg, near Cartoyuca, *Ehrenberg* 1858 (P). OAXACA: Cuicatlán, *Conzatti* 3991 (US), *Nelson* 1872 (US); Oaxaca, *Arson s. n.* (L, S), *Conzatti* 2165 (F), *Pringle* 4580 (G), 4861 (M, MO, P, UC, US, W); San Geronimo, *Purpus* 7147 (A, F, MO, UC, US); Tehuantepec, *Orcutt* 3455 (F, MO, US); Tomelin, *C. L. Smith* 855 (MO, UC, US); Tuxtepec, *Martinez-Calderón* 90 (MO, UC, US). YUCATAN: Campeche, *Fogg* 21757 (MO), *C. L. Lundell* 900 (F, MO, UC, US); Cabal, *Steggerda* 16 (F); Chichankanab, *Gaumer* 1490 (F), 1869 (A, F, MO, UPS, US); Itza, *C. L. & A. A. Lundell* 7464 (MO, US), *Steere* 1104 (MO), 1363 (F); Izamal, *Gaumer* 610 (A, F, MO); Mérida, *Schott* 431 (F); precise locality not known, *Lundell* 4768 (A, F), *Fogg* 21765 (MO), *Gaumer* 24047 (F, MO, P, US).

SOUTH AMERICA.—

BRITISH GUIANA. Georgetown Botanical Garden, *Dahlgren & Persaud s. n.* (F).

COLOMBIA. BOLIVAR: Cartagena, *Billberg* 205 (S), *Cufodontis* 31 (W), *Killip & Smith* 14161 (A, GH, US), *Schott* 851 (F); Cienaga, *R. R. Castañeda* 984 (MO); Turbaco, *Killip & Smith* 14191 (A, GH, US), *Pennell* 4759 (F, GH, K, MO, US). CAUCA: Dagua, *Liebmann* 5091 (F, GH), *Pennell* 5265 (GH, US). CUNDINAMARCA: Bogotá, *Cespedel s. n.* (P), *Triana s. n.* (P). HUILA: Neiva, *Perez-Arbelaes* 735 (MO, US). MAGDALENA: Magdalena, near Codazzi, *Haught* 2316 (A, MO, US), *Pittier* 1574 (US); Sierra Nevada de Santa Marta, *Barkley* 18 C 511 (MO); Santa Marta, *Bertero s. n.* (P), *Juan Giacometto* 1027 (MO), *Purdie* 407 (P), *H. H. Smith* 1648 (A, F, GH, L, MO, P, S, US), 1649 (F, GH, MO, P, US), 1654 (P), 2097 (A, F, GH, L, MO, P, S, UC, US). SANTANDER: Santander, *J. A. Molina & Barkley* 18 S 256 (MO). PRECISE LOCALITY UNKNOWN: *Karsten* 17b (W).

ECUADOR. GUAYAS: Salao, *Eggers* 14535 (M, S, US); Guayaquil, *Anderson s. n.* (S), *Asplund* 5125 (P, UPS, US), *Jameson* 514 (G), *Spruce* 6302 (P, S, W). MANABI: Manabi, *Haught* 2982 (MO, US), *Solis* 10641 (F); Savana ad Faura, *Mille* 989 (F).

PERU. AMAZONAS: Bagua, *Diáz s. n.* (MO). LAMBAYEQUE: Chiclayo, *Ramon Ferreyra* 7610 (US), *Lopez Miranda* 288 (MO, US); Pelillo, *Soukup* 4198 (US). LIBERTAD: La Libertad, *A. Raimondi* 741 (MO). LORETO: Santa Lucia, *Ule* 6805 (L). PIURA: Chaura, between Cauchaque and Buenos Aires, *Ramon Ferreyra* 10949 (MO). SAN MARTIN: Huallaga, cerca a Bella Vista, *Ramon Ferreyra* 10085 (MO).

VENEZUELA. ARAGUA: *H. Pittier* 14038 (US). DISTRITO FEDERAL: Caracas and Puerto Cabello, near El Zigzag, *E. Pittier* 75 (US); Catia and Las Trincheras, *E. Pittier* 8 (US); Curucuri Valley near Maiquetia, *H. Pittier* 13388 (A, F, MO, P, US); Curucuri

vicinity, *H. Pittier 10282* (GH, US); between Caracas and La Guaira, *Rose 21020* (US); La Guaira, *Curran & Haman 854, 886* (GH, US). LARA: Carora, *Jahn 179* (US); Río Tocuyo, *Tamayo 314* (US). MERIDA: El Molino, *Steyermark 56218* (F, MO); Tovar, *Fendler 2206* (GH); MIRANDA: Chaco, *Williams 11189* (F). TRUJILLO: La Cerba, *Reed 961* (US); La Concepción, *Reed 1094* (US); San Pablo de Mendoza, *H. Pittier 13329* (US). ZULIA: Isla San Carlos, *Curran & Haman 800* (GH, US). northern Venezuela, precise locality not known, *Curran & Haman 784* (GH), *803* (GH, US), *Goudot s. n.* (P).

INDIA. MADRAS: Madras, *Woodward s. n.* (MO). UTTAR PRADESH: Dehra Dun, *Bhatnagar s. n.* (MO); Lucknow, *Hiralal s. n.* (MO), *Srivatsava s. n.* (MO).

AUSTRALIA. QUEENSLAND: Brisbane, near Rockhampton, *Simmonds s. n.* (A), *Standish s. n.* (A), cult. C. S. I. R. O. 5428 (MO).

4. *RAUVOLFIA VIRIDIS* R. & S. Syst. Veg. 4:805. 1819. (T.: *Humboldt & Bonpland s. n.*, *photo!*)

R. psychotrioides H. B. K. Nov. Gen. et Sp. 3:231. 1819. (T.: *Humboldt 69!*)

R. nitida Lam. Encyc. Tab. 2:304. 1819, *non R. nitida* Jacq. 1760.

R. lamarkii A. DC. in DC. Prodr. 8:337. 1844. (T.: *Bertero s. n.*, *photo!*)

R. latifolia A. DC. in DC. Prodr. 8:339. 1844. (T.: *Sieber 74!*)

R. latifolia var. *minor* Muell.-Arg. in Linnaea 30:396. 1860. (T.: *Sieber 268!*)

R. lanceolata Griseb. Fl. Br. W. Ind. 408. 1864, *nom. nud.*, *non R. lanceolata* A. DC. 1844.

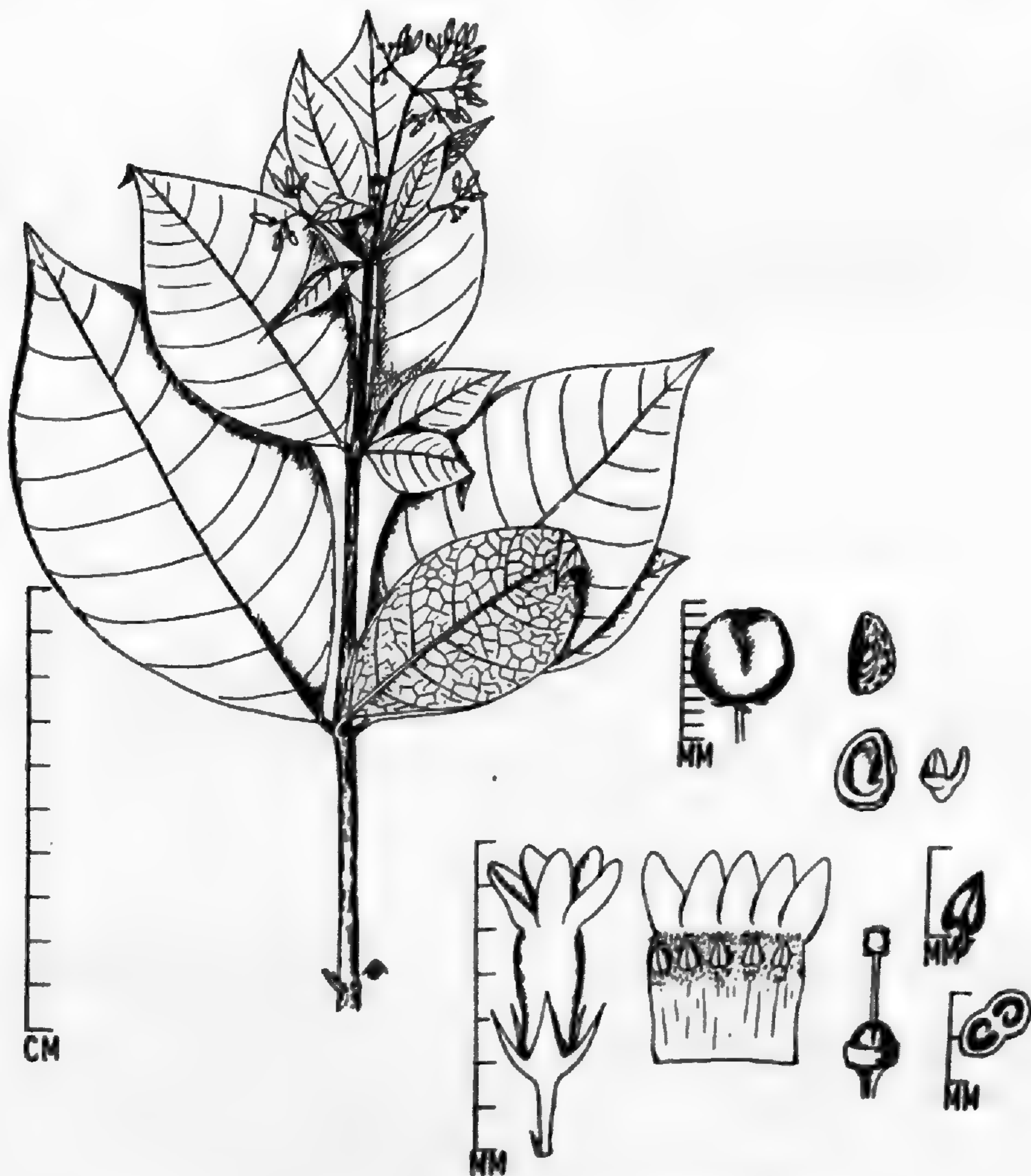


Fig. 4. *Rauvolfia viridis* R. & S. (*Humboldt 69*)

Shrubs up to 2 m. tall; branches terete, puberulent when young, but glabrous later, the nodes with very few pectinate glands in the axil and on the petiole. LEAVES slightly anisophyllous, quaternate, or rarely ternate, shortly petiolate, ovate or broadly ovate-elliptic, acute to acuminate at the tip, tapering at the base, the largest leaves 5–15 cm. long and 3–5 cm. broad, the smallest leaves 2–4 cm. long and 1.5–3.0 cm. broad, membranaceous, glabrous above and minutely puberulent beneath generally or along the midrib and the secondary veins, the secondary veins particularly distinct beneath, sharply arcuate, 8–15 pairs, the tertiary veins and the veinlets forming a distinct network; petiole 2–8 mm. long. INFLORESCENCES terminal or rarely lateral, several- to many-flowered; peduncles slender, 1–4 cm. long, 2- or 3-branched, glabrous or puberulent, minutely bracteate, the pedicels slender, 2–4 mm. long. FLOWERS small; calyx deeply 5-lobed, the lobes ovate, acuminate or cuspidate, 1.0–1.5 mm. long, glabrous; corolla tubular or narrowly urceolate, white, the tube slender, 2.5–3.0 mm. long, glabrous or rarely scantily puberulent without and poorly pilose within near the throat, the throat slightly constricted, the lobes ovate, obtuse, 2.0–2.5 mm. long, about 1 mm. broad, glabrous; stamens 5, included, inserted near the throat, the anthers ovate, acute, about 1 mm. long, the filament distinct, about 0.5 mm. long; ovary 2-carpellary, syncarpous, subspherical, about 1.5 mm. high and 2.0 mm. in diameter, the disc annular, 0.5 mm. wide, the style slender, 1.5–2.0 mm. long, the stigma-head depressed-capitate, 0.5 mm. high, obscurely bilobed. FRUIT spherical or subspherical, slightly flattened, 5–7 mm. in diameter, glabrous, 2-seeded, the stones ovate, flat ventrally, convex dorsally, distinctly rugose; seeds ovate, slightly curved, albuminous, testa submembranaceous, the albumen fleshy, the embryo deeply arcuate, the cotyledons ovate, obtuse, 2–3 mm. long, the hypocotyl terete, about as long as the cotyledons.

Scattered shrubs from near sea-level to about 1000 meters altitude, on coral cliffs and along hill-sides on sandy shady beaches, near mangrove swamps but on dry soil. In arid meadow regions at higher altitudes. Flowering and fruiting from April to October. Lesser Antilles, Colombia and Venezuela.

COMMON NAMES: Colombia—*Cruceto*, *Mata Penos*, and *Venenito*. Lesser Antilles—*Antigua Balsam*, *Bitterbush*, *Billyache*, *Bois Lait* and *Milky Bush*, *Snakeberry Tree*. Venezuela—*Bole de Berraco*.

This species can easily be distinguished from its related species by the slightly anisophyllous leaves with the very distinct vein network and the mostly terminal inflorescences, with the corolla-tube and the lobes almost equal in the flowers. It can also be distinguished from *R. nitida* Jacq. by its usually broad leaves with deeply arcuate secondary veins, the slender peduncles and the acuminate calyx-lobes.

McVaugh⁴⁵ has recently shown that Roemer & Schultes' name, *R. viridis*, has the priority over the till-now more familiar Kunth's name, *R. psychotrioides*. Markgraf⁴⁶ was correct in his recognition of the identity of *R. latifolia* A. DC

⁴⁵ McVaugh, R., in *Taxon* 4:84. 1955.

⁴⁶ Markgraf, F., in *Fedde, Rep. Spec. Nov.* 20:114. 1924.

with *R. lamarkii* A. DC., but yet he maintains *R. lamarkii* as distinct from *R. psychotrioides* mainly perhaps on geographical grounds. The characters that Markgraf used in his key for separating the two species, such as short- and long-acuminate, glabrous or hairy on the midrib, the pilosity in the throat of the corolla, the shape of the stigma-head, all intergrade and cannot be used. The distribution of the species from Puerto Rico to Venezuela and Colombia is nothing unusual.

LESSER ANTILLES.—

ANTIGUA: Box 872 (MO, UC, US), *Wüllschaegel* 342 (M, W).

BARBUDA: northeast of Codrington, Box 605 (US).

DOMINICA: *Hodge* 674 (NY); *Lloyd* 829 (NY).

GRENADA: Belair, *Beard* 1201 (GH, S, US), *Broadway s. n.* (GH, MO, NY, P); La Pointe, *Eggers* 6461 (A, P, US); leeward side of Chatham Bay, *C. P. Cooper III* 202 (NY).

GUADELOUPE: Le Moule, *H. Steble* 951 (NY), 981 (P), *H. & M. Steble* 6994, 7022 (US). PRECISE LOCALITY UNKNOWN: *Bena* 5337 (US), *Duss* 6 (P), 2614 (GH, MO, NY, US), *Forstrom* 807 (S), *Perrotet s. n.* (P), *Quentin* 213 (P), *L. C. Richard s. n.* (P).

MARTINIQUE: Case Pilote, *Hahn* 1503 (P, S), *Mouret* 226 (P); St. Anne, *H. & M. Steble* 6164 (US); Valle des Pierre, *Hahn* 1459 (G, GH, NY, P, US). PRECISE LOCALITY NOT KNOWN: *Duss* 1225 (NY, US), *Sieber* 74 (M, P, W).

MONTserrat: *Schafer* 46 (NY, US).

PUERTO RICE: CULEBRA ISLAND: *Britton & Wheeler* 69a (NY, US). GUAYAMA: Guayama, *Goll et al.* 517 (NY). HUMACAO: Fajardo lighthouse, *Heller* 1186 (NY, US), *Sintenis* 1194 (GH, M, P, S, US), 1195 (P). MAYAGUEZ: Guanica, *Fogg* 21775 (MO). PONCE: Ponce to Playa, Las Cucharas, *N. L. & E. G. Britton & Marble* 1951 (GH, US); Cayo Muertos, *N. L. Britton, Cowell & Stewardson Brown* 504S (NY, US). SAN JUAN, San Juan, *Sintenis* 2806 (L); precise locality unknown, *Plée* 610 (P), *Sargent* 195 (US), *Underwood & Griggs* 628 (NY, US). VIEQUES ISLAND: Cerra Encanta, *Schafer* 2541, vicinity of Isabela Segunda, *Schafer* 2560 (NY, US).

ST. BARTHELEMY: *Forström s. n.* (S), *Goes s. n.* (S, UPS), *Questol* 228 (NY), 907 (US).

ST. CROIX: *A. E. Ricksecker* 407 (GH, MO, NY, UC, US), *J. J. Ricksecker* 333 (P), *Thompson* 284 (US), 298 (GH, NY, P), 350 (GH).

ST. EUSTATIUS: *Boldingh* 1235B (L), *Suringar s. n.* (L).

ST. JAN: Bethania, hillside woods, *N. L. Britton & Schafer* 193 (NY, US).

ST. KITTS: *N. L. Britton & Cowell* 254, 351 (NY).

ST. MARTIN: *Boldingh* 2361B (L, P), *Rijgersmaa s. n.* (S).

ST. THOMAS: *Börgeson* 27B6B (S), 66B (NY), *N. L. & E. G. Britton & Schafer* 124 (NY), *N. L. & E. G. Britton & Marble* 401, 1296 (NY, US), *Eggers* 183 (G, L, M, P, UPS), *Eggers s. n.* (GH, W), *Ehrenberg s. n.* (MO), *Jalmarsson s. n.* (S), *Holton s. n.* (NY), *Poiteau s. n.* (P).

ST. VINCENT: *H. H. & G. W. Smith* 557 (GH, NY).

TRINIDAD: *Sieber* 268 (MO, P, W); TOBAGO: *Broadway s. n.* (GH, MO, P, US); Buccoo Point, *Cheesman* 298 (MO).

VIRGIN ISLANDS: Virgin Gorda, *Fishlock* 75 (NY).

SOUTH AMERICA.—

COLOMBIA. ATLANTICO: Barranquilla, *Dugand* 125,958 (F), 4822 (MO), *Dugand & Jaramillo* 3213, 3217 (US), *Elias* 14,189 (US), *Paul* C34 (US); Puerto Colombia, *Elias* 1014 (F). BOLIVAR: Cartegena, *Dugand & Jaramillo* 3374 (US), *Heriberto* 38, 354 (US), *Schott s. n.* (F). MAGDALENA: Santa Marta, *Espiña* 47 (US), *Perez-Arbelaez* 4816, 5860 (US).

VENEZUELA. ARAGUA: Ocumare, *H. Pittier* 14035 (US), *Williams* 10170 (F). CARA-BOBO: road from Puerto Cabello to San Felipe, *H. Pittier* 8872 (GH, US); Maracay, *Vogel*

1395 (M). DISTRITO FEDERAL: Caracas, *Curran & Haman 1093* (GH, US). MIRANDA: Guatire, *H. Pittier 7844* (GH, US); Santa Lucia, *Holt 548* (P); precise locality not known, *H. Pittier 5979, 11052* (GH, P, US). MONAGAS: Río Caribe, *Curran & Haman 1269* (GH, MO, UC). NUEVA ESPARTA: Isle Margarita, *Johnston 135* (F, G, GH, UC, US, W), *Miller & Johnston 43* (F, GH, MO, P, US). SUCRE: Cristóbal Colón, *Broadway 103, 109* (GH, US); Cumaná, *Humboldt 69* (P); southwest of Cuchivano, *Steyermark 62789* (F, MO). YARACUY: entrance to San Filipe, *Steyermark 55855* (F). ZULIA: Perija, *Tejira 13* (GH, US); Tovar, *Fendler 612* (K, GH, MO); precise locality not known, *Kuntze v74* (F).

5. *RAUVOLFIA MORICANDII* A. DC. in DC. Prodr. 8:340. 1844. (T.: *Blanchet 1007!*)

Plants with branches ternate or quaternate, cylindrical or obscurely angular, glabrous. LEAVES ternate or rarely quaternate, slightly anisophyllous, sparsely glandular at base, short-petiolate, narrowly elliptic, caudate-acuminate, gradually attenuate at both ends, entire, 3–8 cm. long, 1.0–2.5 cm. broad, submembranaceous, glabrous, dark green above and pale green beneath, secondary veins delicate, indistinct above, distinct beneath, transverse, many; petioles 2–8 mm. long. INFLORESCENCES terminal, 6- to 15-flowered, peduncles slender, 1–3 cm. long, 2- or 3-branched, bracteate, bracts minute, pedicels filiform, 4–6 mm. long. FLOWERS small; calyx deeply 5-lobed, the lobes deltoid, acuminate, about 1 mm. long; corolla salverform, the corolla-tube slender, 4–5 mm. long, about 1 mm. in di-



Fig. 5. *Rauvolfia moricandii* A. DC. (*Blanchet 1007*)

anther at the base, glabrous without, sparsely villous within along the upper half, the throat constricted, the corolla-lobes ovate, obtuse, 2.0–2.5 mm. long, about 1 mm. broad; stamens 5, inserted near the throat, the anthers ovate, acuminate, the filaments short, about 0.5 mm. long; pistil bicarpellary, hemisyncarpous, the ovary subspherical, about 1 mm. high and about 1 mm. in diameter, with 2 ovules in each locule on an axile placenta, the disc annular, narrow, about 0.5 mm. high, the style common, columnar, 2.0–2.5 mm. long, glabrous, the stigma-head sub-cylindrical, about 1 mm. high, obscurely biapiculate. FRUITS not observed.

Northeast Brazil: Bahia.

This must be a comparatively rare species. Amongst all the material borrowed from the different herbaria, including that of the Rio de Janeiro garden, I have not come across any more specimens of this species. The paucity of the petiolar glands, the rather long corolla-tube, and the hemisyncarpous ovary, characteristic of this species, are exceptional to the section to which it is presently assigned. It is conceivable that with the study of more material this species may well be shifted to the section MACROVOLFIA.

BRAZIL. BAHIA: precise locality not known, *Blanchet 1007* (G).

SERIES 2. TERNIFOLIAE A. S. Rao, ser. nov.

Folia in quoque nodo ternata rariusve quaternata, folio majore 3–5 cm. longo. Inflorescentiae folium majorem subaequant. Species typica: *R. ligustrina* R. & S.

KEY TO THE SPECIES

- A. Leaves mucronulate, the largest leaf at each node less than twice as long as broad. Twigs, leaves and peduncles with a fuscous pubescence. Northeastern Brazil.6. *R. blanchetii*
- AA. Leaves acute, the largest leaf at each node more than twice as long as broad. Twigs, leaves, and peduncles glabrous or with a whitish pubescence.
- B. Leaves (at least the young ones), young twigs, and peduncles with a whitish pubescence, rarely glabrous. Inflorescences spreading; peduncles 2- or 3-branched, pedicels 5–8 mm. long. Calyx-lobes ovate, acute. Paraguay and south-central Brazil.7. *R. mollis*
- BB. Leaves, young twigs, and peduncles glabrous, or leaves puberulent along the midrib only beneath. Inflorescences rather congested; peduncles unbranched or rarely 1- to 2-branched, pedicels 2–4 mm. long. Calyx-lobes lanceolate, acuminate. Cuba; Mexico to Colombia, Bolivia, Venezuela, and northern Brazil.8. *R. ligustrina*
6. RAUVOLFIA BLANCHETTI A. DC. in DC. Prodr. 8:340. 1844. T.: *Blanchet 2718!*, *2769!*)

Shrubs; branches 2-, 3- or 4-chotomously branching, terete, fuscous-pubescent, the nodes with very few axillary glands ascending the petiole. LEAVES ternate to quaternate, slightly anisophyllous, shortly petiolate, ovate to ovate-elliptic, acute, mucronulate, abruptly attenuate at the base, 1–4 cm. long, 1–3 cm. broad, membranaceous, glabrous to puberulent above and pubescent beneath, the secondary veins 4–8 pairs, rather indistinct, the vein network hardly distinct; petioles 1–3 mm. long. INFLORESCENCES terminal and lateral, few-to many-flowered; peduncles slender, dichotomously branching, 1–3 cm. long, puberulent, the pedicels slender,

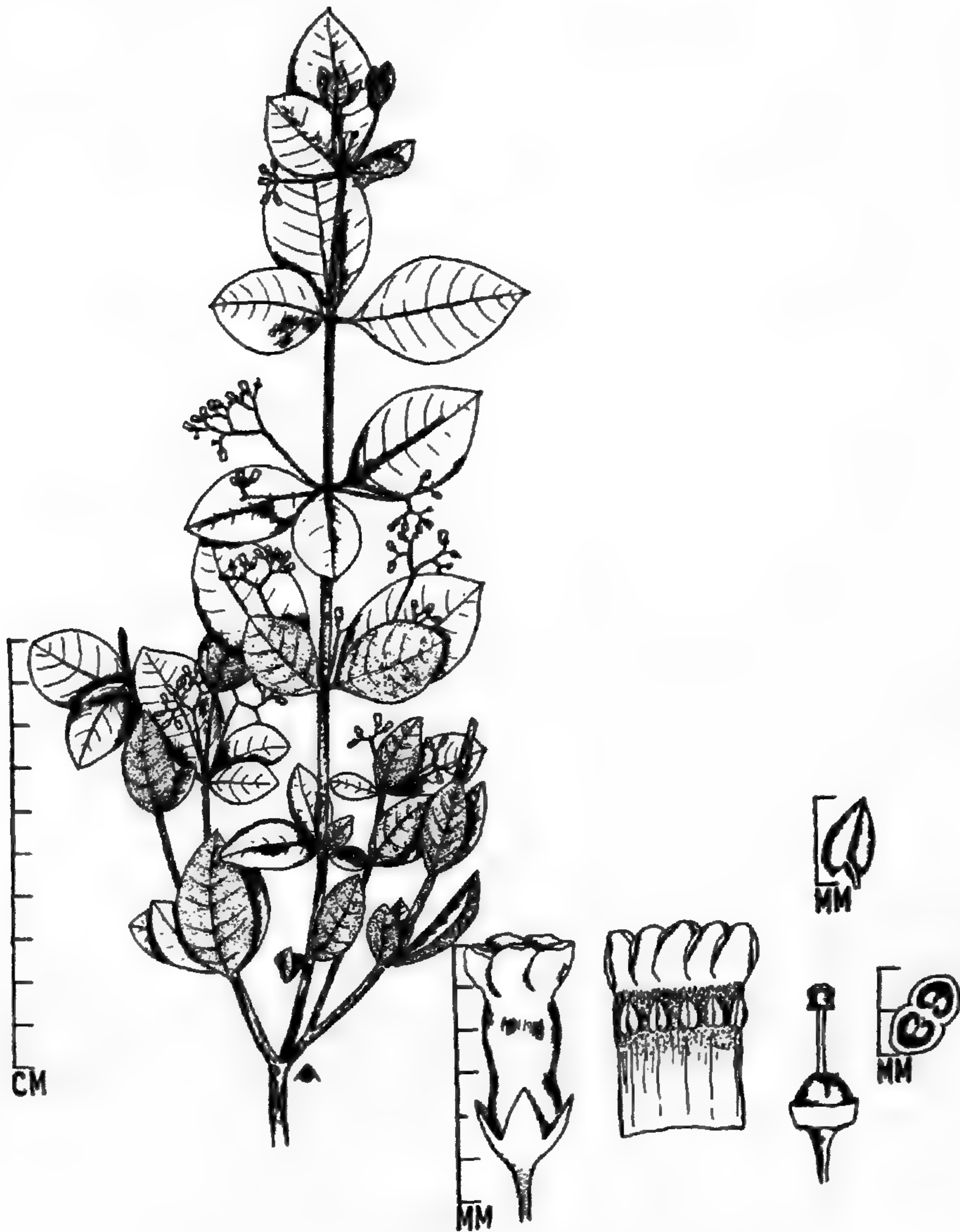


Fig. 6. *Rauvolfia blanchetti* A. DC. (Blanchet 2718)

2–4 mm. long, puberulent. FLOWERS small; calyx deeply 5-lobed, the lobes ovate, acute, about 1.5 mm. long, glabrous; corolla tubular or indistinctly urceolate, the tube slender, 2–3 mm. long, glabrous or rarely puberulent without, densely villous within near the throat, the throat scarcely constricted, the lobes ovate to subrotund, obtuse, 1.5–2.0 mm. long, the stamens 5, included, inserted near the throat, the anthers ovate, acute, about 1 mm. long, the filaments distinct, about 0.5 mm. long; ovary 2-carpellary, syncarpous, spherical, about 1.5 mm. in diameter, the ovules 1–2 in each locule on an axile placenta, the disc annular, about 0.5 mm. broad, the style columnar, 1.5–2.0 mm. long, glabrous, the stigma-head subcapitate, about 0.5 mm. high, obscurely bilobed. FRUITS spherical when young, 2-seeded.

I have not seen ripe fruits. Mueller-Argoviensis⁴⁷ has depicted mature fruits in his illustration of *R. blanchettii*. The fruits are obviously like those of the other members of this section.

⁴⁷ Mart. Fl. Bras. 6¹: tab. 9, fig. 1. 1860.

This species can be distinguished from all the related species by its fuscous-pubescent twigs, the mostly ternate, ovate-elliptic, mucronate-tipped, puberulent leaves, the inflorescences mostly few-flowered and with dichotomously branching, pubescent peduncles, and flowers with ovate, acute calyx-lobes.

Plants of northeastern Brazil.

BRAZIL. BAHIA: Monte de la Jacobine and Villa de Barra, *Blanchet 2718* (G, F, P), 2769 (G); Joazeiro, *Martinus 2370* (M). ESPIRITO SANTO: Itapemirim, *Glaziou 11183* (P).

7. *RAUVOLFIA MOLLIS* S. Moore, in *Trans. Linn. Soc. Ser. II.* 4:393. 1895. (T.: S. Moore 950, photo!)

R. divergens Mgf. in *Fedde, Rep. Spec. Nov.* 20:115, 119. 1924. (T.: *Fiebrig 4664!*)

Shrubs 1–2 m. tall; branches di- or trichotomous, terete, glabrous, or with a whitish pubescence, the nodes with a few axillary glands ascending the petiole.

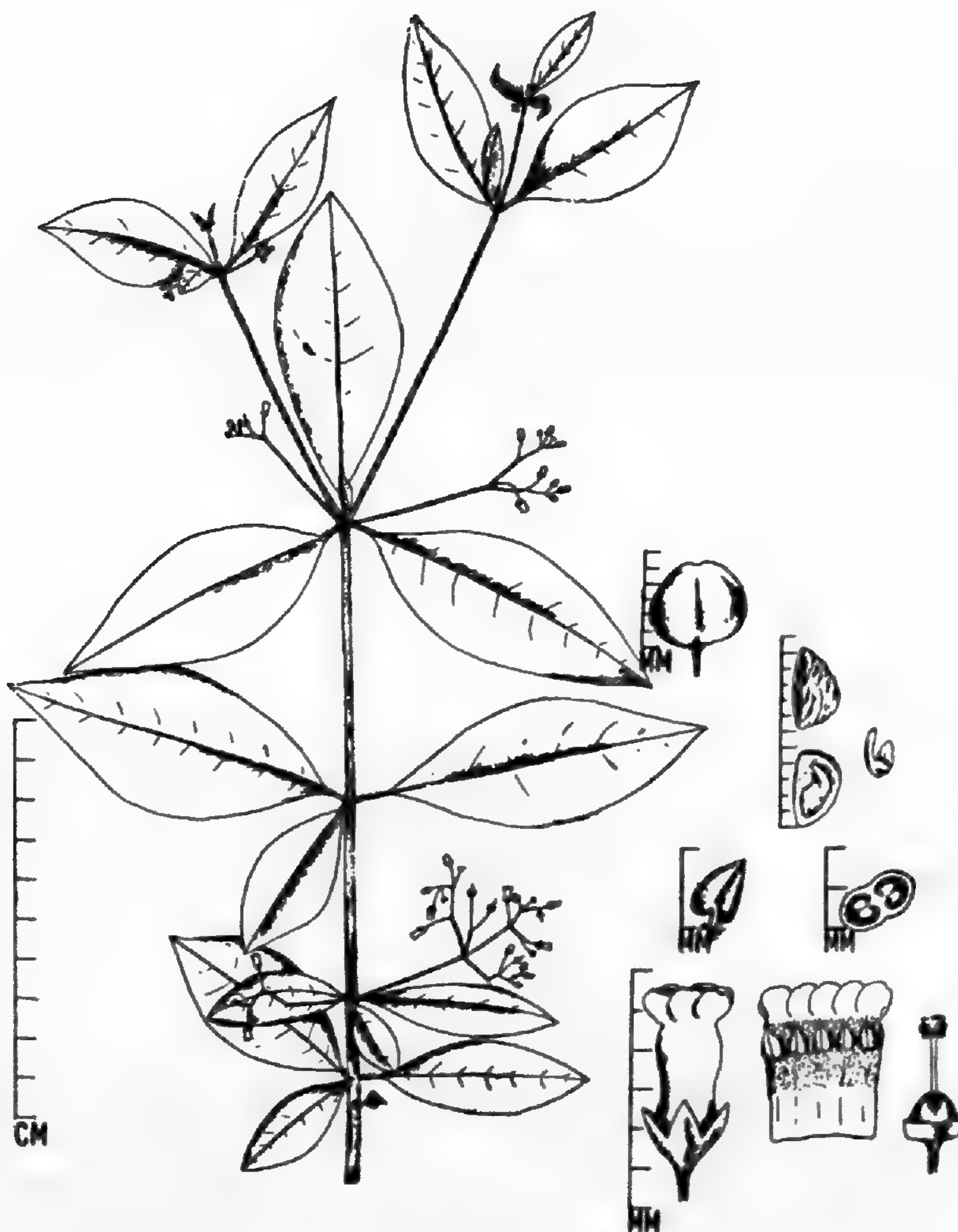


Fig. 7. *Rauvolfia mollis* S. Moore (E. Hassler 7400)

LEAVES ternate to very rarely quaternate, slightly anisophyllous, shortly petiolate, ovate-elliptic to narrowly elliptic, acute, attenuate at the base, 1–5 cm. long, 0.5–3.0 cm. broad, membranaceous to subcoriaceous, glabrous above, generally puberulent to puberulent only along the midrib beneath, the secondary veins and the vein network obscure; petiole 1–5 mm. long. INFLORESCENCES terminal and lateral, few- to many-flowered; peduncles glabrous to puberulent, slender, 1–4 cm. long, dichotomously branched, the branches usually divergent, minutely bracteate, the pedicels slender, 5–8 mm. long, glabrous to puberulent. FLOWERS small; calyx deeply 5-lobed, the lobes ovate, acute, 1.0–1.5 mm. long, glabrous or ciliate; corolla urceolate, white; the tube slender, 2.0–3.5 mm. long, glabrous without, villous within near the throat, the throat a little constricted, the lobes obovate to rotund, rounded, 1.0–1.5 mm. long; stamens 5, included, inserted near the throat, the anthers ovate, acute, about 1 mm. long, the filament distinct, about 0.5 mm. long; ovary 2-carpellary, syncarpous, subglobose, about 1.5 mm. in diameter, the ovules 1–2 in each locule on an axile placenta, the disc annular, about 0.5 mm. broad, the style columnar, 1.5–2.0 mm. long, glabrous, the stigma-head depressed-capitate, constricted in the middle, about 0.5 mm. high, obscurely bilobed. FRUITS spherical to subspherical, 4–6 mm. in diameter, glabrous, 2-seeded, the stones ovoid, flat ventrally, bulged dorsally, distinctly rugose; seeds ovate, slightly curved, albuminous, the testa membranaceous, the albumen carnose, the embryo deeply arcuate, the cotyledons ovate, obtuse, 2.0–2.5 mm. long, the hypocotyl terete, about as long as the cotyledons.

In dry fields and in inundated secondary forests. Flowering from September to December; fruiting from December through February. Paraguay and central-southern Brazil.

R. mollis can easily be mistaken for the more widespread *R. ligustrina*. However, it can be distinguished by the often whitish pubescence of its twigs, leaves, and peduncles, by the more branched, conspicuously divergent inflorescences, and the flowers with ovate calyx-lobes.

The leaf shape and the whitish pubescence of the twigs, leaves and peduncles are extremely variable. This is particularly evident in a suite of specimens of Malme from the type locality of *R. mollis*. The type specimen of *R. divergens* Mgf. does not indicate any distinctive character to justify its retention as a distinct species. I am, therefore, merging it with *R. mollis*.

BRAZIL. MATO GROSSO: Corumba, *Hoebne 4280* (US), *Malme 2736* (S, UPS); Cuyaba, *Malme 2679, 2679a* (S); Santa Cruz de Sierra do Rio dos Bugres, *Lindman 2885* (UPS), *A 2885* (S). RIO DE JANEIRO: Rio de Janeiro, *Dusén 139* (S).

PARAGUAY. BOQUERÓN (CHACO): 21° latitude, *Fiebrig 1278* (G, P, S), *1350* (G, P); between Río Apa and Aquidaban, *Fiebrig 4634* (G, K); Villa Sana, *Fiebrig 4664* (G, GH, P, M, S); San Genaro, Isla Margarita, *Meyer 18.600* (MO). PRECISE LOCALITY UNKNOWN: *Anisits 2230, 2655* (S), *Hassler 7400* (A, G, MO, P, S, UC, W).



Fig. 8. *Rauvolfia ligustrina* R. & S. (Humboldt 1480)

8. *RAUVOLFIA LIGUSTRINA* R. & S. Syst. Veg. 4:805. 1819. (T.: Humboldt & Bonpland s. n.)

R. ternifolia H. B. K. Nov. Gen. et Sp. 3:232. 1819. (T.: Humboldt 1480!)

R. parvifolia Bert. ex Spreng. Syst. 1:834. 1825. (T.: Bertero s. n. !)

R. parvifolia var. *cubana* A. DC. in DC. Prodr. 8:340. 1844, nom. nud.

R. parvifolia var. *tomentella* Muell.-Arg. in Linnaea 30:394. 1860. (T.: Sieber 326!)

R. alphonsiana Muell.-Arg. l. c. (T.: Poeppig s. n. !)

R. indecora Woodson, in Ann. Mo. Bot. Gard. 24:12. 1937. (Stork 2800!)

Shrubs 1–3 m. tall; branches dichotomous, terete, glabrous, the nodes with axillary glands ascending the petiole. LEAVES ternate, slightly anisophyllous, shortly petiolate, ovate to ovate-elliptic, acute to acuminate and broadly acute to rarely obtuse at the base, the largest leaves at the nodes 3–5 cm. long, 1–3 cm. broad, the smallest 1–3 cm. long, 0.5–1.5 cm. broad, membranaceous, glabrous or puberulent along the midrib beneath, secondary veins distinct, arcuate, 4–10 pairs,

the vein network obscure; petiole 1–3 mm. long. INFLORESCENCES terminal and lateral, few- to rarely many-flowered; peduncles slender, 1–3 cm. long, 2- or rarely 3-branched, the secondary peduncles rather congested, glabrous, or minutely puberulent, the pedicels slender, 2–4 mm. long, glabrous. FLOWERS small; calyx deeply 5-lobed, the lobes lanceolate, acuminate, 1.5–2.0 mm. long, glabrous; corolla urceolate, white, the tube slender, 2.0–3.5 mm. long, glabrous without and pilose within near the throat, the throat slightly constricted, the lobes ovate to subrotund, rounded, 1.0–1.5 mm. long; stamens 5, included, inserted near the throat, the anthers ovate, acute, about 1 mm. long, the filament distinct, 0.5 mm. long; ovary 2-carpellary, syncarpous, subspherical, about 1.5 mm. high, 2 mm. in diameter, the ovule 1 in each locule on an axile placenta, the disc annular, 0.5 mm. broad, the style columnar, 1.5–2.0 mm. long, glabrous, the stigma-head calyptriform, about 1 mm. high, obscurely bilobed. FRUITS spherical to subspherical, 5–7 mm. in diameter, glabrous, 2-seeded, the stones ovoid, flattened ventrally, convex dorsally, distinctly rugose; seeds ovate, slightly curved, albuminous, testa membranaceous, the albumen carnose, the embryo deeply arcuate, the cotyledons ovate, obtuse, 2.0–2.5 mm. long, the hypocotyl terete, about as long as the cotyledons.

Chiefly in moist situations, near sea-shore in coastal thickets, in river plains, savannas, and wet meadows; from sea-level to 1000 m. altitude. Flowering and fruiting from April to September. Cuba; Mexico to Colombia, Bolivia, Venezuela, Surinam, and northeastern Brazil.

COMMON NAMES: Brazil, Maranhão—*Paratudo*; Paraíba—*Mamao de Sapo*. Colombia—*Contra* and *Venenito*. El Salvador—*San Jose*. Mexico—*Cbirillo* and *Veneno*.

R. ligustrina can easily be recognized by its ternate, mostly ovate-elliptic, acuminate leaves, the rather congested, mostly few-flowered, lateral inflorescences, and the flowers with lanceolate, acuminate calyx-lobes.

Roemer & Schultes' name, *R. ligustrina*, has priority over the Kunthian name *R. ternifolia*, as shown by McVaugh.⁴⁸ The several specific names here are mainly due to an inadequate appreciation of variation in leaf characteristics. Markgraf, while correctly recognizing the identity of *R. alphonsiana* with *R. parvifolia*, still maintained the distinction between *R. parvifolia* and *R. ternifolia*. He has used as his key characters leaf size and inflorescence flower-number. Similarly, Woodson differentiates his *R. indecora* "by its nearly isophyllous, subsessile leaves, which are minutely puberulent beneath, and its larger drupes." These characters, however, are very variable and do not help in maintaining the distinctions.

ANTILLES.—

CUBA. HAVANA: Havana, *Baker 2640* (NY, UC), *Leon 7191* (MO, NY), *Leon & Roca 7251, 7252* (MO, NY), *Van Hermann 673* (NY), *Wilson 1345* (A, G, NY, P, UC, US, W). MATANZAS: Matanzas, *Alain 4078* (MO), *Baker 2421* (UC). ORIENTE: Bayate, *Ekman 5927* (S). PINAR DEL RIO: *Roig 1733* (NY), *Sbafer 11887* (MO, NY, US). SANTA CLARA (LAS VILLAS): Cienfuegos, *Combs 180* (GH, MO, NY, P, US); Sagua, *N. L.*

⁴⁸ McVaugh, R., in *Taxon* 4:84. 1955.

Britton & Wilson 306, 369 (NY), *Howard 5582* (GH, NY); Santa Clara, *Baker 4963* (NY, UC, US), *Ekman 16859* (S), *Leon 9223, 9447* (MO). PRECISE LOCALITY UNKNOWN: *Poeppig s. n.* (L, P, W), *Wright 2943, 2944* (G, GH, MO, NY, P, S).

TRINIDAD: Moruga, coastal thicket, N. L. *Britton & Broadway 2460* (GH, US), *Broadway 2263* (G), *2680* (G, US), *9010* (A, MO), *9265* (A, G); St. Augustine, *Baker 1* (MO). PRECISE LOCALITY UNKNOWN: *Sieber 326* (P, MO), *Trinidad Botanical Garden 2772* (US).

CENTRAL AMERICA.—

COSTA RICA. GUANACASTE: Bebedero, *Brenes 12579* (F); Nocoya, *Jorge León 4286, 4287* (MO).

EL SALVADOR. LA PAZ: La Paz, *Choussy 19* (US). LA UNION: Laguna de Maquigue, *Standley 20910* (US). SAN MIGUEL: Laguna de Olomega, *Standley 20996* (US), *Tucker 949* (US). SONSONATE: Acajutla, *Salvador Calderón 1654* (US).

GUATEMALA. ESCUINTLA: San Jose, *Kellerman 4570* (US), *Standley 64198* (F, MO), *Merck & Co. s. n.* (MO). SUCHITEPEQUEZ: south of Tiquisate, *Steyermark 47806* (F).

MEXICO. CHIAPAS: Paderon, *Matuda 16273* (F, MO), *16927* (F), *2734* (A, MO, US), *2687* (A, F, MO). OAXACA: Oaxaca, *Matuda extra 5* (MO). JALISCO: Tuxpán, *Mexia 1042* (A, F, G, MO, P, UC, US).

SOUTH AMERICA.—

BOLIVIA. BENI: Río Madre de Dios, *Kuhlmann 581* (RB); junction of R. Beni and R. Madre de Dios, *Rusby 2388* (F, GH, MO, W), *2389* (F, GH, P, US).

BRAZIL. BAHIA: Bahia, *RB 47482* (RB). CEARA: Ceara, *Allemão 974* (P), *Drouet 2707* (F, GH, S, US), *Ducke s. n.* (RB), *Hoehne 7544* (F). MARANHÃO: *Ducke s. n.* (RB), *Hoehne 3430* (F); near Lorenda, *Krukoff 2047* (A, F, G, M, MO, S, US). PARA: Montelegrè, *Ducke 23* (P, RB, S, US). PARAIBA: J. C. de Moraes *890* (MO), *Xavier 103* (MO). PERNAMBUCO: Fernando de Noronha, *Mosley s. n.* (P), *Ridley, Lea & Ramage 83* (GH); Pernambuco, *Gardner 1063* (G, GH, S, US, W). PIAUÍ: *Netto 40* (F).

COLOMBIA. ATLANTICO: *Dugand 4541* (US), *Dugand & Bariga 2307* (US), *Elias 1425* (F, MO, P, US); Río Magdalena, *Dugand & Jaramillo 2748, 3262* (US); Barranquilla, *Elias 1076* (F, G, MO, US). BOLIVAR: Cartagena, *Otto 804* (W); Florencia, *Perez Arbelaez 636* (US); San Martín, *Curran 28, 75* (GH, US), *408* (GH), *Dugand 528* (F, MO); Río Tucurínca, foothills of Sierra Nevada, *Dugand 1025* (MO); San Pedro Alejandrino, R. R. *Castañeda 74* (F); Monteiro, Zainum, *Molina & Barkley BO. 115* (MO, US), *Pennell 4140* (GH, MO, US).

SURINAM: Surinam River, *Focke 1287* (GH).

VENEZUELA. ARAGUA: Maracay, *Vogel 1455* (M). DISTRITO FEDERAL: Betel, *Clarendon 67* (US); around Caracas, *H. Pittier 9717* (G, US); Losa, *Tamayo 197* (MO). MERIDA: Tovar, *Fendler 2347* (G, GH, MO, P, US).

SECTION II. MACROVOLFIA (Pichon) A. S. Rao, emend.

§ GRANDIFLORAE Mgf. in Fedde, Rep. Spec. Nov. 20:116. 1924.

§ HESPEROVOLFIA Pichon, in Bull. Soc. Bot. Fr. 94:32, 33. 1947.

SERIES 3. LATIFOLIAE A. S. Rao, ser. nov.

Rami floriferi apice foliosi, cataphyllis super quoque nodo manifestis, hoc aucto nodo verticillato unico. Folia ca. bis longiora quam latiora (usque ter longiora in *R. polyphylla*) basi obtusa vel rotundata. Inflorescentiae terminales. Species typica: *R. polyphylla* Benth.

