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A Partial Revision of *Paullinia* (Sapindaceae) for Ecuador, Peru, and Bolivia. Part I.

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SUMMARY

The species of *Paullinia* known from the Central Andean countries and adjacent areas are treated, and discussions presented on the taxonomy of some of the more problematical taxa. Only the taxa of section *Paullinia* (= *Neurotoechus* Radlk.) are treated here, the remaining taxa to be covered in a subsequent publication. The section is divided into several new infrasectional taxa, two new species and two new varieties are described, and the status of several taxa are changed. The identification key is supplemented by two plates illustrating features of capsule, inflorescence, and stem morphology used in the key to species. Three of the new taxa are illustrated by a full plate each.

I. INTRODUCTION

Paullinia is a genus of the Sapindaceae having between 150 and 200 species, all restricted to the Western Hemisphere with the exception of *P. pinnata* L. which occurs in both the American and African Tropics. Within the Sapindaceae, *Paullinia* is most closely related to the large genus *Serjania*, the two being separated solely by characters of the fruit; in *Paullinia* the maturing pistil becomes a dehiscent capsule, in *Serjania* it develops into three samaras.

The present treatment is a revision of the species found in Ecuador, Peru, and Bolivia, with occasional comments on taxa found outside that area. In the "Flora of Peru" (*Fieldiana: Bot.*, vol. 13, part III-A, no. 2. 1956) Macbride included a total of 54 species of *Paullinia* that had been collected in Peru or that could be expected there.

Only the species of Section I, *Paullinia* (=Sect. *Neurotoechus* Radlk.) are treated here; the remainder of the genus will be treated

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in part II, to be published later. Of Macbride's 54 species, 11 belong definitely to section *Paullinia*. Five species of this section that were not included by Macbride are now known from Peru, but since several of the species that Macbride listed are reduced or modified in this revision, the results are, for Peru, a total of 16 taxa belonging to only 12 species. For Ecuador, this treatment gives four taxa belonging to three species; and for Bolivia, six taxa belonging to five species, with the probable occurrence there of two more species.

II. NOTES ON THE BIOLOGY OF *Paullinia*

With the exception of Radlkofer's detailed studies in the anatomy of the Sapindaceae, little has been published on either the structure or functional biology of *Paullinia*. Some of the morphological features found in this genus suggest adaptation for specialized biological functions, especially those related to pollination and dispersal mechanisms.

The following notes include some of the hypotheses I have formed in the course of this study, to which are added references to pertinent literature. Any hypothesis about the probable function of morphological features must, of course, remain conjectural pending study of living plants in the field. I am aware, too, that their consideration is not central to this taxonomic study, but it is hoped that discussions of these matters may encourage others to initiate studies in the functional biology of these tropical taxa.

There are aspects of the biology of *Paullinia* other than those mentioned below that deserve some discussion but their inclusion must be deferred to part II of this study. Among these are the very interesting forms of dispersal mechanisms that seem to have evolved in this genus. Discussion of a possible phylogeny of the species of *Paullinia* is also deferred to part II.

1. ANATOMY AND MORPHOLOGY

Because of Radlkofer's special interests in plant anatomy, the family Sapindaceae is, from the standpoint of anatomy and morphology, probably one of the more thoroughly studied of the large tropical families of dicotyledons. In one of his larger publications he presented a new classification of the Sapindaceae (Radlkofer, 1890) based, at least in part, on the results of his anatomical studies. His system of classification in the genus *Paullinia* (Radlkofer, 1895) made extensive use of the anatomical

features of stem, leaf, and capsule, in addition to the standard use of floral morphology.

His classification divided the genus into 13 sections that were distinguished primarily on the basis of anatomical structure, with special emphasis on the anatomy of the capsule. This system of classification is a relatively natural one, but the morphological and anatomical characters on which it is based are somewhat difficult to recognize. This is partly because some of these characteristics occur only rarely outside the Sapindaceae, consequently, are unfamiliar to most taxonomists; and partly because of a lack of illustrations of critical features. Finally, difficulty may arise because Radlkofer's descriptions are replete with terminology unfamiliar to taxonomists. It is apparent that most taxonomists who have published new taxa of *Paullinia* since Radlkofer's monograph have generally not understood his sections nor the anatomical and morphological features by which he distinguished them. Certain of these features, especially those that occur in sect. *Paullinia*, deserve some discussion.

A distinctive appearance of the dried capsule is the primary feature on which section *Paullinia* is recognized. The capsule's outer surface is covered with a system of ridges or nerves that are closely packed, parallel to each other, longitudinally oriented but curving away from the lines of dehiscence and converging on the midline of each valve (pl. I). All species of the section exhibit this feature and only in occasional immature fruits is it indistinct.

Another feature of taxonomic significance found in section I is the presence of composite wood. This is an unusual development of the vascular system of the stem and branches that apparently occurs only in a few lianaceous genera. Within this section it is most markedly developed in certain species of subseries *Alatae* (pl. II). The presence and degree of development of this feature is roughly correlated with the occurrence of other distinguishing features but most striking is its correlation within subseries *Alatae* with ecological conditions. It is most strongly developed in such species of the lowland tropical rain forest as *P. exalata*, *P. largifolia*, and *P. alata* ssp. *loretana* in the western part of the Amazon Basin. In the Pacific and Caribbean drainages, *P. alata* ssp. *loretana* again shows highly developed composite wood, especially in the areas of almost continuous high humidity such as the premontane forest of Western Ecuador, and from the Chocó of

Colombia through Panama to the Caribbean lowlands of Costa Rica.

By contrast, *P. elegans* ssp. *elegans* of the seasonably dry forests and savannahs of eastern and southern Brazil, Paraguay, southeastern Bolivia, and northeastern Argentina has a form of composite wood in which the peripheral bundles have little secondary growth, remaining small while the central bundle grows normally.

In the remaining subseries and series of section *Paullinia*, the peripheral bundles are either weakly developed or entirely lacking (wood simple). All these have species that occur in the wet lowland rain forest of Amazonia, but, on the basis of other characteristics, I am inclined to think that these species probably evolved outside that humid forest area, having entered during either the Pleistocene or Holocene, while several other taxa seem still to occupy only areas peripheral to the rain forest.

2. POLLINATION BIOLOGY

The literature of pollination biology contains little mention of *Paullinia*, but in the course of this study I have encountered structural features very suggestive of adaptation for specialized pollination mechanisms. Possibly the earliest mention of *Paullinia* in pollination literature was by Müller (1873). The statement, as translated by Thompson (1883), was to the effect that the flower of *Serjania cuspidata* St. Hil. "resembles the labiate type and like *Paullinia* L. is protandrous." In fact, the flowers of *S. cuspidata*, as in many species of *Paullinia*, are functionally unisexual.

The flower is zygomorphic; the filaments are of unequal length and as a group curve downward against the two adaxial sepals then recurving upward to bring the anthers in contact with the hooded scales on the upper (abaxial) petals. In this respect they resemble the position of the stamens as found in many species of *Cassia*. The four petals are asymmetric, grouped toward the top (abaxial side) of the flower, and each bears a large scale or flap arising on the inner surface near the base. The scales are often nearly as large as the petals and are generally of two types; the two upper scales are markedly crested or hooded and usually more or less bilaterally symmetrical, the two lateral scales are usually asymmetrical, often are furnished with long hairs on the inner surface and a fringed margin, and the apical hood or crest is less well developed or in some species entirely lacking. The apex of the crests are of thicker,

perhaps glandular tissue. I have reasoned that the hood of the scale may contain accumulated nectar within, derived either from glands within the crest or from glands in the fleshy lobes of the disc that project up into the hooded scales. If this assumption is correct then it is likely that the pollinator enters the flower from above (i.e., pollination is sternotribic, the pollen being deposited on the dorsal surface of the pollinator) forcing a way between the anthers and the upper scales and perhaps gaining leverage by grasping the hairs and fringe of the lateral scales. Pollination mechanisms such as this are well known for many papilionoid legumes. While in staminate flowers the reduced, non-functional pistil is small and symmetrical, in functionally pistillate flowers the pistil is larger, curves toward the two lower sepals, the style recurving upward to bring the stigmas in close proximity to the upper scales; again the resemblance to the flowers of many of the Leguminosae is apparent.

In most species the flowers are borne in spicate, racemose, or sometimes paniculate thyrses which are produced singly in the leaf axils or at the apex of a shoot. In contrast to this are a few species in which the inflorescence is always ramiflorous or cauliflorous, i.e., produced on older, leafless branches or mainstems. Some examples are *P. alata*, *P. exalata*, and *P. hemiptera*, all of section *Paullinia*, and in other sections of the genus such species as *P. trilatera*, *P. metensis*, and *P. tenera*.

In these species the inflorescences are produced at the nodes on usually leafless, older stems. These inflorescences are generally borne in clusters of two to several at a node, each being a very condensed, shortened, paniculate thyrses. As a result of the condensation and clustering, the mature flowers seem to be borne in a hemispheric arrangement. The combination of cauliflory and the hemispheric inflorescences are very suggestive of certain bat pollinated plants. Perch requirements of the bats probably select for cauliflory and ramiflory on sturdy older branches. It also seems reasonable to assume that the much condensed inflorescences are shortened to keep the flowers within reach of the perch area. These ideas are only assumptions, and it should be remembered, as Faegri and Van der Pijl (1966, p. 166) have pointed out, that some cases of cauliflory are related to seed dispersal by bats rather than to pollinator requirements. Discussion of dispersal biology is deferred to the next publication on the genus.

In other species of *Paullinia*, for example, *P. scaberula* R. E. Schultes, *P. turbacensis*, and some undescribed taxa such as

Woodson & Schery 163, from Panama, the cauliflorous inflorescences are somewhat elongated, not forming a densely flowered hemispheric cluster. I am still unable to formulate any ideas about the adaptive significance of this latter form of cauliflory.

III. GUIDE TO THE TAXONOMIC TREATMENT

1. CITATION OF TAXONOMIC LITERATURE

An exhaustive review of the literature on *Paullinia* has been presented by Radlkofer (1896, 1931-1934) and it is not necessary to repeat it here. In the following text, literature citations will be limited to: 1) the protolog, 2) the two Radlkofer publications, and 3) for those taxa not treated by Macbride (1956) it is so indicated.

Throughout the Sapindaceae Macbride listed a number immediately following the date of the protolog, and separated from it by a semicolon. That number corresponds to the page on which that species is described by Radlkofer (1931-1934) in the "Pflanzenreich."