KEY TO THE SPECIES

- A. Calyx-lobes ovate. Corolla-tube 6–8 mm. long.
- B. Leaves ovate or ovate-elliptic. Peduncles equal to or up to 4 times as long as the petioles.
- C. Leaves membranaceous or subcoriaceous, 1.5–2.5 cm. broad, petioles 1.0–1.5 cm. long. Peduncles slender, 3–4 times as long as the petioles. Northeastern Brazil...9 *R. mattfeldiana*
- CC. Leaves delicately membranaceous or strikingly coriaceous, 3–6 cm. broad, petioles 2.0–3.5 cm. long. Peduncles stout, as long as the petioles or up to 2.5 times as long.
- D. Leaves strikingly coriaceous. Peduncles as long as, or 1.5 times longer than, the petioles, pedicels 0.8–1.0 cm. long. Corolla-tube lilac-colored, 1.5–2 times as long as the corolla-lobes. Venezuela.....10. *R. pachyphylla*
- DD. Leaves delicately membranaceous. Peduncles 2.0–2.5 times as long as the petioles, pedicels 0.3–0.5 cm. long. Corolla-tube yellow, as long as or 1.25 times longer than the corolla-lobes. Colombia.....11. *R. leptophylla*
- BB. Leaves lanceolate. Peduncles shorter than the petioles. Northwestern Brazil.
.....12. *R. polyphylla*
- AA. Calyx-lobes lanceolate or deltoid. Corolla-tube 10–24 mm. long.
- E. Leaves with 5–11 pairs of distinctly arcuate secondary veins 8–12 mm. apart,
- F. Petioles 1.5–2.0 cm. long. Inflorescences 20-to many-flowered. Calyx-lobes deltoid, 1.0–1.5 mm. long.
- G. Leaves mostly 4 at node, membranaceous. Anthers 2.0–2.5 mm. long; ovary sulcately marked. Fruit bilobed, reniform. Northwestern Brazil and Peru.....13. *R. sprucei*
- GG. Leaves mostly 5 at node, subcoriaceous. Anthers 1.0–1.5 mm. long; ovary smooth. Fruit globose. Northwestern Brazil.....14. *R. paraensis*
- FF. Petioles 0.5–1.0 cm. long. Inflorescences 1- to 5-flowered. Calyx-lobes lanceolate, 2.5–3.5 mm. long. Northwestern Brazil and Peru.....15. *R. macrantha*
- EE. Leaves with 12–20 pairs of scarcely arcuate or almost transverse secondary veins 4–7 mm. apart. Northwestern Brazil.....16. *R. pentaphylla*

9. *RAUVOLFIA MATTFELDIANA* Mgf. in Fedde, Rep. Spec. Nov. 20:117, 120. 1924. (T.: *Ule 7114!*)

Shrubs 2–5 m. tall; branches 2-, 3- or 4-chotomous, terete to slightly 4-angled, sparsely lenticellate, glabrous, the base of young branches with caducous cataphylls 2–3 mm. long, about 1 mm. broad, the nodes with pectinate glands confined to the axil. LEAVES in verticils of 4 or 5 at the tips of twigs, slightly anisophyllous, short-petiolate, ovate-elliptic, acute to acuminate, attenuate at the base, the largest leaves 4–7 cm. long, 1.5–2.5 cm. broad, the smallest 2–4 cm. long, 1.0–1.5 cm. broad, membranaceous to subcoriaceous, glabrous, secondary veins and the vein network obscure above but distinct beneath; petioles slender, 1.0–1.5 cm. long. INFLORESCENCES terminal, lax, comparatively few-flowered, corymbose; peduncles slender, 2–4 cm. long, usually geminate, 2- to 3-branched, minutely bracteate, the bracts subulate, about 2 mm. long, the pedicels slender, 10–15 mm. long, glabrous. FLOWERS rather small; calyx deeply 5-lobed, the lobes ovate, acute, 1.5–2.0 mm. long, glabrous; corolla tubular, slender, 6–7 mm. long, glabrous without and pilose within along the upper half, the throat not constricted, the lobes linear-ovate, obtuse, 3–4 mm. long, 1.5–2.5 mm. broad; stamens 5, included, inserted near the throat, the anthers ovate, apiculate, 1.5–2.0 long, with a callosity on the back at the point of insertion, the filament obscure; ovary 2-carpellary, hemisyncarpous, obovoid, about 2.5 mm. high and 2 mm. in diameter, the ovules 1–2 in each locule on a ventral placenta, the disc annular, about 0.5 mm. broad, the style columnar, 3.0–3.5 mm. long, glabrous, the stigma-head cylindrical, a little narrowed in the

middle, obscurely bilobed. FRUITS deeply bilobed when young, 2-seeded.

In the fields near hilly areas; flowering in November. Northeastern Brazil.

The terminal verticils of rather small leaves with the distinct vein network beneath, the few-flowered, slender-peduncled inflorescences, the rather long pedicels of the fairly small tubular flowers, are characteristics which help in distinguishing this species from its related species.

BRAZIL. BAHIA: Bahia, Serra de Sincora, *Ule 7114* (G, L). MINAS GERAES: Minas Geraes, Tapanahoacanga, *Pohl 3462* (W).

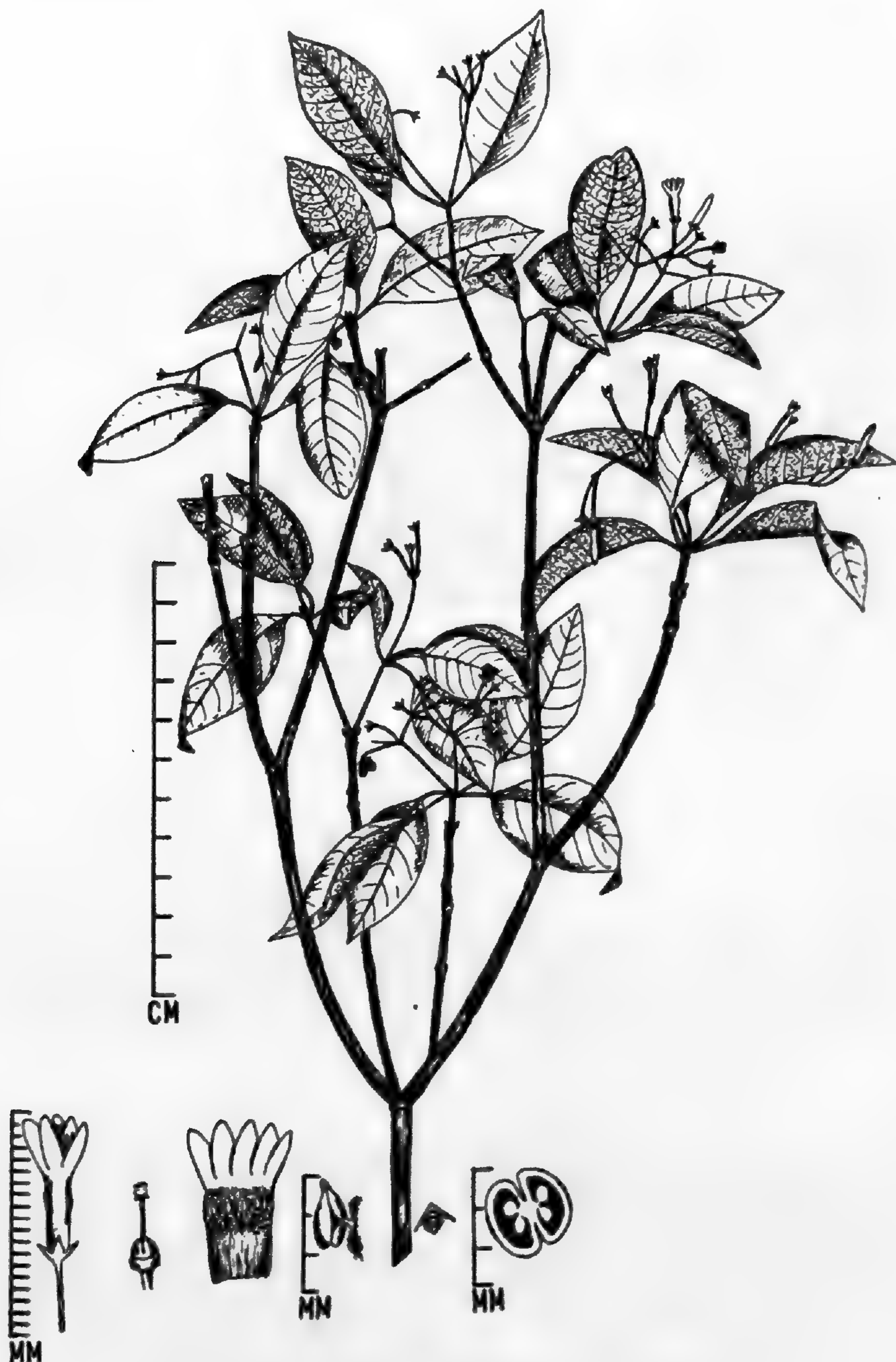


Fig. 9. *Rauvolfia mattfeldiana* Mgf. (*Ule 7114*)

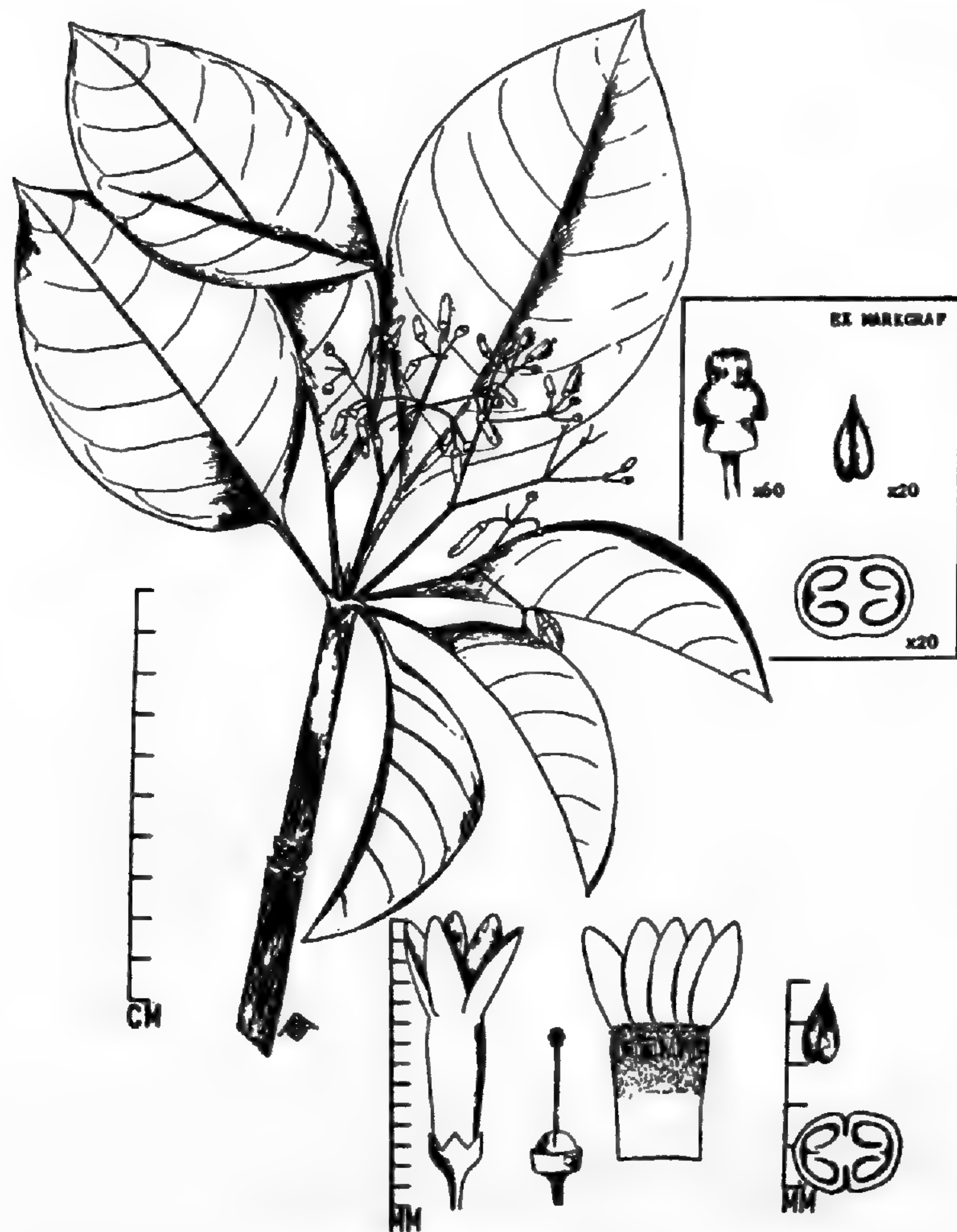


Fig. 10. *Rauvolfia pachyphylla* Mgf. (Ule 8736 photo, and Pittier 9465).

10. *RAUVOLFIA PACHYPHYLLA* Mgf. in Fedde, Rep. Spec. Nov. 20:117, 121. 1924.
(T.: Ule 8736, photo!)

Aspidosperma quadriovulatum Pitt. in Bol. Cient. y Tecn. Mus. Com. Venez. 1:66. 1925.
(T.: Pittier 9465!)

Shrubs 1–2 m. tall; branches 2- or 3-chotomous, terete, prominently lenticellate, the nodes with many distinct, pectinate glands confined to the axil and with a verticil of cataphylls or their scars immediately above. LEAVES 4–6 at node usually at the tips of twigs, long-petiolate, elliptic to obovate-elliptic, acuminate, abruptly attenuate at the base, 10–15 cm. long, 5–7 cm. broad, strikingly coriaceous, glabrous, the secondary veins distinct on both surfaces, 6–8 pairs 10–15 mm. apart, arcuate, faintly joining at the margin to form a marginal vein on either side; petioles stout, 2–3 cm. long. INFLORESCENCES terminal, many-flowered; peduncles 2–3, dichotomously branched, stout, 3–4 cm. long, glabrous, minutely bracteate, the pedicels stout, 8–10 mm. long, glabrous. FLOWERS rather small; calyx 5-lobed, the lobes ovate, acuminate, glandular-dentate at the margin, about 1.5 mm. long, 1 mm. broad, the corolla tubular, lilac to dark violet in color

(Ule), about 7 mm. long, 2 mm. in diameter, glabrous without, pilose within near the throat, the throat a little constricted, the lobes ovate, obtuse, about 4 mm. long, 3 mm. broad; stamens 5, included, inserted near the throat, the anthers ovate, acuminate, about 1 mm. long, the filament obscure; ovary 2-carpellary, syncarpous, with 2 ovules in each locule on an axile placenta, the disc annular, the style columnar, the stigma-head cylindrical, constricted at the two ends, biapiculate.

Between rocks, amongst undershrubs, 900 to 1,600 m. altitude. Flowering May, June. Venezuela and Mount Roraima in British Guiana.

The type specimen of *R. pachyphylla* is presumably lost in the general destruction of the Berlin Herbarium. However, the type photo which I had for comparison includes Markgraf's drawings of the flower dissections. This was helpful in tracking down the identity of Pittier's *Aspidosperma quadriovulatum*. Woodson⁴⁹ had already determined this as a *Rauvolfia*.

VENEZUELA. BOLIVAR: Ptari-Tepui, southeast-facing slopes, *Steyermark 60022* (F).
DISTRITO FEDERAL: quebrada de San Lázaro, near Caracas, *H. Pittier 9465, 11062* (US).

11. *RAUVOLFIA leptophylla* A. S. Rao, spec. nov.

Arbor circa 15 m. alta; ramulis sparse lenticellatis griseis plus minusve quadrangulatis basi ramulorum novorum caducis ibique cataphyllis praeditis. FOLIA

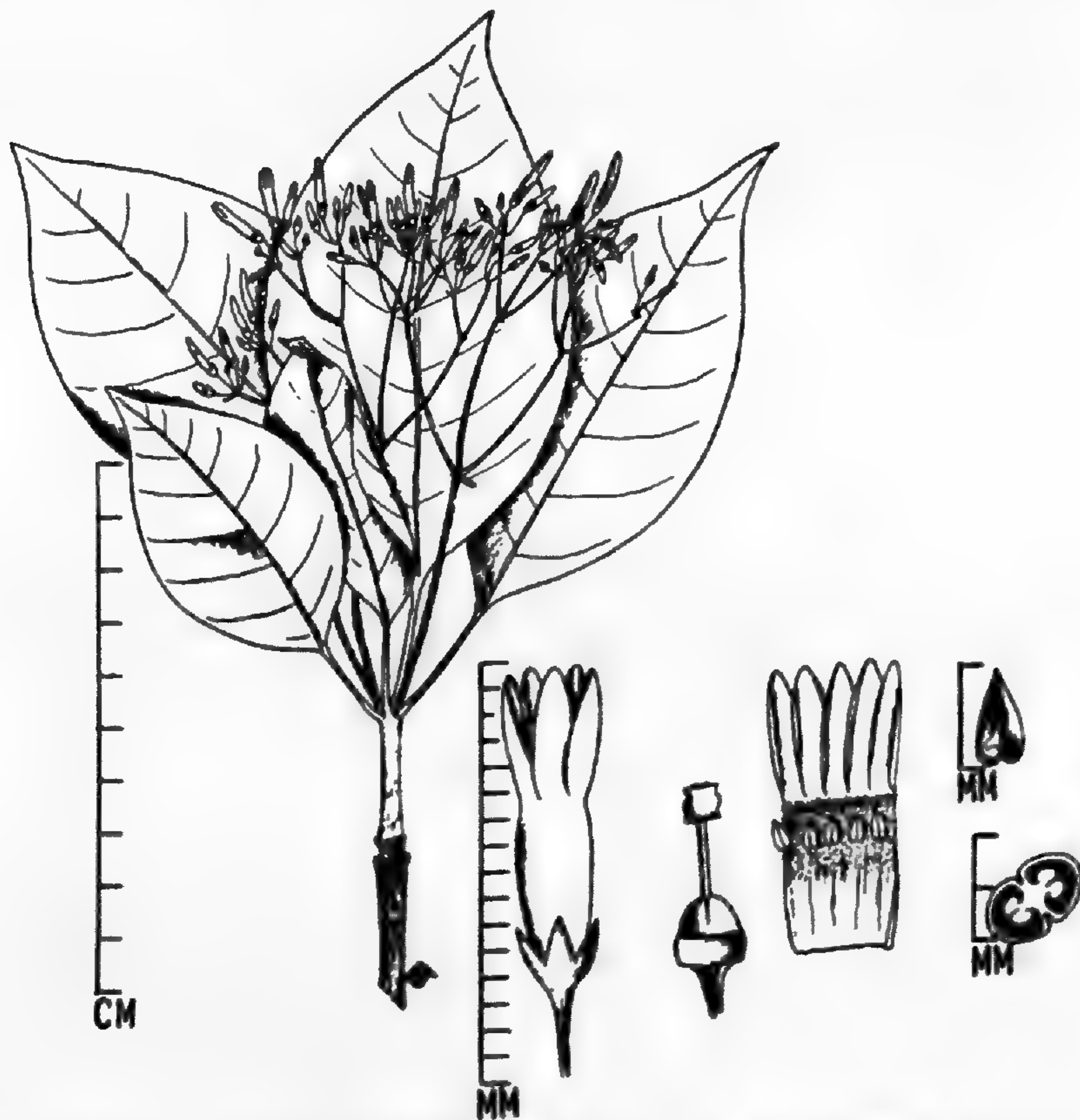


Fig. 11. *Rauvolfia leptophylla* A. S. Rao (*R. R. Castañeda 309*)

⁴⁹ Woodson, R. E., in *Ann. Mo. Bot. Gard.* 38:129. 1951.

tenuissima in apices ramulorum 5-verticillata glabra late elliptica inaequalia, majoribus 9–12 cm. longis 4–5 cm. latis, minoribus 5–6 cm. longis 3.0–3.5 cm. latis, nervis 9–15 in utroque latere arcuatis; petiolo 2.0–3.5 cm. longo eglandulo. INFLORESCENTIAE terminales corymbosae multiflorae, pedunculis binis 5–6 cm. longis glabris, pedicellis 3–5 mm. longis gracilibus. FLORES majusculi; calycis lobis 1.5–2.0 mm. longis circa 1 mm. latis glabris; corollae tubo flavido 6–7 mm. longo extus glabro intus in dimidio superiore praesertim supra insertionem staminum piloso, lobis lineari-ovatis obtusis, 4–5 mm. longis 1.0–1.5 mm. latis; staminibus 5 inclusis sub faucibus insertis, antheris ovatis acutis circa 1 mm. longis subsessilibus; ovarii bicarpellatis semiconnatis obovoides circa 2.5 mm. altis 2.0 mm. diametro 4-ovulatis; disco annulare circa 0.5 mm. alto, stylo 3.0–3.5 mm. longo, clavunculo calyptriformi circa 1 mm. alto, obtuse bilobato. FRUCTUS desunt.

Trees about 15 m. tall; branches terete or faintly 4-angular, sparsely lenticellate, glabrous, the base of young branches with caducous cataphylls, the nodes with pectinate glands confined to the leaf axils. LEAVES in verticils of 5 at the tips of twigs, slightly anisophyllous, long-petiolate, elliptic, acuminate, attenuate at the base, the largest leaves at the node 9–12 cm. long, 4–5 cm. broad, the smallest 5–6 cm. long, 3.0–3.5 cm. broad, delicately membranaceous, glabrous, secondary veins 9–15 pairs, arcuate, equally obscure on both surfaces; petiole stout, 2.0–3.5 cm. long. INFLORESCENCES terminal, many-flowered, corymbose; peduncles slender, 5–6 cm. long, usually geminate, 2- or 3-branched, glabrous, minutely bracteate, the pedicels slender, 3–5 mm. long, glabrous. FLOWERS rather large, calyx campanulate, deeply 5-lobed, the lobes ovate, acute, 1.5–2.0 mm. long, about 1 mm. broad, glabrous; corolla salverform, yellowish, the tube slender, 6–7 mm. long, glabrous without, villous within along the upper half, scarcely constricted at the throat, the lobes linear-ovate, obtuse, 4–5 mm. long, 1.0–1.5 mm. broad; stamens 5, included, inserted near the throat, the anthers ovate, acute, about 1 mm. long, subsessile; ovary 2-carpellary, hemisyncarpous, obovoid, about 2.5 mm. high, 2 mm. in diameter, the ovules 2 in each locule on an axile placenta, the disc annular, about 0.5 mm. high, the style columnar, 3.0–3.5 mm. long, glabrous, the stigma-head calyptriform, about 1 mm. high, obscurely bilobed. Fruits not seen.

COLOMBIA. MAGDALENA: San Sebastián de Rábago, Romero R. Castañeda 900, TYPE (MO).

12. *RAUVOLFIA POLYPHYLLA* Benth. in Hook. Jour. Bot. 3:241. 1841. (T.: Robert Schomburgk 891!)

R. polyphylla var. *connivens* Benth. ex Muell.-Arg. Mart. Fl. Bras. 6¹:31. 1860. (T.: Spruce 1896!)

R. polyphylla var. *divergens* Benth. ex Muell.-Arg. l. c. (T.: Spruce 1837!)

Trees or shrubs with di- or tri-chotomous, terete to slightly quadrangular, glabrous branches, the nodes with pectinate glands confined to the axil. LEAVES in verticils of 4–5 at the tips of twigs, slightly anisophyllous, long-petiolate, ovate-lanceolate, acute to acuminate at the tip, obtuse to abruptly attenuate at the base,

the largest leaves 11–15 cm. long, 3–5 cm. broad, the smallest 4–6 cm. long, 1–3 cm. broad, membranaceous, glabrous, secondary veins 5–10 pairs, arcuate, equally evident on both surfaces; petioles fairly slender, 1–3 cm. long. INFLORESCENCES terminal, few-flowered, corymbose; peduncles slender, 10–15 mm. long, glabrous, bracteate, the bracts linear-lanceolate, about 1.5 mm. long, the pedicels slender, 2–5 mm. long, glabrous. FLOWERS white, odorous; calyx deeply 5-lobed, the lobes

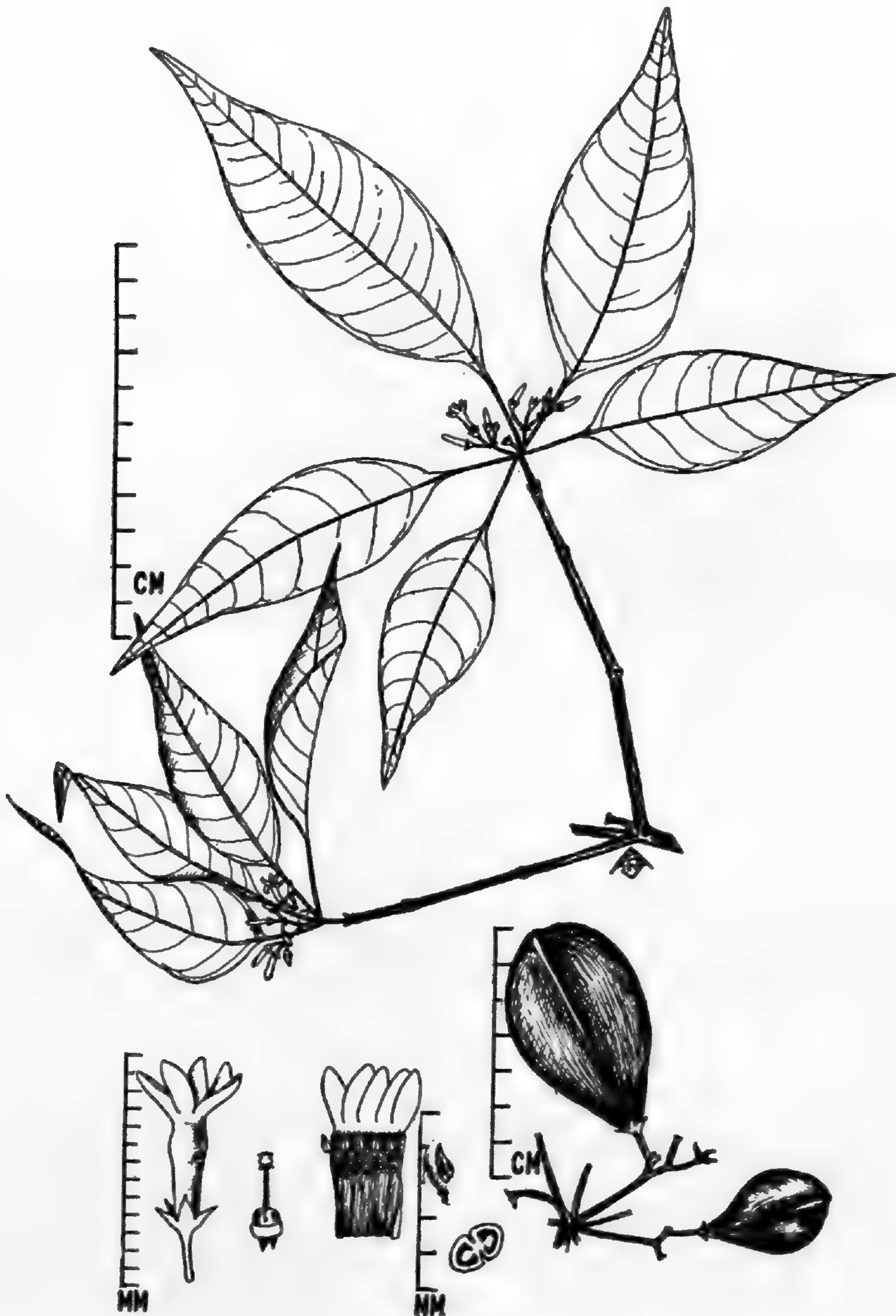


Fig. 12. *Rauvolfia polyphylla* Benth. (R. Spruce 3821, and 1896)

ovate, acute to acuminate, 1.5–2.0 mm. long, 1.0–1.5 mm. broad, glabrous; corolla tubular, white, a little dilated near the throat, 6–8 mm. long, glabrous without, villous within along the upper half, rather densely near the anther tips, the lobes linear-ovate, obtuse, 4–5 mm. long, 2.0–2.5 mm. broad; stamens 5, included, inserted near the throat, the anthers ovate, acute to acuminate, 1.0–1.5 mm. long, with a dorsal callosity at the point of insertion, the filament about 0.5 mm. long; ovary 2-carpellary, fused at the very base, obovoid, about 2.5 mm. high, 2 mm. in diameter, the ovule 1 in each locule on a ventral placenta, the disc annular, about 1 mm. broad, the style linear, 3.0–3.5 mm. long, glabrous, the stigma-head cylindrical, constricted at the two ends, about 1 mm. high, obscurely bilobed. FRUITS deeply bilobed, compressed, pear-shaped, 15–19 mm. long, 14–15 mm. broad, glabrous.

Chiefly near dry river beds and on the banks of streams; flowering from September to November and fruiting in December. Northern Brazil and Guiana border.

This species can easily be recognized by its ovate-lanceolate leaves and the peduncles much shorter than the petioles.

The two varieties, obviously based on the characters of the leaves and the fruits, do not deserve to be maintained, as both the characters are variable and are of no taxonomic significance.

BRAZIL. AMAZONAS: Mañaos, Río Taruma, Igapo ad ripas infra cataractum minorum, *Ducke 626* (F, MO, RB, US); Cucuhy, Río Negro, Igarape Macacumy, *Ducke s. n.*, RB 30117 (RB); secus Río Negro, inter Barcellos et San Gabriel, *Spruce 1896* (P, W); inter Barra et Barcellos, *Spruce 1837* (G, GH, MO, W); ad flumen Guainia et Río Negro supra ostium flumini Cusquiari, *Spruce 3821* (P, W); Brasilia australis, without precise locality, *Riedel s. n.* (G, P).

GUIANA: *Robert Schomburgk 891* (W).

13. *RAUVOLFIA SPRUCEI* Muell.-Arg. in Mart. Fl. Bras. 6¹:34. 1860. (T.: *Spruce 1732!*)

R. lauretiana Woodson, in Ann. Mo. Bot. Gard. 18:541. 1931. (T.: *G. Klug 35!*)

Trees 8–25 m. tall; branches terete, sparsely lenticellate, bark dark brown, crackled or longitudinally striated, the nodes with glands confined to the axil. LEAVES in whorls of 4, rarely 3 or 5, at the tips of twigs, slightly anisophyllous, long-petiolate, ovate to rhombic-ovate, acute to acuminate, abruptly attenuate at the base, the largest leaves 9–15 cm. long, 5–8 cm. broad, the smallest leaves 5–8 cm. long, 3–5 cm. broad, membranaceous, glabrous, the secondary veins 7–10 pairs, arcuate, rather obscure above, very distinct beneath; petioles stout, 1.5–3.5 cm. long. INFLORESCENCES terminal, many-flowered; peduncles 1–4 cm. long, dichotomously branched, the secondary peduncles often longer than the primary peduncle, glabrous, bracteate, the bracts ovate, acuminate, about 1.5 mm. long, the pedicels slender, 5–12 mm. long, glabrous. FLOWERS conspicuous; calyx deeply 5-lobed, the lobes broadly deltoid, broadly acute to obtuse, 1.0–1.5 mm. long, about 2 mm. broad, the margin minutely ciliate, glabrous; corolla tubular, whitish with crimson

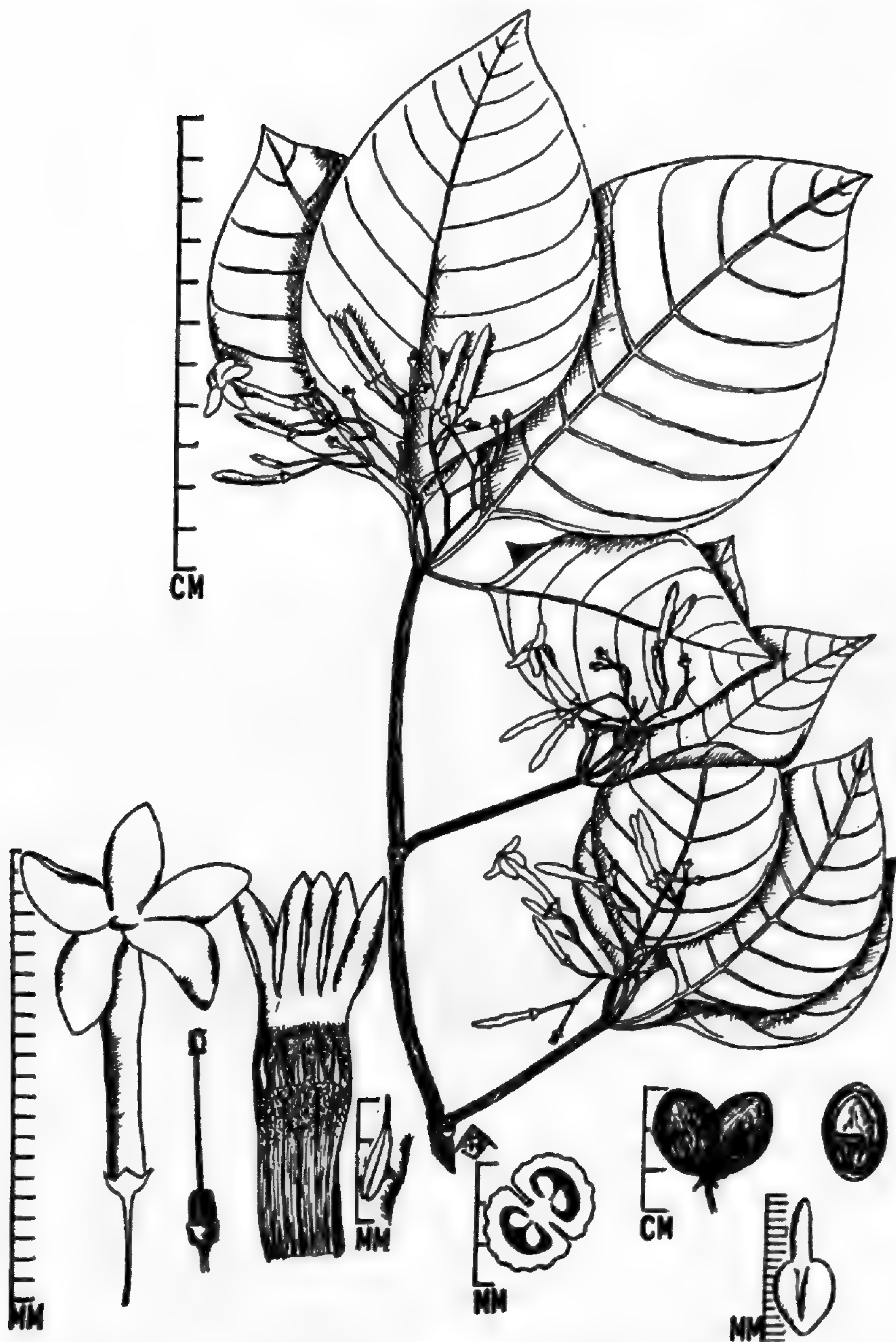


Fig. 13. *Rauvolfia sprucei* Muell.-Arg. (Spruce 1732, Mexia 6415)

streaks, 12–20 mm. long, about 2 mm. in diameter, glabrous without, sparsely pilose within near the throat, the throat scarcely dilated, the lobes obovate, obtuse, 5–8 mm. long, 3–5 mm. broad; stamens 5, included, inserted a little below the throat, the anthers ovate, acuminate, 2–3 mm. long, with a callosity on the back at the point of insertion, subsessile; ovary 2-carpellary, hemisyncarpous, cylindrical, about 3 mm. high, 2 mm. in diameter, sulcately marked, the ovules 2 in each locule on an axile placenta, the style filiform, 5–12 mm. long, glabrous, the stigma-head calyptriform, about 1.5 mm. high, biapiculate. FRUITS reniform, bilobed when both carpels develop, but often ovoid, with only one carpel developing, 20–25 mm. high, 14–16 mm. broad, the stones ovate, compressed, faintly rugose, 19–24 mm.

long, 9–15 mm. broad, the seed ovate, albuminous, the testa membranaceous, the albumen fleshy, the embryo erect, about as long as the seed, the cotyledons ovate, obtuse, 5–9 mm. long, 3–5 mm. broad, the hypocotyl terete, as long as the cotyledons, superior.

Trees on the banks of rivers and overflowed creeks; 100–110 m. altitude. Flowering from September to October; mature fruits in January. Northwest Brazil and northern Peru.

R. sprucei is closely allied to *R. paraensis*, and indeed it is often difficult to distinguish one from the other. However, *R. sprucei* usually bears leaves in 4's, the leaves are quite membranaceous, and more often rhombic-ovate. The peduncle is regularly dichotomous in branching, and very often the secondary peduncles are longer than the primary peduncle. The anthers are longer, the ovary sulcately marked. The fruits are reniform, bilobed.

BRAZIL. AMAZONAS: Barra, *Spruce 1732* (G, GH, K, W) Ilha de Bacaba, *Fröes 21307* (F, K); mouth of Rio Embira, *Krukoff 4683* (A, G, M, MO, S, UC, US).

PERU. LORETO: Marañon von Iquitos, *Tessmann 5107* (NY, S); Mishuyacu, near Iquitos, *Klug 35* (US), Rancho Indiana, *Mexia 6415* (GH, K, MO, S, US); Tarapoto, *Spruce 3856* (K, W).

14. RAUVOLFIA PARAENSIS Ducke, in Arch. Jard. Bot. Rio de Janeiro 4:167. 1925. (T.: Ducke, RB 43!)

R. amazonica Mgf. in Notizblatt 9:960. 1926. (T.: Ducke, RB 917 & RB 11, 395!)

Trees up to about 20 m. tall; branches trichotomous, terete, sparsely lenticellate, the nodes with pectinate glands confined to the axil, LEAVES in whorls of 5, rarely 2, 3, 4, or 6, at the tips of twigs, slightly anisophyllous, long-petiolate, ovate to ovate-elliptic, acute to acuminate, abruptly attenuate at the base, the largest leaves 9–18 cm. long, 5–9 cm. broad, the smallest leaves 8–12 cm. long, 3–7 cm. broad, membranaceous to subcoriaceous, glabrous, the secondary veins 6–10 pairs, arcuate, more distinct beneath; petioles stout, 1.5–4.5 cm. long. INFLORESCENCES terminal, many-flowered; peduncles geminate, 2- or 3-chotomously branched, 2–18 cm. long, glabrous, bracteate, the bracts ovate, acute, about 1 mm. long, the pedicels slender, 5–10 mm. long, glabrous. FLOWERS conspicuous; calyx deeply 5-lobed, the lobes broadly deltoid, acute, about 1.5 mm. long, 2 mm. broad, glabrous; corolla tubular, white with scarlet streaks (according to Ducke), 12–20 mm. long, about 2 mm. in diameter, glabrous without, sparsely pilose within near the throat, the throat a little dilated, the lobes ovate, obtuse to rounded, 3–6 mm. long, 2–4 mm. broad; stamens 5, included, inserted near the throat, the anthers ovate, acute, 1.0–1.5 mm. long, with a callosity on the back at the point of insertion, subsessile; ovary 2-carpellary, hemisyncarpous, cylindrical, 2.5–3.5 mm. high, about 2 mm. in diameter, smooth, the ovules 2 in each locule on an axile placenta, the disc annular, about 1 mm. broad, the style filiform, 6–15 mm. long, glabrous, the stigma-head drum-shaped, about 1 mm. high, bilobed. FRUITS globose, 3–4 cm. in diameter, 2-seeded, one of them often abortive, the stones fusi-

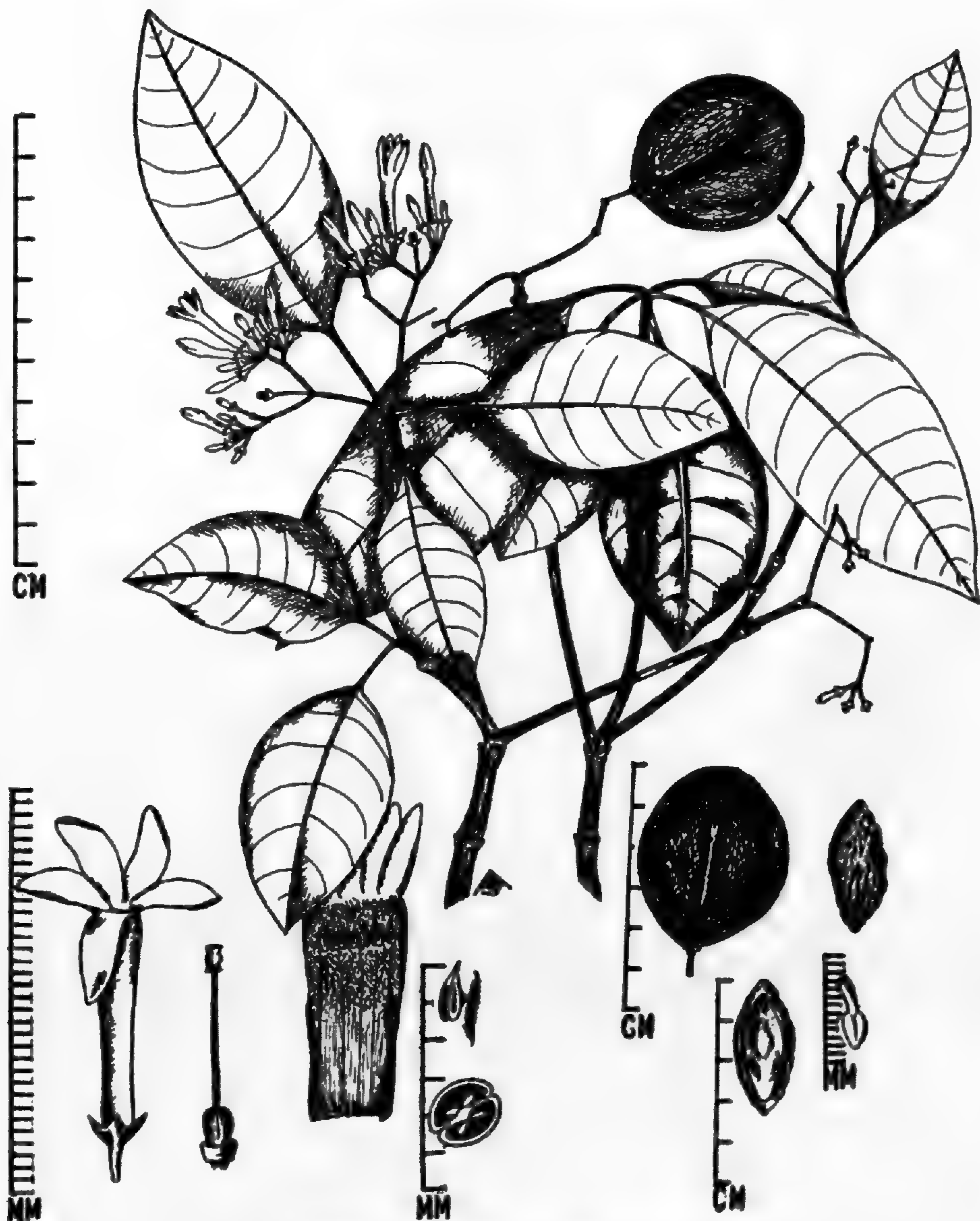


Fig. 14. *Rauvolfia paraensis* Ducke (Ducke RB 43)

form, compressed, rugose, 3.0–3.5 cm. long, about 1 cm. broad, the seed elliptic, albuminous, the testa membranaceous, the albumen carnosae, the embryo about half as long as the seed, erect, the cotyledons ovate, obtuse, 4–5 mm. long, 2.0–2.5 mm. broad, the hypocotyl terete, equal in length to the cotyledons.

Trees in non-inundated primary forests; flowering from September to January, ripe fruits in May. Northern and northwestern Brazil.

COMMON NAME: Brazil, Pará—*Gogo de Guariba*.

This species is closely related to *R. sprucei* and *R. pentaphylla*. It differs from the former in having mostly elliptic, coriaceous leaves in 5's; the primary peduncles usually much longer than the secondary peduncles; the flowers with shorter anthers and smooth ovaries and the fruits globose. It differs from the latter species in having fewer distinctly arcuate secondary veins and slightly larger fruits.

Markgraf has differentiated his new species *R. amazonica* from *R. paraensis* thus:—

2. Blätter 3 zu bis 4, gröber, längliche-elliptisch (vorn kurz zugespitzt), mit 6 bis 8 Paar Seitennerven; Kronzipfel $\frac{1}{3}$ bis $\frac{1}{2}$ so lang wie die Kronröhre; Fruchtknoten doppelt so hoch wie die stumpfen Kelchzipfel.....*R. paraensis*
3. Blätter zu 3, eiförmig, vorn lang zugespitzt, mit 5 bis 8 Paar Seitennerven; Kronzipfel etwa $\frac{2}{3}$ so lang wie die Kronröhre, Fruchtknoten doppelt so hoch wie die spitzen Kelchzipfel.....*R. amazonica*

I have examined a good number of Ducke's specimens from the Rio de Janeiro Garden Herbarium and elsewhere. I have measured and analyzed the leaf and flower characteristics on which Markgraf has based his *R. amazonica*. I find a considerable variation in the number of leaves per node, their shape and structure clearly varying with age of the twigs. There is a similar variation in the flower too. In view of this, I agree with Ducke, who collected and described *R. paraensis*, in including *R. amazonica* (RB 917, 11395) under that name. Hence, I am merging *R. amazonica* with *R. paraensis*.

BRAZIL. AMAZONAS: Borba (Rio Madeira), *Ducke 74* (A, F, MO, US), 30115 (RB); Esperança, ad ostium fluminis Jauary, *Ducke 1118* (K, MO, RB, US); Santa Izabel, Rio Negro, *Ducke 23950* (A, RB, S, US); São Paulo de Olivença, basin of Rio Solimoes, *Krukoff 8996* (A, F, MO, P, US). PARA: Belem, *Ducke 785* (F, MO, US), 43 (RB, US); Boa Vista, Rio Tapajos, *Ducke 11391* (RB, S, US); Macajubim, *Ducke 11395* (RB); Santa Izabel, Estrada de Ferro do Braganca, *Ducke 917* (G, P, RB, S, US); Juruty Velho (Civ. Para), *Ducke 2159F* (G, with 917, P, RB, S, US); Villa Nova, Rio Tapajos, *Pires 3577, 4021* (MO).

SURINAM. Brownsweeg, *Zaandam 6885* (L), *Lanjouw 1255* (S, MO); precise locality not known, *RB 21835, 27412* (RB).