2. CITATION OF GEOGRAPHICAL DATA

In citation of collection localities it has sometimes seemed useful to add to the terse information from the specimen label, placing my additions or comments in brackets. This is done, in most cases, either to pinpoint a collection site or to clarify some element of confusion. An example of the latter is the citation under *P. alata* ssp. *alata* of *Llewellyn Williams 7262* from San Roque, in Dept. San Martín. One might suppose this to be San Roque de Cumbasa, located about 12 km. from Tarapoto and accessible by road, but this is not the case. Rather, it refers to San Roque (on present day maps usually only "Roque") near the upper Río Sisa about 50 km. from Tarapoto. At the time that Mr. Williams collected there in 1930, the principal route between Tarapoto and Moyobamba, the departmental capital, passed through the latter-named San Roque. At present the highway passes to the east of Tabalosas leaving all the upper Río Sisa drainage (including Roque) relatively inaccessible.

Many of the collection sites for tropical South American specimens are very difficult to locate. This is especially true of many older collections, such as those of Pearce, Haenke, and some of Martius' collections, but is true as well for some twentieth century collectors. This difficulty is due to a number of things,

including lack of comprehensive gazetteers; the impermanence of small settlements and villages (especially in the areas of tropical rain forest); difficulties in transcribing place names derived from local dialects; and confusion in orthography (e.g., Sangabán, in Dept. Puno, Perú has been variously cited as San Gabán, San Gaván, and Sangaván). To treat these matters properly, they should be dealt with in a gazetteer-like compilation of collection localities, but that also is beyond the scope of this study.

3. CITATION OF HERBARIUM SPECIMENS AND PHOTOGRAPHS OF SPECIMENS

Among the citations of specimens are citations of photographs from Field Museum's botanical "phototype" collection¹. Most of these are photographs of New World collections found in European herbaria and were photographed by Macbride or his assistants from 1929 through 1939. Not all are photos of type specimens, but those not types are often referred to as "authentic" specimens, i.e., specimens cited in critical or important works. These are cited by negative number and by reference to the herbarium where the specimen was housed when photographed. Thus, "(Photo ex M: F neg. 6002)" refers to negative no. 6002, a photograph of a Martius collection (the type of *P. trilatera* Radlk.) in the herbarium at M (Botanische Staatssammlung, Munich, Germany). Of special importance are the photographs of specimens in the Berlin herbarium (over 5,900 negatives), many accompanied by fragments taken from the sheet photographed. Positive prints from all the negatives are mounted on herbarium paper and interfiled in the herbarium at Field Museum.

Herbarium specimens will be cited as follows: *Woytkowski 6630* (F, MO-2, US) to indicate I have examined the one herbarium sheet of *Woytkowski 6630* that exists in the herbarium at Field Museum, the two sheets at the Missouri Botanical Garden, and the single sheet in the United States National Herbarium.

The abbreviations for herbaria are those of the *Index Herbariorum* (Lanjouw and Stafleu, 1967). Certain collections are cited by abbreviations as follows:

U.C.B.P. — A series of collections made by Mildred Mathias, Dermot Taylor, and José Schunke Vigo, in a project sponsored by the Departments of Botany and Pharmacology of the University of

¹ Field Museum has several photograph collections, each with a separate series of negative numbers. Therefore, when requesting prints, please indicate "Botany Phototype" followed by the negative number.

California at Los Angeles. The collection numbers of this series are distinct from those of José Schunke Vigo's personal collection number series. Thus, *U.C.B.P. (José Schunke V.) 5739* is a *Paullinia* collected in 1962, while *José Schunke V. 5739* is a species of Marantaceae collected in 1972.

Goodspeed Exped. - Collections made by several collectors working under the direction of T. H. Goodspeed of the University of California, Berkeley. Between 1935 and 1947 there were four expeditions to the Andean countries of South America, involving several collectors or teams of collectors. The collection numbers were those of the expedition series and were continuous through the four expeditions. The collections from these expeditions are often cited by collector and number with no indication that the number belongs to the Goodspeed Expeditions series rather than to the collectors own number series.

Subsequently, there were three more expeditions under the direction of Paul Hutchinson. These did not follow the number sequence of the earlier expeditions, using instead, Hutchinson's own collection numbers beginning with *P. C. Hutchinson No. 2* on the fifth expedition.

The first five Goodspeed Expeditions were reviewed, with the collectors and itineraries summarized, by Goodspeed and Stork (1955).

IV. TAXONOMIC TREATMENT

Paullinia L. emend. Radlk. in Engler & Prantl, *Naturl. Pflanzenfam.* III, 5: 305. 1895. [For synonymy see Radlk. *Monographia Paullinia* pp. 71-76, in *Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss.* 19: 67-381. 1896.]

Lianas or scandent shrubs; stems with one to several distinct vascular bundles and referred to as being simple (when only one) or composite (when more than one). Leaves compound (rarely a unifoliate leaf may be produced as an anomaly on an otherwise 3-foliolate or 5-foliolate plant); mostly pinnate or bipinnate, sometimes ternate or biternate, or rarely palmate (in sect. *Castanella*); stipules usually present, persistent or deciduous; petiole and rachis often wing-margined; leaflets membranous to coriaceous, often pellucid punctate or lineate, often having a network of semi-pellucid lactiferous canals that are orange-colored by transmitted light, tertiary venation reticulate or often clathrate, margin usually serrate, serrate-dentate, lobate, or rarely subentire, the teeth often gland tipped. Inflorescence generally single and apical or in the leaf axil, sometimes several in a fascicle then usually produced at the nodes of older, leafless stems (ramiflorous or cauliflorous); basically a thyse but usually the branches modified into cincinni which may be borne on a racemose,

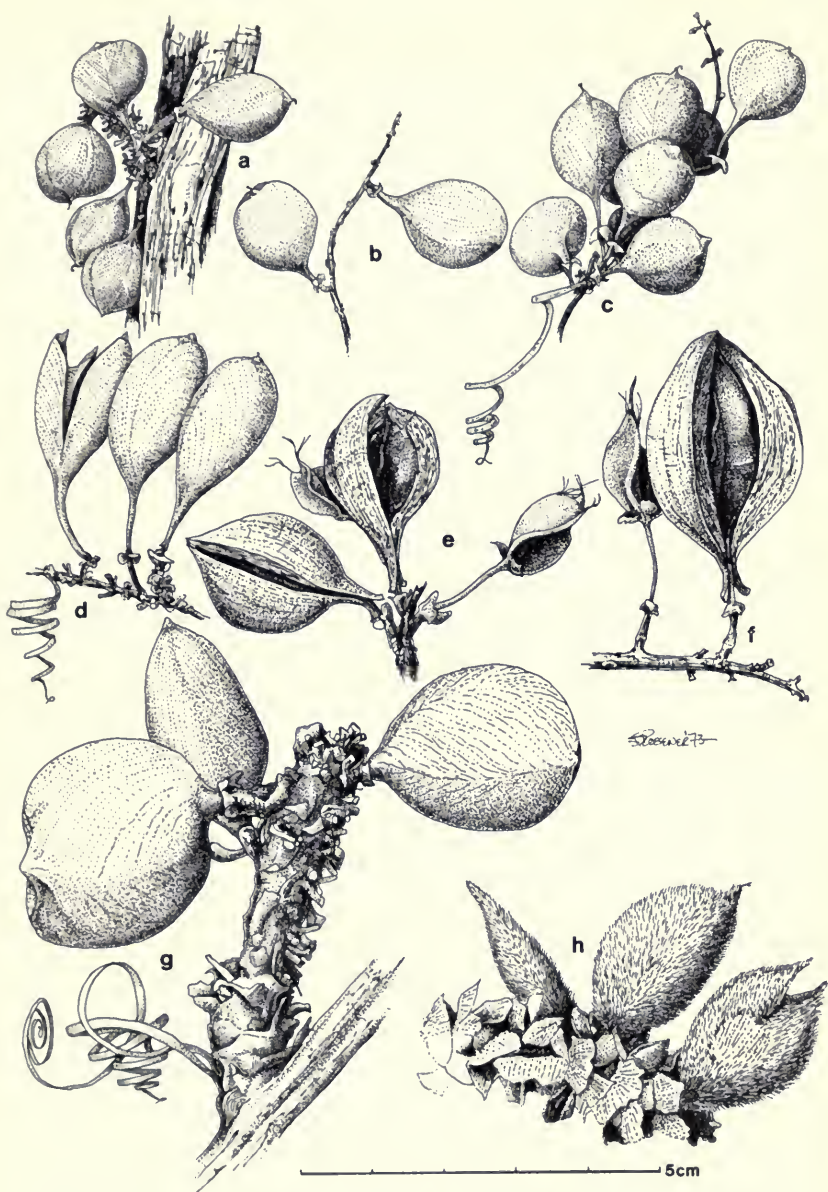


PLATE I. Capsules of sect. *Paullinia*. a, *P. alata* ssp. *loretana*; from Wurdack 1977. b, *P. elegans* ssp. *neglecta*; from U.C.B.P. (Schunke) 6200 and L.I. Williams 6626. c, *P. elegans* ssp. *elegans*; from M.M. Job 960 (coll. in Argentina). d, *P. tumbesensis*; from Dodson & Thien 1285. e, *P. obovata* var. *obovata*; from Woytkowski 5375. f, *P. obovata* var. *polymorpha*; from J. Steinbach 7102. g, *P. bracteosa*; from U.C.B.P. (J. Schunke V.) 6314. h, *P. eriocarpa*; from Woytkowski 5634.

paniculate, or even a corymbose inflorescence; the cincinnus usually subtended by a bract, the flowers by bracteoles. Flowers polygamous or often unisexual, zygomorphic (usually bilaterally symmetric), sepals 5 or sometimes 4 by fusion of the two lowermost, imbricate, free or fused near the base; petals 4, imbricate, free, each bearing on the abaxial surface a petaloid, usually hooded and fringed, glandular scale; scales of the two lateral petals asymmetric, the hood lacking or less developed than on the upper scales; scales of the two upper petals usually markedly hooded, bilaterally symmetrical or less often asymmetrical, sometimes provided with one or two conical or knobby or variously shaped apical projections; disc present, glandular, inequilateral; stamens 8, length slightly unequal, somewhat connivent and slightly upturned toward the apex thus forming a keel-like cluster; pistil often short stipitate, ovary 3-locular, one ovule in each cell, style 1, apically 3-lobed. Fruit a dehiscent capsule, stipitate or sessile; valves septicial, dorsally winged or wingless. Seeds with a usually lustrous black seedcoat and partly enclosed in a fleshy, usually white aril.

Section I. Paullinia. Section *Neurotechus* Radlk. Monogr. Paull. 108. 1895. Pflanzenreich IV, 165: 223. 1931.