15. *RAUVOLFIA MACRANTHA* K. Sch. ex Markgraf, in Fedde, Rep. Spec. Nov. 20: 117, 120. 1924. (T.:*Ule 5174!*)

R. micrantha K. Sch. ex Ule in Engl. Bot. Jahrb. 40:136. 1907. (*nom. nud., sphalm.*)

Shrubs up to 6 m. tall; branches 2-, 3-, or 4-chotomous, terete, glabrous, the bark longitudinally wrinkled, the nodes with axillary glands. LEAVES in whorls of 4, slightly anisophyllous, short-petiolate, ovate to broadly ovate-elliptic, acute to acuminate at the tip, abruptly attenuate at the base, the largest leaves 8–10 cm. long, 4–7 cm. broad, the smallest 3–6 cm. long, 2–4 cm. broad, membranaceous, the secondary veins 5–7 pairs, arcuate, distinct on both surfaces; petioles slender 0.5–1.0 (1.5) cm. long. INFLORESCENCES terminal, few-flowered; peduncles geminate, slender, 1–3 cm. long, bracteate, the bracts lanceolate, about 1.5 mm. long, the pedicels slender, 5–8 mm. long, glabrous. FLOWERS conspicuous; calyx deeply 5-lobed, the lobes lanceolate, acuminate, 2.5–3.5 mm. long, glabrous; corolla salverform, white (Ule), 15–20 mm. long, about 2 mm. in diameter, glabrous without, villous within for more than half of the upper part, a little dilated near the throat, the lobes ovate, broadly acute to obtuse, 5–6 mm. long, 3–4 mm. broad; stamens 5, inserted about 3 mm. below the throat, in the region of the dilatation, the anthers linear-ovate, acuminate, 2–3 mm. long, with a dorsal callosity,

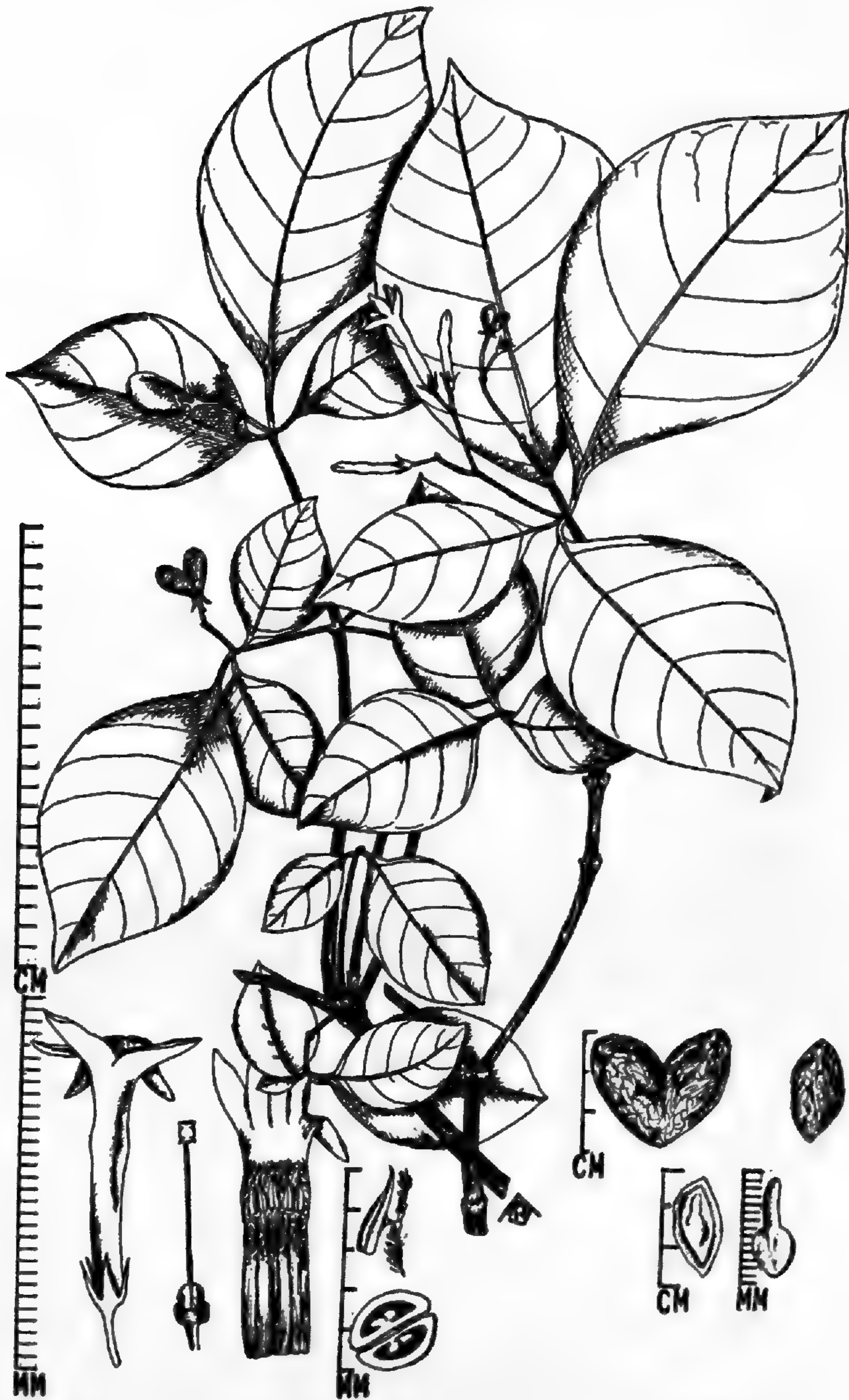


Fig. 15. *Rauvolfia macrantha* (Ule 5174 and Krukoff 6698)

subsessile; ovary 2-carpellary, almost apocarpous, cylindrical, about 2.5 mm. high, 2 mm. in diameter, glabrous, the ovules 2 in each locule on a ventral placenta, the disc annular, about 1 mm. broad, the style linear, 10–12 mm. long, glabrous, the stigma-head cylindrical, narrowed at the two ends, about 1.5 mm. high, obscurely bilobed. FRUITS obcordate, deeply bilobed, often only one carpel developing, then ovoid, rounded, 2.5–3.5 cm. high, about 2.5 cm. broad, 2-seeded, the stones elliptic, a little flattened, faintly rugose, 2.0–2.5 cm. long, about 1 cm. broad, the seed

elliptic, compressed, albuminous, the testa membranaceous, the albumen fleshy, the embryo as long as the seed, the cotyledons ovate, obtuse, 5–6 mm. long, 3–4 mm. broad, the hypocotyl terete, equal in length to the cotyledons.

In high forest, on river banks; flowering August to November; mature fruits in December. Northwestern Brazil.

R. macrantha is closely related to *R. sprucei* but can be distinguished from it and all the other related species by its few-flowered inflorescences with short, slender peduncles and the flowers with lanceolate, acuminate calyx-lobes, and the obcordate fruits.

BRAZIL. AMAZONAS: Japura, *Ducke 6772* (RB); Humayta municipality near Livramento, on immediate shore of river, *Krukoff 6698* (A, MO, S, US); São Paulo de Olivença, near Palmares, *Krukoff 8262, 8422* (A, F, G, MO); basin of creek, Belem, *Krukoff 8871* (A, F, G, MO, US); Marary, Rio Juruá, *Ule 5174* (G, L).

16. *RAUVOLFIA PENTAPHYLLA* (Hub.) Ducke, in Arch. Jard. Bot. Rio de Janeiro 3:244. 1922. (T.: *Ducke 11038!*)

Couma pentaphylla Hub. in Bol. Mus. Goeldi 7:124. 1913, *nom. nud.*

R. duckei Mgf. in Fedde, Rep. Spec. Nov. 20:121. 1924. (T.: *Ducke 16544!*)

Trees about 25 m. tall; branches verticillate, terete, glabrous, the nodes with prominent axillary glands. LEAVES in 5's, slightly anisophyllous, short-petiolate, ovate to obovate-elliptic, acute to acuminate, abruptly attenuate at the base, the largest leaves 10–15 cm. long, 4–6 cm. broad, the smallest 4–7 cm. long, 2–3 cm. broad, firmly membranaceous to coriaceous, the secondary veins 12–20 pairs, transverse, very little curved at the margins and uniting to form marginal veins, equally distinct on both surfaces; petioles stout, 1.5–3.0 cm. long. INFLORESCENCES terminal, many-flowered; peduncles geminate, stout, 3–6 cm. long, bracteate, the bracts ovate, acute, about 1 mm. long, the pedicels slender, 2–6 mm. long, glabrous. FLOWERS conspicuous, odorous (Ducke); calyx deeply 5-lobed, the lobes ovate, acute, about 1.5 mm. long, 2 mm. broad, glabrous; corolla infundibuliform, white with purplish streaks (Ducke), the tube slender, 12–18 mm. long, about 2 mm. in diameter, glabrous without, villous within near the throat, the throat a little dilated, the lobes ovate, obtuse, 6–12 mm. long, 3–5 mm. broad; stamens 5, inserted near the throat, the anthers ovate, acute, 1.0–1.5 mm. long, with a dorsal callosity, subsessile; ovary 2-carpellary, hemisyncarpous, cylindrical, about 2.5 mm. high, 2 mm. in diameter, glabrous, the ovule 1 in each locule on an axile placenta, the disc annular, about 1 mm. high, the style columnar, 10–15 mm. long, glabrous, the stigma-head cylindrical, bulged in the middle, obscurely bilobed. FRUITS subglobose to globose, 2.5–3.0 cm. in diameter, 2-seeded, the stones elliptic, 2.0–2.5 cm. long, about 1 cm. broad, faintly rugose, the seed slightly compressed, albuminous, the testa membranaceous, the albumen carnose, the embryo erect, the cotyledons elliptic, 4–5 mm. long, 2.5–3.0 mm. broad, the hypocotyl terete, equal in length to the cotyledons.

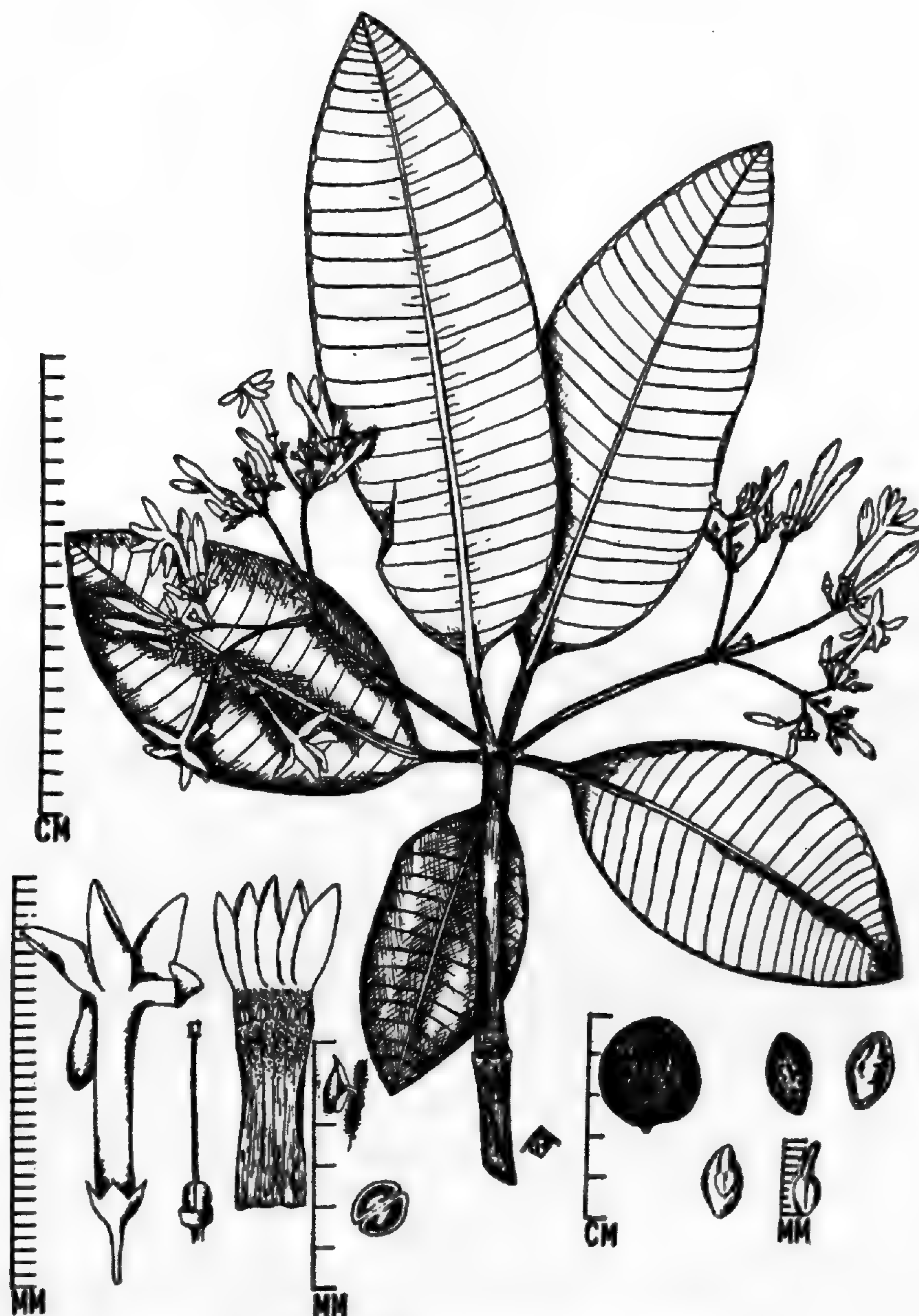


Fig. 16. *Rauvolfia pentaphylla* Ducke (Ducke 11038)

In non-inundated forests; flowering from June to December; mature fruits in March, April. Northern Brazil.

COMMON NAMES: Brazil, Amazonas—*Itapeua Grande*, *Marfim*, and *Muirá Jussara*. Ducke has pointed out that the last name is also used for *Aspidosperma duckei*, which is a tree resembling *R. pentaphylla*.

This species very much resembles *R. paraensis*, but can be distinguished by its leaves with numerous, quite transverse secondary veins, and the smaller fruits. As in *R. paraensis*, here also there is considerable variation in the leaf and flower characteristics. Hence, there is no reason for the continued distinction of *R. duckei*. Ducke has cited several numbers in his original description. Of these I have not seen 11032, but 11038 I find well represented in the several herbaria.

The Macbride type photograph collection includes a photo of *Ducke 11038* from the Berlin Herbarium. I am, therefore, designating *Ducke 11038* (RB) as the type of *R. pentaphylla*.

BRAZIL. AMAZONAS: Mañaos, *Ducke 492* (A, F, MO, US), *Ducke RB 22426* (P, RB, US), *Ducke RB 23941* (RB, S, US). AMAPÁ: Porto Platon, Rio Araguari, *Pires & Silva 4784* (MO). PARÁ: Belterra, *Black 47-942* (NY); Cajutuba, *M. da Costa 273* (F, MO); Gurupa, *Ducke 11038 = RB 13298* (G, P, RB, US), *Ducke 16544 = RB 13299* (G, P, RB, US).

SERIES 4. ANGUSTIFOLIAE A. S. Rao, ser. nov.

Rami floriferi prorsus foliosi, cataphyllis non manifestis, hoc aucto nodis verticillatis pluribus. Folia 3- vel 4-plo longiora quam latiora (ca. 2-plo longiora in *R. steyermarkii*) basi attenuata. Inflorescentiae aut terminales aut laterales. Species typica: *R. grandiflora* Mart.

KEY TO THE SUBSERIES

- A. Leaves linear or obovate, 0.2–2.5 cm. broad. Corolla-tube 8–20 mm. long, constricted at the throat; corolla-lobes obovate, obtuse. Cuba.....Subseries 1. CUBANAE
- AA. Leaves elliptic, 3–5 cm. broad. Corolla-tube 5–12 mm. long, constricted at the throat; corolla-lobes oblong, acute. Andes of Peru, Bolivia and Argentina.
.....Subseries 2. ANDINAE
- AAA. Leaves obovate or elliptic, 3–7 cm. broad (sometimes less than 3 cm. broad in *R. weddelliana* and *R. paucifolia*, but not obovate). Corolla-tube 4–20 mm. long, not constricted at the throat; corolla-lobes ovate, acute or obtuse. Greater Antilles and northern regions of South America.....Subseries 3. GRANDIFLORAE

SUBSERIES 1. CUBANAE A. S. Rao, subser. nov.

Folia linearia vel obovata 0.2–2.5 cm. lata. Corollae tubus 8–20 mm. longus, faucibus constrictis; lobis obovatis obtusis. Species typica: *R. cubana* A. DC.

KEY TO THE SPECIES

- A. Herbaceous subshrubs 1–5 dm. tall. Leaves linear. Corolla purplish-violet; calyx-lobes membranaceous, acuminate. Fruits deeply 2-lobed, the lobes acute or slightly beaked. Oriente.....17. *R. linearifolia*
- AA. Woody shrubs 2–8 m. tall. Leaves obovate. Corolla white; calyx-lobes coriaceous, obtuse. Fruits bilobed at the top, the lobes obtuse or broadly acute, but not beaked.
 - B. Leaves mostly 4-nate. Corolla-tube 8–10 mm. long, glabrous in the throat, the lobes half as long as the tube. Oriente.....18. *R. salicifolia*
 - BB. Leaves mostly 3-nate. Corolla-tube 12–20 mm. long, villous in the throat, the lobes almost as long as the tube. Western provinces of Cuba and the Isle of Pines...19. *R. cubana*

17. RAUVOLFIA LINEARIFOLIA Brit. & Wils., in Mem. Torr. Bot. Club 16:94. 1920. (T.:*Schafer 1754!*)

Shrubs 1–5 dm. tall; branches slender, terete, 2-chotomously branching, glabrous, the nodes with minute glands confined to the leaf-axils. LEAVES in whorls of 3, scarcely anisophyllous, shortly petiolate, linear, acute to acuminate, attenuate, at base, 2–6 cm. long, 0.2–0.5 cm. broad, membranaceous, the midrib distinct on both surfaces but the secondary veins obscure; petioles slender, 1–3 mm. long.

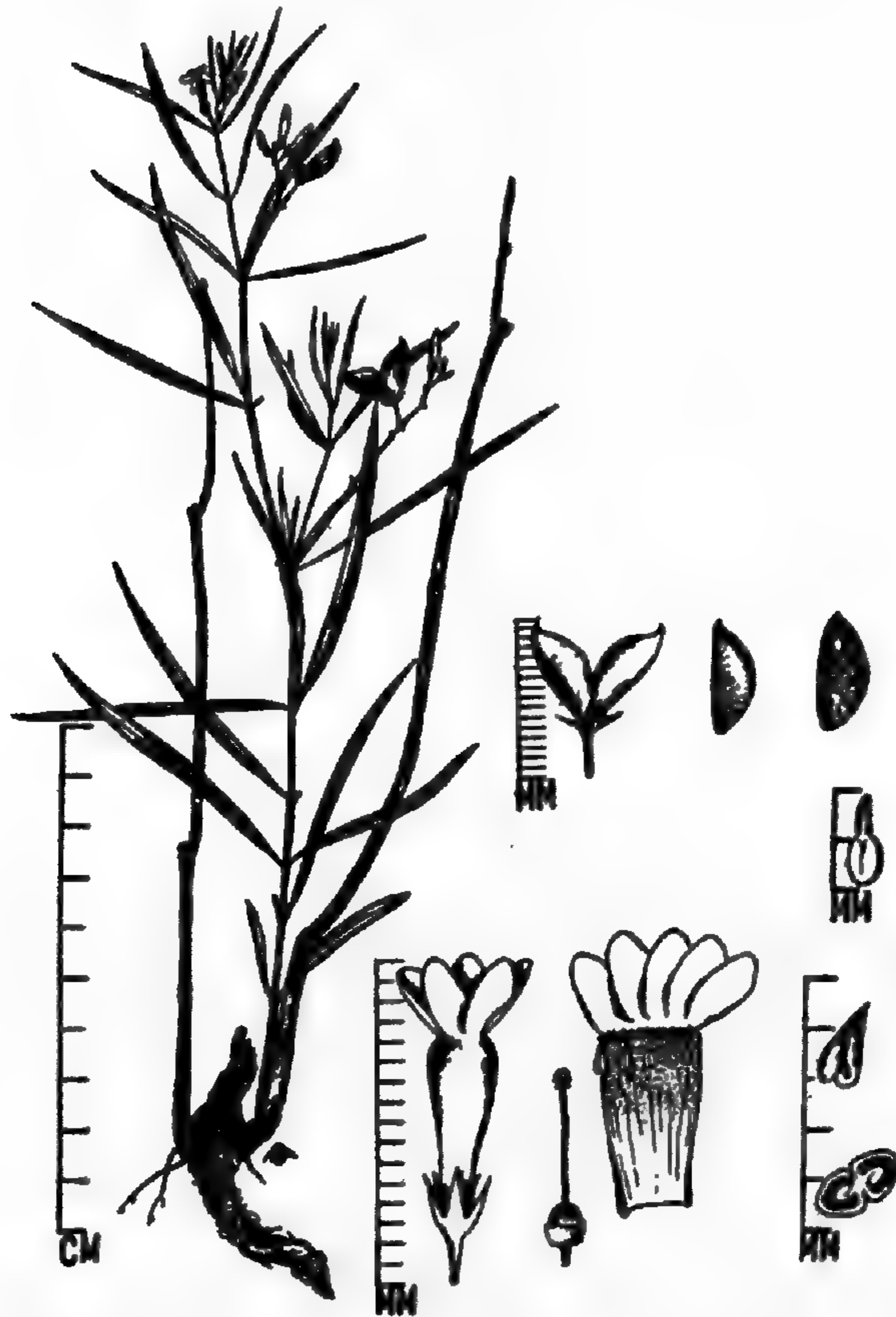


Fig. 17. *Rauvolfia linearifolia* Brit. & Wils.
(Ekman 9552).

INFLORESCENCES terminal, few-flowered, cincinnate; peduncles slender, 1–3 cm. long, glabrous, bracteate, the bracts lanceolate, about 1.5 mm. long, the pedicels slender, 2–5 mm. long, glabrous. FLOWERS conspicuous; calyx deeply 5-lobed, the lobes lanceolate, 1.5–2.0 mm. long, glabrous; corolla salverform, pale purplish-violet (Ekman), the tube slender, 8–10 mm. long, about 1.5 mm. in diameter at the base, glabrous without, villous within along the top half, constricted at the throat, the lobes ovate-elliptic, obtuse to rounded, 4–5 mm. long, 1.5–2.5 mm. broad; stamens 5, inserted near the throat, the anthers linear-ovate, about 1.5 mm. long, the filament about 0.5 mm. long; ovary 2-carpellary, connate at the base, obovoid, about 1.5 mm. high and 1.5 mm. in diameter, the ovule 1 in each locule on a ventral placenta, the disc annular, about 1 mm. high, the style linear, 5–6 mm. long, glabrous, the stigma-head drum-shaped, about 1 mm. high, obtusely bilobed. FRUITS deeply bilobed, the lobes widely divergent, flattened, semi-lunate, acuminate or slightly beaked, 9–12 mm. long, 2.5–3.0 mm. broad, the stones elliptic, smooth, the seed elliptic, flattened, albuminous, the testa membranaceous, the embryo erect, small (probably abortive), the cotyledons elliptic, rounded, about 1 mm. long, 0.5 mm. broad, the hypocotyl terete, equal in length to the cotyledons.

On limestone hills and in the savannas; flowering from April to September; ripe fruits in October and November. Oriente Province in Cuba.

Rauvolfia linearifolia is the shortest of all the American Rauvolfias. It is characterized by its narrow, linear leaves, the few-flowered, slender-peduncled inflorescences, the flowers with lanceolate calyx-lobes, and the compressed, widely divergent, slightly beaked fruits. In all the fruits analyzed the embryos were very small and indicated abortive development. The plants appear to propagate more often vegetatively from the root-stocks. The plants of this species are endemic, and apparently rare in Cuba.

CUBA. ORIENTE: Sierra de Nipe, *Ekman 1733, 5913, 5939, 9552, 9685, 15304 (S); Shafer 1754 (NY)*.

18. *RAUVOLFIA SALICIFOLIA* Griseb. in Mem. Am. Acad. N. S. 8:519. 1863. (T.: *Wright 1386!*)

Shrubs or trees up to 8 m. tall; branches 2-, 3- or 4-chotomous, terete, glabrous, the nodes with distinct pectinate glands in the leaf-axils. LEAVES in whorls of 4, scarcely anisophyllous, shortly petiolate, narrowly obovate to oblanceolate, broadly acute to obtuse, cuneate at the base, 2-7 cm. long, 1-2 cm. broad, coriaceous, slightly lustrous above, opaque beneath, the midrib distinct on both surfaces but the secondary veins obscure; petioles slender, 3-8 mm. long. INFLORESCENCES



Fig. 18. *Rauvolfia salicifolia* Griseb. (*Wright 1386*)

terminal, few-flowered; peduncles rather stout, 2–6 cm. long, glabrous, bracteate, the bracts ovate, acute, about 1 mm. long, the pedicels rather stout, 2–4 mm. long, glabrous. FLOWERS conspicuous; calyx campanulate, deeply 5-lobed, the lobes occasionally unequal, ovate, obtuse, about 1.5 mm. long, 1 mm. broad, coriaceous, the margin minutely glandular-dentate; corolla salverform, white (Wright), the tube slender, 8–10 mm. long, about 1.5 mm. in diameter at the base, glabrous without and within near the throat and sparsely villous below the stamens, constricted at the throat, the lobes oblique-obovate, rounded, 5–6 mm. long, 3.0–3.5 mm. broad; stamens 5, inserted near the throat, the anthers ovate, acute, about 1 mm. long, subsessile; ovary 2-carpellary, hemisyncarpous, obovoid, about 2.5 mm. high, 2 mm. in diameter, the ovules 2 in each locule on an axile placenta, the disc annular, about 1 mm. high, the style linear, 5–6 mm. long, glabrous, the stigma-head subcapitate, about 1 mm. high, obscurely bilobed. FRUITS obcordate, slightly bilobed, the lobes obliquely obovate, obtuse, broadly acute to obtuse, 13–14 mm. long, 6–8 mm. broad, the stones slightly flattened, faintly rugose, the seed albuminous, the testa membranaceous, the albumen fleshy, the embryo about half as long as the seed, erect, the cotyledons ovate-elliptic, 3.0–3.5 mm. long, 1.5–2.0 mm. broad, the hypocotyl terete, equal in length to the cotyledons.

On limestone hills, in open forests and amongst Pines; flowering from June to November; ripe fruits in January and February. Oriente province in Cuba.

COMMON NAME: Cuba, Oriente—*Corazon de Paloma*.

Rauvolfia salicifolia is closely related to *R. linearifolia* and *R. cubana*. It can be distinguished from the former by its broader, obtuse, coriaceous leaves, the rather stout peduncles with white flowers, the calyx-lobes stiff and obtuse, and the fruits which are obscurely bilobed and obtuse. It can be distinguished from the latter by its narrower and longer leaves, and smaller flowers with the corolla-lobes about half as long as the tube. Like *R. linearifolia*, this species is endemic to Oriente province, Cuba.

CUBA. ORIENTE: *Alain* 3310, 3319, 3673 (MO), *Carebia* 3823 (NY), *Clement* 3566, 3605, 4390 (MO), *Ekman* 3322, 3514, 4147, 6145, 6688, 9078 (S), 6329 (P, S), *Howard* 5942 (GH, NY, US), 6104 (GH, MO, NY, UC), *Corta* 2.038 (W), *Leon & Clement* 23046 (MO), *Leon, Clement & Alain* 22523 (MO), *Leon, Victorin & Clement* 20785 (MO), *Roig* 65 (MO), *Sbafer* 3529, 3687 (GH, NY), 4238 (GH), 8144 (NY), 8364 (NY, US), *Wright* 1386 (G, GH, MO, P, S, W), 2946 (G, GH, MO, P, S).

19. RAUVOLFIA CUBANA A. DC. in DC. Prodr. 8:339. 1844. (T.: *Sagra* 535, *photo!*)

Shrubs or small trees, 2–5 m. tall; branches 2- or 3-chotomous, terete, glabrous, the nodes with distinct pectinate glands limited to the leaf-axils. LEAVES in whorls of 3, scarcely anisophyllous, shortly petiolate, obovate, obtuse, cuneate at the base, 1–6 cm. long, 1–2 cm. broad, coriaceous, lustrous above, opaque beneath, the midrib distinct on both surfaces but the secondary veins obscure; petioles 2–4 mm.

long. INFLORESCENCES terminal, few-flowered; peduncles slender, 2–5 cm. long, glabrous, bracteate, the bracts ovate, acute, about 1 mm. long, the pedicels slender, 6–11 mm. long, glabrous, FLOWERS rather large; calyx deeply 5-lobed, the lobes ovate, obtuse, 2–3 mm. long, 1.0–1.5 mm. broad, coriaceous, the margins glandular-dentate; corolla salverform, white, odorous (R. de la Sagra), the tube slender, 12–20 mm. long, about 2 mm. in diameter, glabrous without, villous within near the throat and along the base of the stamens, constricted at the throat, the lobes obovate-elliptic, rounded, 10–14 mm. long, 5–7 mm. broad; stamens 5, inserted near the throat, the anthers ovate, acute, 1.0–1.5 mm. long, the filament about 1 mm. long; ovary 2-carpellary, hemisyncarpous, cylindrical, about 2.5 mm. high, 2 mm. in diameter, the ovules 2 in each locule on an axile placenta, the disc annular, about 1 mm. high, the style filiform, 10–14 mm. long, glabrous, the stigma-head cylindrical, about 1 mm. high, 2-apiculate. FRUITS broadly obovate, bilobed, the lobes obovate, flattened, broadly acute to obtuse, 10–12 mm. high, 5–7 mm. broad (often only one carpel developing, then the fruit ellipsoid), the stones faintly rugose, the seed albuminous, the testa membranaceous, the albumen fleshy, the

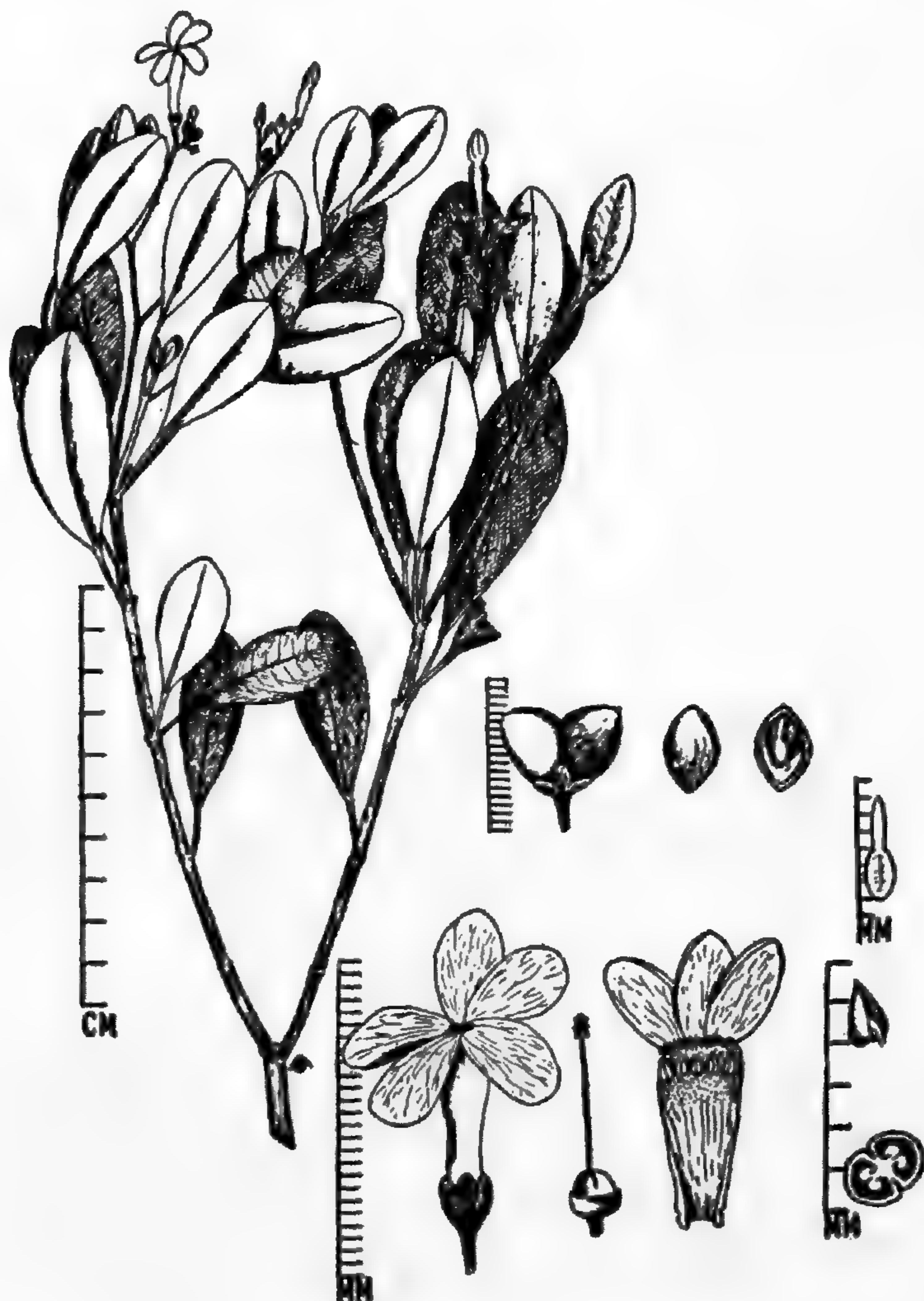


Fig. 19. *Rauvolfia cubana* A. DC. (Wright 2947)

embryo erect, a little more than half as long as the seed, the cotyledons elliptic, about 3 mm. long, 2 mm. broad, the hypocotyl terete, as long as the cotyledons.

On limestone hills, in savannas and in swampy regions along river banks; flowering from April to August; ripe fruits in October to December, western Cuba, and the Isle of Pines.

Rauvolfia cubana resembles *R. salicifolia* very much but can be distinguished from it by its larger flowers with the calyx-lobes larger, the corolla-lobes about as long as the tube and the throat villous, and the broadly obcordate, smaller fruits. *R. cubana* also is an endemic of Cuba, but confined to the western provinces and the Isle of Pines.

CUBA. HAVANA: *N. L. Britton, Cowell & C. de LaTerre 13345* (NY), *Ekman 10022, 12583* (S), *Leon 5208* (NY), *Leon, Ekman et al, 9096* (NY), *Leon & Roca 7712* (NY), *L. C. Richard 13* (P), *Roig 3* (NY), *Shafer 72* (NY). PRECISE LOCALITY UNKNOWN: *Sagra 414, 815* (P), *Wright 2947* (G, GH, MO, NY, P, S, US, W). ISLE OF PINES: *N. L. Britton & Wilson 14876* (GH, NY, US), *Ekman 11842* (S), *Jennings 212, 615* (GH, NY, US), *Killip 44082* (US). PINAR DEL RIO: *N. L. Britton & Cowell 9987* (NY), *N. L. & E. G. Britton & Gager 7014* (NY, US), *N. L. Britton & Gager 7328* (US), *Leon & Charles 4914* (NY). SANTA CLARA (LAS VILLAS): *N. L. Britton, Earle & Wilson 4599* (NY), *N. L. Britton & Wilson 5744* (US), *Combs 245* (G, GH, MO, NY, P), *Ekman 17069* (S), *Jack 7540* (A, NY, S, US), *8684* (A, NY, S), *Leon 9246* (NY), *Van Hermann s. n.* (L).

SUBSERIES 2. ANDINAE (Mgf.) A. S. Rao, stat. nov.

§ ANDINAE Mgf. in Fedde, Rep. Spec. Nov. 20:118. 1924.

KEY TO THE SPECIES

- A. Leaves 3 times as long as broad. Corolla-tube 5–6 mm. long, the throat villous; calyx-lobes cuspidate, the margin entire. Andes of Bolivia and northern Argentina.....20. *R. schueli*
 AA. Leaves 4 times as long as broad. Corolla-tube 8–12 mm. long, the throat glabrous; calyx-lobes lanceolate, the margin glandular-dentate. Andes of Peru.....21. *R. andina*

20. RAUVOLFIA SCHUELI Speg. in Physis 3:337. 1917, *ex char.* (T.: *Spegazzini s. n.*)

R. boliviana Mgf. in Fedde, Rep. Spec. Nov. 20:122. 1924. (T.: *Hieronimus & Lorentz 962, photo!*)

Shrubs or small trees 2–6 m. tall; branches 2-, 3- or 4-chotomous, terete, sparsely lenticellate, the bark grayish and slightly wrinkled longitudinally, the nodes with glands confined to the leaf-axils. LEAVES in whorls of 3 or 4, scarcely anisophyllous, long-petiolate, elliptic, acuminate, attenuate at the base, 4–12 cm. long, 1–4 cm. broad, membranaceous to subcoriaceous, opaque on both surfaces, the secondary veins many, arcuate, rather obscure above and more distinct beneath; petioles 1–2 cm. long. INFLORESCENCES terminal, many-flowered, corymbose; peduncles slender, 2–4 cm. long, glabrous, bracteate, the bracts ovate, acute, about 1 mm. long, the pedicels slender, 3–6 mm. long, glabrous. FLOWERS conspicuous; calyx deeply 5-lobed, the lobes cuspidate, acuminate, about 2 mm. long; corolla



Fig. 20. *Rauvolfia schubli* Speg. (Venturi 9634)

salverform, white, fragrant (Pearce), the tube slender, 5–6 mm. long, about 1.5 mm. in diameter, glabrous without and sparsely pilose within near the throat, constricted at the throat, the lobes ovate-oblong, acute, 3.0–3.5 mm. long, about 1 mm. broad; stamens 5, inserted near the throat, the anthers ovate, acute, about 1 mm. long, subsessile; ovary 2-carpellary, hemisyncarpous, ovoid, about 2 mm. high, 1.5 mm. broad, the ovules 2 in each locule on an axile placenta, the disc annular, about 0.5 mm. high, the style linear, 3.0–3.5 mm. long, glabrous, the stigma-head cylindrical, with a hairy corona at the base, about 0.5 mm. high, 2-apiculate.

I have not seen any fruits. Spegazzini has described the drupes as reniform, about 10 mm. in diameter and 5–6 mm. high, blue-black. Markgraf has described the mericarps as subglobose, 2-seeded, 5 mm. broad, 7 mm. high, black.

Densely branching shrubs or small trees in open woods and in sandy loam; flowering from May to October. The Andean regions of Bolivia and northern Argentina.

COMMON NAME: Bolivia—*Lecheron del Monte*.

I have not seen Spegazzini's type of *R. schubli*. All efforts to locate the specimens in the important herbaria of Argentina have been in vain. However, Dr.

Theodoro Meyer of the National University of Tucumán, who has collected the species from both type localities and has studied them extensively, informs me that he considers *R. boliviana* of Markgraf synonymous with *R. schueli*. Evidently Markgraf was unaware of Spegazzini's species when he described *R. boliviana*. I agree with Dr. Meyer and am including *R. boliviana* under *R. schueli*.

ARGENTINA. JUJUY: San Pedro, near Río Lavagin, southeast of San Pedro de Jujuy, *Eyerdam & Beetle 22524*, (GH, UCL); Sierra de Santa Barbara, *Venturi 9634*, (GH, S). SALTA: Yaquiásmé, *Meyer 18.003* (MO).

BOLIVIA: precise locality not known, *Pearce s. n.*, K. no. 2253/54 (K).

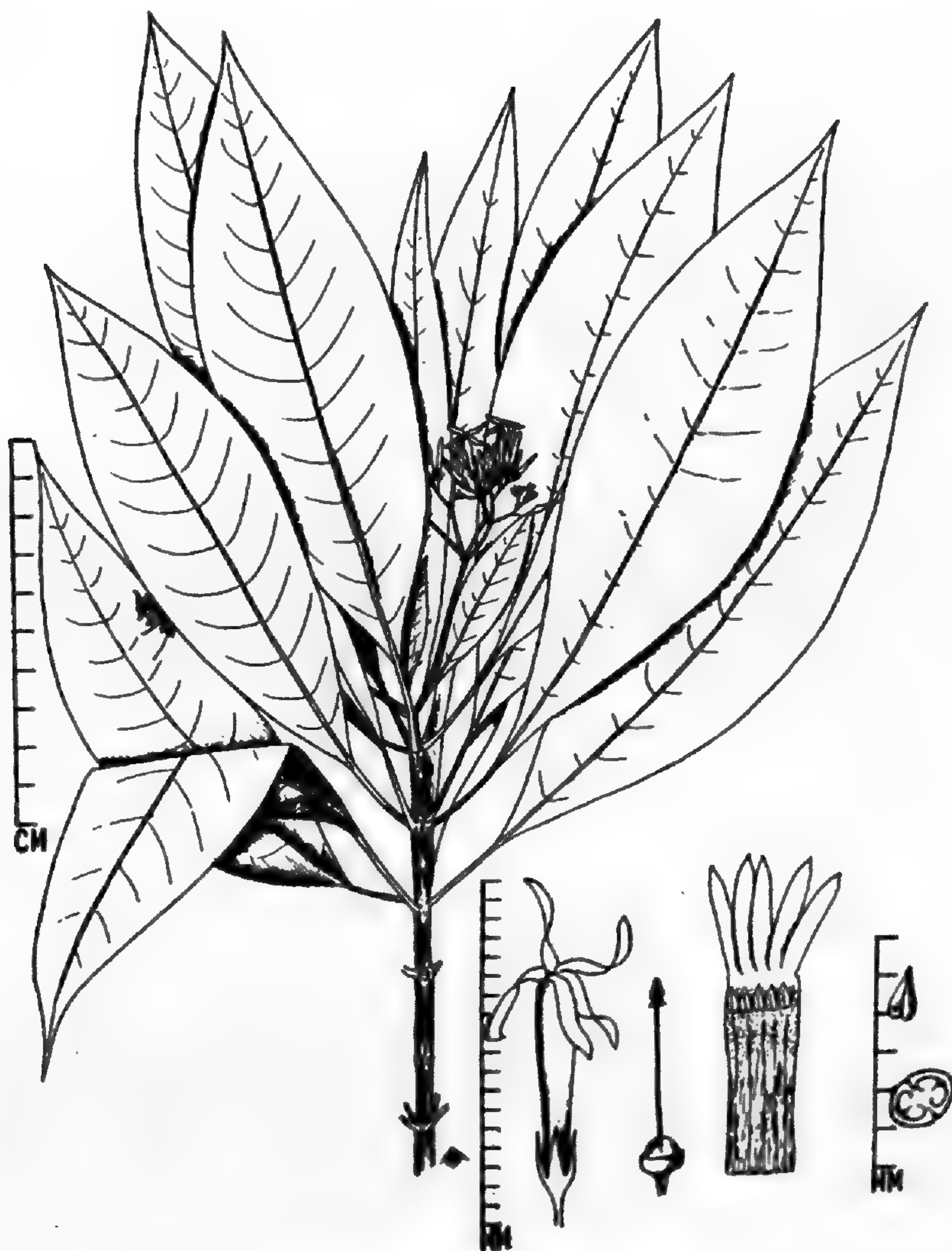


Fig. 21. *Rauvolfia andina* Mgf. (Weberbauer 7112)

21. RAUVOLFIA ANDINA Mgf. in Fedde, Rep. Spec. Nov. 20:122. 1924. (T.: *Weberbauer 7112!*)

Shrubs 5–7 m. tall; branches terete, sparsely lenticellate, the bark gray, slightly wrinkled, the nodes with glands confined to the leaf-axils. LEAVES in whorls of 3 or 4, scarcely anisophyllous, long-petiolate, elliptic-oblong, acuminate, attenuate

at the base, 8–20 cm. long, 2–5 cm. broad, membranaceous, the secondary veins many, obscure above, a little more distinct beneath; petioles 2–3 cm. long. INFLORESCENCES terminal, many-flowered, corymbose; peduncles stout, 1–5 cm. long, glabrous, bracteate, the bracts ovate, acute, about 1 mm. long, the pedicels slender, 4–6 mm. long, glabrous. FLOWERS relatively large; calyx deeply 5-lobed, the lobes lanceolate, acuminate, 2.0–2.5 mm. long, the margin glandular-dentate; corolla salverform, white, the tube slender, 8–12 mm. long, about 1.5 mm. in diameter at the base, glabrous without and within near the throat, but sparsely villous below the stamens, constricted at the throat, the lobes linear, acute, 5–6 mm. long, 1.0–1.5 mm. broad; stamens 5, inserted near the throat, the anthers ovate, acute, about 1.5 mm. long, subsessile; ovary 2-carpellary, hemisyncarpous, cylindrical, about 2.5 mm. high, 2 mm. in diameter, the ovules 2 in each locule on an axile placenta, the disc annular, about 1 mm. high, the style linear, 7–8 mm. long, glabrous, the stigma-head cylindrical with a hairy corona at the base, about 1 mm. high, 2-apiculate.

I have seen no fruits. Markgraf has described the fruits as obcordate, 1 cm. high, 1 cm. broad, about 0.5 cm. thick, red in the immature state, and 2-seeded.

On rocky and stony soil in river valleys, 1200–1700 m. altitude; flowering in April and May. Andes of Peru.

PERU. CAJAMARCA: Cajamarca, cerca a San Miguel, camino a Asuncion, Ramon Ferreyra 7086 (US); Jaen, valley of the R. Huancabamba, near Pomahuaca, Weberbauer 7112 (GH, US).

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m

SUBSERIES 3. GRANDIFLORAE (Mgf.) A. S. Rao, stat. nov.

§ GRANDIFLORAE Mgf. in Fedde, Rep. Spec. Nov. 20:116. 1924.

KEY TO THE SPECIES

- A. Corolla-tube 10–20 mm. long, 2–3 times as long as the corolla-lobes, inflated 2–3 mm. below the orifice.
- B. Leaves oblanceolate or narrowly elliptic, 5–20 cm. long. Peduncles 8- to many-flowered. Corolla-tube 2.5–3.0 times as long as the corolla-lobes; calyx-lobes ovate or deltoid, 1.0–1.5 mm. long.
- C. Leaves distinctly petiolate, coriaceous. Corolla-tube 10–12 mm. long. Fruits reniform. Colombia and Peru.....22. *R. sanctorum*
- CC. Leaves obscurely petiolate, membranaceous. Corolla-tube 12–20 mm. long. Fruits obcordate. Eastern Brazil.....23. *R. grandiflora*
- BB. Leaves obovate or elliptic, 2–4 cm. long. Peduncles 1- to 6-flowered. Corolla-tube about 2 times as long as the corolla-lobes; calyx-lobes lanceolate, 2.5–3.0 mm. long. Eastern Brazil.....24. *R. paucifolia*
- AA. Corolla-tube 4–9 mm. long, about as long as or 1.5 times as long as the corolla-lobes (except in *R. sessilifolia* 10 mm.), not inflated or inflated immediately at the orifice.
- D. Leaves sessile or with petioles 2–10 mm. long.
- E. Leaves sessile or with petioles 2–4 mm. long. Corolla-tube 8–10 mm. long.
- F. Leaves membranaceous, ovate to oblong-ovate, sessile. South-central Brazil.25. *R. sessilifolia*
- FF. Leaves coriaceous, broadly or narrowly elliptic; petioles 2–4 mm. long. South-central Brazil.....26. *R. weddelliana*
- EE. Leaves with petioles 5–10 mm. long. Corolla-tube 4–7 mm. long.

- G. Leaves abruptly attenuate at the base, upper surface opaque, secondary veins distinct, 4–5 mm. apart. Inflorescences longer than the subtending leaf, with ternately or quaternately divided peduncles. Calyx-lobes oblong-ovate, obtuse. Venezuela.....27. *R. steyermarkii*
- GG. Leaves gradually attenuate at the base, upper surface lustrous, with many distinct secondary veins 1–3 mm. apart, or upper surface opaque with obscure secondary veins. Inflorescences with dichotomously branched peduncles, about as long as the subtending leaf. Calyx-lobes ovate, acute or rounded.
- H. Leaves mostly in whorls of 4, elliptic, upper surface lustrous with innumerable secondary veins 1–3 mm. apart. Pedicels stout, 4–8 mm. long; calyx-lobes rounded. Antilles.....28. *R. nitida*
- HH. Leaves mostly in whorls of 3, oblanceolate or obovate, upper surface opaque with obscure secondary veins. Pedicels slender, 10–15 mm. long; calyx-lobes acute.
- I. Leaves membranaceous or subcoriaceous. Cymules umbellate; corolla-tube about 2 times as long as the corolla-lobes; ovary free almost to the base. Northeast Brazil.....29. *R. babiensis*
- II. Leaves coriaceous. Cymules corymbose; corolla-tube about as long as the corolla-lobes; ovary fused almost to the top. Dominican Republic, Guadeloupe and Dominica.....30. *R. biauriculata*
- DD. Leaves with petioles 12–40 mm. long.
- J. Leaves obovate or obovate-oblong, coriaceous, opaque on both surfaces.
- K. Leaves usually in whorls of 4, obovate, secondary veins arcuate. Calyx-lobes acute; corolla purpurascens. Panama.....31. *R. purpurascens*
- KK. Leaves usually in whorls of 3, obovate-oblong to elliptic-oblong, secondary veins transverse. Calyx-lobes obtuse; corolla white. Costa Rica.....32. *R. sarapiquensis*
- JJ. Leaves elliptic, coriaceous or membranaceous, opaque on both surfaces or lustrous above.
- L. Leaves coriaceous, lustrous above. Secondary and tertiary peduncles slender. Corolla-tube slender, about 1 mm. in diameter at the base, reddish-violet; calyx-lobes about 1 mm. long. Ovary hemisyncarpous. Peru and Bolivia.....33. *R. praecox*
- LL. Leaves membranaceous, opaque on both surfaces. Secondary and tertiary peduncles stout. Corolla-tube stout, about 1.5 mm. in diameter at the base, white; calyx-lobes about 1.5 mm. long. Ovary apocarpous. Southeastern Brazil.....34. *R. sellowii*

22. *RAUVOLFIA SANCTORUM* Woodson, in Ann. Mo. Bot. Gard. 18:543. 1931.
(T.: Killip & Smith 15392!)