The principal distinguishing features of this section are based on the morphology of the mature capsule as follows; capsule wall markedly striated (especially in the dried state) with numerous, parallel, fine ridges and grooves; the ridges formed by elongate, fibrous bundles in the mesocarp; striations longitudinally oriented but in at least the upper half of the capsule diverging from the lines of dehiscence (the margins of the valves) to converge along the mid-line of each valve; capsules stipitate except in series *Eriocarpae*.

Although the following characters may not serve to distinguish this section from all others of the genus, they are often helpful in identification of herbarium specimens. The leaves ternate or 5-foliolate pinnate; no known species of this section have more than 5 leaflets nor are decompound. Stipules usually longer than broad, acute to acuminate (except *P. eriocarpa* q.v.). Wood simple or composite. Fasciculate, cauliflorous inflorescences in several species. Sepals all free (in some species of the other sections the two lower sepals may be fused along their adjoining margins in varying degrees).

Infraclassical subdivisions: On the following pages the species are grouped in three series, one of which is divided into three subseries. The subseries are to some extent intergradient but do, I believe, represent natural clusters of closely related species. I have recognized the species clusters at the hierarchical levels of subseries and series rather than that of subsection and section, as more correctly reflecting the close natural relationships between the species clusters of section *Paullinia*. It may be that series *Eriocarpae* should be elevated to subsectional status, but I believe that the information now available does not yet support such a change.

KEY TO THE SUBDIVISIONS OF SECTION *Paullinia*

- A. Capsules sessile or rarely subsessile, fusiform to ellipsoidal to ovoid, sparsely pubescent (in *P. leiocarpa*) to densely lanate (in *P. eriocarpa*), valves moderately thick; wood composite; branchlets sparsely to densely pubescent; leaves 5-foliolate pinnate. Trinidad and Panama to Brazil and Peru.....series C. *Eriocarpace*
- AA. Capsules usually stipitate, fusiform to obovate to pyriform, glabrous or sometimes sparsely pubescent; wood simple or composite; branchlets glabrous to moderately pubescent (but never densely lanate); leaves unifoliolate to 5-foliolate pinnate.
- B. Capsule valves mostly 5-8 mm. thick; placenta persistent; capsule large, mostly 3-6 cm. long; wood mostly composite; leaves 5-foliolate pinnate. Mexico and the West Indies to Bolivia and Brazil.....series B. *Obovatae*
- BB. Capsule valves thin, mostly 2 mm. thick or less; placenta dehiscing with the valves or sometimes persistent; capsules small or large; wood simple or composite; leaves 1- to 5-foliolate. Distributed throughout the range of the genus.....series A. *Paullinae*
- Consisting of the following three subseries:
- C. Capsules narrowly cylindrical or narrowly claviform, often falcately curved; wood simple to weakly composite; leaves 3-foliolate, rachis not winged. Mexico and the West Indies south to the Caribbean Coast of South America and southeast along the coast to Pará State, Brazil.....subseries 1. *Paullinae*
- CC. Capsules broadly claviform to obovate to pyriform, usually straight; wood simple or composite; leaves 1- to 5-foliolate, rachis winged or wingless.
- D. Capsules short (mostly 15-20 (30) mm. long); capsule wall thin, somewhat pliable (often compressed out of shape in dried material) and leathery; wood mostly composite. Costa Rica south to Brazil, Uruguay and northern Argentina.....subseries 2. *Alatae*
- DD. Capsule long (mostly 2.5-3.5 cm. long); capsule wall thin but rigid; wood simple or composite. Distributed throughout the range of the genus.
subseries 3. *Pinnatae*

ARTIFICIAL KEY TO SPECIES OF SECTION *Paullinia*

Illustrations of characters used in the key indicated by asterisk (*).

1. Inflorescences fascicled, condensed, and cauliflorous (pl. I, fig. a).
 2. Inflorescences single and axial (pl. I, figs. b, c).
 3. Simple wood (pl. II, figs. d, e).
 4. Composite wood (pl. II, figs. a, b, c).
 5. Clathrate tertiary venation (pl. V).
- A. Leaves with winged petiole and rachis (wing sometimes very narrow, e.g., *P. spicata*).
- B. Inflorescences condensed and cauliflorous* (clustered on the older, mostly leafless stems), thyrsoid-paniculate usually about as broad as long.

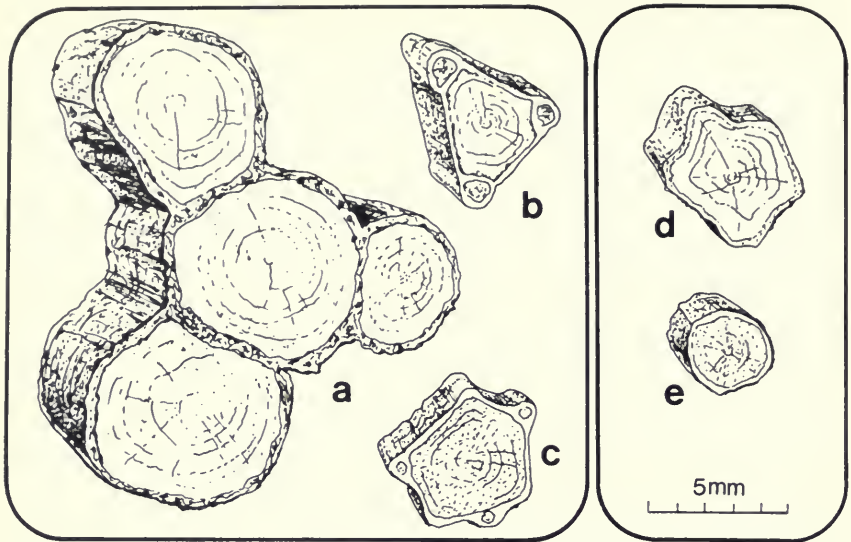


PLATE II. Stem cross-sections illustrating principle variations found in section *Paullinia*. Wood composite in figures a, b, and c; wood simple in figures d and e. a, *P. alata* ssp. *loreтана*; from Wurdack 1977 (F). b, *P. elegans* ssp. *neglecta*; from Vargas 16076 (US). c, *P. eriocarpa*; from Woytkowski 5069 (US). d, *P. clavigera* var. *bullata*; from U.C.B.P. (Mathias & Taylor) 5530 (F). e, *P. hemiptera*; from Ll. Williams 6856 (F).

C. Wood simple*; capsules clavate (endemic to the area around Tarapoto, Peru).
7. *P. hemiptera*

CC. Wood composite*; capsules usually pyriform.

D. Leaves trifoliolate (central and western part of Amazon Basin).

1. *P. largifolia*

DD. Leaves 5-foliolate (widely distributed; along the Pacific Coast from Panama to southern Ecuador and in the Amazon Basin from about 1,000 m. alt. along the east side of the Andes, eastward to Pará State, Brazil, and southward to Sta. Cruz, Bolivia).2. *P. alata*

BB. Inflorescences borne singly* in the axils of the leaves or terminal on the branch, racemose or spicate.

E. Inflorescence bracts broad and rounded or broadly acute at the tip, never acicular, at least 3 mm. wide, usually wider; wood simple*, stems usually stout.

F. Branchlets, inflorescences, and leaves beneath pubescent; capsules estipitate, ellipsoidal or fusiform, densely lanate with yellow-golden pubescence; lower bracts of inflorescence often as broad as long (central and eastern Colombia south to southeast Peru).....13. *P. eriocarpa*

FF. Branchlets and leaves glabrous or branchlets sometimes tomentose; capsules usually stipitate; inflorescence bracts always with length several

times the width (Costa Rica and Panama to Amazonian Bolivia and Brazil).

11. *P. bracteosa*

EE. Inflorescence bracts acuminate, usually acicular; wood composite* or simple*.

G. Valves of the capsules (3) 5-8 mm. thick; wood simple* (Amazonia and the Guianas)12. *P. imberbis*

GG. Valves of the capsules ca. 2 mm. thick; wood simple* or composite*.

H. Petiole and rachis narrowly winged, wing 0.5-1.0 mm. wide on each side; wood inconspicuously composite* (western Ecuador and Dept. Tumbes, Peru).8. *P. tumbesensis*

HH. Petiole and rachis broadly winged, at least 3 mm. on each side; wood composite* or simple*.

I. Leaves large, mostly (15) 20-40 cm. long; leaflets mostly 12-18 cm. long by (4) 5-7 cm. wide; petiole wing mostly 5-8 mm. on each side; wood inconspicuously composite* to simple* (Mexico to Brazil).

6. *P. clavigera*

II. Leaves small, mostly 11-18 cm. long; leaflets mostly 5-12 cm. long by 2-3.5 cm. wide; petiole wing mostly 3-5 mm. on each side; wood inconspicuously composite* (northeastern Argentina, Paraguay and probably adjacent parts of Brazil and Bolivia).

5. The narrow-leaved form of *P. pinnata*

AA. Leaves with petiole and rachis wingless.

J. Inflorescences clustered on older, mostly leafless stems (cauliflorous)*, thyrsoid-paniculate, condensed and usually about as broad as long; wood complex* (central and western parts of the Amazon Basin).....3. *P. exalata*

JJ. Inflorescences single*, axillary or terminal on mostly leafy branches, spicate or racemose; wood composite* or simple*.

K. Leaflet with tertiary venation clathrate*; capsule valves mostly 5-8 mm. thick; wood simple* (Peru and Bolivia).10. *P. obovata*

KK. Leaflet with tertiary venation clathrate* or reticulate; capsule valves mostly less than 2.5 mm. thick; wood simple* or composite*.

L. Leaflet with tertiary venation reticulate; wood composite*.....4. *P. elegans*

LL. Leaflet with tertiary venation clathrate*; wood simple*.....9. *P. spicata*

Series A. *Paulliniae*.

Capsules stipitate, mostly pyriform (seed-bearing part sometimes subglobose) or in a few species narrowly clavate or cylindrical and sometimes falcate-curved (e.g., *P. cururu*); capsule wall often thin, usually 2 mm. or less in thickness, in some species showing the effects of compression in dried, pressed specimens (e.g., *P. alata* and *P. elegans*). Leaves trifoliolate or 5-foliolate, pinnate; tertiary venation of the leaflets

generally reticulate, never markedly clathrate (?); petiole and rachis winged or wingless.

Subseries 1. *Paulliniae*.

Capsules narrowly cylindrical or narrowly claviform, usually falcate-curved, capsule wall somewhat rigid.