Trees 3–4 m. tall; branches slender, drooping, terete, the bark olive-gray, glabrous, the nodes with pectinate glands confined to the leaf-axils. LEAVES in whorls of 3, rarely 4, slightly anisophyllous, long-petiolate, elliptic to elliptic-oblanceolate, acuminate, cuneate at the base, 8–20 cm. long, 3–8 cm. broad, coriaceous, the secondary veins equally prominent on both surfaces, many, arcuate; petioles stout, 1–3 cm. long. INFLORESCENCES terminal, solitary or paired, few-flowered; peduncles slender, 2–5 cm. long, glabrous, bracteate, the bracts ovate, acute, about 1 mm. long, the pedicels slender, 4–8 mm. long, glabrous. FLOWERS conspicuous; calyx deeply 5-lobed, the lobes ovate, acuminate, about 1.5 mm. long; corolla infundibuliform, white, the tube slender, 10–12 mm. long, about 1.5 mm. in diameter, glabrous without and within the orifice, but distinctly pilose near the tip and base of the stamens, the throat dilated 2–3 mm. below the orifice, the lobes



Fig. 22. *Rauvolfia sanctorum* Woodson (Killip & Smith 15392)

obovate-oblong, about 4 mm. long, 2 mm. broad; stamens 5, inserted 2–3 mm. below the orifice, the anthers ovate, acuminate, about 2 mm. long, subsessile; ovary 2-carpellary, connate at the base, obovoid, about 3 mm. high, 2 mm. broad, the ovule 1 in each locule on a ventral placenta, the disc annular, about 1 mm. high, the style slender, 4–5 mm. long, glabrous, the stigma-head broadly drum-shaped, about 1 mm. high, obscurely bilobed. FRUITS reniform, 2-seeded, the lobes 13–15 mm. high, 7–9 mm. broad, the stones broadly ellipsoid, a little compressed, faintly rugose, the seed albuminous, the testa membranaceous, the albumen fleshy, the embryo erect, the cotyledons ovate, obtuse, about 4 mm. long, 2 mm. broad, the hypocotyl terete, as long as the cotyledons, superior.

In dense forests, along the slopes of hills, 100 to 1500 m. altitude; flowering and fruiting November to December. Colombia and Peru.

This is closely related to *R. grandiflora* but differs from it by its stout-petioled, somewhat leathery leaves, the few-flowered inflorescences, and the kidney-shaped fruits. The geographical distribution is also different.

COLOMBIA. SANTANDER: northern slopes of Mesa de los Santos, *Killip & Smith 15315* (GH, NY, US), *15392* (A, GH, MO, NY, S, US).

PERU. LORETO: Mishuhuaca near Iquitos, *Killip & Smith 29928* (US).

23. *RAUVOLFIA GRANDIFLORA* Mart. ex A. DC. in DC. Prodr. 8:341. 1844. (T.: *Martius 908!*)

R. affinis Muell.-Arg. in Mart. Fl. Bras. 6¹:34. 1860. (T.: *Sellow s. n., photo!*)

R. affinis var. *subulata* Muell.-Arg. l. c. ex char. (T.: *Sellow 315*)

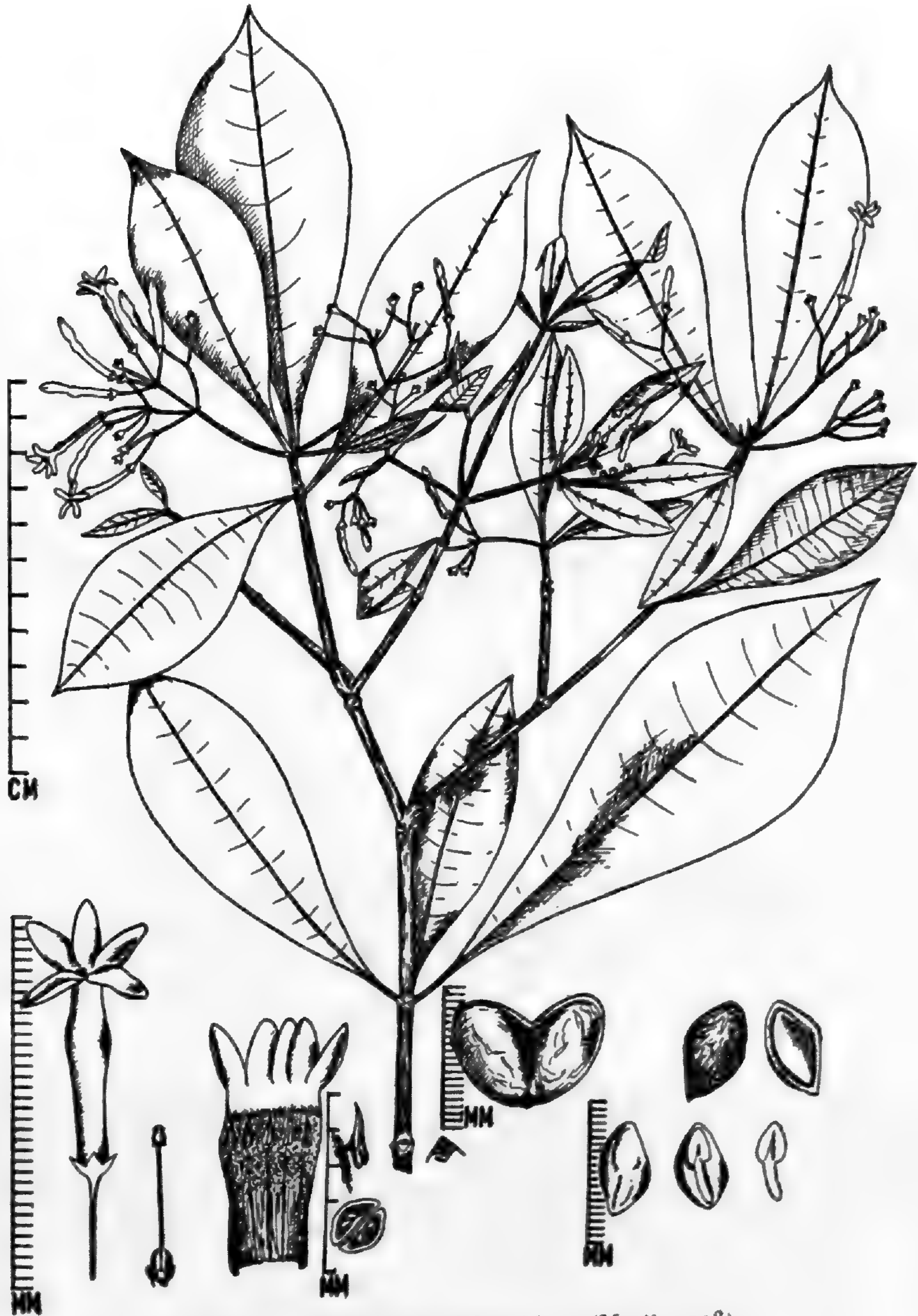


Fig. 23. *Rauvolfia grandiflora* Mart. (*Martius 908*)

Shrubs 1–6 m. tall; branches 2-, 3- or 4-chotomous, terete, glabrous, the nodes with pectinate glands confined to the leaf-axils. LEAVES in whorls of 3 or 4, slightly anisophyllous, shortly petiolate to sessile, obovate to oblong-lanceolate, acuminate, cuneate at the base, 5–15 cm. long, 1.5–4.5 cm. broad, membranaceous, the secondary veins equally evident on both surfaces, several, arcuate; petioles slender, 2–5 mm. long, or absent. INFLORESCENCES terminal and lateral, few- to many-flowered; peduncles slender, 1–4 cm. long, glabrous, the pedicels slender, 8–12 mm. long, glabrous. FLOWERS relatively large; calyx deeply 5-lobed, ovate, acute to acuminate, about 1.5 mm. long; corolla salverform, white to pale violet (*vide* Mendes Magalhaes), the tube slender, 12–20 mm. long, about 2 mm. in diameter at the base, glabrous without and within near the orifice, but villous at the tip and near the base of the stamens, the throat dilated from 3–4 mm. below the orifice, the lobes ovate, obtuse, 4–8 mm. long, 2–3 mm. broad; stamens 5, inserted 3–4 mm. below the orifice, the anthers ovate, acuminate, about 2 mm. long, sessile; ovary 2-carpellary, fused at the very base, obovoid, about 2.5 mm. high, 2 mm. in diameter, the ovules 1–2 in each locule on a ventral placenta, the disc annular, about 1 mm. high, the style columnar, 8–12 mm. long, glabrous, the stigma-head cylindrical, about 1.5 mm. long, obscurely bilobed. FRUITS obcordate, 2-seeded, the lobes ovoid, 15–20 mm. long, 10–15 mm. broad, (often only one carpel developing, then the fruit ovoid), the stones ovoid, slightly compressed, faintly rugose, the seed ovate, albuminous, the testa membranaceous, the albumen fleshy, the embryo as long as the cotyledons.

Near river banks and on road-sides. Flowering from September to December; ripe fruits in January and February. Eastern Brazil.

This species can be distinguished from the very closely related *R. sanctorum* by its membranaceous, extremely short-petioled, almost sessile leaves, the more open and many-flowered inflorescences and the obcordate fruits.

There is considerable variation in the size and number of leaves per node, as also in the branching of the peduncles and the relative proportion between the corolla-tube and the lobes of the flowers. In view of this, I see no justification for separate recognition of *R. affinis*, and *R. affinis* var. *subulata*, both of Mueller-Argoviensis. I am hence treating them as synonymous with *R. grandiflora*.

BRAZIL. BAHIA: *Blanchet* 105 (P), 211 (G), 2314 (G, P); Muritiba, *Blanchet* 3468 (W). ESPIRITO SANTO: Rio Doce, *Kuhlman* 121 (RB); Goitacozes, Rio Doce, *Kuhlmann* 6448 (RB); MINAS GERAES: Belo Horizonte, Governador Valadares, *Mendes Magalhaes* 4-431 (MO). PERNAMBUCO: Dois Irmãos, Rio Garca, *Autenour* 89627 (RB); RIO DE JANEIRO: Rio de Janeiro, *Baretto* 4014 (F), *Glaziou* 639 (P), 7751 (P), *Horto Florestal*, RB 61277, 62875 (RB, MO), *Kuhlmann* 42421 (RB); Santa Maria Magdalena, *Constantino* 2757 (RB), *St. Hilaire* b²197 (F, P, US). PRECISE LOCALITY NOT KNOWN: *Martius* 908 (G, GH, L, M, MO, P, W).

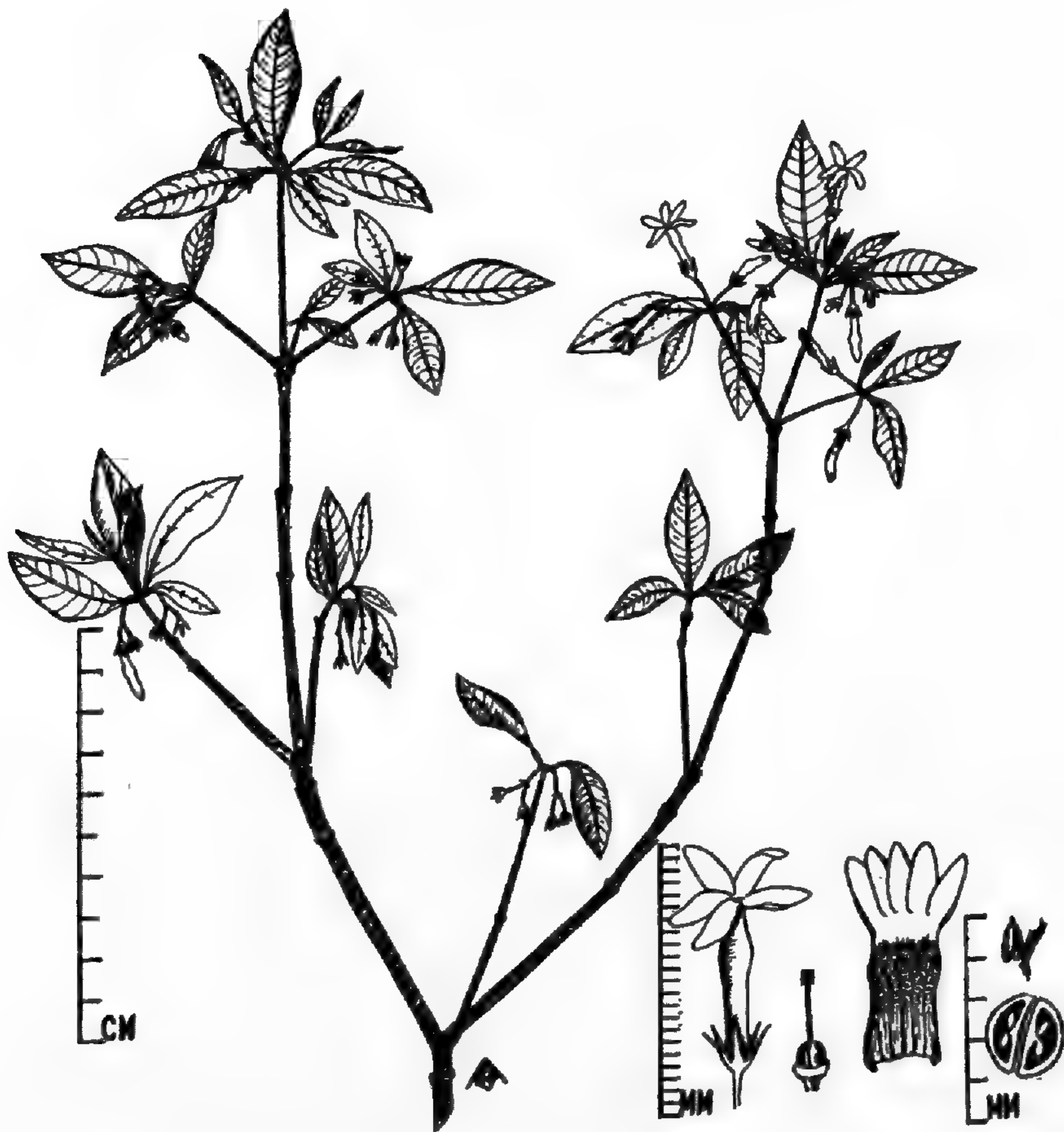


Fig. 24. *Rauvolfia paucifolia* A. DC. (Blanchet 2020)

24. RAUVOLFIA PAUCIFOLIA A. DC. in DC. Prodr. 8:340. 1844. (T.: Blanchet 2020!)

Shrubs ?; branches 2- or 4-chotomous, slender, terete or slightly 4-angular, lenticellate, the nodes relatively distant, with pectinate glands confined to the leaf-axils. LEAVES in whorls of 4 or sometimes 3, slightly anisophyllous, shortly petiolate to subsessile, elliptic or obovate, acuminate, attenuate at the base, 2–4 cm. long, 1–2 cm. broad, membranaceous, the secondary veins 6–10 pairs, arcuate, distinct on both surfaces; petioles slender, 2–4 mm. long, or absent. INFLORESCENCES terminal or lateral, few-flowered; peduncles slender, 0.5–2.0 cm. long, glabrous, minutely bracteate, the pedicels slender, 8–12 mm. long, glabrous. FLOWERS relatively large; calyx deeply 5-lobed, the lobes lanceolate, acuminate, 2–3 mm. long; corolla salverform, the tube slender, 10–12 mm. long, about 2 mm. in diameter at the base, glabrous without and within near the orifice, but villous at the tip and near the base of the stamens, the throat dilated 2–3 mm. below the orifice, the lobes ovate, obtuse, 4–5 mm. long, 2.0–2.5 mm. broad; stamens 5, inserted 2–3 mm. below the orifice, the anthers ovate, acute, about 1 mm. long, subsessile; ovary 2-carpellary, fused at the very base, subglobose,

about 2.5 mm. in diameter, the ovules 2 in each locule on a ventral placenta, the disc annular, about 1 mm. high, the style columnar, 3–4 mm. long, glabrous, the stigma-head subcapitate, about 1 mm. high, obscurely bilobed. FRUITS not known.

On hills near rivers and streams; flowering during September. Eastern Brazil.

Rauvolfia paucifolia is easily distinguished from all its related species by its slender branches with rather distant nodes and fairly small leaves, and the very few-flowered short inflorescences.

BRAZIL. BAHIA: Jacobina, Serato do Rio São Francisco, *Blanchet 2920* (G, W).
ESPIRITO SANTO: Serra do Itabapoana, *Glaziov 11182* (P).

25. RAUVOLFIA SESSILIFOLIA S. Moore, in Jour. Bot. (Brit.) 42:103. 1904. (T.: *Robert 494, photo!*)

Plants with slender, terete, lenticellate, glabrous branches, the nodes with glands confined to the leaf-axils. LEAVES in whorls of 3 to 4, scarcely anisophyllous, sessile, ovate to ovate-oblong, acute to shortly acuminate, narrowed at the base, 5–8 cm. long, 2–4 cm. broad, membranaceous, the secondary veins 10–16 pairs, slightly arcuate, evident above, obscure beneath. INFLORESCENCES terminal and lateral, many-flowered, corymbose; peduncles slender, about 3 cm. long, glabrous, bracteate, the bracts subulate, about 2 mm. long, the pedicels slender, about 5 mm. long, glabrous. FLOWERS conspicuous; calyx deeply 5-lobed, the lobes ovate, acute, about 1 mm. long; corolla salverform, the tube slender, about 10 mm. long, glabrous without and within, except near the stamens, pilose; stamens 5, inserted near the throat, the anthers linear, about 1.5 mm. long; ovary 2-carpelled, oblong, obtuse, about 2 mm. high, the disc annular, about 1 mm. high. FRUITS not known.

Flowering in September. South-central Brazil.

According to Spencer Moore, *R. sessilifolia* is closely related to *R. weddelliana*, but differs from it by its ovate or ovate-oblong sessile leaves, its shorter pedicels and the corolla-tube about twice as long as the lobes.

26. RAUVOLFIA WEDDELLIANA Muell.-Arg. in Mart. Fl. Bras. 6¹:32. 1860. (T.: *Weddel 2966!*)

R. elliptica Malme, in Bihang till K. Sv. Vet.-Akad. Handl. Afd. III. 24¹⁰:13. 1899. (T.: *Malme 1444B!*)

Shrubs or subshrubs 0.5–1.0 m. tall; branches few, slender, terete, glabrous, not lenticellate, the nodes with pectinate glands confined to the leaf-axils. LEAVES in whorls of 3 to 4, scarcely anisophyllous, shortly petiolate, broadly to narrowly elliptic, acute to short-acuminate, narrowed at the base, 5–11 cm. long, 1–4 cm. broad, subcoriaceous to coriaceous, the secondary veins 12–18 pairs, slightly arcuate and meeting on either side to form a delicate marginal vein, a little obscure above, more distinct beneath; petioles slender, 2–4 mm. long.

INFLORESCENCES terminal and lateral, geminate or ternate, many-flowered, corymbose; peduncles slender, 3–4 cm. long, glabrous, bracteate, the bracts lanceolate, about 2 mm. long, the pedicels slender, 5–12 mm. long, glabrous. FLOWERS conspicuous; calyx deeply 5-lobed, ovate, acute, about 2 mm. long, corolla



Fig. 25. *Rauvolfia weddelliana* Muell.-Arg. (Hassler 10696)

salverform, roseate (*vide* Hassler), the tube slender, cylindrical, 8–9 mm. long, about 2 mm. in diameter at the base, glabrous without, villous within near the throat and near the stamens, the lobes ovate, broadly acute to obtuse, 4–5 mm. long, about 2 mm. broad; stamens 5, inserted near the throat, the anthers ovate, acute to acuminate, about 2 mm. long, subsessile; ovary 2-carpellary, hemisyncarpous, subspherical, about 2 mm. in diameter, the ovules 2 in each locule on an axile placenta, the disc annular, about 1 mm. high, the style columnar, 3–4 mm. long, glabrous, the stigma-head subturbinate, about 1 mm. high, obscurely bilobed. FRUITS reniform, 2-seeded, the lobes obovoid, 14–16 mm. long, 10–13 mm. broad, often only one carpel developing, then the fruit obovoid, the stones distinctly rugose, the seeds obovate, albuminous, the testa membranaceous, the albumen fleshy, the embryo about as long as the seed, erect, the cotyledons ovate, obtuse, about 4 mm. long, 3 mm. broad, the hypocotyl terete, about 5 mm. long.

In dry fields and on slopes of hills; flowering from September to February; ripe fruits in March and April. South-central Brazil and Paraguay.

This species resembles *R. paucifolia* to some extent, but can be distinguished from it by its elliptic leaves and long-peduncled, many-flowered inflorescences.

My study of the two type sheets respectively of *R. weddelliana* and *R. elliptica* confirms what Spencer Moore had already concluded, that *R. elliptica* is conspecific with *R. weddelliana*. Mueller-Argoviensis has cited, in his original description, two specimens: *Riedel 637* and *Weddell 2966*. All the Riedel sheets that I have examined are unnumbered but I have no doubt that these sheets are isotypic with what Mueller has mentioned. However, the prominently lenticellate twigs with oblanceolate leaves, and the flowers with very short corolla-tube and lobes make this referable to *R. babiensis* rather than *R. weddelliana*. Accordingly, I am designating for *R. weddelliana*, *Weddell 2966* (P) as the type.

BRAZIL. MATO GROSSO: Santa Anna da Chapada, *Malme 1444B* (S), *Malme s. n.* (G, S, UPS, US); precise locality not known, *Robert s. n.* (MO); between Goyaz and Cujaba, *Weddell 2966* (P).

PARAGUAY. AMAMBAY: Sierra de Maracaju, *Hassler 5044* (A, G, MO, P, S, UC, W); Sierra de Amambay, *Hassler 10696* (G, P, W); Cerro Torín, *Meyer 18.541* (MO).

27. *RAUVOLFIA STEYERMARKII* Woodson, in *Fieldiana: Bot.* 28³:502. 1953. (T.: *Steyermark 57428!*)

Shrubs about 6 m. tall; branches verticillate, terete, glabrous, profusely lenticellate, the nodes with distinct pectinate glands confined to the leaf-axils. LEAVES in whorls of 3 to 5, scarcely anisophyllous, shortly petiolate, elliptic to obovate-elliptic, shortly acuminate, obtuse at the base, 5–10 cm. long, 3–4 cm. broad, subcoriaceous, the secondary veins many, 4–5 mm. apart, slightly arcuate, equally evident on both surfaces; petioles stout, 5–10 mm. long. INFLORESCENCES terminal, 3- or 4-nate, much branched, many-flowered; peduncles stout, 4–5 cm. long, glabrous, bracteate, the bracts ovate, acute, about 1 mm. long, the pedicels stout, 3–5 mm. long, glabrous. FLOWERS relatively small; calyx deeply 5-lobed,

the lobes oblong-ovate, obtuse, about 2 mm. long, corolla salverform, greenish-white, fragrant (*vide* Steyermark), the tube slender, 5–6 mm. long, about 1 mm. in diameter at the base, glabrous without, villous within near the throat and the stamens, the lobes oblique-ovate, rounded, about 2.0–2.5 mm. long, about 1.5 mm. broad; stamens 5, inserted near the throat, the anthers ovate, acute, about 1 mm. long, the filament about 1 mm. long; ovary 2-carpellary, apocarpous, obovate, about 2 mm. high, 1.5 mm. in diameter, the ovules 2 in each locule on a ventral placenta, the disc annular, about 1 mm. high, the style columnar, 2.5–3.0 mm. long, glabrous, the stigma-head subcapitate, about 1 mm. high, obscurely bilobed. FRUITS not known.

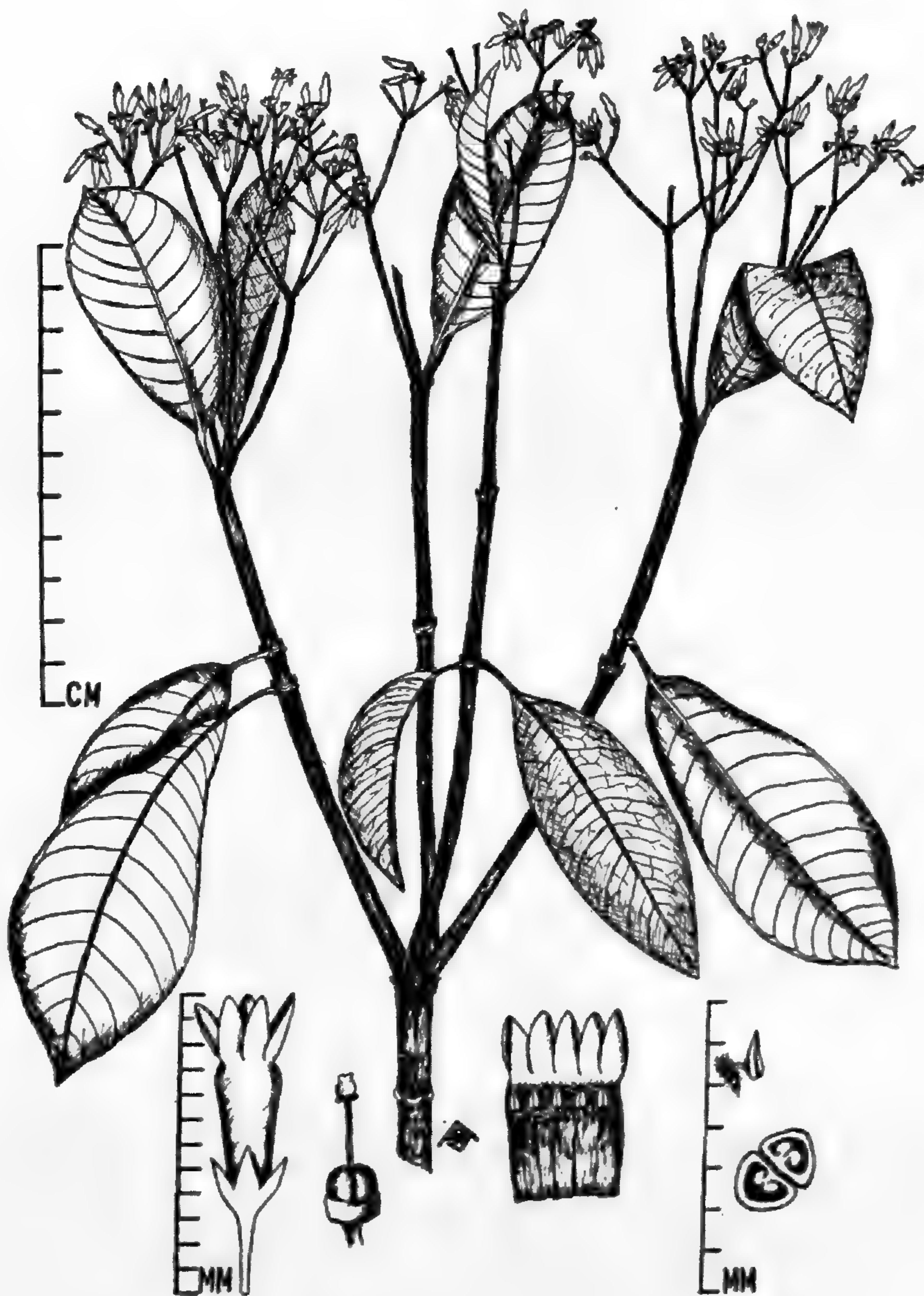


Fig. 26. *Rauvolfia steyermarkii* Woodson (Steyermark 57428)

Along river banks, at altitudes between 1820 and 2130 meters; flowering in July. Venezuela.

Rauvolfia steyermarkii is easily distinguished by its verticillate branches, bearing at their tips the ternate or quaternate, profusely flowered inflorescences.

VENEZUELA. TACHIRA: between Tabor and Villapaez, along Río Tachira, by Colombian-Venezuelan boundary, *Steyermark* 57428 (F, MO).

28. *RAUVOLFIA NITIDA* Jacq. Enum. Pl. Carrib. 14. 1760; Select. Stirp. Amer. 47. 1763, *ex char.*, not *R. nitida* Lamarck, 1819.

R. angustifolia Salisb. Prodr. 146. 1796, *nom nud.*

R. nitidissima Steud. Nom. Bot. ed. 1. 682. 1821, *nom. nud.*

R. canescens Descourt. Fl. Ant. 3:151. 1827, *ex char. et icon.*, not *R. canescens* L. 1762.

R. lanceolata A. DC. in DC. Prodr. 8:337. 1844. (T.: *Wydler* 290!), not *R. lanceolata* Griseb. 1864.

R. nitida Sessé & Moc. Fl. Mex. 53. 1887, *ex char.*

Shrubs or trees 2–15 m. tall; branches 2-, 3- or 4-chotomous, terete, the bark coarse, gray, prominently lenticellate, the nodes with pectinate glands confined to the leaf-axils. LEAVES in whorls of 4, rarely 2, 3, or 5, ovate-elliptic to oblong-elliptic, acute to shortly acuminate, gradually to abruptly attenuate at the base, 3–15 cm. long, 2–5 cm. broad, subcoriaceous, the secondary veins many, almost transverse, distinct on both surfaces, the upper surface lustrous, the lower opaque; petioles 5–10 mm. long. INFLORESCENCES terminal and lateral, few- to many-flowered, corymbose; peduncles stout, repeatedly dichotomously branched, 1–4 cm. long, glabrous, minutely bracteate, the pedicels stout, 2–5 mm. long, glabrous. FLOWERS relatively small; calyx deeply 5-lobed, the lobes broadly ovate, obtuse to rounded, about 1.5 mm. long; corolla salverform, white (*fide* J. G. Jack), the tube stout, 5–6 mm. long, about 1.5 mm. in diameter at the base, glabrous without, villous within along the upper half, the lobes broadly ovate, rounded, 3–4 mm. long, 2–3 mm. broad; stamens 5, inserted near the throat, the anthers ovate, acute, about 1.5 mm. long, subsessile; ovary 2-carpellary, hemisyncarpous, subglobose, about 2 mm. in diameter, the ovules 2 in each locule on an axile placenta, the disc annular, about 1 mm. high, the style columnar, about 3 mm. long, glabrous, the stigma-head subcapitate, about 1 mm. high, obscurely biapiculate. FRUITS subglobose, faintly emarginate, 10–12 mm. long, 15–18 mm. broad, 2-seeded, the stones ovoid, stout at the base, compressed above, faintly ridged, the seed ovate, slightly curved at the base, albuminous, the testa chartaceous, the albumen fleshy, the embryo about as long as the seed, the cotyledons ovate, obtuse, slightly curved at the tip, about 4 mm. long, 2 mm. broad, the hypocotyl terete, about as long as the cotyledons.

On sandy and stony soil, on hills, in the forests and in pastures, at altitudes from sea-level to 600 m. Flowering from September to March; ripe fruits in March and April. The West Indies.

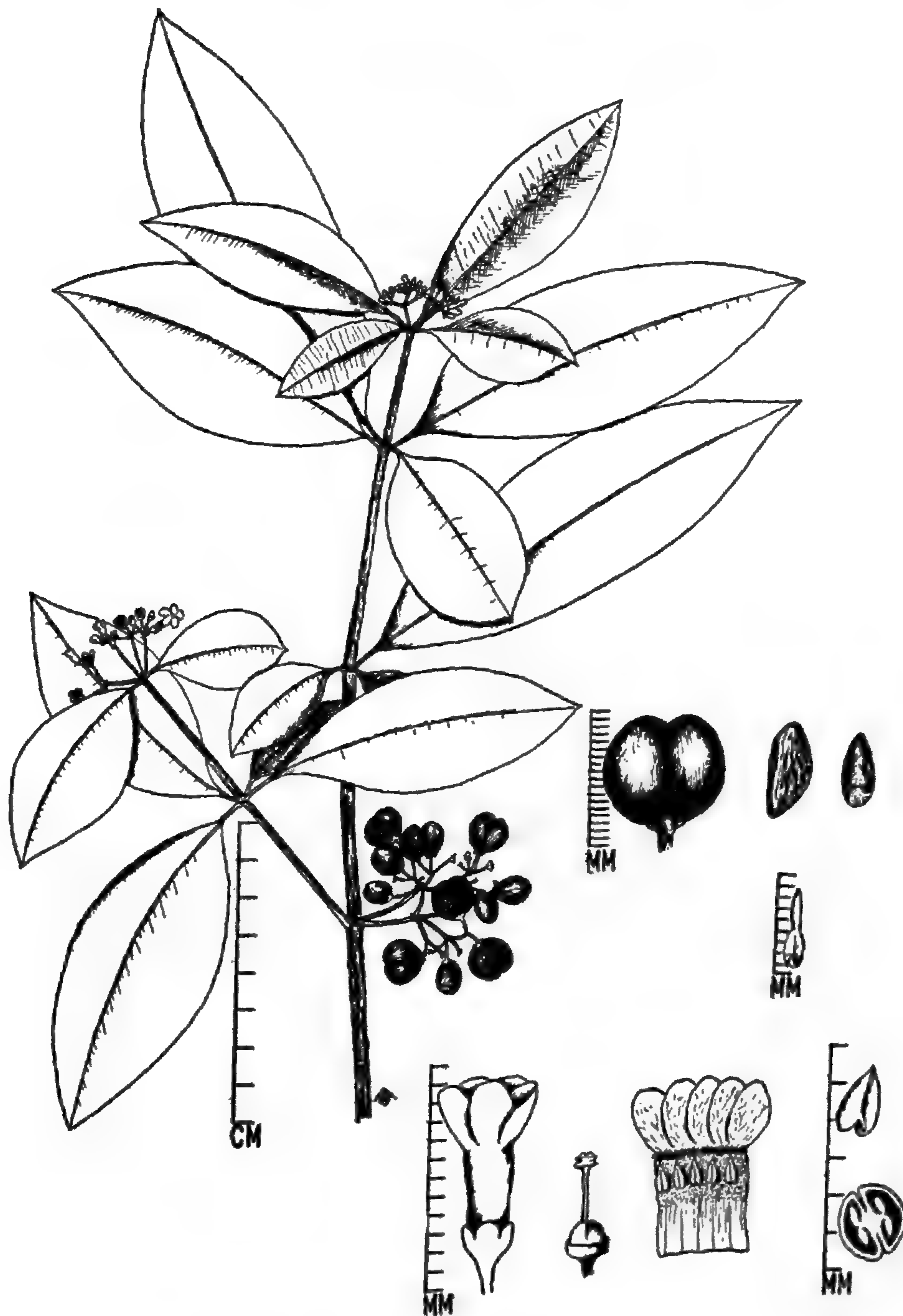


Fig. 27. *Rauvolfia nitida* Jacq. (A. A. Heller 6190)

COMMON NAMES: *Bois Lait*, *Glass Wood*, *Juan Primero*, *Lechoso*, *Palo del Leche*, *Palo del Rey*, *Sucheli Blanco*.

This species is easily recognized by its glistening, elliptic leaves with innumerable close-knit secondary veins, and the inflorescences with repeatedly dichotomously branching, stout peduncles carrying innumerable small white flowers on stout short pedicels.

Rauvolfia nitida is one of the two species that Plumier originally founded under the trinomial *Rauvolfia tetraphylla angustifolia*. Since Linnaeus' time much

confusion has occurred on the synonymy of this species. Rendle⁵⁰ has ably clarified this situation. Recently, however, Feuell⁵¹ has been led to a fresh error in mistaking Descourtilz's *R. canescens* (= *R. nitida*) for *R. canescens* L., and has consequently ascribed the poisonous properties of *R. nitida* to *R. canescens*.

I have seen two specimens from the Trinidad Botanical Gardens. These are obviously the same that Cheesman⁵² refers to in his account of Apocynaceae. Since there has been no further collection of *R. nitida* from Trinidad, Cheesman has concluded that this is a doubtful record.

UNITED STATES. FLORIDA: Miami, Coconut Grove, Fennell 651 (MO) (Cultivated).
ANTILLES.—

BAHAMAS: Brace 346 (NY). NEW PROVIDENCE: Delaport, N. L. Britton & Brace 306 (A, GH, MO, NY, US).

CUBA. HAVANA: Leon 660, 3696 (NY), Sagra s. n. (P, W). ISLE OF PINES: N. L. Britton & Wilson 14864 (NY, US). MATANZAS: Matanzas, N. L. & E. G. Britton & Shafer 96 (NY). ORIENTE: Baraçoá, Ekman 4440 (S), 5145 (P, S), Leon 11863, 12143 (NY); Bayate, Ekman 6112 (S); Cupey, Ekman 6325 (S); Papayo, Ekman 9324 (S); Manacal, Ekman 9390 (S). SANTA CLARA (LAS VILLAS): Cienfuegos, Combs 296 (GH, MO, NY, P, US), Jack 5089 (A, S, US), 5154 (A, P, US); Soledad, Jack 4977 (A, P), 5427, 5685 (A, P, US), 5653 (A), 6735 (US), 7426 (A, S, US), Howard 6591 (GH, S, US); Mina Carlota, Howard 5631 (GH, MO, NY, UC, US), 5694 (GH, NY). PRECISE LOCALITY UNKNOWN: Rugel 751 (NY), Wright s. n. (S), 397 = 1384 (G, GH, MO, NY, P, US), 400 (S), 1383 (G, GH, P).

JAMAICA. Blue Mountains, below Berurcks, Parkins 1195 (A, GH), hillside, Potsdam to Lover's Leap, N. L. Britton 1131 (NY), Santa Cruz Mountains, Harris 5402 (US), 5850 (NY), 9743 (NY, US); Tepe near Troy, Harris 11071 (NY, US), 11113 (NY, US). PRECISE LOCALITY UNKNOWN: Alexander s. n. (GH, NY, P).

HISPANIOLA.—

DOMINICAN REPUBLIC: Azua, J. N. Rose 4054 (NY, US); Barahona, Fuertes 318 (GH, L, MO, NY, P, S, US), Von Tuerckheim 2831 (GH, L, MO, P, S, US, W); Ciudad Trujillo, Allard 14627 (S, US), Schiffino 126 (US), 160 (GH); Constanza, Abbott s. n. (US); Higuey, R. A. & E. S. Howard 9760, 9770 (GH, MO, NY), Higuey to Gato, Taylor 449 (NY); Puerto Escondido, R. A. Howard 12140 (MO); Santiago de los Caballeros, Jimenez 2706 (MO); Sierra del Pala, Eggers 1900 (L, M, P). PRECISE LOCALITY UNKNOWN: Eggers 2518 (NY, US), Ekman 14294 (S, US), Poiteau s. n. (P), Sagra s. n. (P), Von Tuerckheim 2692 (M, NY, P), 3485 (GH, L, M, MO, NY, P, S, US, W), 1385bis (GH), Valeur 678 (MO, NY, P, S, US), Wright 219 (US), Wright, Perry & Brummel 407 (US).

PUERTO RICO. HUMACAO: Coamo to Caguas, N. L. Britton & Cowell 1380 (NY); vicinity of Coamo Springs, N. L. & E. G. Britton & Brown 6424 (NY, P, US), 6481 (NY), Underwood & Griggs 460 (NY, US); Humacao, Blanner 50 (P); near San Germán, Miller 1626 (US); Yabucoa, Sintenis 5036 (G, M, P, S). AGUADILLA: Rincon, Sintenis 5680 (L, P). GUAYAMA: Guayama, Kuntze 511 (NY); Cayey, Sintenis 2372 (G, L, MO, P); Jobos, Goll 517, 518 (US). MAYAGUEZ: Monte Mesa, N. L. Britton & Hess 2716 (NY, US); Río de Maricao, N. L. Britton, Stevens & Hess 2421 (NY, US); Punta Guaniquilla, N. L. Britton, Cowell & Brown 4571 (GH, MO, NY, P, US); Parquera, N. L. & E. G. Britton 9926 (NY); vicinity of Mayaguez, Cowell 695 (NY, US), Fogg 21770 (MO); Yauco, Garber 42 (GH, NY); Guanica, Sintenis 3372 (GH, NY, US), 3835 (NY, P, US); Lajas, Sargent 522 (US); road from Yauco to Guayanilla, Underwood & Griggs 599 (NY, US). SAN JUAN: Bayamon, The Hellers 403 (A, NY, US), Sintenis 1193 (GH, M, NY, S, US),

⁵⁰ Rendle, A. B., Proc. Linn. Soc. Lond. 149³:106. 1937.

⁵¹ Feuell, A. J., in Colon. Pl. & An. Prod. 5:5. 1955.

⁵² Cheesman, E. E., in Flora of Trinidad and Tobago 2³:153. 1947.

1194bis (G); Martin Pena, *Stevenson 1872* (US), Point Cangrejos, *Stevenson 522* (US). PONCE: Ponce to Penuelas, *N. L. & E. G. Britton & Marble 1753* (GH, MO, NY, US); Penuelas, *Sintenis 4786* (M, S, US, W); Ponce, *Heller 6190* (A, GH, L, MO, NY, P, US). VIEQUES ISLAND: Santa Maria to Caballo Colorado, *Shafer 2680, 2684* (NY, US). MONA ISLAND: *Stevens 6318* (NY). PRECISE LOCALITY UNKNOWN: *Wydler 290* (G, L), *Plée s. n.* (P), *Poiteau s. n.* (P), *L. C. Richard s. n.* (P), *Riedel s. n.* (P).

ST. CROIX: Prosperity Garden, *Raunkiaer s. n.* (US), *Benzon s. n.* (MO), *A. E. Ricksecker 362* (GH, MO, NY, UC, US), *J. J. Ricksecker 428* (MO, P, US); Fredericksted, *J. N. Rose 3515* (NY), *Thompson 98* (GH, NY), *803, 876* (S).

ST. KITTS: *Fairchild s. n.* (A, MO, US).

ST. THOMAS: Pearl to Bonne Resolution, *E. G. Britton & Marble 1325* (MO, NY, US); near Solbjerg, *Eggers s. n.* (S); Signal Hills, *Eggers 385* (G, L, M, P, US, W). PRECISE LOCALITY UNKNOWN: *Bertero s. n.* (M), *Krebs s. n.* (NY), *L. C. Richard s. n.* (P), *Riedel s. n.* (P).

VIRGIN ISLANDS: St. John, *Morrow 167* (US); Tortola, Belmont sand dunes, *Fisblock 430* (NY), *Shafer 1156, 1178* (NY, US), *N. L. & E. G. Britton & Kemp 89* (NY).

ANTILLES (WEST INDIES): precise locality unknown, *Swartz s. n.* (S), *Sessé & Moçino 675, 1449* (F), *Ridley s. n.* (P), *Vahl 5209* (L).

GUADELOUPE: *Alleizette s. n.* (L).

MARTINIQUE: *Plée s. n.* (P).

TRINIDAD: *Trinidad Botanic Garden Herb. 1931* (US); woods of Chaguanas, *Prestoe 1448* (NY).

29. *RAUVOLFIA BAHIENSIS* A. DC. in DC. Prodr. 8:339. 1844. (T.: *Blanchet 3186!*)

Plants with trichotomous, rarely dichotomous, terete, glabrous, prominently lenticellate branches, the nodes with distinct pectinate glands confined to the leaf-axils. LEAVES in whorls of 3, oblanceolate to obovate, shortly acuminate, cuneate at the base, 3–12 cm. long, 1.0–4.5 cm. broad, subcoriaceous, the secondary veins barely visible on both surfaces; petioles 5–10 mm. long. INFLORESCENCES terminal, geminate or ternate, few-flowered, umbellate; peduncles slender, 3–4 cm. long, glabrous, minutely bracteate, the pedicels slender, 10–15 mm. long, glabrous. FLOWERS relatively small; calyx deeply 5-lobed, the lobes ovate to deltoid, acute, about 2 mm. long; corolla infundibuliform, the tube slender, 6–7 mm. long, about 2 mm. in diameter at the base, glabrous without, densely villous nearly to the base within, the lobes ovate, broadly acute, 4–5 mm. long, about 2 mm. broad; stamens 5, inserted near the throat, the anthers subulate, about 2 mm. long, subsessile; ovary 2-carpellary, free nearly to the base, obovoid, about 2.5 mm. high, about 2 mm. in diameter, the ovules 2 in each locule on a ventral placenta, the disc annular, about 1 mm. high, the style columnar, 3–4 mm. long, glabrous, the stigma-head subcapitate, about 1 mm. high, obscurely bilobed. Fruits unknown.

Near river banks and on road-sides; flowering during December. Eastern Brazil.

The densely lenticellate, trichotomous, terete twigs, with the terminal, prominently umbellate inflorescences carrying long-pedicelled flowers, serve to distinguish this species from the related *Rauvolfias*.

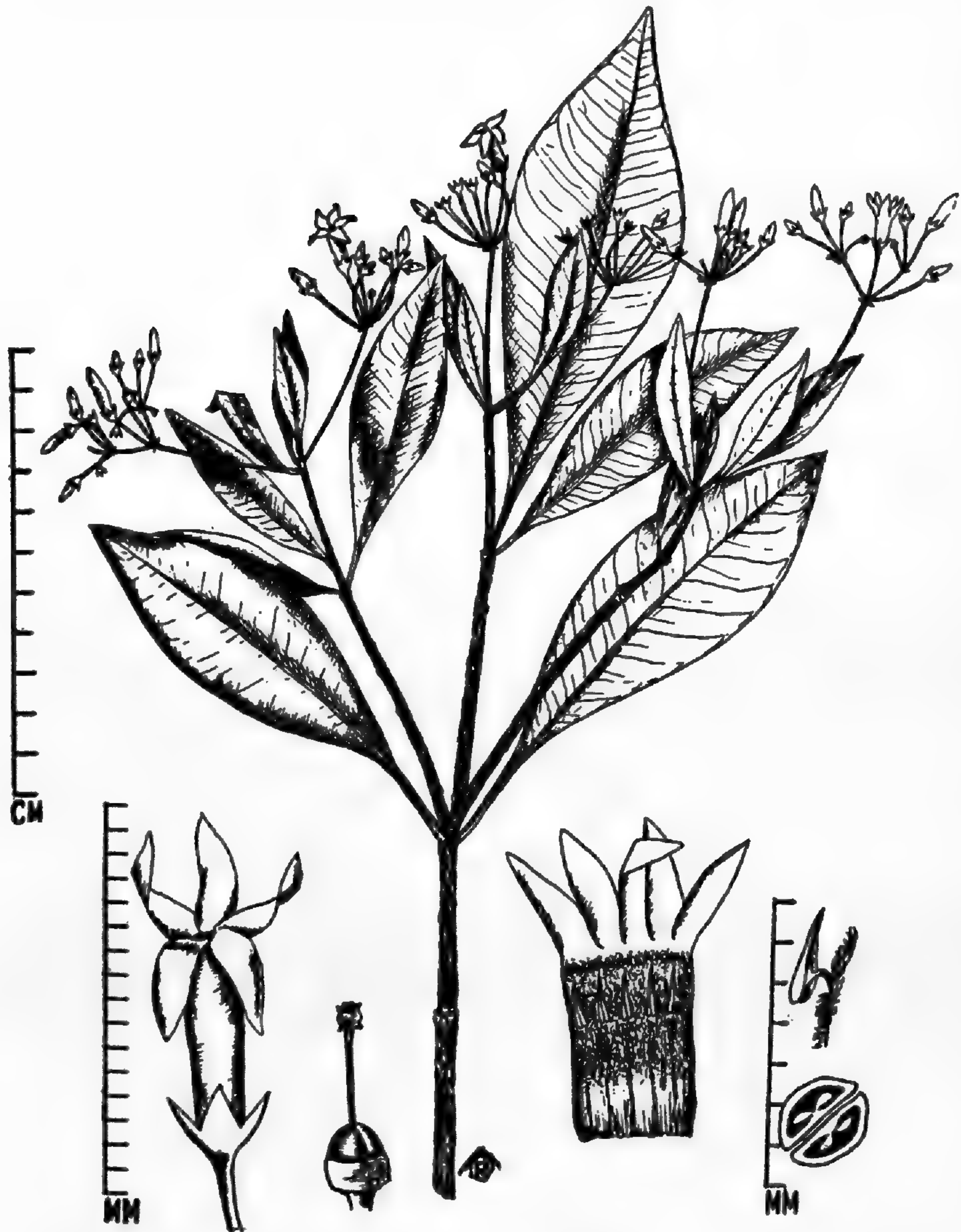


Fig. 28. *Rauvolfia babiensis* A. DC. (Blanchet 3186)

BRAZIL. BAHIA: basin of Rio Santa Ana, road to Pontal, *Krukoff 12698/63* (NY); precise locality not known, *Blanchet 3186* (G, W); *Riedel s. n.* (G, GH, P, W).

30. *RAUVOLFIA BIAURICULATA* Muell.-Arg. in *Linnaea* 30:396. 1860. (T.: *Sieber s. n.* !)

Shrubs or trees 3–9 m. tall; branches 2- or 3-chotomous, terete, glabrous, the bark gray, wrinkled longitudinally, slightly lenticellate, the nodes with distinct pectinate glands in the leaf-axils only. LEAVES in whorls of 3, rarely 4, shortly petiolate, oblanceolate to obovate, shortly acuminate to caudate, cuneate at the base, 5–12 cm. long, 2.0–3.5 cm. broad, coriaceous, the secondary veins obscure on both surfaces, the two surfaces opaque; petioles 5–10 mm. long. INFLORESCENCES terminal, few-to many-flowered, corymbose; peduncles repeatedly 2-branched,



Fig. 29. *Rauvolfia bianriculata* Muell.-Arg. (Eggers 674)

slender, 3–5 cm. long, glabrous, minutely bracteate, the pedicels slender, 5–10 mm. long, glabrous. FLOWERS relatively small; calyx deeply 5-lobed, the lobes deltoid, acute, about 1.5 mm. long, the margin minutely glandular-dentate; corolla salverform, roseate (*vide* Howard), the tube slender, 4–6 mm. long, about 1 mm. in diameter at the base, glabrous without, villous within along the upper half, the lobes obliquely oblong-elliptic, obtuse, 4–5 mm. long, 2–3 mm. broad; stamens 5, inserted near the throat, the anthers ovate, acuminate, about 2 mm. long, subsessile;

ovary 2-carpellary, fused almost to the top, obovoid, about 2.5 mm. high, 2 mm. in diameter, the ovules 1 in each locule on an axile placenta, the disc annular, about 1 mm. high, the style columnar, about 3 mm. long, glabrous, the stigma-head cylindrical, about 1 mm. high, obscurely bi-apiculate. FRUITS obcordate, 2-seeded (often only one carpel developing, then the fruit ellipsoid and 1-seeded), the lobes ellipsoid, 12–15 mm. long, 5–8 mm. broad, the stones distinctly rugose, the seed albuminous, the testa membranaceous, the albumen fleshy, the embryo erect, the cotyledons ovate, obtuse, about 3 mm. long, 2 mm. broad, the hypocotyl terete, about as long as the cotyledons.

In dense humid forests, on hills, at altitudes between 500 and 800 m. Flowering from June to December; ripe fruits in January to March. Antilles: Dominican Republic, Dominica, and Guadeloupe.

COMMON NAME: *Bois Lait-montagne*.

Rauvolfia biauriculata resembles greatly *R. babiensis*, but can be differentiated from it by its slightly lenticellate, wrinkle-barked twigs with markedly leathery leaves, and the terminal dichotomously branching peduncled, corymbose inflorescences bearing flowers with the corolla-tube almost as long as the lobes.

I have seen the two Ritter and Sieber specimens that Mueller has cited in his description. The Sieber sheet carries distinctly the annotation "Trinitas." However, Cheesman⁵³ considers this a doubtful record, as he has found no evidence for the occurrence of this species in Trinidad.

ANTILLES. DOMINICAN REPUBLIC: precise locality unknown, *Ritter s. n.* (W). DOMINICA: Pleasant Valley, *Eggers 674* (G, GH, L, M, P, UC, US, W). GUADELOUPE: Fort Baines Jaunes, *Steble, Quentin et Bena 5601* (US), *Steble 702* (US); trail from St. Cloud to Soufrière above Baines Jaunes, *Howard 11794* (MO); Grand Bois, *Quentin 726* (P). PRECISE LOCALITY UNKNOWN: *Duss 8* (P), *2544* (GH, MO, NY, UPS, US), *L. C. Richard s. n.* (P). TRINIDAD: *Sieber s. n.* (W).

31. RAUVOLFIA PURPURASCENS Standl. in Trop. Woods 16:11. 1928; Field Mus. Publ. Bot. 4:255. 1929. (T.: *G. P. Cooper 516!*)

Stout liana?; branches subterete, glabrous, the bark wrinkled longitudinally, scarcely lenticellate, the nodes with distinct pectinate glands confined to the leaf-axils. LEAVES in whorls of 4, long-petiolate, obovate, broadly acute to shortly acuminate or obtuse, cuneate at the base, 5–16 cm. long, 3–7 cm. broad, membranaceous to coriaceous, the secondary veins several, arcuate, joining at the margins to form marginal veins, distinct on both surfaces, the two surfaces opaque; petioles stout, 12–20 mm. long. INFLORESCENCES terminal, lax, few- to many-flowered, paniculate; peduncles slender, 3–6 cm. long, glabrous, minutely bracteate, the pedicels slender, 3–6 mm. long, glabrous. FLOWERS relatively small; calyx deeply 5-lobed, the lobes ovate, acute, about 2 mm. long; corolla salverform, purpurascens (*vide G. P. Cooper*), the tube slender, 6–7 mm. long, about 1 mm. in diameter at the base, glabrous without, villous within near the throat and the stamens, the lobes

⁵³ Cheesman, E. E., in *Flora of Trinidad and Tobago* 2³:153. 1947.

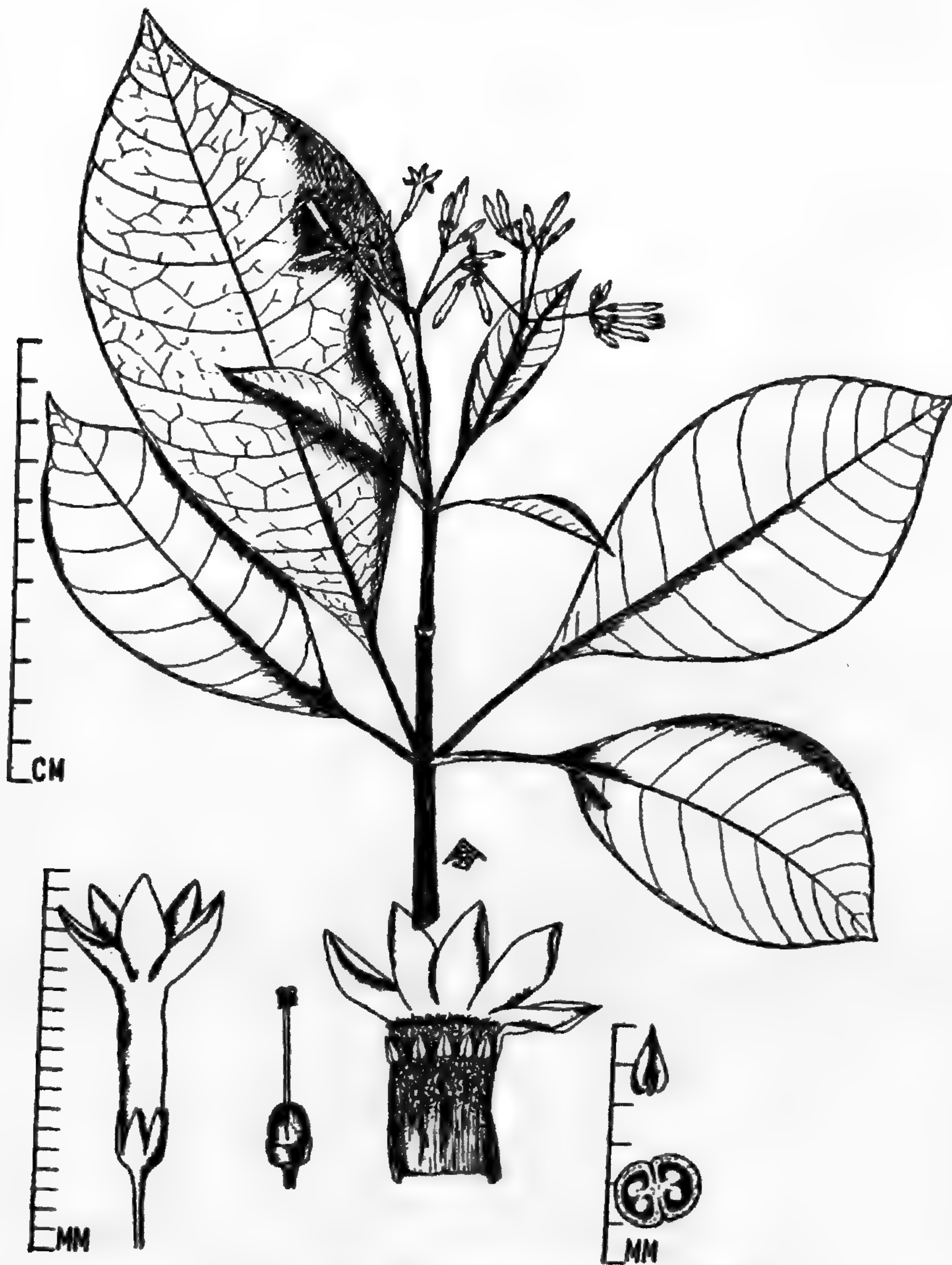


Fig. 30. *Rauvolfia purpurascens* Standl. (Cooper 516)

obovate, broadly acute to obtuse, 5–6 mm. long, 2–3 mm. broad; stamens 5, inserted near the throat, the anthers ovate, acute, about 1.5 mm. long, subsessile; ovary 2-carpellary, hemisyncarpous, cylindrical, about 3 mm. high, 2 mm. in diameter, the ovules 2 in each locule on an axile placenta, the disc annular, about 1 mm. high, the style columnar, 3–4 mm. long, the stigma-head subcapitate, about 1 mm. high, obscurely bi-apiculate. FRUITS unknown.

Flowering from January to March. Panama: Cricamola Valley. The branches bearing whorls of 4 long-petioled, obovate leaves with distinct, arcuate secondary veins, and the terminal, loose, paniculate inflorescences distinguish *R. purpurascens* from the related species of *Rauvolfia*.

PANAMA. BOCAS DEL TORO: region of Almirante, Cricamola Valley, Cooper 516 (F, G, US).

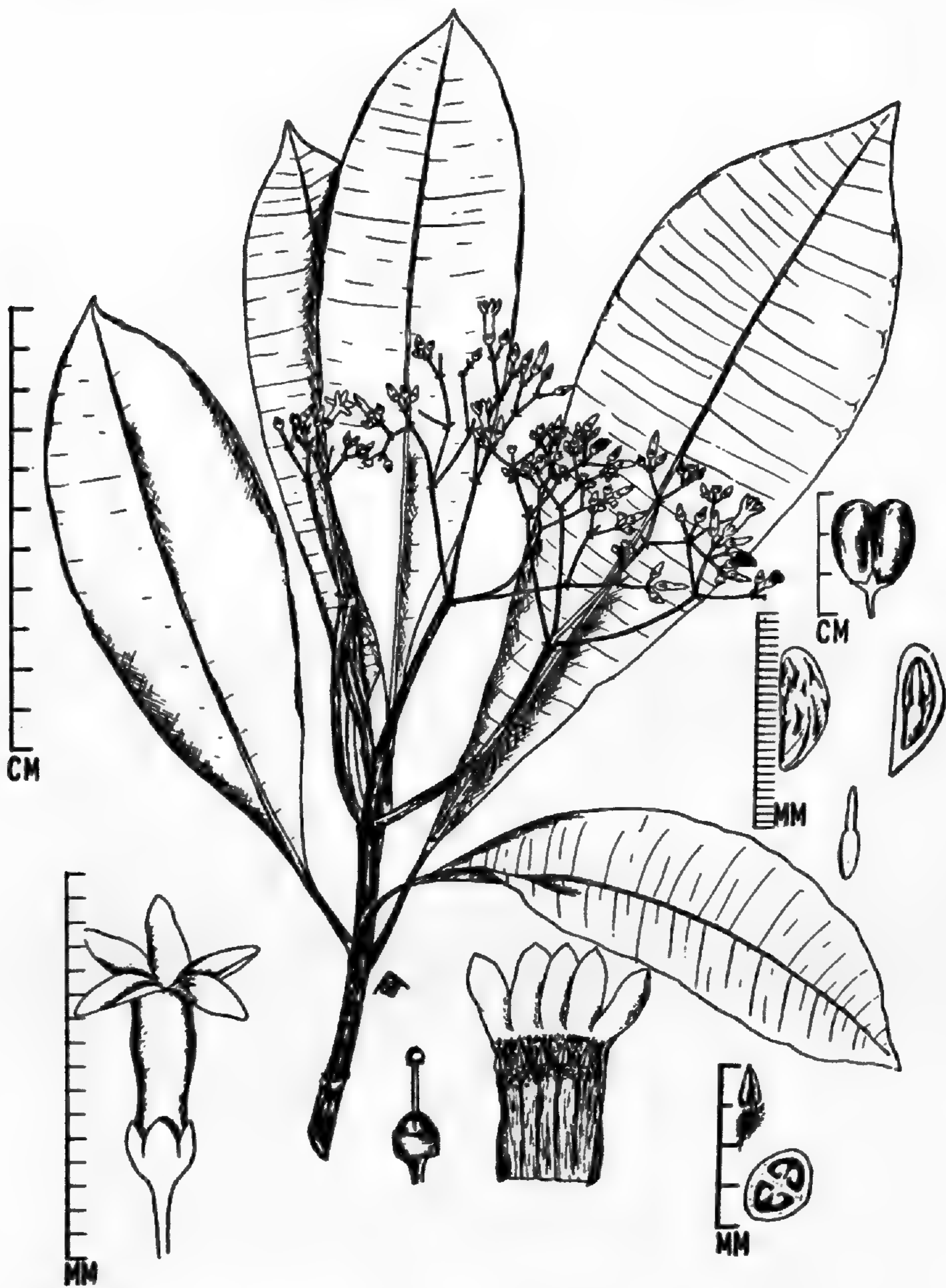


Fig. 31. *Rauvolfia sarapiquensis* Woodson (*Skutch 3556*, and *Mora s. n.*)

32. *RAUVOLFIA SARAPIQUENSIS* Woodson, in *Ann. Mo. Bot. Gard.* 28:271. 1941.
(T.: *Skutch 3556!*)

Trees about 15 m. tall; branches terete to subangular, the bark dark gray, glabrous, the nodes with distinct pectinate glands confined to the leaf-axils. LEAVES in whorls of 3, long-petiolate, oblong-ob lanceolate to oblong-elliptic, shortly acuminate, attenuate at the base, 15–25 cm. long, 4–7 cm. broad, coriaceous, the secondary veins several, almost transverse, equally evident on both surfaces, the two surfaces opaque; petioles stout, 1.5–2.5 cm. long. INFLORESCENCES terminal, ternate, many-flowered, corymbose; peduncles stout, 5–6 cm. long, 2- or 3-branched, glabrous, minutely bracteate, the pedicels stout, 4–5 mm. long, glabrous.

FLOWERS relatively small; calyx deeply 5-lobed, the lobes broadly ovate, obtuse, about 2 mm. long, fleshy; corolla salverform, white (*vide* Skutch), the tube stout, 5–7 mm. long, about 1.5 mm. in diameter at the base, glabrous without, villous within near the throat and the stamens, the lobes elliptic to ovate-elliptic, obtuse, about 4 mm. long, 2 mm. broad; stamens 5, inserted near the throat, the anthers ovate, acute, about 1 mm. long, the filament about 1 mm. long; ovary 2-carpellary, hemisyncarpous, obovoid, about 2.5 mm. high and 2 mm. broad, the ovules 2 in each locule on an axile placenta, the disc annular, about 1 mm. high, the style linear, about 2 mm. long, glabrous, the stigma-head subglobose, about 1 mm. high, obscurely bilobed. FRUITS slightly bilobed, the lobes obovate, about 18 mm. high, 8 mm. broad, the stones distinctly rugose, the seed albuminous, the testa membranaceous, the albumen fleshy, the embryo erect, the cotyledons oblong, obtuse, about 5 mm. long, 2 mm. broad, the hypocotyl terete, about as long as the cotyledons.

On hill slopes at altitudes of about 1500 m.; flowering in February. Costa Rica.

The oblong-elliptic, rather leathery leaves with almost transverse secondary veins, and the many-flowered, much-branched inflorescences distinguish this species from the rest of the Central American species of *Rauvolfia*.

COSTA RICA. Vara Blanca de Sarapiquí, north slope of central Cordillera, between Poas and Barba volcanoes, *Skutch 3556* (A, MO, US); Buena Vista de San Carlos, *H. B. Mora s. n.* (MO).

33. RAUVOLFIA PRAECOX K. Sch. ex Markgraf, in Fedde, Rep. Spec. Nov. 20:119. 1924. (T.: *Ule 6256!*); ex Ule in Engl. Bot. Jahrb. 40:400. 1908, *nom nud.*

Trees 15–30 m. tall; branches subangular to terete, 2-, 3- or 4-chotomous, the bark gray, lenticellate, the nodes with distinct pectinate glands confined to the leaf-axils. LEAVES in whorls of 3 or 4, long-petiolate, narrowly elliptic, acute or acuminate to obtuse, attenuate at the base, 5–15 cm. long, 2–5 cm. broad, coriaceous, the secondary veins several, slightly arcuate, meeting at the margins to form two marginal veins equally evident on both surfaces, the upper surface lustrous, the lower opaque; petioles slender, 2–3 cm. long. INFLORESCENCES terminal, often at the tips of defoliated twigs, many-flowered, paniculate; peduncles ternate, 2- or 3-branched, 2–4 cm. long, glabrous, minutely bracteate, the pedicels slender, 6–9 mm. long, glabrous. FLOWERS relatively small; calyx deeply 5-lobed, the lobes ovate, acuminate, about 1 mm. long; corolla salverform, reddish-violet (*vide* Ule), the tube slender, 5–7 mm. long, about 1 mm. in diameter at the base, glabrous without, scantily pilose within near the throat and the stamens, the lobes ovate, broadly acute to obtuse, 4–6 mm. long, about 2 mm. broad; stamens 5, inserted near the throat, the anthers ovate, acuminate, about 1 mm. long, subsessile; ovary 2-carpellary, hemisyncarpous, obovoid, about 2 mm. high, 1.5 mm. broad, the ovules 2 in each locule on an axile placenta, the disc annular, about 1 mm. high, the style linear, 3–5 mm. long, glabrous, the stigma-head cylindrical, about 1 mm. high, obscurely bilobed. FRUITS not seen.



Fig. 32. *Rauvolfia praecox* K. Sch. (Ule 6256)

On river banks in dense forests; flowering from July to October. Bolivia, Peru and Western Brazil.

COMMON NAME: Bolivia—*Amargo*.

Rauvolfia praecox has been confused in the past with *R. sellowii*, which is eastern Brazilian in its distribution. It can be distinguished by its long-petioled, glistening, elliptic leaves and the terminal inflorescences with a profusion of reddish-violet, slender flowers.

BRAZIL. AMAZONAS: near mouth of Rio Embira, tributary of Rio Taracua, lat 7.30° s., long. 70.15° w., *Krukoff 5018* (A, F, G, M, MO, P, S, US).

BOLIVIA. SANTA CRUZ: Sara, Buena Vista, banks of Río Surutu, *Steinbach 6536* (A, F, M, MO, S, US), *6561* (F, G, MO, S, UC, W).

PERU. LORETO: Iquitos, *Ule 6256* (G, L).

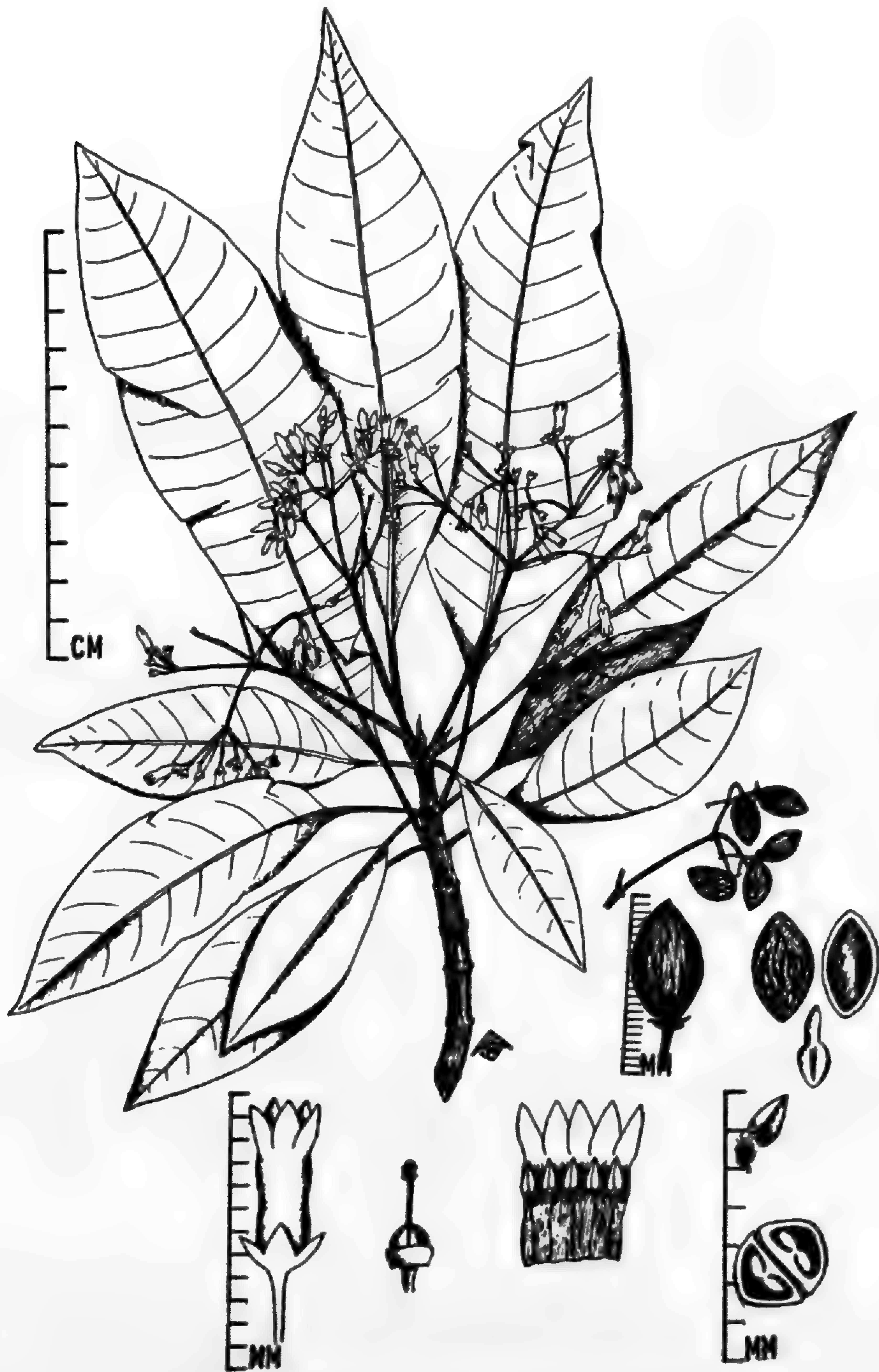


Fig. 33. *Rauvolfia sellowii* Muell.-Arg. (*Weir 173*)

34. RAUVOLFIA SELLOWII Muell.-Arg. in Mart. Fl. Bras. 6¹:34. 1860. (T.: *Sellow 238*)

Trees with branches verticillate, terete, the bark gray, longitudinally wrinkled, the internodes short, the nodes with distinct pectinate glands confined to the leaf-axils. LEAVES in whorls of 4, long-petiolate, oblong-obovate to oblong-elliptic, obtuse-acuminate, attenuate at the base, 6–20 cm. long, 3–6 cm. broad, membranaceous, the secondary veins several, arcuate, equally evident on both surfaces, the upper surface greenish, the lower dull grayish green; petioles slender, 2–3 cm. long. INFLORESCENCES terminal, ternate, many-flowered, corymbose; peduncles stout, 3–5 cm. long, 3- or 4-branched, glabrous, minutely bracteate, the pedicels slender, 3–5 mm. long, glabrous. FLOWERS relatively small; calyx deeply 5-lobed, the lobes broadly ovate, acute, about 1.5 mm. long; corolla salverform, white (*vide* Sellow), the tube stout, 5–7 mm. long, about 1.5 mm. in diameter at the base, glabrous without, scantily villous within near the stamens, the lobes ovate, broadly acute to obtuse, 2–3 mm. long, about 1.5 mm. broad; stamens 5, inserted near the throat, the anthers ovate, acute, about 1.5 mm. long, subsessile; ovary 2-carpellary, apocarpous, subglobose, about 2 mm. high, 1.5 mm. in diameter, the ovules 2 in each locule on a ventral placenta, the disc annular, about 1 mm. high, the style linear, 3–4 mm. long, glabrous, the stigma-head cylindrical, about 1 mm. high, obscurely bilobed. FRUITS apocarpous, drupelets ellipsoid, 12–16 mm. long, 7–10 mm. broad, the stones distinctly rugose, the seed ellipsoid, albuminous, the testa membranaceous, the albumen fleshy, the embryo about as long as the seed, erect, the cotyledons ovate, obtuse, about 7 mm. long, 3 mm. broad, the hypocotyl terete, about as long as the cotyledons.

In dense forests on hill slopes, flowering from September to December; ripe fruits in February to March. Southeastern Brazil.

Rauvolfia sellowii is distinguished by its twigs with short internodes, the oblong-elliptic membranaceous leaves, the much-branched many-flowered inflorescences, and the ellipsoid apocarpic fruits.

BRAZIL. MINAS GERAES: Cidade de Caldos, *Henschen* 866 (F, US). PARANA: Capao Grande, *Dusén* 7631 (S). RIO DE JANEIRO: Rio de Janeiro, *Glaziou* 2915, 6045 (P), 1045 (K). SÃO PAULO: Monte Alegre, *Kuhlmann* 7995 (UC), *Mosén* 1457 (S), São Paulo, *Mello & Mosén* s. n. (S). PRECISE LOCALITY UNKNOWN: *Burchell* 4678 (K), *Glaziou* s. n. (P), *Regnell* 111866 (P, S, UPS, US), *Sellow* s. n. (K), *Weir* 173 (K).

DUBIOUS SPECIES

Rauvolfia arborea Larrañaga, *Escritos* D. A. Larrañaga, Atlas 1: pl. 132. 1927 (Publ. Inst. Hist. Geog. Uruguay).

Rauvolfia bilabiata Larrañaga, *Escritos* D. A. Larrañaga, 2:85. 1923.

Neither the illustration of the first species nor the description of the second is sufficient to refer the above two to any known species.

Rauvolfia oppositiflora Sessé & Moç. in *La Naturaleza*, Ser. 2¹:32. 1888. The description is insufficient to refer this to any known species.

Rauvolfia rhombosiae Mgf. in Notizblatt 15:384–385. 1941. I have not been able to examine any representative material of this species. From the original description, I am inclined to treat it as synonymous with *R. sanctorum* Woodson.

EXCLUDED SPECIES

Rauvolfia dentata Tafalla, ex D. Don, in Edinb. New Phil. Jour. 10:237. 1831 = CITHAREXYLUM DENTATUM D. Don, *l. c.* 1831.

Rauvolfia flexuosa Ruiz & Pav. Fl. Peruv. 2:26. 1799 = CITHAREXYLUM FLEXUOSUM (R. & P.) D. Don, in Edinb. New Phil. Jour. 10:237. 1831.

Rauvolfia glabra Cav. Icon. 3:50, *tab.* 297. 1794 = VALLESIA DICHOTOMA Ruiz & Pav., Fl. Peruv. 2:26. 1799.

Rauvolfia laevigata Roem. & Schult. Syst. 4:805. 1819 = MALOUETIA JASMINOIDES A. DC. in DC. Prodr. 8:379. 1844.

Rauvolfia longifolia A. DC. *l. c.* 338 = TONDUZIA LONGIFOLIA (A. DC.) Mgf. in Fedde, Rep. Spec. Nov. 20:112. 1924.

Rauvolfia lycioides Cav. in Anal. Cienc. Nat. 5:69. 1802. This is a species of *Citharexylum* according to my observation of the type specimen from the Paris Herbarium.

Rauvolfia macrophylla Ruiz & Pav. Fl. Peruv. 2:26. 1799 = CITHAREXYLUM RETUSUM D. Don, in Edinb. New Phil. Jour. 10:237. 1831.

Rauvolfia oppositifolia Spreng. Neue Entdeck. 3:33. 1822 = TABERNAEMONTANA OPPOSITIFOLIA (Spreng.) Urb. Symb. Antill. 4:493. 1910.

Rauvolfia pubescens Roem. & Schult. Syst. 4:805. 1819 = CITHAREXYLUM MOLLE Jacq., *fide* Index Kewensis.

Rauvolfia spinosa Cav. in Anal. Hist. Nat. 1:43. 1799; Icon. 6:16, *tab.* 526. 1801. My observation of the type from the Madrid Herbarium indicates that this is also a species of *Citharexylum*.

Rauvolfia stenophylla Donn. Sm. in Bot. Gaz. 44:115. 1907 = TONDUZIA LONGIFOLIA (A. DC.) Mgf. in Fedde, Rep. Spec. Nov. 20:112. 1924.

Rauvolfia strempeleioides Griseb. Cat. Pl. Cub. 170. 1866 = STREMPELIOPSIS STREMPELIOIDES (Griseb.) Benth. in Benth. & Hook. Gen. Pl. 2:702. 1866.

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Italicized numerals refer to collectors' numbers, *s. n.* (*sine numero*) to unnumbered collections; parenthetical numerals refer to the number assigned to the species conserved in this revision.

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ENUMERATION OF THE SPECIES

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1. *woodsoniana* Standl.
2. *littoralis* Rusby
3. *tetraphylla* L.
4. *viridis* R. & S.
5. *morilandii* A. DC.

SERIES 2. TERNIFOLIAE

6. *blanchetii* A. DC.
7. *mollis* S. Moore
8. *ligustrina* R. & S.

SECTION II. MACROVOLFFIA

SERIES 3. LATIFOLIAE

9. *mattfeldiana* Mgf.
10. *pachyphylla* Mgf.
11. *leptophylla* A. S. Rao
12. *polyphylla* Benth.
13. *sprucei* Muel.-Arg.
14. *paraensis* Ducke
15. *macrantha* K. Sch.
16. *pentaphylla* Ducke

SERIES 4. ANGUSTIFOLIAE

SUBSERIES 1. CUBANAE

17. *linearifolia* Brit. & Wils.
18. *salicifolia* Griseb.
19. *cubana* A. DC.

SUBSERIES 2. ANDINAE

20. *schueli* Speg.
21. *andina* Mgf.

SUBSERIES 3. GRANDIFLORAE

22. *sanctorum* Woodson
23. *grandiflora* Mart.
24. *paucifolia* A. DC.
25. *sessilifolia* S. Moore
26. *weddelliana* Muel.-Arg.
27. *steyermarkii* Woodson
28. *nitida* Jacq.
29. *bahiensis* A. DC.
30. *biauriculata* Muel.-Arg.
31. *purpurascens* Standl.
32. *sarapiquensis* Woodson
33. *praecox* K. Sch.
34. *sellowii* Muel.-Arg.

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Roman type indicates accepted, preëxisting names; *italics* indicates synonyms; **bold face** indicates novelties; subgeneric categories are in CAPITALS.

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ADDENDUM: To the list of "Dubious Species" on p. 346 add:

Rauwolfia brasiliensis Spreng. Syst. 1:834. 1825. Due to insufficient description, both A. DeCandolle and Mueller-Argoviensis have also treated this as a dubious species.

EXPLANATION OF PLATE 3

Historical illustrations of *Rauwolfia* (see page 255)

Fig. 1. Plate 236 from Burmann's edition of Plumier's 'Plant. Amer. Gen.' 1755.

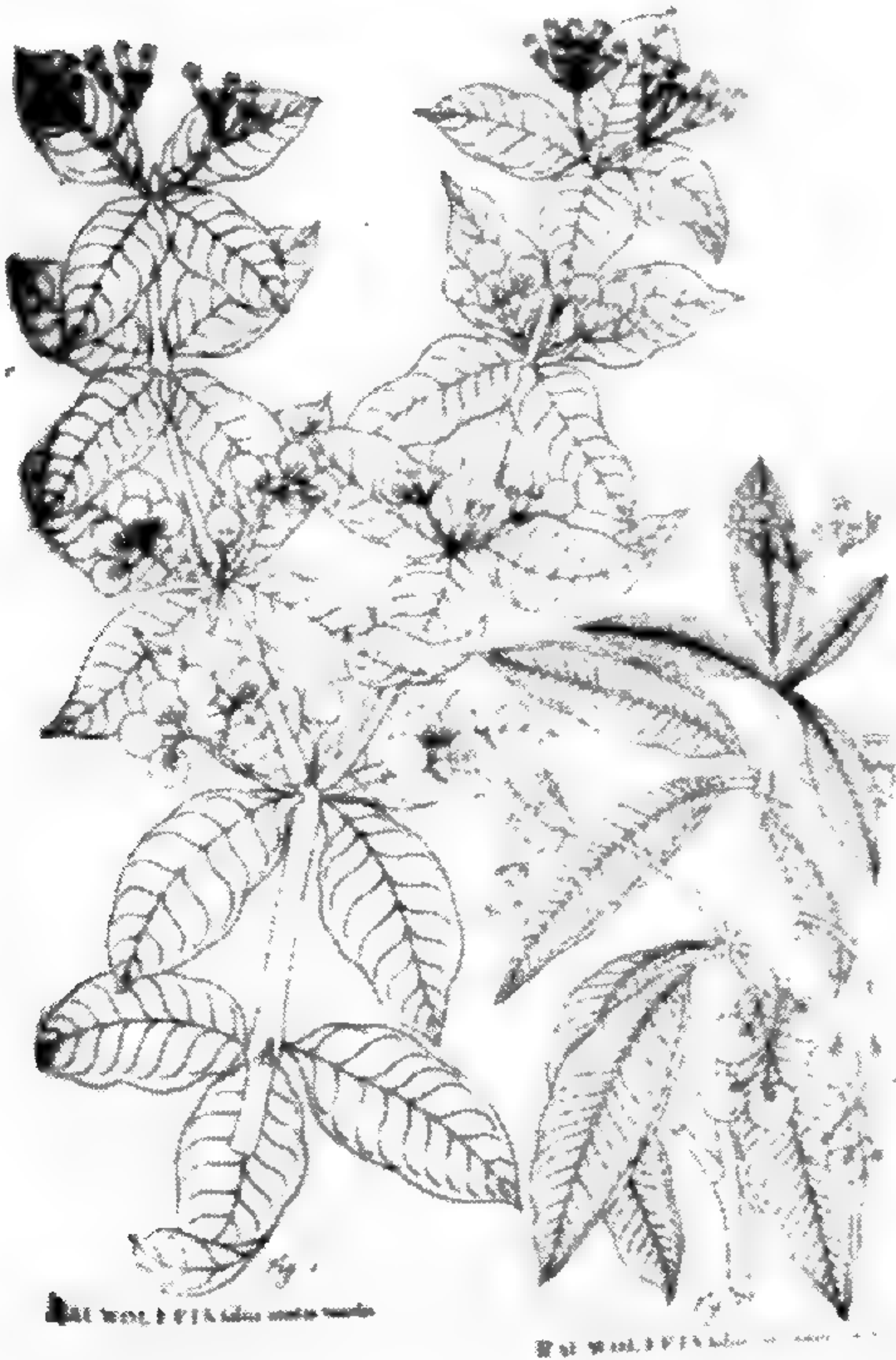
Fig. 2. Illustration of *R. tomentosa* from Jacquin (Obs. Bot. pl. 36. 1763).

Fig. 3. Ehret's drawing of a plant in the Chelsea Garden on which Linnaeus based his *R. tetraphylla*.

Fig. 4. Patrick Browne's illustration of *R. canescens* in the Linnean Herbarium.

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Savage, Catalogue no. 491

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Annals of the Missouri Botanical Garden



NOVEMBER, 1956

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Annals

of the

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Vol. 43

NOVEMBER, 1956

No. 4

A NEW FOSSIL PLANT FROM THE NEW ALBANY SHALE WITH SOME COMMENTS ON THE ORIGIN OF LAND VASCULAR PLANTS*

PART 1. CROCALOPHYTON, A NEW TRANSITIONAL SEA-LAND PLANT

HENRY N. ANDREWS AND KAREN S. ALT**

Introduction:—

The Devonian-Mississippian black shales of the east-central states have yielded in recent years a fossil flora that is remarkable in the unique and diversified nature of the plants. Within this broader area the New Albany shale of Kentucky and Indiana has produced an exceptional wealth of plant fossils. It is noteworthy that so great a variety of plant groups has been described since the collections from this area and horizon are not abundant. Few, if any, of the plants composing the flora are known with a completeness that is in any way satisfactory, yet in spite of the fragmentary nature of the specimens, they reveal plants that are novel in their morphology and anatomy and disclose major taxonomic groups hitherto unknown. The additional fact that several competent paleobotanists have not found it possible to agree on the affinities of certain constituents of the flora is indicative of its exotic nature.

It is the purpose of the present paper to record a distinctive and particularly problematical new member of the flora from a locality in Kentucky. In view of its perplexing taxonomic status a discussion follows (Part 2) dealing generally with some of the problems of the evolution of land plants which seem to be inextricably related to the particular problem of our fossil's affinity.

The geology of the New Albany shale has been dealt with in the comprehensive study by Campbell (1946) and the fossil plants of the area with which we are concerned have been described by Read and Campbell and by Hoskins and Cross. It seems unnecessary to review these previous paleobotanical studies although we

* The publication of this investigation was aided by a grant from the National Science Foundation.

** Henry Shaw School of Botany of Washington University. St. Louis, Mo.

have included in the "Literature Cited" section a fairly complete list of the contributions on the subject.

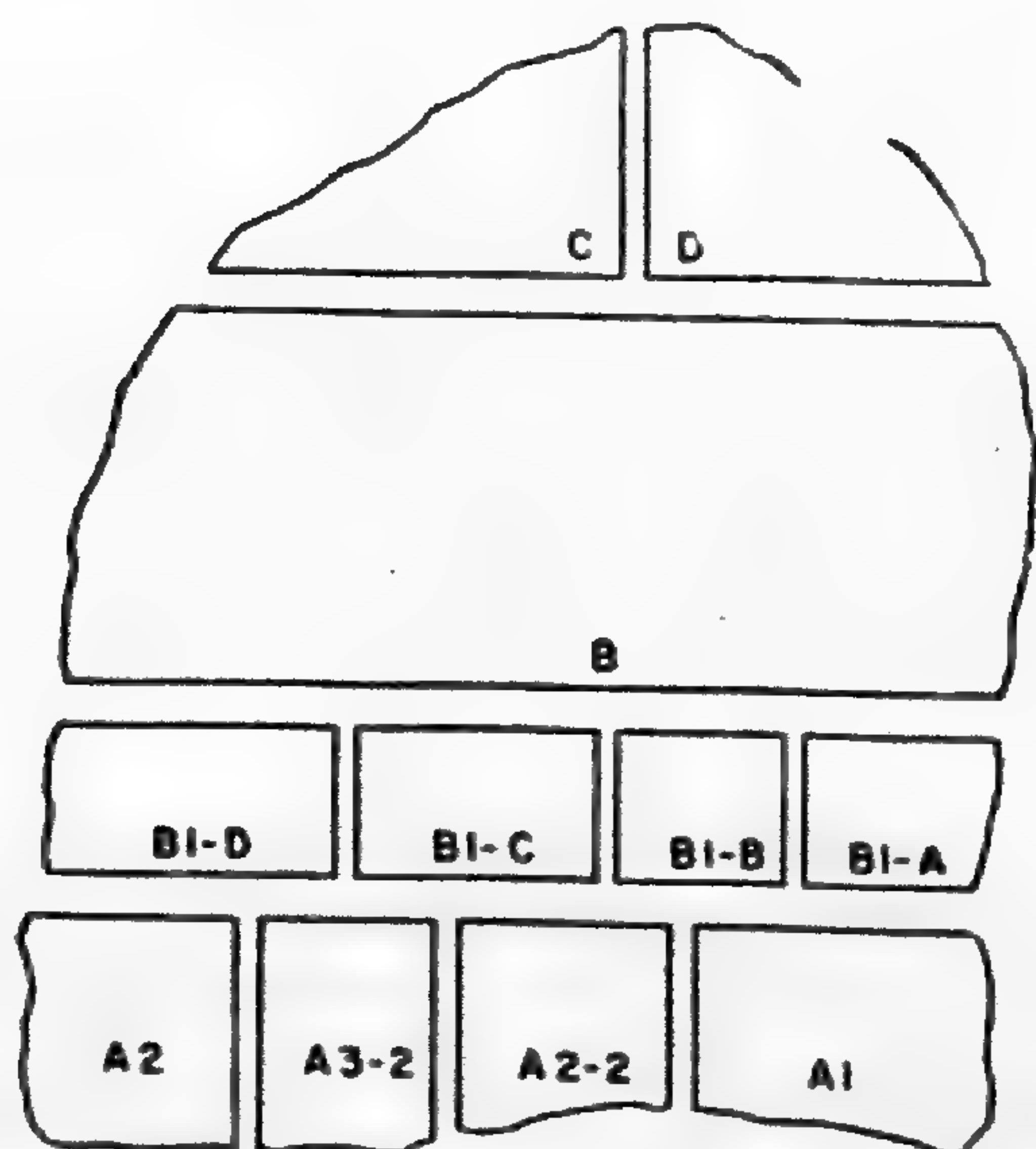
The reader will perhaps agree, if from only a casual glance at the illustrations, that a few additional words of introduction may be justified. Our study of this fossil has proven to be a fascinating if somewhat precarious venture; fascinating in that it is anatomically the most unique fossil that has ever come into this laboratory, and precarious in that its affinities remain, at the conclusion of our studies, quite uncertain. Suggestions are offered on later pages concerning its possible position in the plant kingdom, but, quite admittedly, these are speculative although we hope that these speculations may prove to be of some significance.

It was evident from an initial inspection of the fossils that the cellular organization was highly unique, so much so in fact that consideration was given to the possibility that it was of animal origin. However, detailed studies of the cellular structure have left no doubt as to its plant nature, and other botanists who have been kind enough to examine our preparations have agreed on this point.

Description:—

The following description is based on two specimens that were collected several years ago by Mr. Charles B. Read (U. S. Geological Survey) from the New Albany shale at a locality near Boston, Kentucky. We are indebted to Dr. S. H. Mamay, who is in charge of the Geological Survey's Paleozoic plant collections, for kindly placing the two specimens in our hands for study. The specimens and all figured slides are now preserved in the collections of the U. S. National Museum.

Since the two specimens are very nearly identical in size and form and the surfaces revealed, under low magnification, apparently identical anatomical



Text-fig. 1. Longitudinal profile through specimen U.S.N.M. No. 40797, showing surfaces from which thin sections were prepared.



Text-fig. 2. Longitudinal section through the major axis showing the stratified organization of the fossil. Strands are shown in black.

structure, only one (No. 40797) was used in the preparation of thin sections. Later it proved to be necessary to make a longitudinal cut through the second specimen (No. 40798) and a study of this left no doubt as to the validity of the original supposition that both represent the same species.

The specimens are conical (pl. 4, fig. 1) being about 12 cm. tall, and the diameters of the more or less oval base measure approximately 5.5 by 11.5 cm. Externally the specimens are of a light grayish color, irregularly but not deeply pitted. The irregularly broken aspect of their basal structure suggests that we are dealing with the terminal portion of a trunk or branch of some sort. It may be noted, however, that the horizontal orientation of the supposedly conducting tissue offers some reason to believe that the specimens represent complete or nearly complete plants; this possibility will be discussed on a later page.

Text-fig. 1 presents in profile the plan that was followed in studying specimen No. 40797. Numerous transverse and longitudinal sections were prepared from the A, B, C and D blocks, sufficient to insure a representative coverage of the internal structure.

Although the preservation of the specimens is excellent the original plant material has been highly replaced by phosphate of the calcium-magnesium group. This lack of a sufficient mineral-organic differential, combined with the fact that the specimens are rather soft and porous, prevented the use of the peel technique. No difficulty was encountered, however, in preparing ground thin sections. The blocks to be sectioned were allowed to stand in melted resin for a few minutes before affixing to the slide. The only particular caution found to be necessary was very careful grinding in the last stages due to the softness of the petrification.

The general organization of the fossil, which has been given the new generic name *Crocalophyton* is shown diagrammatically in text-figs. 2 and 3. The specimens are composed of but two tissues, one consisting of ray-like strands made up of transversely elongated cells, the strands being enclosed in a thick-walled, nearly isodiametric parenchyma. Whether the term parenchyma is appropriate may be questioned; it is at least as fitting as any that we are aware of. The strands are shown in black in both figures. Text-fig. 3 is taken from the lower surface of the B1 block. The figure was prepared from four transverse sections taken from B1A, B1B, B1C and B1D as shown in text-fig. 1. After each section was photographed, the strands were inked; the four photos were then pasted together and a tracing prepared of the entire cross-section. Text-fig. 2 is a diagram of the arrangement of the same tissue system in a median longitudinal surface; this was prepared from a free-hand sketch of the surface as it appeared under a binocular microscope. It may be noted that these figures are intended to show the approximate organization of the larger strands and that the photos should be relied upon for a precise portrayal of their structure and pattern of organization.



Text-fig. 3. General organization of the strands in transverse section prepared from the basal surface of the B 1 block.

The Strands:—

The term *strand* is applied to the highly unique ray-like tissue system of the fossil. The cells composing the strands are transversely elongate and pitted; they are presumed to have functioned as a radially conducting system and are tentatively thought to be a primitive tracheidal or sub-tracheidal cell type.

In their organization the strands, as shown in text-fig. 3, tend to radiate from the central part of the specimen toward the periphery; this is, however, only a very general tendency. It will help to clarify the nature of this curious tissue if we glance next at fig. 3, which is a photograph of a representative portion of the cross-section. It shows an area of approximately 1.0×1.5 cm. considerably enlarged. A comparison of this with text-fig. 3 reveals the fact that the latter does not include the numerous smaller strands that occur in many parts of the specimen.

There are few strand terminations in the central part of the fossil although occasionally the smaller ones end blindly. They form for the most part a continuous and highly complex anastomosing system; a few continue to the extreme periphery of the fossil and some end abruptly within a few millimeters of the periphery.