This subseries is erected to contain *P. cururu* L., the type species of the genus (judging by a photograph of the type of *P. nitida* H.B.K. it may also belong here). It is distributed from Mexico and the West Indies, to the Caribbean and Atlantic Coasts of Columbia, Venezuela, the Guianas and Brazil (Territory Amapá and Pará State), but does not occur in Ecuador, Peru, or Bolivia nor in areas adjacent to their borders.

Subseries 2. *Alatae* D. Simp. subser. nov.

Capsulae pyriformes; partibus semeniferentibus plerumque subglobosis et aliquantum radialiter trilobatis; valvis illis subseriebus 1 et 3 minus rigidis.

Capsules pyriform; the seed-bearing part often subglobose and radially 3-lobed; the wall less rigid than in subseries 1 and 3, such that in dried material the wall often seems to have been squashed in the drying press. Wood usually composite.

This subseries should probably include, in addition to the species given below, *P. densiflora* J. E. Smith, *P. fasciculata* Radlk., and *P. macrophylla* H.B.K.

Type species: *P. alata* (R. & P.) G. Don.

1. *Paullinia largifolia* Radlk. Bot. Jahrb. 37: 149. 1905. Pflanzenreich IV, 165: 241, no. 2. 1931. Not included in "Flora of Peru."

Liana; the stem with composite wood, 3-angled in cross-section. Leaves trifoliolate; petiole winged, 8-11 cm. long, maximum width (including wings) 6-12 mm.; terminal leaflet 15-24 cm. long by 10-15 cm. wide, broadly ovate, obtuse to truncate at base; lateral leaflets elliptic, broadly acute at base, in the type 18 cm. long by 10.5 cm. wide (fide Radlk.), in the Peruvian collection cited below, as small as 8 cm. long by 5.2 cm. wide; all leaflets subentire, obsolete callose dentate, chartaceous to subcoriaceous, glabrous above except pubescent on veins, uniformly short pilose beneath; petiolules in type ca. 8 mm. long, in Peruvian collection ca. 2 mm. long (i.e., leaflets subsessile). Inflorescences condensed, clustered on older, leafless stems. Fruit unknown.

Type: *Ule 5816* (B, destroyed?).

PERU: [Dept. Loreto: Prov. Alto Amazonas;] edge of forest, Fortaleza, [near] Yurimaguas, *Ll. Williams 4317* (F, US).

BRAZIL: Amazonas: [village of] Belém [on the Rio] Juruá Miry, *Ule 5816* (photo ex B: F neg. 5606).

Easily distinguished by trifoliolate leaves with winged petiole, cauliflorous, condensed inflorescences and striate, wingless capsules.

The Peruvian collection closely resembles the type, differing only in the leaves being smaller in all dimensions except width of winged petiole. Radlkofer describes the leaflet texture as chartaceous but from the photograph of the Berlin type it is certainly as thick as that of the Peruvian specimen which I prefer to describe as subcoriaceous.

2. *Paullinia alata* (R. & P.) G. Don, Gen. Syst. 1: 660. 1831. Radlk., Monogr. Paull. 125, no. 3. 1895. Pflanzenreich IV, 165: 242, no. 4. 1931. *Simarillaria alata* Ruiz et Pavón, Flora Peruv. et Chil. IV: t. 340. 1802 [the unpublished text of vol. IV is reproduced in Anal. Inst. Bot. Cavanilles vol. 12, 13, 14, 15; for *S. alata* see vol. 12: 158-159. 1953]. *P. rhizantha* Poepp. & Endl. Nov. Gen. & Sp. 3: 36, pl. 243. 1844. Radlk. Monogr. Paull. 127, no. 4. 1895. Pflanzenreich IV, 165: 243, no. 5. 1931.

Stem wood usually markedly composite and 3-angled. Leaves pinnate with 5 leaflets; petiole and rachis winged. Inflorescences short, condensed, fascicled on the older stems. Fruit wall markedly striate, usually only 1-2 mm. thick in dried specimens.

In the Pflanzenreich, Radlkofer notes that *P. rhizantha* may not be distinct from *P. alata*. An isotype specimen of *P. rhizantha* (Poeppig 2239) at F resembles the isotype of *P. alata* (Ruiz & Pavón s.n.) at F more than any other specimen in the herbarium! The separation of the two by Radlkofer on the basis of branchlets 3-angled versus 6-angled is, I believe, of little taxonomic significance in this complex and variable species.

The form of cauliflory in this species as also in *P. largifolia* and *P. exalata*, suggests an adaptation to either pollination or seed dispersal by bats.

The specimens at hand do exhibit morphological variations that roughly correlate with differences in geographical distribution. Subspecies *loretana* has large, papery leaflets and is found mostly in the Amazon Basin lowlands. Subspecies *alata* has smaller leaflets that are subcoriaceous to coriaceous and occurs principally in "ceja de la montaña" forests on the Eastern Cordillera and, in Ecuador, on the Western Cordillera and in the lowland forests between that and the Pacific Coast. Material from the humid lowland forests of Costa Rica, Panama, and the Chocó of Colombia more nearly fit subsp. *loretana*. In Peru, the two subspecies are

allopatric in the middle valley of the Huallaga River and near the foothills at the western edge of the Basin (as, for example, at Yurimaguas), but this zone of allopatry probably does not extend above 800 or 900 m. altitude nor eastward more than 50 km. from the foothills of the Cordillera.