The strands vary from one to nine cells wide and are vertically elongate sheet or ray-like structures. One must, as in the case of wood rays, observe tangential and radial sections in order to acquire an understanding of their 3-dimensional structure. While they present a superficial similarity to the wood rays of a conifer or dicotyledon it is evident from text-fig. 3 and fig. 3 that they are by no means comparably oriented.

Referring to fig. 3 (pl. 4) it will be noted that two lines have been drawn in the lower right portion of the photo. When a longitudinal section is prepared in the "A-A" plane (referred to as *tangential*) the rays appear as shown in fig. 4 (an

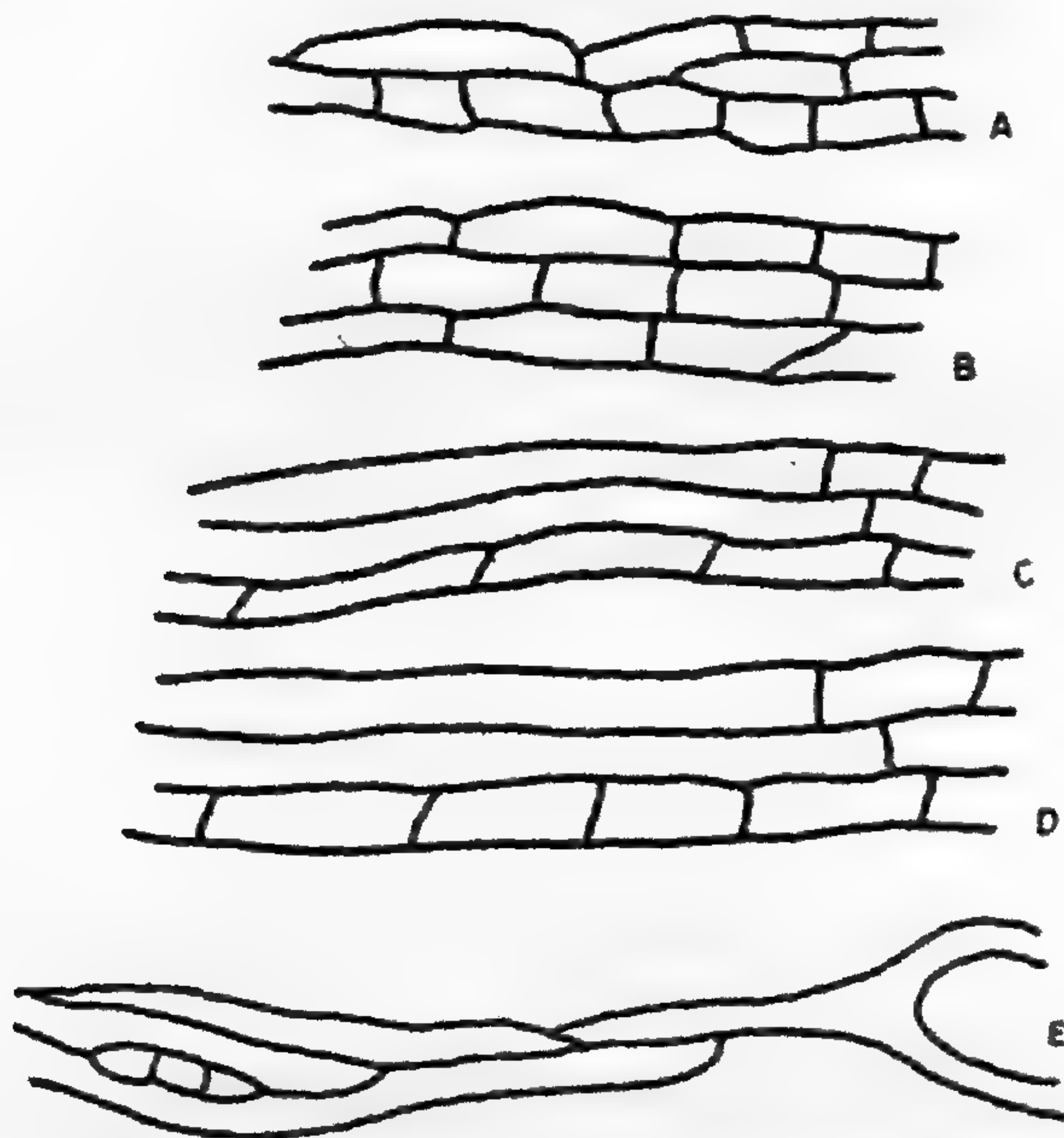
appreciably higher magnification than fig. 3); and longitudinal sections prepared in the "B-B" plane (referred to as *radial*) reveal the rays as shown in fig. 5.

The strands are about 1 cm. high and, as shown in the longitudinal profile (text-fig. 2), they are distinctly stratified. Thus a transverse section taken between the strand areas will reveal no strands. Most of them terminate blindly although a few continue to the periphery of the specimen (text-fig. 3). The tortuous pattern of the strands is emphasized in fig. 2 (and parts of fig. 3) where they present a circular pattern in transverse view.

There is no externally delimiting tissue. The only evidence which suggests that the original surface of the fossil is intact is the close similarity of the two specimens. It is of course possible that some outer tissue or tissues was lost prior to fossilization.

Detailed Structure of the Strands:—

Any transverse section (figs. 3, 6, 7) clearly reveals the variation in the width of the strands which may take place within a few millimeters due to the anastomosing pattern of this tissue and to the frequent intercalation of parenchyma cells.

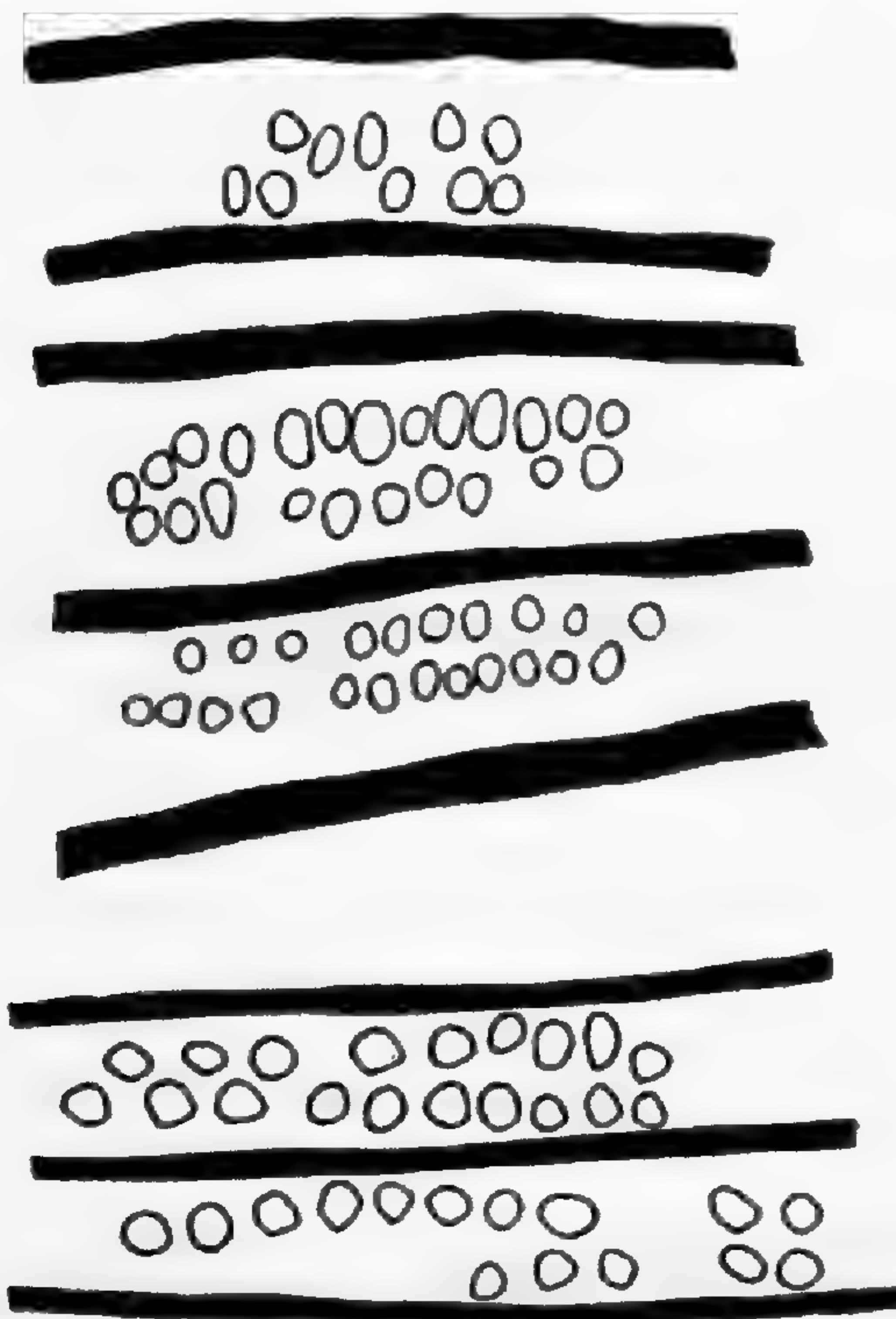


Text-fig. 4. Representative portions from several strands showing shape of strand cells.

One of the most striking characteristics of the strands is the organization of the cells in very nearly perfect vertical rows; this is clearly shown in tangential sections (fig. 4). The cells are transversely elongate, their length appearing to be extremely variable. In tangential view the strand cells are approximately square, being $38\ \mu$ in diameter, while their length, as observed in cross-section (figs. 6, 7), varies between 105 and $230\ \mu$. Some cells, however, have been followed for a considerably greater distance without any evidence of terminations, but where they have been observed they are for the most part transverse. Representative portions of strands are shown in text-fig. 4 where figures A, B and E were drawn

from strands in transverse section and figures C and D from radial sections. While some of the cells possess a tapering end, transverse or only slightly oblique end walls are more usual.

The pitting in the strand cells is particularly interesting. In our initial suite of slides many of the cells displayed obscure striations that were suggestive of some sort of wall sculpturing but it was not until several radial sections were examined with considerable care that clearly defined pits were found. Knowing then what to look for they were found in several slides and we are reasonably confident that the pitting is uniform on both the transverse and radial walls of most or all of the strand cells. In fig. 5a and 5b are shown portions of two particularly well-preserved strand cells in radial view, and the structures which are interpreted as pits appear in two rows wherever they have been observed with clarity. Text-fig. 5 shows pitting in cells from two selected areas. No indication



Text-fig. 5. Pitting in the "radial" walls of the strand cells.

of a border has been noted and the slightly angular outline renders them somewhat distinct from the bordered pits of most vascular plants.

The Parenchyma:—

The only cell type other than the strand cells is the tissue enclosing the strand cells which has been referred to as parenchyma. This consists of cells which are variable only within rather narrow limits and are for the most part isodiametric; rarely are these cells more than twice as long as broad. A representative portion of the parenchyma is shown in fig. 10. The transverse diameter of the parenchyma cells (fig. 10), based on measurements of 140 cells, was found to vary between

45 and 122 μ , with an average of 80 μ ; in longitudinal view (fig. 9) their length, based on measurements of 70 cells, varies from 52 to 165 μ , with an average of 100 μ .

The above figures are based on what is termed, as a matter of convenience, "ordinary" parenchyma, referring to the relatively large areas where the parenchyma is not associated intimately with the strands (fig. 3) or with the purely parenchymatous "inter-strand" portions of the specimen (text-fig. 2). The parenchyma between closely associated strands consists of cells that are slightly elongated vertically and arranged in regular rows, assuming an organization comparable with that of the strand cells. Fig. 11 shows a representative portion of such parenchyma between two strands appearing at the extreme left and right edges of the photo. Parenchyma cells in such areas also may show a tendency to be elongated transversely; this is evident between some of the strands illustrated in fig. 3.

Aside from these structural variations, which certainly are not extreme when compared with the generally bizarre characteristics of the fossil, there is no evidence to suggest any appreciable differences in the functional nature of the tissue.

The walls of the parenchyma cells are rather thick, being approximately 6–7 μ . This character may appear exaggerated due to the difficulty of distinguishing, in the photos, between the actual cell wall and the mineral layer in the periphery of the lumen.

Although we have stated that the parenchyma and strands constitute the only two cell types, one other structure may possibly be distinct. It may be noted that all of the photos which include any appreciable quantity of the fossil (figs. 3, 4, 8) display open areas or apparent breaks. In a very few instances we have observed structures which suggest that some sort of secretory areas may be present. It is apparent, for example in fig. 12, that the central cells are in an advanced stage of disintegration but whether this cavity is a secretory structure or simply decay cannot be determined for sure. In only two or three cases we have observed that the parenchyma cells are radially aligned (fig. 13) in such areas. These are so few that it is problematical as to whether any significance can be attached to them.

The Ontogeny of Crocalophyton:—

The arrangement of the strand cells and closely associated parenchyma in very nearly perfect vertical rows (figs. 4, 11) seems to imply meristematic activity of some sort. Judging from the characteristic alignment of these cells they were formed by an apical meristem which laid down, successively, the strand and inter-strand layers or, at an early stage in the plant's development, several meristematic areas were differentiated. Whether the strands may be termed "xylary" is certainly debatable. The cells are perhaps best termed "pre-tracheidal"; they are elongate and pitted and probably served as conducting elements but the organization and orientation of the strands can only be said to be unique.

If the argument presented in Part 2 is in any way valid the organization of the fossil is not as surprising as may at first appear. Meristematic activities are perhaps

more varied in plants than is generally realized, and it is more than likely that the algae, from which we suppose land vascular plants arose, experimented rather widely in this way and in some cases succeeded.

Without necessarily implying a brown algal ancestry for any of the dominant pteridophytic groups of the Devonian it is difficult to study living representatives, such as *Pterygophora* with its stipe of radially aligned cells, "annual rings," and its trumpet cells (Smith, 1939), without visualizing tendencies that were used to advantage in the creation of a land flora.

With reference to the habit of land vascular plants it is evident that xylary systems evolved along many different lines. Of particular interest here is *Schizopodium davidi* (Harris, 1929) from the Devonian of Australia. It is described as having an outer wood zone "intermediate between primary and secondary wood", the tracheids being cubical, vertically elongate, radially elongate or tangentially elongate, and apparently not formed by a clearly defined cambial meristem. This "outer xylem" may be considered a fumbling attempt (probably one of many) of the plant to produce secondary wood. *Crocalophyton* may be looked upon as a plant in which a unique, and apparently unsuccessful, mode of meristematic activity made its appearance. It is perhaps most aptly summarized in the words of one botanist who examined our illustrations, as a "kind of foolish experiment" that was involved in the evolution of land plants.

*Crocalophyton readi*¹ gen. et sp. nov.

Diagnosis of the Genus and Type Species: Conical-shaped structure, about 12 cm. tall with a roughly oval base measuring approximately 5.5×11.5 cm.; stratified in a plane perpendicular to the long axis and consisting of strand-parenchyma bands alternating with parenchyma bands; strands about 1 cm. high, generally radiating from the center but forming a highly irregular system frequently branching and anastomosing and contorted to the extent of forming a loop, or series of loops, 1-9 cells wide (transverse), with the cells arranged in vertical rows; strand cells horizontally elongated with mostly transverse end walls and two rows of apparently simple pits in the longitudinal walls.

Type specimen: United States National Museum, No. 40797.

Locality: near Boston, Kentucky.

Horizon: New Albany shale; Upper Devonian or lowermost Mississippian.

Affinities: On the basis of our own observations and the opinions of specialists familiar with the various cryptogamic groups, *Crocalophyton* shows no evident relationship to any known thallophyte, bryophyte or pteridophyte. Since its affin-

¹ On the assumption that this was a plant that lived in a habitat transitional between strictly aquatic or dry land, the first syllable of the generic name is taken from the Greek *krokale*, meaning beach or seashore; the specific name is in recognition of Charles B. Read's studies of the New Albany shale plants.

ities are so very vague we have felt that nothing is to be gained at the moment by setting up any new taxon such as a family or order. A more detailed consideration of the possible relationships of the fossil is included in Part 2.

PART 2. SOME COMMENTS ON THE ORIGIN OF LAND VASCULAR PLANTS
AND THE TAXONOMIC POSITION OF CROCALOPHYTON

HENRY N. ANDREWS

In his introduction to a consideration of the problems of Jurassic paleobotany Harris (1947) made the following comment:

Most of the "problems" of paleobotany are those questions which we feel we would like to be able to answer but cannot because our knowledge is incomplete. Such problems are often ephemeral. In time some are answered; some are left aside by progress because they cease to be interesting, or are later realized to be meaningless;

I would supplement this with a paleobotanical proverb that has been attributed to D. H. Scott, although most paleobotanists must have felt at one time or another, that: "fossil plants frequently create more problems than they solve". This is not intended as a facetious comment; it points to the great complexity and diversity of organization that existed in many groups and we are forcefully reminded on occasion of the necessity of altering our concepts of the lines of racial origin and development within a group.

The problem of the origin of vascular plants has been with us for a long time; it is not one of the ephemeral ones and if it is solved, at least in part, it will have proved to have been a multi-faceted problem involving development along several (or many) morphological lines. Many of us have become accustomed to look upon *Rhynia* as *the* primitive land plant; there is now concrete evidence to suggest that it is *a* primitive vascular plant representing a particular line of pteridophytic evolution. In the following pages I should like to discuss what seems to me to be the nature of the problem; this is essentially a review although it may possibly assist in clarifying the issues that are involved. The discussion is also aimed specifically at the question as to just why *Crocalophyton* does not conform to any taxonomic category in the plant kingdom.

The structure of *Crocalophyton* is quite unlike that of any known alga. The possibility that it might be a member of the Phaeophyta was considered, but the organization of the strands could be correlated in no way with the anatomy of any brown alga. Several competent algologists have examined the illustrations and have readily agreed that the plant has no place in the algae. As to the vascular cryptogams there is equally little to choose from. *Crocalophyton* is unique in the ray-like organization of the strands with their radially elongated, pitted cells arranged in vertical rows. The pits show no evidence of a border, and the shape of the cells is not closely comparable with that of a tracheid.

Thus, lacking any clues that might suggest affinities with a known group of plants it can be considered only on its own merits.

On the supposition that the strands constitute a conducting tissue of sorts a guess may be made as to the plant's mode of life. The stratification of the strands, being separated by rather broad bands of distinctly non-conducting tissue (the parenchyma), combined with the radial elongation of the strand cells, would seem to imply that whatever transport capacity the strands served was primarily transverse rather than longitudinal. It is also unlikely that such a plant could have attained any great height if it existed in a strict land habitat. If we next assume that it lived submerged at a depth of as much as several fathoms, as do some of the Phaeophyta, the trunk might have attained a considerable length but in such a habitat it is difficult to understand why so profusely developed a conducting system was needed. Since plants do seemingly strange things that do not always conform with our understanding of their "needs", this possibility need not be entirely ruled out.

If we postulate next an intermediate habitat, approximately in the tidal zone,² a possible case for the strands may be made. A relatively short but stout trunk attached to the rocks between low and high tide marks, and perhaps even somewhat beyond the latter, lacking a root system or any other specialized organ of water intake, would necessarily have to depend upon the absorption of water by the surface of the trunk. Assuming a fairly strong absorption capacity for the exterior surface the strand system could have readily conducted the water throughout the trunk.

The assumption that *Crocophyton* is a primitive semi-land plant, yet can be assigned to no living or fossil group, would seem to call for further explanation. Two general problems may have some real bearing on the subject. The first is the gap that exists between the earliest land vascular plants and the algae from which they are presumed to have evolved. The second, and I believe correlative, problem is the evolutionary pattern that exists in any major group of plants. Briefly, the concept that I wish to explore is that any large group (lycopods, articulates, "ferns", psilophytes, etc.) is highly polyphyletic and the transitional members between it and the group(s) above it, if it so evolved, may be expected to be correspondingly varied.

As a starting point, a few comments might be made on the origin of the algae as well as their pre-Paleozoic and early Paleozoic record. The earliest record of structurally preserved thallophytes is that reported by Tyler and Barghoorn (1954) wherein they describe fossils that are tentatively assigned to the blue green algae and "simple fungi" from rocks in southern Ontario that are dated as being in the vicinity of 1300 million years and possibly much older. These authors note that, "Since the pre-Cambrian flora with which we are dealing comes from near the base of the Gunflint formation, it seems likely that age may approach 2 billion years."

² It has been called to my attention that the present discussion implies an origin of land vascular plants from marine algae. I wish to acknowledge this criticism and indicate that the evolution of vascular plants from plants of fresh water habitats or waters of varying salinity is not intentionally precluded.

Another recent contribution suggests an even greater age for the algae. In 1941 Macgregor described supposed algal remains from Rhodesia in rocks which have been dated as "at least 2,600 million years" and possibly in excess of 2,700 million years. Since they are not structurally preserved I feel that a considerable element of doubt surrounds these Rhodesian algae; so far as I am aware, the Tyler and Barghoorn report gives us the oldest authentic date of a structurally preserved plant on the earth.

Before returning to the algae, for the purpose of my argument, a few words on the earliest records of vascular plants will be interpolated here. The earliest unquestioned record of such a flora is the mid-Silurian one (*Baragwanathia*, etc.) described by Cookson and Lang from Australia. It is evident that these plants were separated by a broad gulf of evolution from any algal ancestors.

Recently Krishtofovich (1953) has reported a supposed lycopodiaceous plant from the Middle Cambrian of the Aldan Mountain range in Siberia. The plant remains were associated with trilobites (believed to correspond to the *Paradoxides forchhammeri* zone of Western Europe) and according to the author, "Consequently the geological age of the find constitutes no doubt whatever."³

Krishtofovich's *Aldanophyton antiquissimum* is represented by shoots up to 13 mm. wide and 8.5 cm. long which are covered with microphyllous leaves up to 9 mm. in length. "In places a thin rod-conducting bundle may be traced as far as the base of the enations (leaves)". Comparison is drawn with other early lycopods such as *Drepanophycus* and *Baragwanathia* although sporangia were not found in *Aldanophyton*.

There have been several accounts of spores from the Cambrian which are purported to be those of land vascular plants. Several Indian investigators (Jacob et al., 1952, '53a, '53b) have described spores and wood fragments from the Middle and Upper Cambrian of Kashmir, Spiti, and other Indian localities. As many as 43 different spore types are recorded including those referable to Equisetalean plants, "other primitive pteridophytes" and the Pteridospermae. These authors are insistent that their preparations are free of contamination and, although I am prepared to accept the existence of vascular plants in pre-Silurian times, the occurrence of the Pteridospermae in the Cambrian is a matter that will require more substantial proof. Naumova (1949) reports a considerable assemblage of spores from the lower Cambrian blue clay of the Estonia-Latvia-Lithuania area (details of locality are not given) which are presumed to represent bryophytes and pteridophytes.

Since the approximate date at which vascular plants first appeared has some bearing on this discussion the high degree of complexity that already existed in the lowermost Mississippian and Devonian seems significant.

³ Although I have had access to the original publication it is in Russian with no summary in any other language; I am indebted to Dr. Harlan P. Banks, who kindly supplied me with an English translation.

Largely as a result of Florin's important contributions, we are particularly well informed on the evolution of the cordaite-conifer line and certain associated groups. With reference to the origin of this assemblage Florin (1949) notes:

The Ginkgoinae, Cordaitinae, Coniferae and Taxinae undoubtedly belong to the same natural plant group of higher order, . . . but they constitute parallel evolutionary lines which probably were already separated from each other in Upper Devonian or Lower Carboniferous times. At all events, a clear differentiation can be seen as far back as the available fossil records go. [pp. 101-102].

Judging from its stem anatomy the well-known and widely distributed Devonian *Callixylon* is in all probability a coniferophyte and possibly a rather highly specialized member of the group; the fact that it was a large forest tree would suggest that the coniferophytes may date back to an earlier period than the Devonian.

It is also pertinent to note the early appearance of heterosporous ferns, specifically *Archaeopteris latifolia* (Arnold, 1939) from the Upper Devonian (possibly upper Chadakoin) of Pennsylvania, and *Stauropteris burntislandica* (Surange, 1952) from the Lower Carboniferous (Calciferous Sandstone series) of Pettycur, Scotland. Just how these plants fit into the general stream of "fern" evolution is problematical but there can be little doubt that they represent the culmination of a long period of evolution of land vascular plants.

It is perhaps not surprising to find that the angiosperms are not to be excluded from this general retrenchment in time of so many major groups. Under the new binomial *Sanmiguelia lewisi*, Brown (1956) has reported leaves from the Dolores formation (Middle to Late Triassic) of Colorado. They are alternate, large, pleated, monocotyledonous, and closely resemble those of a palm. If this apparent relationship is correct *Sanmiguelia* is the earliest angiosperm on record and suggests a Paleozoic origin for the group.

In view of the evidence, direct and indirect, cited above I do not find it difficult to accept land vascular plants in the Cambrian as a possibility or even a probability.

Next to be considered is the status of the algae during the approximate time when plants were becoming established on the land. A few records based on fairly well-preserved plants indicate the presence of several modern groups of algae in the Devonian. These include smaller algae referable to the Chroococcaceae, Ulotrichaceae and Desmidiaceae from the Onondaga chert of New York (Bashnagel, 1942); Charophyta from the Lower Devonian Downtonian beds (Croft, 1952) of west Podolia (borders of Poland and Russia); fossils referable to the brown and red algae from New York (Fry and Banks, 1955); and the remarkable fungi and algae from the Rhynie chert (Kidston and Lang, 1921). There is abundant evidence that such diversity, comparable with that of today, existed long before the Devonian—Fenton (1946); Fenton and Fenton (1939); Johnson (in Smith, 1951); Pia (in Hirmer, 1927); Walcott (1919), and numerous other references cited by them.

The vast period of time that the algae existed prior to the advent of land plants, even assuming their existence in the Cambrian, is somewhat startling. In a

chart⁴ recently prepared by the U. S. Geological Survey the beginning of Cambrian time dates back 520 million years and the mid-Silurian about 340 million years.

Accepting the mid-Silurian "*Baragwanathia flora*" as the oldest authentic record of vascular plants and subtracting this (340 million years) from the figures of Holmes or Tyler and Barghoorn cited above we find the algae existed from 960 to 1360 million years before the advent of land vascular plants. If we accept Krishtofovich's report of a Siberian lycopod from the Cambrian the figures are decreased by another 100 to 200 million years, but we are still faced with the apparent possibility that the algae existed for one billion years before migration to the land was accomplished.

Unless land vascular plants did evolve much earlier than mid-Silurian times, and by "much earlier" I imply at least several hundred million years, the obvious and baffling question is why was the transition from an aquatic to a land habitat so long delayed? This query is not a new one, and I allude to it only to present two theories that may constitute a fresh approach whether or not they contribute to the solution: *One*, that there existed prior to Silurian (or Cambrian?) times environmental conditions that rendered the transition difficult or impossible. *Two*, that there was a great diversity of plant form involved in the transition and that plants of the *Rhynia* type represent a successful arrival in but one of many different lines that made the try.

As to the environmental factor, I have been intrigued with a suggestion by Rachel Carson in "The Sea Around Us".⁵ Assuming a closer proximity of the Moon to the Earth in pre-Paleozoic times she postulates that the action of the tides may have been vastly greater than at present creating a littoral zone, surrounding the oceans, of such turbulence as to render the landward migration impossible. There are obvious difficulties to accepting this as a significant explanation but it is at least thought-provoking.

The second factor mentioned above, namely, the diversity of plant form that may have been involved in the sea-land transition, may have a real bearing on the taxonomic position of *Crocalophyton*.

Evolution in certain major groups, such as the lycopods or articulates, has been a process of extreme polyphyletic once the basic morphology of the group was established. The guess may be hazarded for larger groups, such as the coniferophytes or angiosperms, that they were polyphyletic from the start. The early land plants (excluding clearly defined representatives of the lycopods or articulates) present a highly complex assemblage; some may be justifiably classified as psilophytes while others do not fit with any degree of comfort into any major category and seem to imply a highly polyphyletic origin from the algae.

Few writers of text-books now portray the "family tree" of the plant kingdom

⁴ Prepared from the Report of the National Research Council, Committee on the Measurement of Geologic Time, 1949-50.

⁵ See p. 158 of the original Oxford University Press edition.

as a great central trunk from which secondary branches progressively arise. Such diagrammatic representations of evolution have passed out of favor because the trunk of the tree failed to materialize, and I think it is clear that this failure was simply due to the fact that the trunk never existed. Although I suspect that this thesis could be successfully argued for any major group I will confine myself to plants with which I have some special interest and which bear on the problem of *Crocalophyton*.

It is becoming apparent, even in non-paleobotanical circles, that the term "psilophyte" cannot be defined with any degree of precision. From the seemingly simple (one might say classical) example of *Rhynia* a considerable diversity of morphology is now known; this has been dealt with briefly but effectively by Miss Leclercq (1954). The complexity in stelar anatomy that exists in Devonian and lowermost Mississippian plants is perhaps not so well known. I refer particularly to the stelar pattern in *Rhynia*, *Asteroxylon* and the assemblage of more complicated forms including *Pietzschia*, *Steloxylon*, *Siderella*, *Cladoxylon*, *Xenocladia*, and *Periastron*.

The problem of relationships among certain of these Devonian and Mississippian fossils is a perplexing one, but, since in some stems only anatomy is known while in others our information is more or less limited to the gross morphology, any postulated relationships are obviously tentative. It is, however, instructive to contrast the stelar anatomy of plants of the *Rhynia* type with the more complex polystelic fossils such as *Steloxylon* and *Xenocladia*. The fragment of the stem of *Xenocladia* described by Arnold (1952a) from the Middle Devonian of New York measures approximately 1×5 cm. in cross-section (suggesting a stem of about 10 cm. diameter) and includes more than 40 steles. Several fragmentary specimens of *Steloxylon* have been collected from the New Albany shale, the largest of which are about 3×6 cm. and are composed of several dozens of steles. The contrast between plants of this sort and those possessing slender monostelic stems presents a deep and broad chasm to be spanned by any evolutionary bridge. It is possible that they may have originated from an earlier, indeed much earlier, common land plant ancestor but since there is no evidence to support this it seems at least equally reasonable to postulate separate ancestry prior to establishment of the land habit.

Taking size and form relationships into consideration, if an early land plant were *originally* large we might expect to find *either* a large stelar unit *or* several centers of stelar organization.

Prototaxites is an example of an early (possibly land) plant with longitudinally aligned conducting cells throughout the trunk. This does not in any way imply a brown algal ancestry for the groups that were successful in accommodating themselves to the land habitat, but I believe it does present potentialities for a conducting system wholly different from the *Rhynia* type.

Crocalophyton affords evidence that a plant of large diameter (as compared with the *Rhynia* type) did exist and it apparently possessed an extensive apical

meristem of a somewhat indecisive character. Conducting cells that are "almost tracheids" were formed but in a very irregular fashion and apparently not constantly, as is evinced by the vertical stratification of "vascular" and non-vascular tissues. Briefly, it may be concluded that *Crocalophyton* is an early land plant wholly different from the classical *Rhynia*.

We are accustomed to look upon *Rhynia* as "typical" or as a central type of the psilophytes; at least it seems to occupy this position in most general accounts and texts. I believe it occupies this position chiefly because of the excellence and completeness of the preservation. What we do know to be a fact is that the early vascular plants were, by Devonian times and probably earlier, a highly complex assemblage. It would seem to follow that these plants were highly polyphyletic; they were radiating out in many directions a few of which became definable as lycopods, articulates, coenopterids, etc. There can be no doubt that we have only a fragmentary picture of this polyphyletic plan; discoveries of the future may or may not clarify the path followed by the more successful groups of the Carboniferous but they will certainly add to the complexity of the polyphyleticism that is already evident.

It seems clear that once a distinctive pattern of organization is established it may radiate in many directions, and there may or may not be a conspicuous channel which leads to another basic pattern. It is evident that the articulates and ferns (and I should think to a somewhat lesser degree the lycopods) diversified rapidly in many directions, although it would seem to be more difficult to define what we mean by a fern than an articulate because of a greater polyphyleticism in the former group.

The degree of morphological diversity that has existed in the algae is enormous, and it is very likely that they were highly diversified in pre-Cambrian times. The point, therefore, that I have attempted to lead to is that in all probability several (or many) groups of algae participated in the attempt to conquer the land. May we possibly explain the diversification of morphology and anatomy that exists in the early lycopods, articulates, the "psilophytes", as well as the many that "do not fit" as representing numerous lines of evolution from the algae rather than just three or four? I believe this viewpoint receives support from other "groups" or plants that defy classification. I allude here to fossils such as *Protosalvinia* and *Prototaxites*.

Arnold (1954) notes:

The position of *Protosalvinia furcata* in the plant kingdom is unknown, but it had evolved to a level ^[6] comparable to that of the lower bryophytes. . . . Not being connected with vascular plant evolution, the rise of *Protosalvinia* during Devonian time was a minor episode of nature, one of many attempts to preserve and perpetuate life by meeting adversity through adaptation and adjustment. This attempt was apparently not more than temporarily successful and was inadequate to insure continuity of the particular line. As far as we know *Protosalvinia* gave rise to no other forms and has no descendants. [p. 299].

⁶ I have underlined the word *level*. There is a subtle distinction between classing a plant as a member of the Bryophytes and saying that it has reached that level.

With reference to *Prototaxites*, the relations of this curious plant have recently been reviewed by Arnold (1952b) in a contribution which includes a description of a beautifully preserved new species. Not only is the taxonomic position of *Prototaxites* very much in doubt but its habitat is as well; suggestions of various authors place it anywhere from the deep sea to a land habitat.

As to *Crocalophyton* I can only conclude that it represents a curious effort, one of a great many, in the struggle to evolve a vascular flora. Very possibly it or its immediate descendants reached a dead end; at any rate it has no known contemporaries with which it may be closely compared.

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EXPLANATION OF PLATE

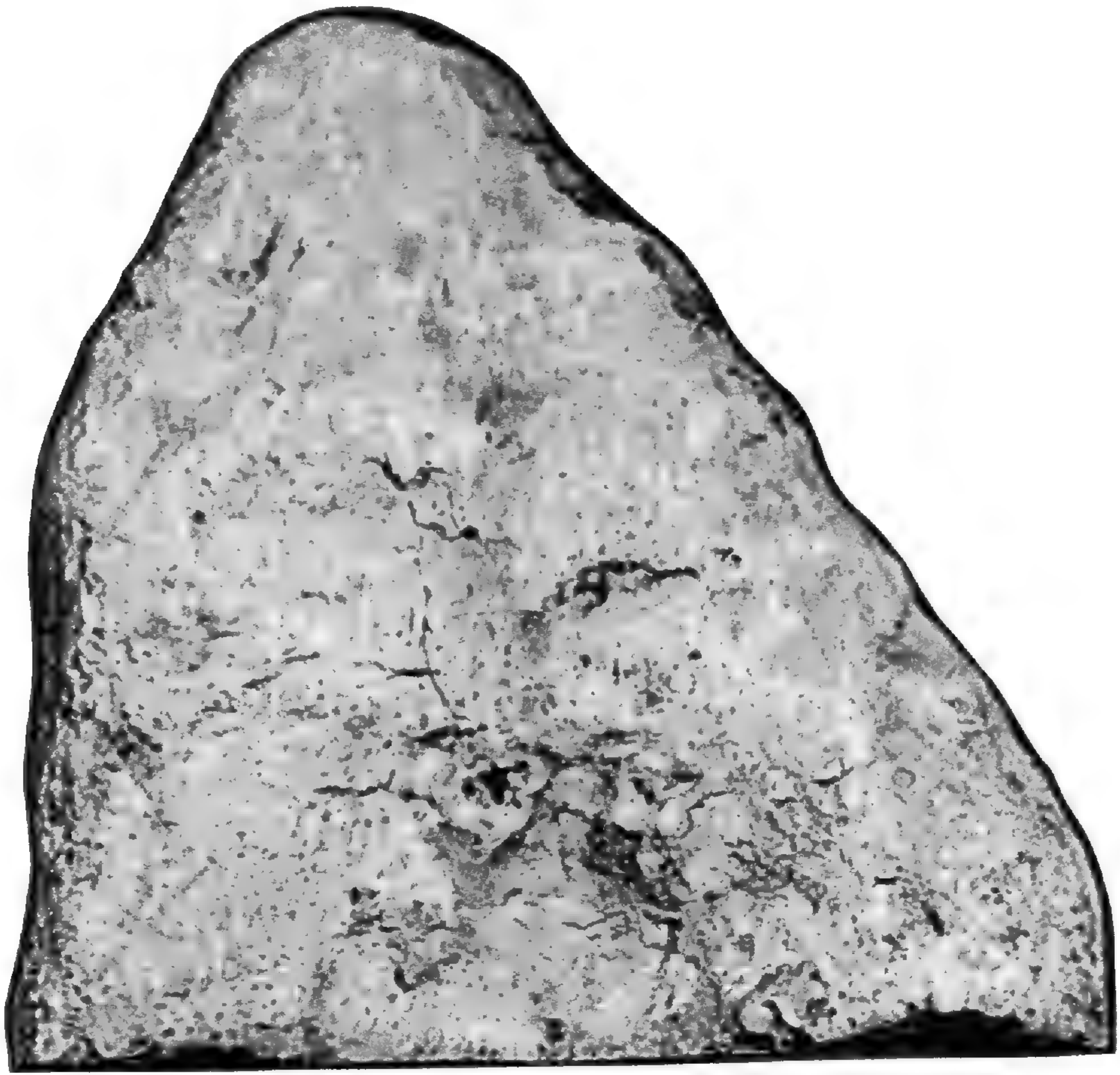
PLATE 4

Crocalophyton readi Andrews and Alt

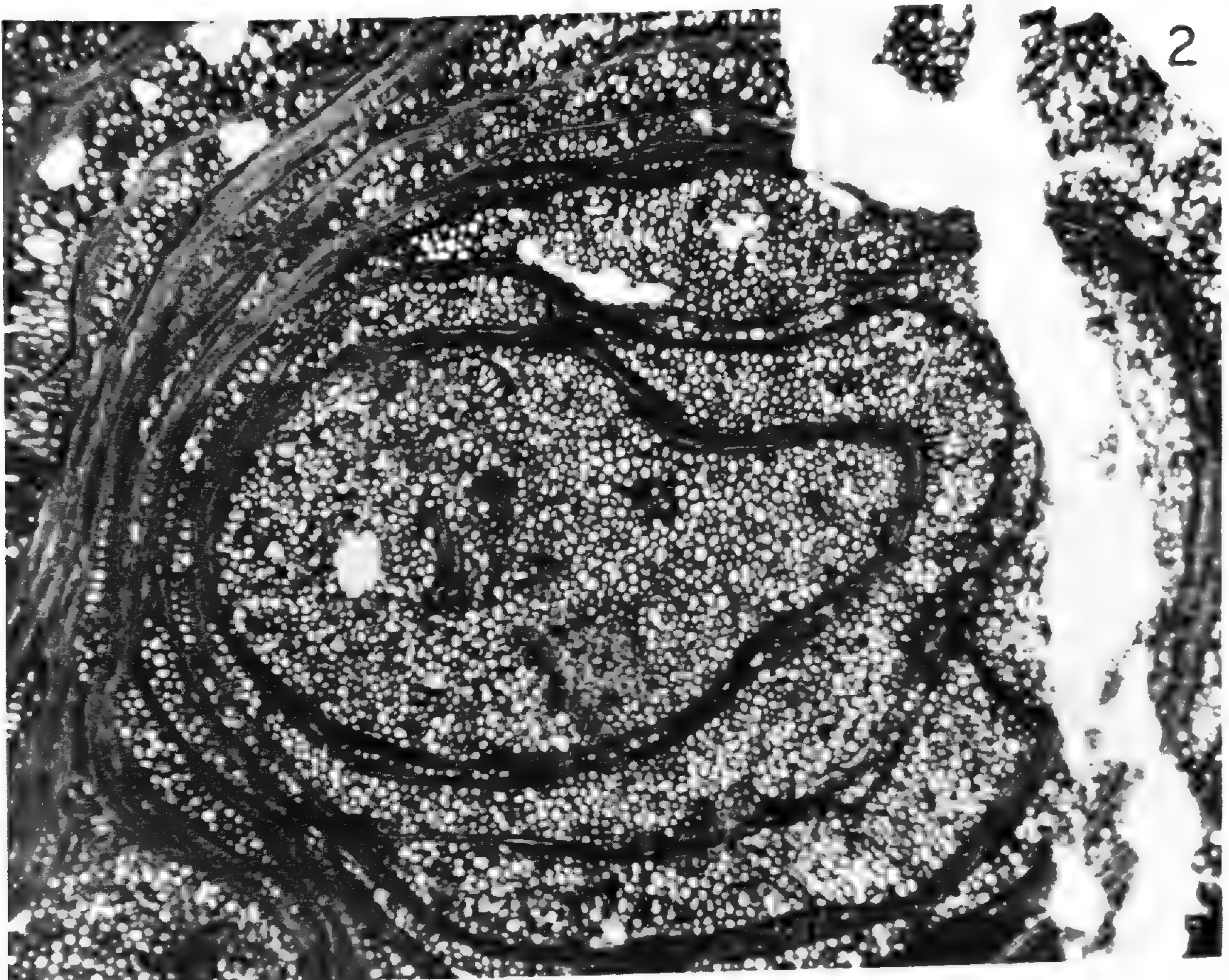
Fig. 1. Specimen No. 40798 (U.S.N.M.), approximately natural size.

Fig. 2. Detail of transverse section showing looped form of strands. 23X. Slide B1C,b1.

NOTE: All figured slides are preserved in the Paleobotanical collections of the United States National Museum. Slide numbers noted herein indicate the position from which they were prepared as indicated in text-fig. 1.

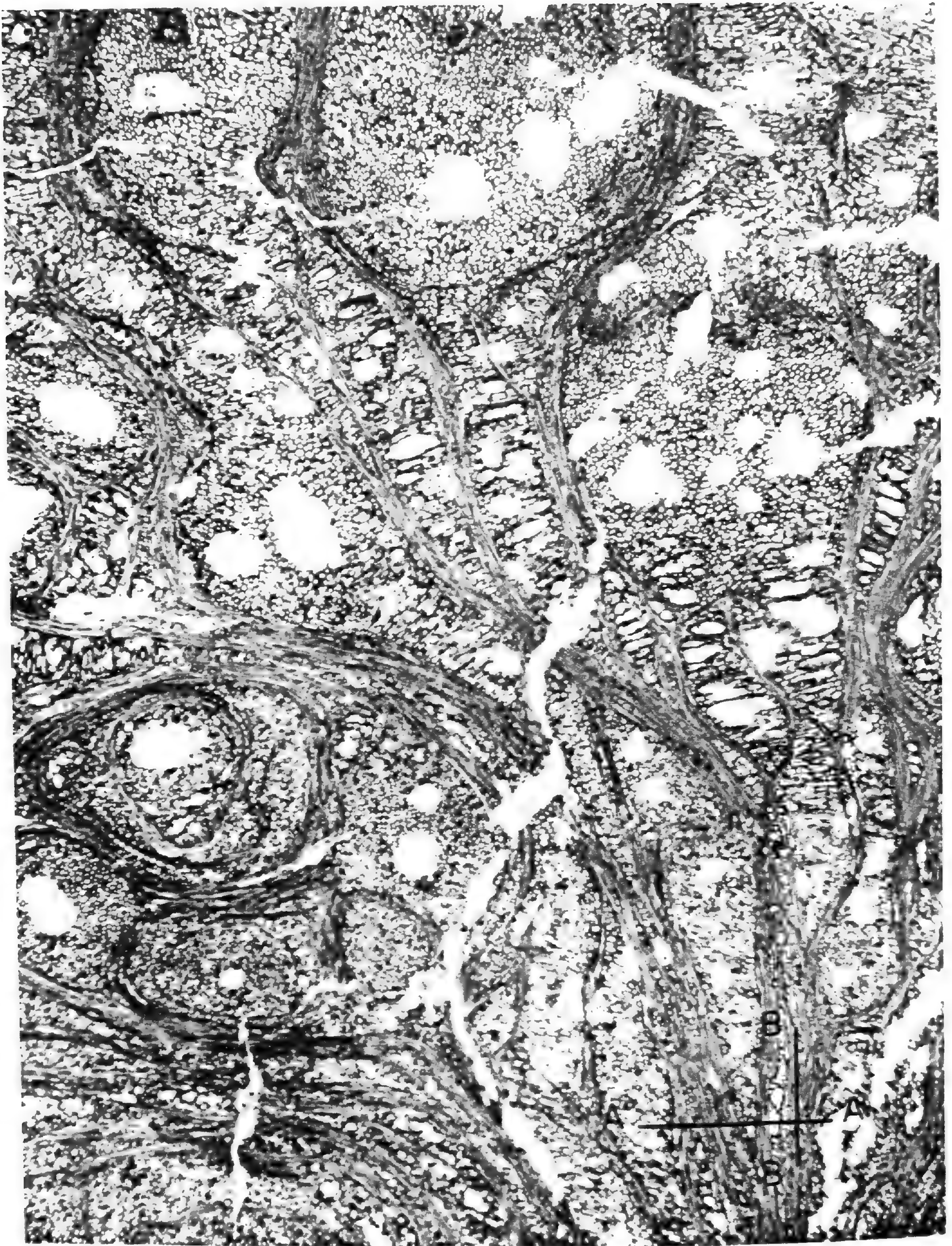


1



2

ANDREWS AND ALT — *CROCALOPHYTON READI*



3

EXPLANATION OF PLATE

PLATE 5

Crocalophyton readi Andrews and Alt

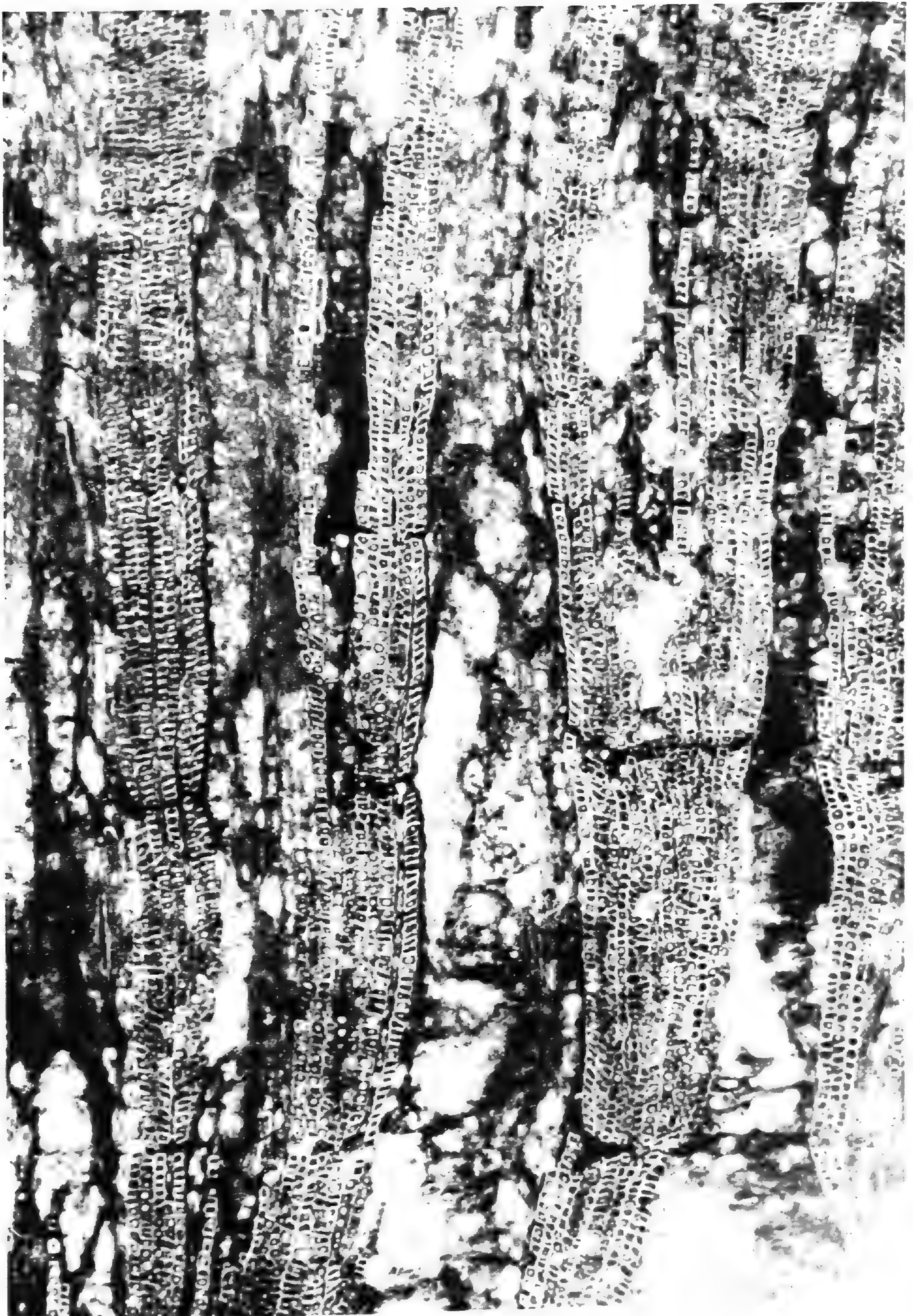
Fig. 3. Transverse view through a representative portion of a strand zone. Line A-A indicates orientation of "tangential" section (see fig. 4); line B-B indicates orientation of "radial" section (see fig. 5). 14X. Slide B1C,b1.

EXPLANATION OF PLATE

PLATE 6

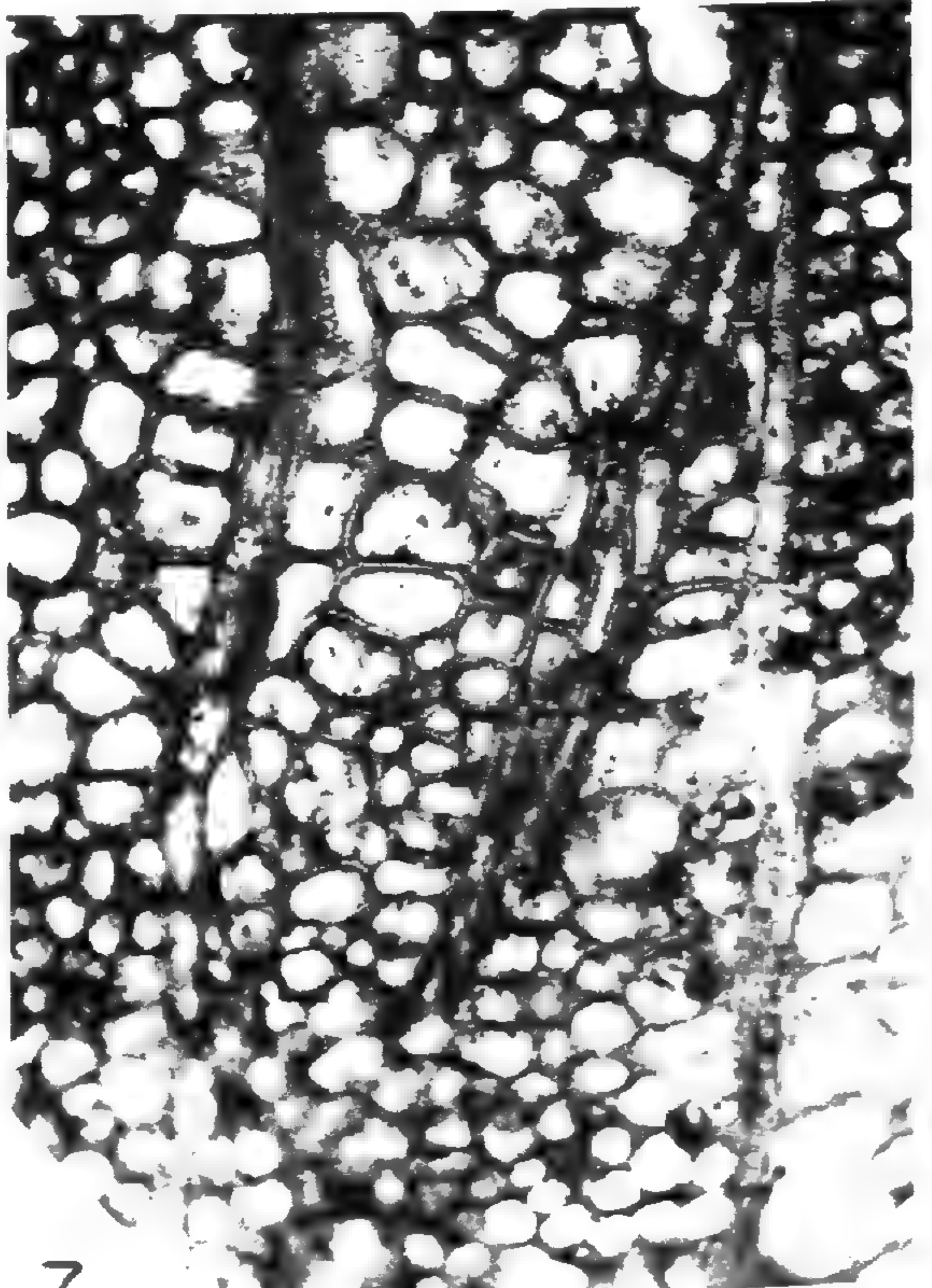
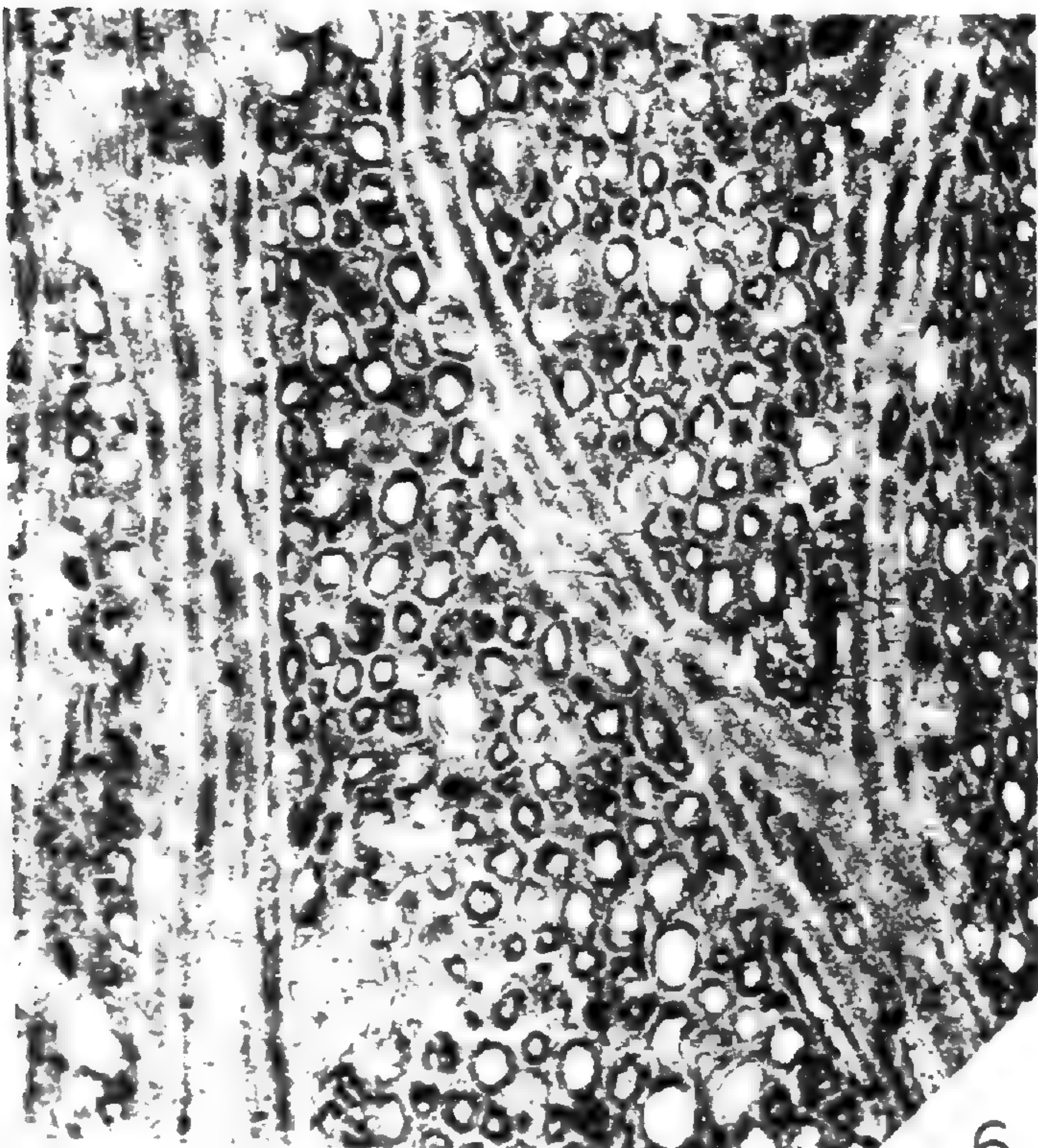
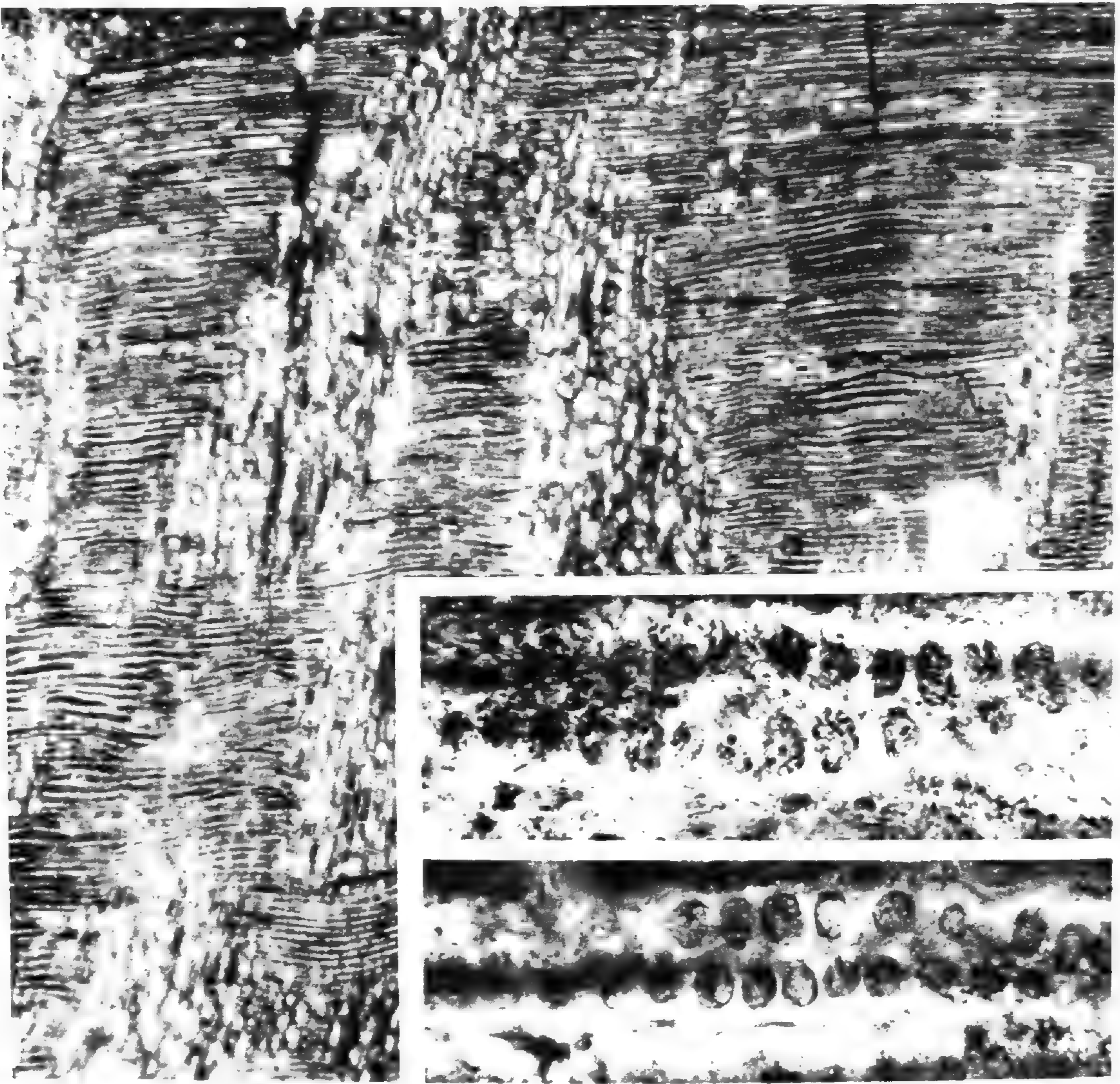
Crocalophyton readi Andrews and Alt

Fig. 4. Strands in tangential view. 40X. Slide A2-2, s2.



4

ANDREWS AND ALT — *CROCALOPHYTON READI*



EXPLANATION OF PLATE

PLATE 7

Crocalophyton readi Andrews and Alt

Fig. 5. Strands in radial view. 32X. Slide A2-1, s1.

Figs. 5A, 5B. Pitting in radial walls of strand cells. About 600X. Slide A2-1, s2.

Figs. 6, 7. Detail of strands in transverse section. 75X: fig. 6, Slide B1-B, b1; fig. 7, Slide A2-2, t1.

EXPLANATION OF PLATE

PLATE 8

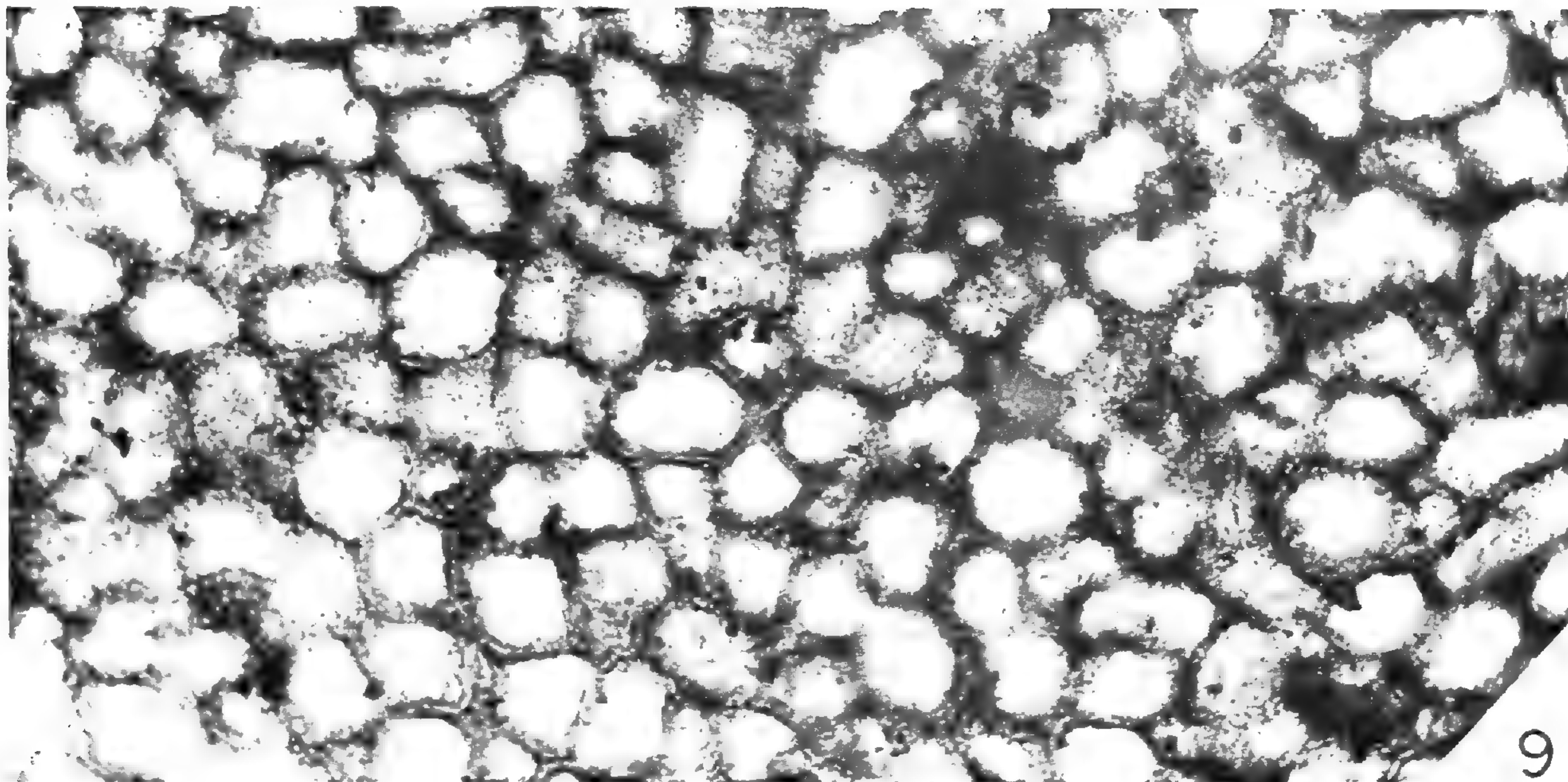
Crocalophyton readi Andrews and Alt

Fig. 8. Longitudinal view showing occasional distortion of the normal "radial" alignment of strands. 34X. Slide A2-2, s2.

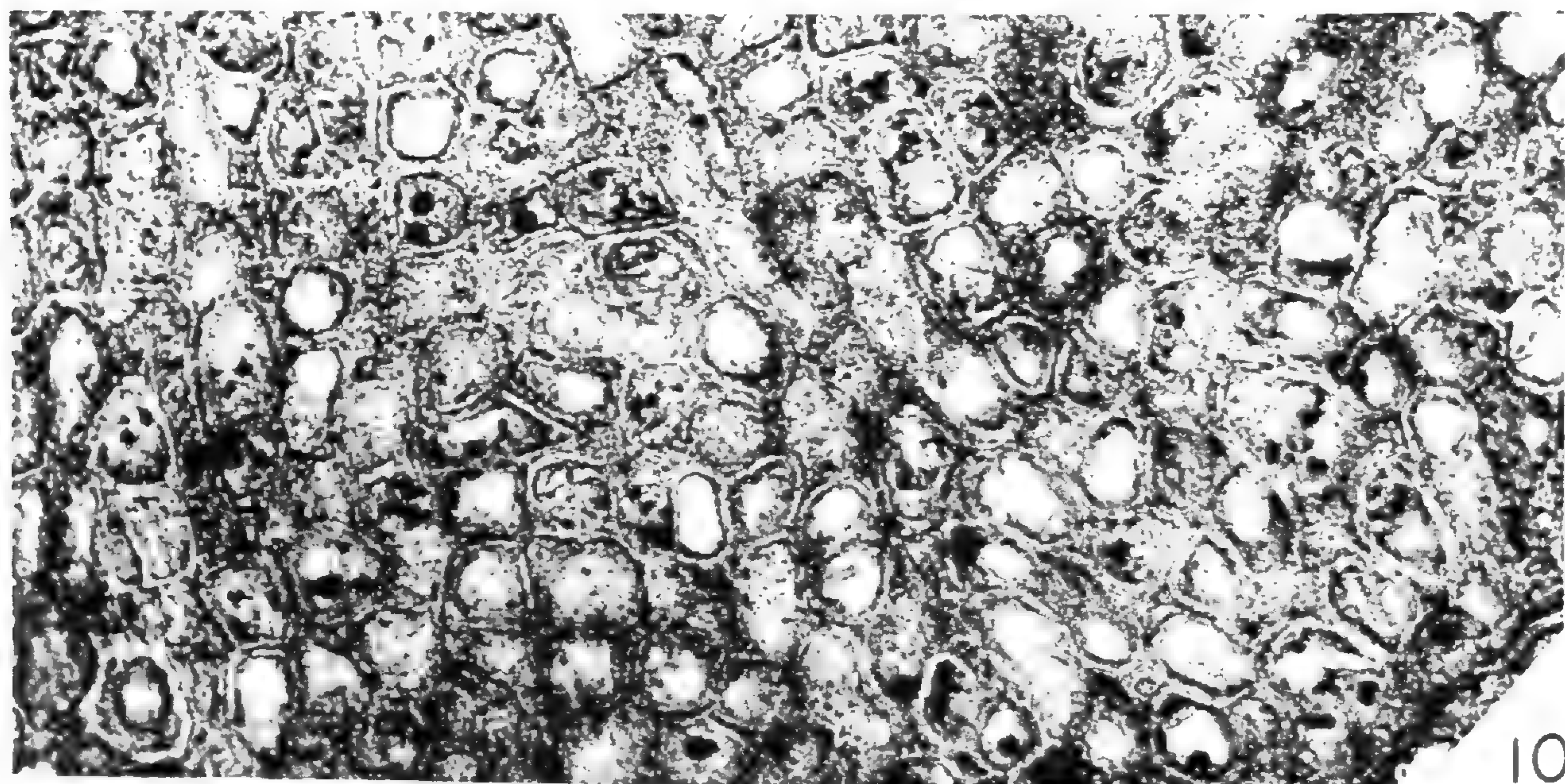


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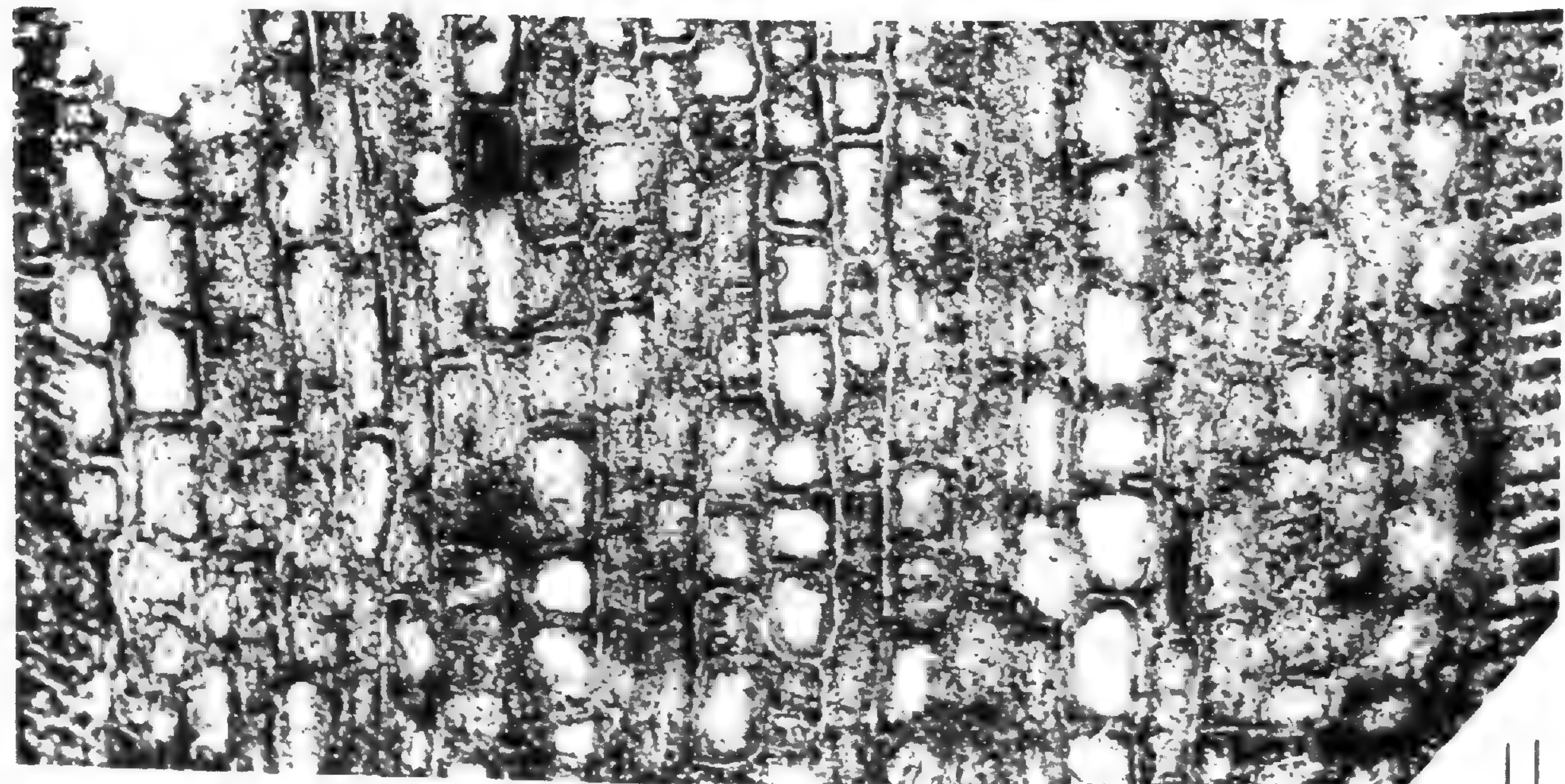
ANDREWS AND ALT — *CROCALOPHYTON READI*



9



10



11

EXPLANATION OF PLATE

PLATE 9

Crocalophyton readi Andrews and Alt

- Fig. 9. Parenchyma in longitudinal section. 100X. Slide A2-2, t2.
Fig. 10. Parenchyma in transverse section. 100X. Slide A2-2, t2.
Fig. 11. Parenchyma associated with strands; tangential section. 100X. Slide Dy, s1.

EXPLANATION OF PLATE

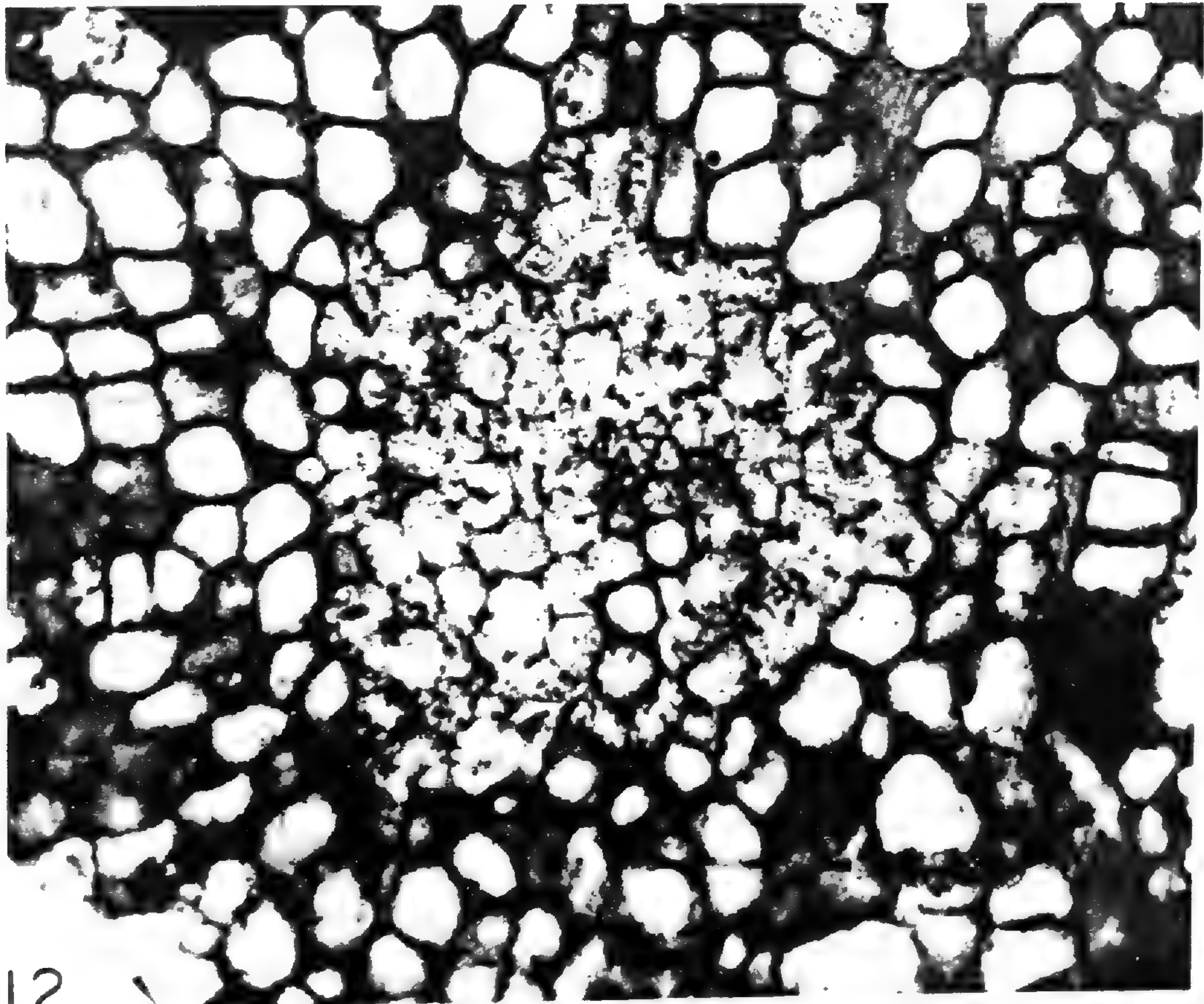
PLATE 10

Crocalophyton readi Andrews and Alt

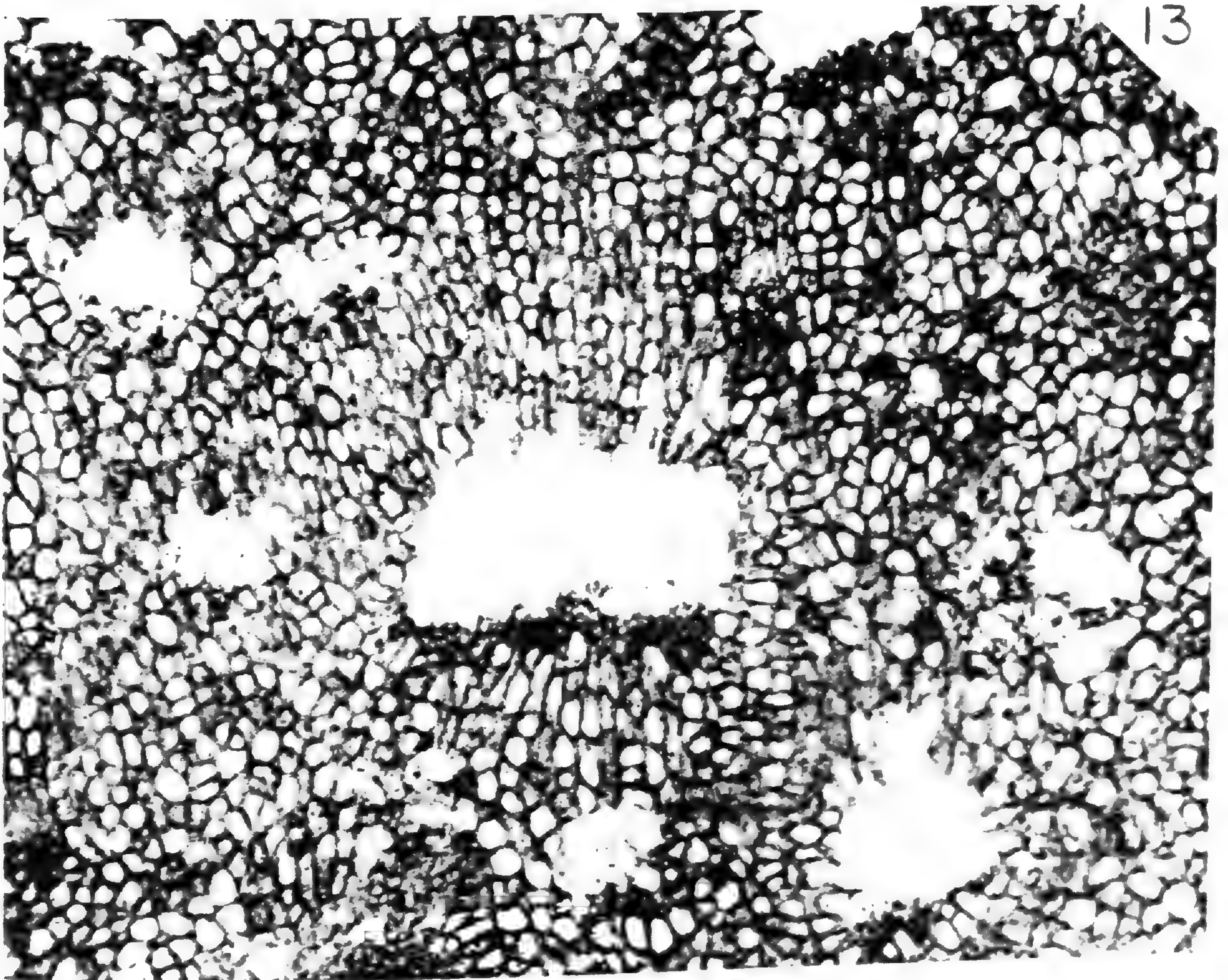
Areas possibly of a secretory nature. For further explanation see text.

Fig. 12. 77X. Slide DY, b1.

Fig. 13. 27X. Slide B1-B, b2.



12



13

A NOTE ON THE NODAL ANATOMY OF *ANKYROPTERIS GLABRA* BAXTER

HENRY N. ANDREWS*

Considerable interest has been centered in the Carboniferous genus *Ankyropteris* since it presents, so far as I am aware, the earliest known instance of axillary branching. A comprehensive understanding of the genus may be gained from the works of Scott (1912), Holden (1930), Read (1938), Baxter (1951) and others cited in these papers. It is the purpose of this note to supplement the description of *A. glabra* Baxter (1951) with particular reference to the nodal anatomy.

The specimen of *A. glabra* described here was found in the same collection of coal balls from which Baxter obtained the type specimen,—the Indiana No. 5 coal about 10 miles north of Booneville, Indiana. This species was delimited from previously described species of *Ankyropteris* on the basis of the lack of multicellular hairs and the origin of the axillary branch from the stem above the point of departure of the leaf trace. When compared with conceivably related species I believe the difference is actually more clear cut. In *A. grayi* Scott, for example, the stele is much more angular, the central mixed pith is more conspicuous, and the trace at the point of departure from the stem stele is triangular, being quite in contrast to the more or less round (in transverse section) trace of *A. glabra*. Similar differences clearly delimit *A. glabra* from *A. corrugata* (Holden, 1930).

On the basis of the type specimen Baxter pointed out that in *A. glabra* the petiole (phyllophore) trace departs from the stem before the axillary stele, the latter remaining attached to the stem stele for another centimeter. In contrast to this, in *A. grayi* a single triangular trace departs from the stem stele and then divides into two, one trace becoming differentiated into the petiole trace and the other into the axillary branch trace.

The specimen under consideration consists of a stem about 12 cm. long bearing the basal portion of two petioles and associated branches. The internodal distance is 7 cm., corresponding to that cited for the type specimen. Since the anatomy of the two nodes differs somewhat from each other as well as from the type specimen it may be convenient to consider them separately.

Node 1.—The node is identified by the departure from the stem stele of a strand or "common trace" (pl. 11, figs. 1, 2) that is of essentially the same organization as the stem stele itself, differing only in its smaller size. It is not until this is distinctly separate (fig. 3) that it shows evidence of differentiating into a leaf trace and an axillary branch stele. In fig. 4 the two are separate, the leaf trace being a slender, tangentially elongated strand and the axillary branch trace being more or less circular in transverse section. The leaf trace next divides into two essentially equal strands one of which passes off to the right, as shown in fig. 5,

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and the other presumably develops into the main petiole strand, although preservation beyond this point is very poor. The significance of this early division of the petiole trace is not clear. It may possibly be interpreted as a dichotomy of the rachis, as is known in certain of the sphenopterid fronds and in *Telangium affine*.

Node 2.—The departure of the common trace at first follows the same pattern described above; that is, it separates from the stem stele *and then* becomes differentiated into an axillary branch stele and petiole trace (fig. 6). The latter, starting as a tangentially elongated bar, develops into the characteristic H-shaped *Ankyropteris* leaf (phyllophore) trace (fig. 7).

It is then apparent that the xylary nodal structure presented by this specimen compares more closely with that described for *A. grayi* Scott than for *A. glabra* Baxter. Since the specimen described here was obtained from the same coal ball collection from which Baxter obtained *A. glabra* and the two compare closely in every other way, there was apparently a certain degree of variation in the nodal anatomy. Since this difference, although of considerable anatomical interest, is not sufficient to warrant a distinct specific entity, it seems desirable to emend Baxter's specific diagnosis:

ANKYROPTERIS GLABRA Baxter, emend. Andrews.

Stem oval in transverse section, approximately 14×9 mm.; stele 5-lobed, consisting of very narrow discontinuous rays of small tracheidal cells surrounded by much larger tracheids. Cortex a narrow inner zone of thick-walled cells and a broad outer zone of thin-walled parenchyma; aphaebiae numerous; surface of plant glabrous. Petiole (phyllophore) trace of the *di-epsilon* type. Axillary branch stele arising either from the stem above the point of departure of the petiole trace or from the division of a common trace.

Origin: Identical with that cited for the type specimen by Baxter (1951, p. 440).

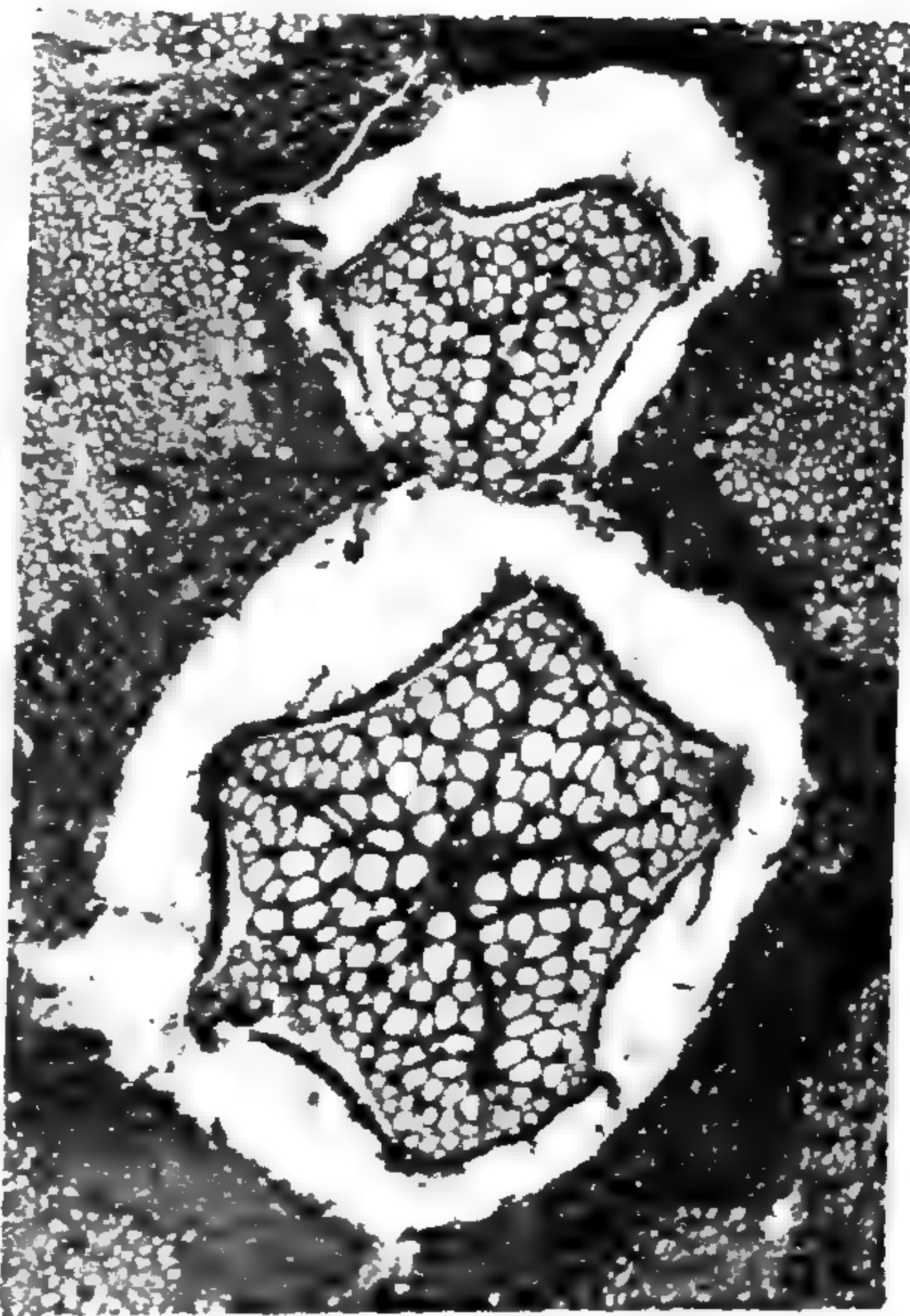
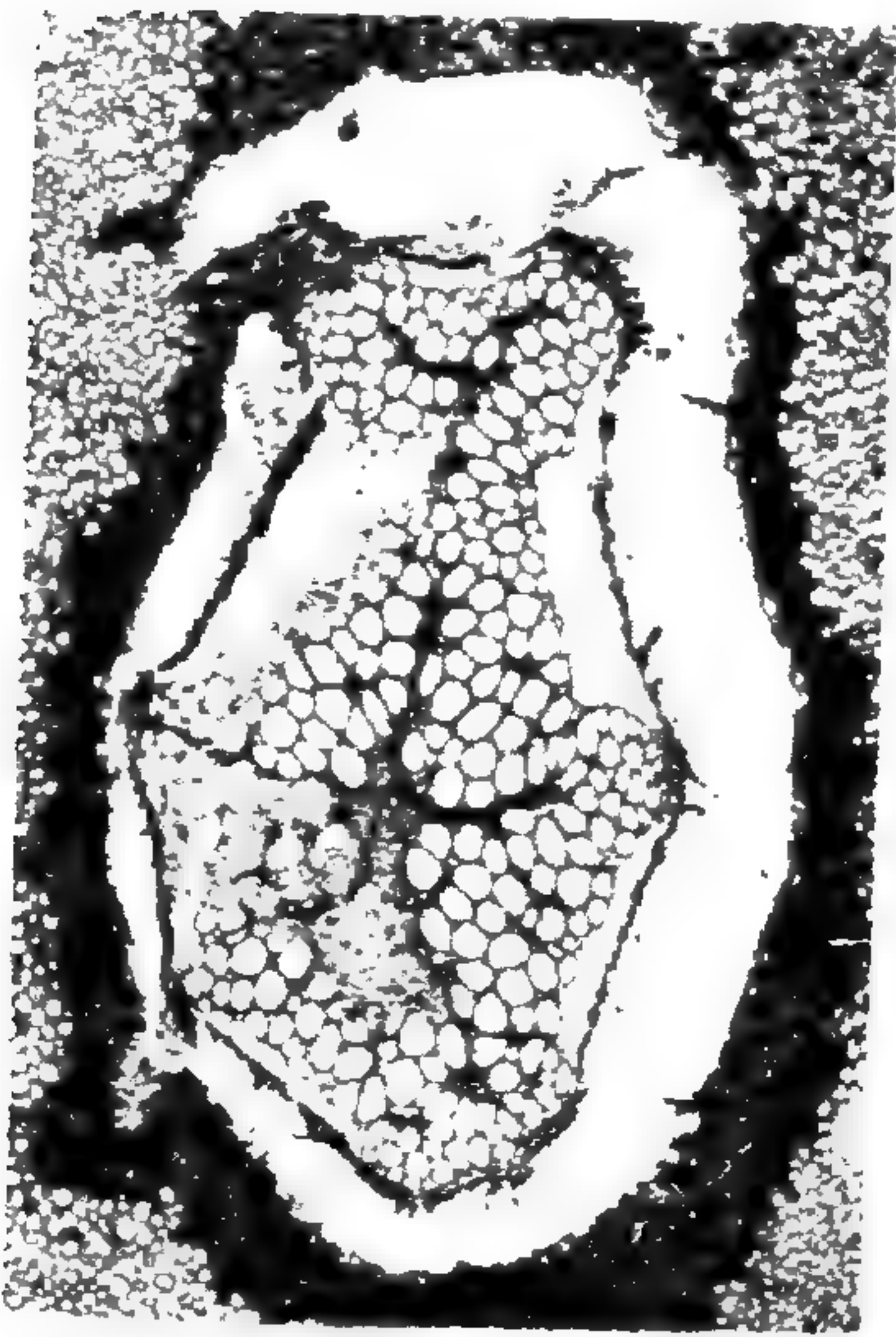
Literature Cited:—

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 Holden, H. S. (1930). On the structure and affinities of *Ankyropteris corrugata*. Phil. Trans. Roy. Soc. Lond. 218B:79–114.
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EXPLANATION OF PLATE 11

Ankyropteris glabra Baxter

Figs. 1–5. Stages in the departure of a petiole trace and axillary branch in Node 1. Fig. 6. Stem stele, branch stele, and trace of Node 2. Fig. 7. Petiole trace at a slightly higher level than shown in fig. 6. Peel preparations as follows: fig. 1, 888 B-t16; fig. 2, B-t4; fig. 3, C-b2; fig. 4, C-b6; fig. 5, C-b10; fig. 6, G-b6; fig. 7, G-b13.



7

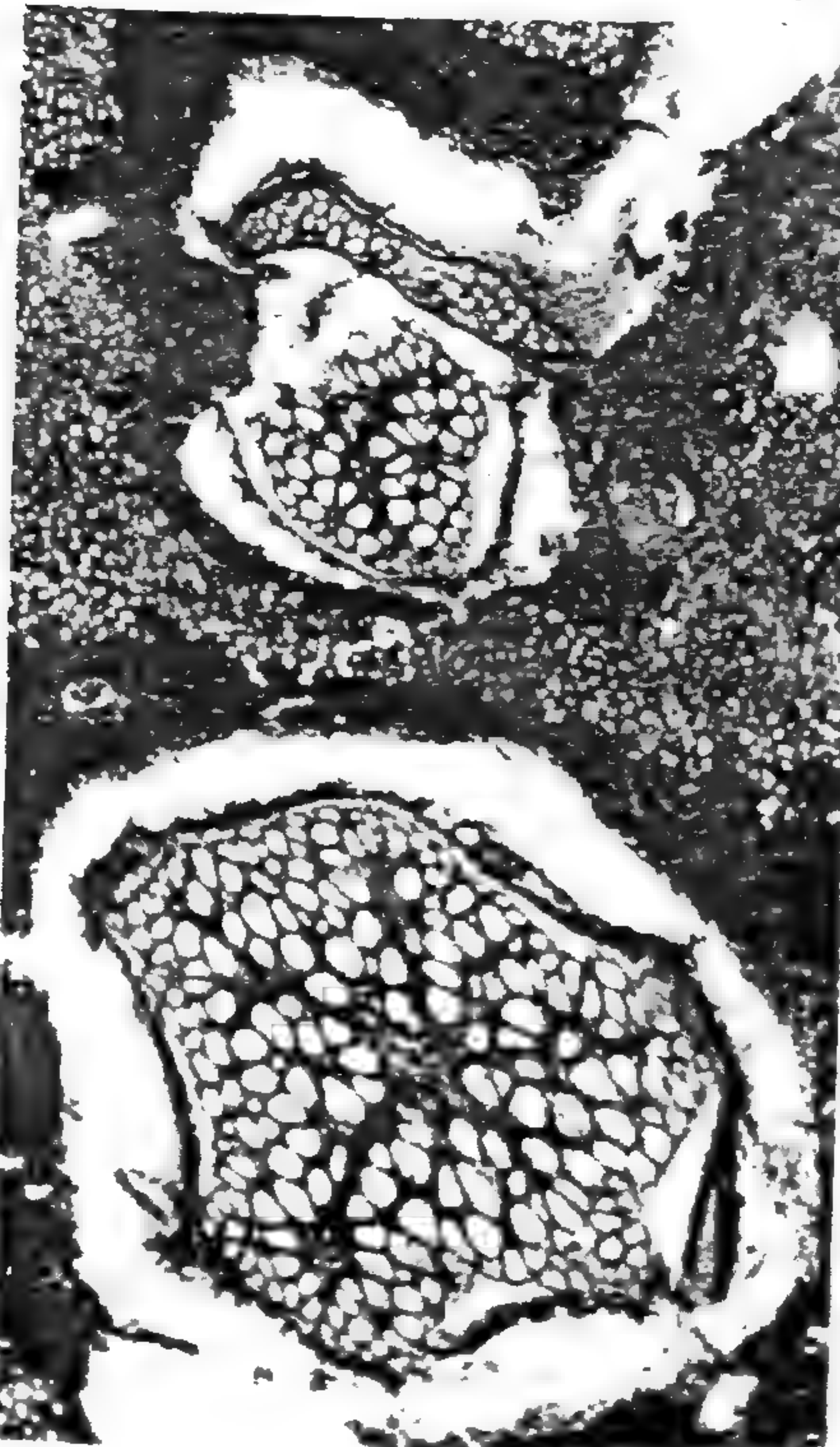
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ANDREWS — ANKYROPTERIS GLABRA

SOME LICHENS OF TROPICAL AFRICA. II. USNEA

CARROLL WILLIAM DODGE*

Through the kindness of Sir Edward Salisbury, Director of the Royal Botanic Gardens at Kew, I have had an opportunity to study a large accumulation of unnamed Tropical and South African lichens, of which nearly half belong in the genus *Usnea*. At about the same time I received a smaller collection from the East African Herbarium at Nairobi, Kenya, through the kindness of Dr. Bernard Verdcourt. I also wish to express my appreciation of the courtesies of Mr. Hamilton, then Acting Curator of the Herbarium of the Art Galleries of the Glasgow Corporation, for permission to study types in the Stirton Herbarium, and of Dr. John Ramsbottom and the late Miss Annie Lorrain Smith at the British Museum, during my stay in these institutions while a John Simon Guggenheim Memorial Foundation fellow in 1930. I am also indebted to Dr. I. Mackenzie Lamb for permission to study specimens at the Farlow Herbarium, and to Dr. Ove Almborn for a few African specimens.

Most of the species previously reported by Motyka¹ were represented in these collections as well as several previously undescribed species. On microscopic study, I have transferred a few of Motyka's species to other sections or subsections and have rewritten my key² to include the new species. Wherever there might be ambiguity, as when a species is somewhat intermediate between sections, I have included it in both. Since some of the South African species also occur in Tropical Africa and the present collections contain some material from South Africa and Madagascar, I have also included species reported by Motyka from those regions, i. e. all species of the African continent and of the adjacent islands south of 15° N. latitude.

Where I have seen specimens, the colors are recorded from comparison with Ridgway (Color standards and color nomenclature. 44 pp. 53 pl. Washington, D. C. 1912). Measurements of the cortex, algal layer, medulla, and axis should not be taken too literally, as proportions of these parts are more constant in a given species than the absolute measurements. It should also be remembered that the thickness of the medulla as given by Motyka includes the algal layer as well as the medulla proper. In groups with a thick medulla, the thickness of the algal

¹ Motyka, J. *Lichenum generis Usnea studium monographicum*. 651 pp. Leopoldi 1936-38.

Motyka, J., & R. Pichi-Sermolli. *Usneae in Missione ad Lacum Tana et Semièn a R. Pichi-Sermolli anno 1937 lectae*. *Webbia* 8:383-404. 1952.

Motyka, J. *O kilku nowych i mniej znanych gatunkach rodzaju Usnea. Species nonnullae novae vel minus cognitae generis Usnea [I.]*. *Frag. Florist. Geobot.* 1²:25-37. 1954.

² Dodge, Carroll W. *Some lichens of Tropical Africa [I]*. *Ann. Mo. Bot. Gard.* 40:271-401. (See pp. 380-383). 1953.

* Missouri Botanical Garden, St. Louis, Mo.

layer does not make much difference in the final ratios of the medulla to cortex or axis, but it does in a few species with a thin medulla, as the algal layer shows less variation in thickness from species to species than the other structures. As far as possible transverse sections of a branch were made just above the first dichotomy or branch, or, if an articulate species, from the middle of the first joint above the first branch. If the basal portion of the plant were missing, I sectioned the basal end of the portion available. As apothecia are often few and apothecial structures are quite constant throughout the genus, I have seldom sectioned the apothecia.

The species numbers in the following key are those used in the present monograph to be continued in the next number of the ANNALS (Vol. 44, No. 1), and the new taxa herein described are numbered as in the key.

KEY TO USNEA IN AFRICA SOUTH OF 15° N.

1. Algae *Trentepohlia*; thallus grayish green, sometimes drying yellowish, rigid, 3–10 cm. tall; axis 250–1150 μ in diameter; medulla compact, usually thinner than the cortex.....ROCELLINAE 2
1. Algae *Trebouxia* or protococcoid.....8
2. Thallus eramulose (rarely a few spinules may grow out *in situ* as short pseudoramuli in *U. perbispidella*)3
2. Thallus clearly ramulose and fertile; exciple reticulate-rugose; axis hollow.....7
3. Apothecia present, marginal cilia rare, distant; surface of the thallus papillate.....4
3. Apothecia absent5
4. Apothecia 8 mm. in diameter, almost eciliate; thallus not spinulose, up to 8 cm. tall; axis hollow; saxicole; S. Rhodesia.....1. *U. cervicornis* Dodge
4. Apothecia 3–5 (–6) mm. in diameter, cilia rare, short, subdistant; thallus spinulose-isidiose from small papillae; axis solid; corticole; S. Sudan and Kenya.....2. *U. perbispidella* Steiner
5. Axis solid, surface not eroded; thallus up to 8 cm. tall; soredia white, isidiose on low tubercles but appearing farinose after isidia are shed; corticole; Uganda, Tanganyika, and Natal.....3. *U. sorediosula* Müll. Arg. in Motyka
5. Axis very slightly lacerate, surface longitudinally eroded and somewhat angular, composed of interwoven strands of thick-walled hyphae; thallus 3–4 cm. tall; soralia farinose, soredia dark fuscous; saxicole.....6
5. Axis lacerate with many small cavities, surface smooth; thallus internodes short below and above, longer in mid-portion, tips recurved, surface minutely verrucose, each verruca producing a single isidium; both saxicole and corticole; Kenya and Uganda.....4. *U. nutans* Dodge
5. Axis hollow, loosely stuffed with brown hyphae; thallus branched near the base, ultimate branches 7 cm. long, densely isidiose-spinulose throughout; saxicole; Tanganyika.....5. *U. Dodoniae* Dodge
6. Medulla K— or slightly yellowing; thallus sparingly dichotomous, 4 cm. tall, 1 mm. in diameter; Southwest Africa*U. bereoensis* (Vainio) Darb.
6. Medulla K red; thallus repeatedly dichotomous, 3 cm. tall, 0.5–0.7 mm. in diameter; southwest Angola.....*U. mossamedana* (Vainio) Darb.
7. Apothecia up to 15 mm. in diameter; exciple ramulose along the ridges; marginal cilia crowded, 2 mm. long; disc white-pruinose; ramuli dense throughout; axis 1.5 mm. in diameter, with a large cavity; arboricole; Uganda.....6. *U. pulvinulata* Dodge
7. Apothecia 5–7 (–10) mm. in diameter; exciple not ramulose; marginal cilia not crowded, 3 mm. long; disc buffy brown, not pruinose; ramuli irregularly disposed, 4–5 mm. long; axis 0.75 mm. in diameter, cavity rather narrow; saxicole; Kenya, Tanganyika.....7. *U. Liechtensteinii* Steiner
8. Axis hollow or loosely stuffed in larger branches; apothecia ciliate, rarely eciliate; thallus smooth or papillate, not scrobiculate; soredia isidiose.....Subg. EUMITRIA 9
8. Axis solid, rarely somewhat lacerate or with a very narrow stuffed cavity.....Subg. EUUSNEA 21

9. Thallus distinctly angled or at least with papillae in dense rows.....10
9. Thallus terete, not angled nor with papillae in dense rows.....11
10. Thallus olive green, 2- to 3-angled; cortex continuous, larger ramuli smooth; soredia isidiose along ridges between the rare ramuli; coastal Kenya, Tanganyika.
.....*U. cristata* Motyka
10. Thallus light brownish olive below, shading through Isabella color to chamois above; cortex subareolate, larger ramuli foveolate, sparsely papillate below; apothecia up to 20 mm. in diameter, exciple smooth or papillate with radial ridges; mountains of Tanganyika.....8. *U. subcristata* Dodge
11. Cavity narrow, or axis lacerate and cavity more or less stuffed with hyphae.....12
11. Cavity very wide and distinct, usually not stuffed.....14
12. Thallus almost eramulose with a few irregular ramuli, persistently ashy green, branches perpendicular, straight or irregularly flexuous, 10 cm. tall, 2 mm. in diameter, tapering gradually to the tips, slightly rugulose, sorediose; Angola.
.....*U. Welwitschiana* Motyka
12. Thallus ramulose, 5-10 cm. tall, branches divergent; fertile, exciple slightly rugulose or smooth.13
13. Medulla rose; ramuli 2 mm. long, slender, perpendicular, dense; apothecia 7 mm. in diameter, exciple ciliate; disc flesh-color, marginal cilia few and short; Kenya to Bechuanaland, (CERATINAE).....85. *U. acanthera* Vainio
13. Medulla white; ramuli 4-5 mm. long, thick, sparse to dense, appressed to the branches; apothecia up to 10 mm. in diameter, exciple and margin eciliate; Kenya, Tanganyika (ROCELLINAE).....7. *U. Liechtensteinii* Steiner
14. Thallus eramulose, sorediose.15
14. Thallus ramulose.17
15. Medulla rose, cavity loosely filled; thallus 20 cm. long; Congo, Kenya.....9. *U. elata* Motyka
15. Medulla white, cavity densely filled with yellow hyphae; thallus 30 cm. long; Madagascar.
.....16
16. Soredia granulose, isidiose from the tubercles over the whole plant.....*U. sororia* Motyka
16. Soredia on capitiform tubercles, 1 mm. in diameter, mostly on the lateral branches.
.....*U. sororia* f. *bisorediata* Motyka
17. Thallus fertile, not sorediose.....18
17. Thallus sterile, sorediose.....19
18. Branches slightly inflated; apothecia 7-10 (-15) mm. in diameter; exciple convex, papillate to ciliate; marginal cilia rare; disc pruinose; medulla rose; Cameroons to Tanganyika.....11. *U. firmula* Motyka
18. Branches not inflated; apothecia up to 20 mm. in diameter, plane; exciple slightly verrucose and venose-rugulose; marginal cilia close; disc cinnamon; medulla white, pale rose next the axis; Uganda, Congo.....12. *U. medio-africana* Dodge
18. Branches not inflated; apothecia 1-2 mm. in diameter; exciple convex, smooth, marginal cilia close; disc carneous, white-pruinose; medulla white; Uganda...10. *U. nana* Dodge
19. Thallus 1-1.2 mm. in diameter, ramulose below, nude above; St. Helena, Cameroons to Tanganyika and south to Réunion.....*U. implicata* (Stirton) Zahlbr.
19. Thallus 2 mm. in diameter, ramulose throughout.....20
20. Thallus remaining greenish ashy, soredia isidiose on tubercles, especially on the ramuli; Madagascar, Tanganyika.....*U. Baileyi* (Stirton) Motyka
20. Thallus drying Mars brown to russet with paler ramuli in the herbarium; a few small tubercles producing single minute isidia, not sorediose; Uganda...13 *U. brunnescens* Dodge
21. Thallus scrobiculate or foveolate, epapillate; flaccid, base not blackened.....FOVEATAE 22
21. Thallus terete or angled, usually more rigid; base often blackened.....27
22. Thallus white to pale green, 14-20 cm. long, not fruticulose, very flaccid; saxicole.....23
22. Thallus darker colored, 9 cm. or less tall, somewhat fruticulose but rather flaccid.....24
23. Thallus white, green-punctate, 14 cm. long (incomplete), 1.5 mm. in diameter, summits capillaceous; apothecia 2 mm. in diameter, lateral on larger branches, eciliate; S. Africa (AMABILES).....*U. primitiva* Motyka
23. Thallus drying clay color, partly somewhat fuscous, 20-30 cm. long, not contorted, 1 mm. in diameter, summits short; apothecia and soredia unknown; Cameroons.
.....14. *U. versicolor* Motyka
24. Thallus flattened, 3 cm. tall, 2 mm. in diameter; apothecia up to 15 mm. in diameter, densely ciliate; Ethiopia.....15. *U. complanata* (Müll. Arg.) Motyka
24. Thallus not distinctly flattened; sorediose.....25

25. Thallus up to 12 cm. tall, 2 mm. in diameter, acutely rugose; Ethiopia to Tanganyika.
.....16. *U. corrugata* Motyka
25. Thallus 6-7 cm. tall, not acutely rugose.....26
26. Branches closely ramulose; soredia in farinose tubercles; Ethiopia to Comoro Islands
(see also f. *eciliata* Motyka).....17. *U. pulverulenta* (Müll. Arg.) Motyka
26. Branches sparsely and irregularly ramulose; soredia isidiose on low ridges, cortex of
larger branches not areolate; French Guinea, Angola to S. Africa, Madagascar and
Comoro Islands.....*U. leprosa* Motyka
27. Thallus articulate with pseudocyphellae but not papillate, inflated, (10-) 25-40 cm. long,
medulla very lax.ARTICULATAE 28
27. Thallus continuous or, if articulate, without pseudocyphellae, often fruticose, papillate,
and ramulose.35
28. Thallus up to 60 cm. long, 2.5 mm. in diameter, pale stramineous; joints 4-10 (-30)
mm. long, only slightly inflated; ramuli 10 mm. long; isidiose on some joints, not
on others; Eritrea to Tanganyika.....18. *U. flavescens* Motyka
28. Thallus (10-) 25-60 cm. long, ramulose or with only an occasional ramulus.....29
29. Pseudocyphellae elevated, conspicuous; thallus stramineous.....30
29. Pseudocyphellae not elevated, rather inconspicuous; thallus usually fuscous in the
herbarium.....31
30. Thallus foveolate, 40-60 cm. long, 2 mm. in diameter; joints 5 (-10) mm. long;
soredia along ridges; pale irregular "cephalodia" often present; Eritrea, Somaliland
and S. Africa.....19. *U. praelonga* Stirton
30. Thallus smooth, up to 40 cm. long, 2 mm. in diameter, joints 0.3-20 mm. long;
apothecia 5 (-10) mm. in diameter, marginal cilia few; Sierra Leone to Cameroons.
.....20. *U. pseudocyphellata* Motyka
31. Thallus up to 30 cm. long, 2.5 mm. in diameter, relatively rigid, joints up to 70 mm.
long, curved; Sierra Leone to St. Helena.....21. *U. speciosa* Motyka
31. Thallus 10-40 cm. long, flaccid, joints 10-30 mm. long, nearly straight.....32
32. Thallus smooth or only slightly deformed.....33
32. Thallus foveate to rugose.....34
33. Thallus 15-25 cm. long, 1-1.4 mm. in diameter, stramineous or pale stramineo-fuscous;
apothecia 5-7 mm. in diameter, exciple smooth, marginal cilia dense and long;
S. Africa and Madagascar.....*U. flexilis* Stirton
33. Thallus up to 60 cm. long, up to 3 mm. in diameter, lurid fuscous, summits long, capilla-
ceous; apothecia rare, 2-4 mm. in diameter, exciple lacunose, marginal cilia few
but long; Kenya to Nyasaland, and Angola.....22. *U. vesiculata* Motyka
33. Thallus 20 cm. long, 1 mm. in diameter, sepia, summits cream buff, joints scarcely
inflated; apothecia and soredia unknown; Tanganyika to S. Africa (STRAMINEAE,
AMOENAE).....30. *U. moniliformis* Motyka
33. Thallus only 10-15 cm. long, 0.5 mm. in diameter, summits inconspicuous, sterile and
esorediose; Ethiopia to Tanganyika.....23. *U. deminuta* Motyka
34. Thallus foveate to scrobiculate on larger joints (25-30 × 4-5 mm.), smooth on
smaller joints (5-10 × 1-1.4 mm.) with small soralia of isidiose soredia on smaller
non-articulate branches; ramuli 5 mm. long on smaller branches; corticole; Ethi-
opia and Kenya.....24. *U. articulata* subsp. *aethiopica* Dodge
34. Thallus foveolate, pale fuscous, up to 20 cm. long, 1-3 mm. in diameter, summits
capillaceous; soredia pale sulfur color in large soralia; saxicole; Kenya, Tangan-
yika and Congo.....25. *U. terrestris* Motyka
34. Thallus partly foveolate to rugose on larger joints, not on others, 20 cm. long; joints
up to 10 × 2 mm. alternating with short joints 0.3 mm. in diameter, reddish
fuscous; no pseudocyphellae; no apothecia nor soredia known; Kenya, Uganda,
Tanganyika (RUBIGINEAE).....79. *U. erubescens* (Stein) Motyka
34. Thallus longitudinally rugose, lurid fuscous, up to 65 cm. long, up to 4 mm. in
diameter, summits short, curved, more densely branched; apothecia about 5 mm.
in diameter, marginal cilia few; Ethiopia.....26. *U. rugosa* Motyka
35. Thallus either persistently stramineous, yellow, or soon becoming fuscous in the herbar-
ium; cortex thin, papery, or, if thicker, very smooth, medulla usually thick and lax
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35. Thallus ashy green, rarely red or, if stramineous, then papillate or tuberculate, seldom
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37. Thallus stramineous, pale yellow or pale fuscous, subarticulate, usually eramulose; sterile (very rarely fertile in *U. gracilis* Ach.).....AMOENAE 39
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39. Thallus persistently stramineous, 0.6 mm. or less in diameter; medulla thicker than the axis, K red; Ethiopia, Kenya and Uganda.....27. *U. Vainioana* Zahlbr.
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40. Ramuli confined to small clusters in upper portions of the branches; joints variable in length, up to 1.3 mm. in diameter, many inflated, clearly annulate; medulla K yellow; St. Helena and Fernando Po.....29. *U. pulchella* Motyka
40. Ramuli very rare or absent, not in clusters; thallus 1 mm. in diameter below, joints 1–3 (–10) mm. long, not constricted nor inflated, less annulate; medulla K—; Kenya to S. Africa.....30. *U. moniliformis* Motyka
41. Thallus rose or copper-rose, medulla K—, 30 cm. long, 2–3 (–4) mm. in diameter; irregularly ramulose; no apothecia nor soredia known; saxicole; Ethiopia.....*U. saxatilis* Motyka
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42. Thallus about 20 cm. long, 2.5 mm. in diameter, soft, foveolate, irregularly articulate, surface indistinctly and minutely papillate; medulla K yellow, then red; Mauritius, Rodriguez, Comoro, and Seychelles and Socotra islands.....31. *U. straminea* Müll. Arg.
42. Thallus 30–35 (–60?) mm. long, branches up to 2 mm. in diameter below, becoming capillaceous above, indistinctly articulate, surface with oblong ridges, farinose; medulla K yellow; apothecia rare, 2–3 mm. in diameter, exciple slightly rugose with few marginal cilia; soredia on ramuli; Kenya, Congo, Uganda and Tanganyika.
.....32. *U. exasperata* (Müll. Arg.) Motyka
43. Thallus longitudinally rugulose and subfoveolate, over 25 cm. long, 1 mm. in diameter, very minutely papillate on some joints, smooth on others, tips capillaceous, densely branched; ramuli close but irregularly disposed; apothecia lateral on secondary branches, up to 10 mm. in diameter; Egypt to Ethiopia and northern Kenya (BARBATAE, PENDULINAE).....33. *U. Pinkertonii* Stirton
43. Thallus up to 20 cm. long, 1.5 mm. in diameter, obliquely or longitudinally rugose, not sulcate, tips capillaceous; ramuli rare and irregularly disposed, longer on the thinner branches; soredia isidiose; Kenya to S. Africa.....35. *U. fusca* Motyka
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44. Main branches up to 2 mm. in diameter; thallus over 40 cm. long, acutely angled and longitudinally rugose, deeply foveate between the ridges; ramuli close, smaller 5 mm. long, mixed with much longer, thick below with obtuse tips; apothecia unknown; isidiose soredia on tubercles on some ramuli; Kenya and Uganda.
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47. Thallus about 15 cm. tall, very indistinctly papillate, papillae cylindrical; ramuli 1–2 mm. long, very slender; Tanganyika, Uganda and N. Rhodesia.
.....40. *U. hispidula* (Müll. Arg.) Motyka
47. Thallus up to 15 cm. tall, with distinct rugi but nearly terete; ramuli irregularly disposed, variable in length and thicker; Tanganyika, Sudan and Madagascar.
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49. Thallus up to 5 cm. tall, 1–1.5 mm. in diameter, old gold to Isabelline; medulla K yellow, becoming red then fuscous (reddish fuscous); soredia isidiose; Kenya and Uganda to S. Africa; Madagascar (*U. pulvinata* Motyka, *p. p.*)
.....43. *U. transvaalensis* Vainio
49. Thallus 4 cm. tall, 1 mm. in diameter, fuscous; medulla K—; soredia in indistinct tubercles; Ethiopia to Tanganyika.....44. *U. ruwenzoriana* Motyka
50. Thallus 7 cm. tall, 1 (–1.5) mm. in diameter, rose to copper-red; medulla K indistinctly yellowish fuscous; soredia in slightly elevated oblong soralia; S. Africa to Madagascar.....*U. Havaasii* Motyka
50. Thallus up to 10 cm. tall, 1.5 (–2) mm. in diameter, ashy green to tawny olive; medulla K—; soredia isidiose in large hemispheric soralia, becoming farinose; Cameroons, Angola, Congo and Uganda.....45. *U. Haumanii* Motyka
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53. Thallus 9 cm. tall, 2 mm. in diameter, tawny olive with cinnamon-buff, subdistant ramuli; apothecia 11–12 mm. in diameter, exciple minutely verrucose with low radial ridges from concrescent axis and ramuli; marginal cilia distant, 10 mm. long; Tanganyika.....49. *U. blepharoides* Dodge
53. Thallus 7–15 cm. tall, deep fuscous in the herbarium; apothecia 10–15 mm. in diameter.....54
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.....50. *U. molliuscula* Stirton
55. Thallus 8 cm. tall, 1.5–2 mm. in diameter; exciple smooth, ramulose; marginal cilia numerous, short, obtuse, thick, almost inflated; Ethiopia to Tanganyika.
.....51. *U. obtusata* Motyka f. *perstrigosa* Motyka

56. Thallus 9–30 cm. long, 1.5 mm. in diameter; soredia isidiose, dispersed over most of the branches, spinules not seen; apothecia 7 mm. in diameter, exciple smooth to foveolate with short spinules; marginal cilia few, short; Kenya to Cape of Good Hope.....52. *U. undulata* Stirton
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57. Thallus about 30 cm. long, 0.6 mm. in diameter; spinules minute; ramuli perpendicular, variously curved, the larger branched; apothecia about 6 mm. in diameter; exciple nearly smooth, marginal cilia dense, variously curved and branched, up to 12 mm. long; Tanganyika to Cape of Good Hope and Madagascar.....53. *U. strigosella* Steiner
57. Thallus about 5 cm. tall, 1.2 mm. in diameter; ramuli 3 mm. long; Cameroons to Kenya, Rhodesia and Lourenço Marques.....54. *U. perspinosa* Motyka
58. Thallus about 9 cm. tall, branches up to 2 mm. in diameter, sulfur to yellowish; sterile; Madagascar.....56. *U. sulphurascens* Motyka
58. Thallus up to 8 cm. tall, 1.5–2 mm. in diameter; ramuli rare; apothecia 3–5 mm. in diameter; Madagascar and Mauritius.....55. *U. luteola* Motyka
58. Thallus 4 cm. tall, 0.5–1.2 mm. in diameter; eramulose (smaller thalline branches simulate ramuli); apothecia 8 mm. in diameter; Madagascar.....*U. chrysoleuca* Motyka
59. Both fertile and sorediose (see no. 58 above, *U. luteola* Motyka and *U. chrysoleuca* Motyka).
59. Sorediose only.60
59. Fertile only; thallus up to 60 cm. long, about 1 mm. in diameter, prostrate with tips of short branches or ramuli forming secondary holdfasts, chamois to deep colonial buff; apothecia 3–5 mm. in diameter, exciple smooth, eciliate (LONGISSIMAE).
.....*U. amaniensis* Dodge
60. Thallus 15 cm. long, persistently osseoleuco-stramineous, 0.6–0.8 mm. in diameter; Madagascar.....*U. Humberti* Motyka
60. Thallus 8.5 cm. (incomplete) long; primary branch 3 mm. in diameter, secondary branches (1–) 1.5 mm. in diameter, becoming fuscous in the herbarium; medulla K red then blackening; Tanganyika.....*U. incrassata* Motyka
61. Thallus unchanging or late becoming fuscous in the herbarium; medulla thick, lax, cortex thin; irregularly branched, papillate tuberculate or sub-smooth, apices rather thick.....DENDRITICAE 62
61. Thallus unchanging, never fuscous; medulla relatively thin, compact; cortex thick, often horny (sometimes scaling and more or less ecorticate); branching more regular.....73
62. Thallus without pseudocyphellae and not white-maculate.....CLADOCARPEAE 64
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64. Thallus about 10 cm. tall, erect or prostrate, rather rigid below, surface subrugose and subfoveate on smaller branches; sterile; Eritrea (BARBATAE, COMOSAE).
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65. Thallus 1–2 mm. in diameter, olive-green, verruculose-papillate; apothecia up to 7 mm. in diameter, exciple sublacunose, verruculose, sorediose; marginal cilia few or none; Kenya to Transvaal.....58. *U. subleprosa* Motyka
65. Thallus 1.5–2 mm. in diameter, pale ashy stramineous, foveolate, impressed, papillae minute, cylindrical; eramulose; Cape of Good Hope.....*U. cornea* Motyka
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66. Exciple papillate.68
66. Exciple foveate to scrobiculate, 10 mm. in diameter; thallus 7 cm. tall, citrine drab to dark olive buff; ramuli close, the shorter 1–3 mm. long, smooth, the longer up to 15 mm. long, isidiose-sorediose in tuberculate soralia; Cameroons to Uganda.
.....59. *U. Ledienii* (Stein) Motyka
67. Apothecia (5–) 10 (–15) mm. in diameter; thallus up to 15 cm. tall, sepia to bone brown in the herbarium; ramuli subdistant on larger branches, closer on smaller branches, 2–10 mm. long, the shorter smooth, the longer somewhat tuberculate but not sorediate; Cameroons to Angola.....60. *U. bispida* Motyka

67. Apothecia 5 mm. in diameter; thallus 10 cm. tall, Saccardo's umber and buffy brown; ramuli wood-brown to avellaneous, subdistant, 5 mm. long; Eritrea to South Africa.....61. *U. ochrophora* Stzbr. in Motyka
67. Apothecia up to 9 mm. in diameter; thallus about 5 cm. tall, buffy clive to yellowish olive; eramulose; Sudan to Tanganyika.....62. *U. subfoveata* Dodge
68. Thallus about 7 cm. long, warm sepia to Verona brown; ramuli 1-10 mm. long, the shorter spinuliform, the longer tuberculate but not sorediate; apothecia 5-8 mm. in diameter; papillae long-capitiform; Eritrea to Tanganyika.....63. *U. trachyna* Motyka
68. Thallus 5 cm. tall, light brownish-olive to Isabelline; ramuli irregularly disposed, 2-3 mm. long, smooth; apothecia up to 15 mm. in diameter; Sierra Leone, Angola and Kenya.....64. *U. scutata* Motyka
69. Thallus becoming pale fuscous, white-spotted, cortex hard; apothecia 4-6 (-15) mm. in diameter; esorediose; Ethiopia and Sudan.....65. *U. albomaculata* Motyka
69. Thallus becoming fusco-sepia, only small pseudocyphellae white, cortex hard; apothecia 10 mm. in diameter; soredia farinose, sulfur yellow on slenderer branches; Ethiopia.*U. abissinica* Motyka
69. Thallus dirty ashy-greenish becoming pale fuscous or yellowish, only small pseudocyphellae white, cortex soft; apothecia 10 mm. in diameter; Ethiopia.51. *U. obtusata* Motyka
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71. Thallus olive green; branches up to 2.5 mm. in diameter; medulla thick (980 μ) soredia isidiouse in punctiform soralia; Cape Verde, Cameroons, Cape of Good Hope.66. *U. Bornmuelleri* Steiner
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72. Branches 2 mm. in diameter, less distinctly papillate, ridges elevated, tops flattened; esorediose; apothecia 10 mm. in diameter, exciple farinose-spotted; Ethiopia and Kenya.....68. *U. serpentaria* Motyka
73. Medulla very thin, white, never rose; thallus fruticulose or, if over 20 cm. long, cortex reddish or reddish-maculate.....SETULOSAE
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76. Eramulose; axis solid or slightly lacerate, surface longitudinally eroded and somewhat angular, composed of interwoven strands of thick-walled hyphae; soralia farinose, soredia dark fuscous.77
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79. Thallus about 8 cm. tall, pale stramineous, 1 mm. in diameter, divergently branched; ramuli dense but somewhat irregularly disposed; soredia isidiose in minute tuberculiform soralia, then eroded and farinose; Madagascar.....*U. ambigua* Motyka
79. Thallus 20 cm. long, pale ashy, 0.9 mm. in diameter below, with minute white tubercles; ramuli irregularly disposed, 10–30 mm. long; Togo, Fernando Po, and St. Helena.
.....72. *U. Lyngei* Motyka
80. Soredia isidiose, covering tubercles, appearing spinulose when tubercles are crowded and farinose after the isidia are shed; thallus 5–6 cm. tall, between deep olive buff and tea green, 1.5 mm. in diameter; ramuli 2–3 (–5) mm. long, irregularly dense; apothecia 3 mm. in diameter (perhaps still immature); Angola...73. *U. Gossweileri* Dodge
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81. Thallus up to 7 cm. tall, 1 (–1.8) mm. in diameter; ramuli dense but fragile, breaking off about 0.2 mm. from the branch and thus appearing very coarsely papillate; apothecia 5 mm. in diameter; Kenya.....76. *U. isabellina* Dodge
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.....77. *U. horridula* (Müll. Arg.) Motyka
83. Thallus closely ramulose, isidiose soredia in tubercles on the lower portion of ramuli; thallus deep olive-buff, pink-maculate, 1 mm. in diameter, acutely few-angled from rows of con crescent papilliform tubercles; Kenya.....78. *U. Dalei* Dodge
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85. Thallus esorediose, reddish fuscous spotted with greenish fuscidulous, 4–5 cm. tall, branches about 1.5 mm. in diameter; apothecia small, exciple tuberculate, rugulose, olive fuscous; Kenya, Tanganyika, Comoro Islands and Madagascar.
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87. Thallus 10 cm. tall, russet below shading to ochraceous-salmon above, up to 0.9 mm. in diameter; soralia small with one to a few isidia, sometimes confluent and appearing farinose after the soredia are shed; Kenya.....82. *U. spilotoides* Dodge
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110. Thallus gray green, 50 cm. or more long, 0.5 mm. in diameter; cortex areolate but not scaling above, sometimes farinose from coalescent scars of fallen isidia; ramuli 3–5 mm. long, dense; short lateral branches tuberculate-isidiose; apothecia 3–4 mm. in diameter, exciple nearly smooth to slightly pitted; marginal cilia few; disc white; Congo.....98. *U. savanarum* Duvign.

1. *USNEA cervicornis* Dodge, sp. nov.

Type: Southern Rhodesia, Makoni Inyanga District, summit of Forest-Hill Kop, 1700 m., on shaded rock face, *Frederick Eyles 827*, at Kew.

Thallus erectus, ad 8 cm. altitudine, 2 mm. diametro, teres, ad axillas complanatus, olivaceo-alutaceus; cortex areolatus, subfoveolatus, minute et irregulariter papillatus, papillis apicibus nigratis; eramulosus. Apothecia lateralia, 8 mm. diametro, margine crenato, eciliato aut cum 1–2 ciliis ad 8 mm. longitudine, ca. 0.5 mm. diametro, subinflatis, apicibus obtusis; discus brunneo-alutaceus, epruinus.

4. *USNEA nutans* Dodge, sp. nov.

Type: Kenya, Northern Frontier Province, Mt. Kulal, 1935 m., on exposed rock, *P. R. O. Bally 5686*, at Kew.

Thallus erectus vel decumbens, rigidus, ca. 8 cm. altitudine, cinnamomeo-alutaceus ad obscure olivaceo-alutaceus in ramis ultimis; hapteron 5 mm. diametro, cum decem vel pluribus ramis perpendiculariter dichotomis, curvatis, apicibus recurvis nutantibusque, teretibus, laevibus; cortex inferne annulatus subareolatusve, superne minute verrucosus; isidia singula; eramulosus, rami ultimi nutantes, laeves, apicibus nigris. Apothecia non visae.

5. *USNEA Dodomae* Dodge, sp. nov.

Type: Tanganyika, Dodoma Prov., Mt. Mpwapwa, 1610–1935 m., saxicole, *P. J. Greenway 2432*, in East African Herb.

Thallus erectus vel decumbens, 10 cm. altitudine, rigidus in virgultis densis ex gompho communi flavo, brunneo-olivaceus, Isabellinusve ad melleus in ramis ultimis; rami 1.5 mm. diametro ad basim nigricantem ad 2 mm. diametro sub dichotomo primo, rami ultimi ad 7 cm. longitudine, flexuosi, eramulosi; cortex inferne fractus et subareolatus, superne laevis; isidia spinulosa fere totam plantam tegentia. Apothecia non visa.

6. *USNEA pulvinulata* Dodge, sp. nov.

Type: Uganda, Kigezi, Kasatoro forest, 1935–2560 m., on trees, *I. R. Dale L39*, at Kew.

Thallus fruticosus, erectus, ad 5 cm. altitudine, ramis 1 mm. diametro, obscure olivaceo-alutaceus, dichotome vel sympodialiter ramosus, internodiis brevibus, pulvinulum hemisphericum formans; cortex inferne nigricans, annulatim fractus subareolatusve, superne laevis; densissime ramulosus, ramuli acuminati, 0.5–3 mm. longitudine, recti; medulla inferne rubra.

Apothecia subterminalia, ad 15 mm. diametro, primum cupulata dein subplana; excipulum tenuiter scrobiculatum, rugis ramulosis; cilia marginalia caespitosa, ca. 2 mm. longitudine, apicibus acuminatis; discus laevis, juventute dense albo-pruinus dein rufus vel subaurantiacus.

8. *USNEA subcristata* Dodge, sp. nov.

Type: Tanganyika, Kondo District, Swaga-swaga Hill, summit, 1775 m., on shrubs, chiefly *Trichalisia cacondensis*, B. D. Burtt 891.

Thallus rigidus, fruticosus, erectus, 7–8 cm. altitudine, inferne pallide brunneo-olivaceus, superne Isabellinus vel melleus; rami basi 2 mm. diametro ad 3 mm. expansi dein ad 1 mm. sub apotheciis, tenuescens, angulati, papillati; cortex subareolatus; rami secundarii 1–1.5 mm. diametro, axi principali similes; ramuli 1–15 mm. longitudine, minores sublaeves, majores foveolati, apicibus rotundatis.

Apothecia terminalia, plana, ad 20 mm. diametro, excipulo laevi vel papillato radialibus cum rugis; cilia marginalia subdistantia in duobus ordinibus disposita, extera crassa, dichotoma, intera 1–2 mm. longitudine, apicibus acutis; discus vinaceo-alutaceus, pruinosis.

10. *USNEA nana* Dodge, sp. nov.

Type: Uganda, Kigezi, Kasatoro, Kabale River, 2256 m., corticole, I. R. Dale L43 p. p. min.

Thallus fruticosus, erectus, ad 4 cm. altitudine, olivaceus, dichotome ramosus, teres, ad 1 mm. diametro superne tenuescens, dense ramulosus; ramuli 1–2 (–4) mm. longitudine, curvati, apicibus obtusis, raro dichotomi.

Apothecia sessilia in ramis tenuibus secundariis, cupulata, 1 (–2) mm. diametro, excipulo laevi; cilia marginalia caespitose radiantia, 1 mm. longitudine; discus concavus, carneus, albo-pruinosis.

12. *USNEA medio-africana* Dodge, sp. nov.

Type: Uganda, Kigezi, Mafuga, 2400 m., on trees, I. R. Dale L41, at Kew.

Thallus erectus, subrigidus, circa 5 cm. altitudine, 1.5 mm. diametro, super basim semel aut bis dichotome ramosus, obscure brunneus, ramulis olivaceo-alutaceis; teres vel subrugosus vel subfoveolatus; ramuli densi, 5–7 mm. longitudine, fragillimi, laeves, apicibus acutis nigricantibus.

Apothecia subterminalia, ad 20 mm. diametro, plana; excipulum foveatum, minute verrucosum, radiantibus cum rugis ex ramulis conrescentibus formatis; cilia marginalia longitudine variabili, ad 8 mm. longitudine; discus cinnamomeus, leviter albo-pruinosis.

13. *USNEA brunnescens* Dodge, sp. nov.

Type: Uganda, Kigezi, Mafuga, 2400 m., on trees, I. R. Dale L41, at Kew.

Thallus erectus, fruticosus, rigidus, ad 10 cm. altitudine, fusco-brunneus, ramulis cinnamomeo-alutaceis; basi bis vel ter dichotomus, ca. 2 mm. diametro, ad 0.3 mm. tenuescens in apicibus obtusis; cortex inferne impressus subareolatusque, sublaevis, superne dense verrucoso-papillatus; ramuli 1–3 mm. longitudine, in ordinibus verticalibus, majores sparse verrucosi, singulis cum isidiis.

24. *USNEA ARTICULATA* (L.) Hoffm. subsp. *aethiopica* Dodge, subsp. nov.

Type: Ethiopia, below Debra Erki, on fir, *Schimper 18*, 21 Oct. 1850. det *U. articulata* v. *intestiniformis* Ach. by Müller Argau at Kew.

Thallus pendens, flaccidus, plus quam 25 cm. longitudine, brunneus; basis 1 mm. diametro, 8 mm. longitudine, annulatus, non nigricans; dichotome ramosus, ramis articulatis, articulis irregularibus, curvatis, cucumiforibus, 4–5 mm. diametro, 25–30 mm. longitudine, foveatis vel scrobiculatis, pseudocyphellatis, vel subrectis, 1–1.4 mm. diametro, 5–10 mm. longitudine minutis cum pseudocyphellis; rami terminales, tenues, fere non articulati, dense ramulosi, ramulis 5 mm. longitudine isidio-sorediosis.

34. *USNEA cameroonensis* Dodge, sp. nov.

Type: Cameroons, *Miss Cheeseman L3*, at Kew.

Thallus pendens, flaccidus, plus quam 55 cm. longitudine, axes principales brunnei vel cinnamomei, ramulis olivaceo-alutaceis; articulati, dichotome ramosi; axillis complanatis, articulis ca. 10 mm. longitudine, 1 (–1.5) mm. diametro, non conspicue inflatis, longitudinaliter rugosis, rugis tenuibus acutis, dorsis fractis farinosisque; ramuli irregulariter dispositi, ad 30 mm. longitudine, basi subarticulati inflatique, ad apicem acutum tenuescentes, tuberculati deformatique; soredia isidiosa. Apothecia non visa.

36a. *USNEA DECIPIENS* Motyka var. *Rhodesiana* Dodge, var. nov.

Type: Southern Rhodesia, Matopos District, top of high granite hill, 1610 m., on tree, *Frederick Eyles 1023*, at Kew.

Thallus pendens, subflaccidus, plus quam 30 cm. longitudine, Isabellinus, infrequenter dichotome ramosus, nec articulatus nec annulatus, longitudinaliter et subreticulate rugosus, rugis subacutis, dorso fracto, inter rugas sulcatus, 1 mm. diametro, superne tenuescens sed sine summitatibus capillaceis; ramuli caespitiosi, 3–15 mm. longitudine; tubercula farinosa sorediosa.

39. *USNEA terricola* Dodge, sp. nov.

Type: Cameroons, Mamoquilles, 2450 m., terricole among mosses and *Stereocaulon* sp., *Miss Cheeseman 25*, at Kew.

Thallus fruticosus, subrigidus, 8–10 cm. altitudine, cinnamomeo-alutaceus, axibus principalibus irregulariter nigro-maculatis, summitatibus obscure olivaceo-alutaceis; basis nigra, dense dichotoma, ramis inferne 1 mm. diametro in medio ad 2–3 mm. dilatatis, dein superne ad 0.5 mm. tenuescentibus; articulatis, articulis 5–20 (–30) mm. longitudine, apicibus constrictis, basalibus sublaevibus, minutis cum pseudocyphellis; cortex fractus, rugis sulphureo-farinosus, isidiosis cum sorediis; superne articulis plus minusve minute verrucosis, rugis plus elevatis et subreticulatis, soraliis majoribus elevatis, sorediis isidiosis. Apothecia non visa.

49. *USNEA blepharoides* Dodge, sp. nov.

Type: Tanganyika, Kilimanjaro, at upper limit of forest, 3000 m., *G. Geilinger 4417*, at Kew.

Thallus fruticosus, pauci-ramosus, prostratus vel suberectus, ca. 9 cm. longitudine, subarticulatus, inferne 2 mm. diametro, ad 1 mm. diametro sub apotheciis tenuescens, subverrucosus, axibus fulvo-olivaceis, ramulis ciliisque cinnamomeo-alutaceis; ramuli subdistantes, 4–5 (–10) mm. longitudine, curvati, basi subarticulati inflatique, sparse papillati, apicibus acuminatis. Apothecia sessilia, geniculata, subplana; excipulum minute verrucosum; cilia marginalia distantia, ad 10 mm. longitudine, acuminata; discus planus, carneus, tenuiter albo-pruinosis.

62. *USNEA subfoveata* Dodge, sp. nov.

Type: Uganda, Bunyoro, Busingoro, on bark of *Jacaranda*, *I. R. Dale L69*.

Thallus fruticosus, erectus, rigidus, 5 cm. altitudine, flavo-ochraceus, dense dichotomus, articulatus, articulis 1–1.5 mm. diametro, 10 mm. longitudine, apicibus constrictis; rami secundarii teretes, subfoveati, papillati in rugis; isidia singula vel bina in apicibus papillarum; eramulosus. Apothecia subterminalia, ad 9 mm. diametro, cupulata, dein plana; excipulum laeve vel verrucosum et subimpressum; cilia marginalia distantia, ad 1.5 mm. longitudine, medio inflata, apicibus subacutis; discus concavus dein planus, ochraceo-alutaceus, tenuiter albo-pruinosis.

73. *USNEA Gossweileri* Dodge, sp. nov.

Type: Angola: Cuanza Sul, Amboim, Capir near the Carloaongo River, 1000 m., on dead trees, *J. Gossweiler 9991*.

Thallus erectus, fruticosus, 5–6 cm. altitudine, olivaceo-alutaceus, inferne sympodialiter, superne dichotome ramosus; rami ca. 1 mm. diametro, annulati, dense verrucosi-tuberculati, teretes; soralia super tuberculos insidentia, isidiosis cum sorediis; ramuli 2–3 (–5) mm. longitudine, irregulariter dispositi, breviores laeves, longiores minute tuberculati. Apothecia rara, sessilia, 3 mm. diametro; excipulum laeve; cilia marginalia subdistantia, 1–2 mm. longitudine, conica; discus carneus albo-pruinosis.

76. *USNEA isabellina* Dodge, sp. nov.

Type: Kenya, Northern Frontier Province, near Buna, summit of Ajao hill, 1030 m., on bushes, *I. R. Dale L71*.

Thallus erectus, rigidus, 7 cm. altitudine, isabellinus; rami 1–1.8 mm. diametro, dichotome ramosi, teretes; cortex laevis, annulatim fractus subareolatusque; ramuli densi fragiles, 2–4 mm. longitudine, crassi, subverrucosi sed non sorediosi; apicibus subnigricantibus; summitates ad 4 cm. longitudine, tenues. Apothecia rara, ca. 5 mm. diametro, lateraliter sessilia, plana vel subconvexa; excipulum laeve, subrugosumve; cilia marginalia distantia, fragilia, longitudine variabilia, plus quam 3 mm. longitudine, ramulis similia; discus avellaneus, tenuiter albo-pruinosis.

78. *USNEA Dalei* Dodge, sp. nov.

Type: Kenya, Northern Frontier Province, near Buna, summit of Ajao hill, 1030 m., on bushes, *I. R. Dale L70*, at Kew.

Thallus pendens, subrigidus, plus quam 16 cm. longitudine, inferne aurantiacocinnamomeus, superne obscure olivaceo-alutaceus, roseo-maculatus; basi subnigricans annulatusque; dichotome ramosus, axibus principalibus ca. 1 mm. diametro ad apicibus tenuescens, acute angulatus ex tuberculis papilliformibus concretescentibus, inter rugis sulcatis, dense ramulosus in rugis corticatis; ramuli 4 (-15) mm. longitudine, curvati flexuose, tuberculati, cum spinulis paucis; summitates tenues, non ramosae nec capillaceae.

82. *USNEA spilotoides* Dodge, sp. nov.

Type: Kenya, Chyulu hills, *H. D. van Someren*, in E. African Herb.

Thallus procumbens aut pendens, subrigidus, ca. 10 cm. longitudine, fulvus, ramulis pallide olivaceo-alutaceis; sympodialiter ramosus, ad 0.9 mm. diametro, ad summitates subcapillaceas tenuescens; inferne articulatus, articulis subinflatis, apicibus constrictis, longitudine variabili, minute albo-verrucosus, sore diis isidiosis; ramuli subdistantes, ca. 1 mm. longitudine, laeves, apicibus acutis; summitates fragiles, ad 20 mm. longitudine, apicibus acuminatis. Apothecia non visa.

83a. *USNEA MEYERI* var. *chondroclada* (Steiner) Dodge, comb. nov.

Usnea chondroclada Steiner, Verhandl. Zool. Bot. Ges. 53:228. 1903.

96. *USNEA amaniensis* Dodge, sp. nov.

Type: Tanganyika, East Usambara, Amani-Maramba, 1030 m., growing in festoons on the topmost branches of tall evergreen rain-forest trees, *P. J. Greenway 4151*, ex Herb. E. African Agr. Res. Sta., Amani.

Thallus prostratus, ramis tenuioribus pendentibus, rigidus, plus quam 60 cm. longitudine, flavo-alutaceus, basi nigrescens, dichotome ramosus, 1 mm. diametro, superne ad summitates capillaceas tenuescens, teres, laevis; cortex annulatim fractus; ramuli 10-20 mm. longitudine, tenuissimi, recti vel curvati, fragiles, apicibus acuminati, minute tuberculati. Apothecia in ramulis sessilia, cupulata dein fere plana, eciliata; excipulum laeve; discus fuscus, albopruinosus.

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