There is considerable variation in presence and amount of pubescence such that I am unable to see any justification for retention of Macbride's variety *pubens*. Although this variation occurs in both subspecies, the type of var. *pubens* can be assigned to subspecies *loretana*. To demonstrate the variation in this feature, the pubescent specimens in each subspecies are listed separately.

2a. subspecies *alata*

Leaves, leaf-bearing branchlets and mature, flowering stems smaller in most dimensions than ssp. *loretana*. Leaves 12.5-22 cm. long; lateral leaflets (4.5) 6.5-8.5 (12) cm. long by (1.8) 2.3-3.6 (5.6) cm. wide; terminal leaflets (5) 6.5-10 (15) cm. long by (1.7) 2.6-4.4 (7) cm. wide; petioles 3.0-4.7 (10) cm. long by 3-5 (9) mm. wide (including wings); usually subcoriaceous.

Type: *Tafalla s.n.*, from Chicoplaya, Peru.

PERU: [Dept. Loreto: Prov. Alto Amazonas;] Yurimaguas, *Poeppig 2239* (isotype F, of *P. rhizantha* P. & E.); Prov. Maynas; Mishuyacu, near Iquitos, alt. 100 m., *Klug 1034* (F, US). — Dept. San Martín: [Prov. Lamas: Dist. Roque;] San Roque [on tributary of Río Sisa; not San Roque de Cumbasa], *Ll. Williams 7262* (F); [Prov. San Martín:] Tarapoto, *Ll. Williams 6092* (F). — Dept. Huánuco: [Prov. Huamalies; Dist. Monzón;] Chicoplaya,¹ *Tafalla s.n.* (isotype F; photo. ex B: F neg. 5589); Cachicoto, alt. 800 m., *Woytkowski 7888* (US); [Prov. Huánuco; Dist. Chinchao;] Pampayacu, 7,000 ft., *Kanehira 46* (F). — Dept. Cuzco: Prov. Convención; Echarate, semi-tropical forest in deep woods, *Goodspeed Exped. (Stork, Horton, & Vargas) 10454* (F).

Pubescent phase: Dept. San Martín: [Prov. Moyobamba;] Zepelacio [now Jepelacio], alt. 1,100-1,200 m., *Klug 3263* (F, MO, US). — Dept. Huánuco: [Prov. Pachitea;] Muña, in Andean forest, [alt. ca. 2,300-2,400 m.] *Woytkowski 5213* (F).

ECUADOR: [Prov. Bolivar:] Western Cordillera, lower valley of [Río] Chimbo, 1,000 m., *Rimbach 196* (F-2).

¹Type locality given in the text for volume IV of Ruiz & Pavon's, *Flora Peruv. et Chil.* (see *Ann. Inst. Bot. A. J. Cavanilles* 12: 159. 1953.) as follows: "Habitat in Peruviae Andium nemoribus Chicoplaya, ubi Joannes Tafalla hanc speciem delineavit et descripsit." For the location of Chicoplaya, see Hodge, W. H., in *Bot. Mus. Leaflet* 14 (6): 143. 1950.

BOLIVIA: [Dept. Beni; Prov. Ballivian;] Rurrenabaque, alt. 1,000 ft., *Mulford Exped. (M. Cardenas) 1257* (US).

I have seen no material of the other collections cited by Radlkofer under *P. rhizantha* but it should be noted that the *R. S. Williams* collections he cites are all from Bolivia and not Colombia as given in the "Pflanzenreich" (see below under subsp. *loretana*).

2b. subspecies **loretana** (Macbr.) D. Simpson stat. nov. *P. alata* (R. & P.) G. Don var. *loretana* Macbr. Field Museum Nat. Hist., Bot. Ser. 13, IIIA (2): 331. 1956. *P. alata* (R. & P.) G. Don var. *pubens* Macbr. *ibid. Plate Ia; plate IIa*.

Leaves larger in most dimensions (except petiole width) than subsp. *alata*, and the texture usually chartaceous in contrast to a more coriaceous texture in ssp. *alata*. Leaves averaging 25-35 cm. long; petioles usually 9-12 (15) cm. long; terminal leaflet generally (10) 12-16 (20) cm. long by (4.5) 6.5-7 (9.5) cm. wide.

Type: *Ll. Williams 2339* from Caballo Cocha, Peru.

PERU: Dept. Loreto: [Prov. Maynas; Dist. Ramón Castilla;] forest, Caballo Cocha on the Amazon River, *Ll. Williams 2339* (holotype F, isotype US); [Dist. Putumayo;] Florida, Río Putumayo at mouth of Río Zubineta, alt. ca. 200 m., *Klug 1993* (F, US); [Dist. Iquitos;] Iquitos, alt. ca. 100 m., *Killip & Smith 27421* (F, US); Villa Olgita, Río Itaya near Iquitos, *U.C.B.P. (Mathias & Taylor) 3909* (F); [Prov. Alto Amazonas; Dist. Balsapuerto;] Balsapuerto, alt. ca. 220 m., *Klug 2879* (F, US); [Prov. Coronel Portillo; Dist. Callería;] Pucallpa, on shores of the lake, Pau-Cocha, alt. 200 m., *Woytkowski 6299* (US, MO); [Dist. Padre Abad;] Aguaytía, in forest, alt. 300 m., *Woytkowski 5364* (F). — Dept. Amazonas: Prov. Bagua; [Dist. Aramango;] left bank of Río Marañon above Cascades de Mayasi (opposite km. 278 of Marañon road), elev. 425-500 m., *Wurdack 1977* (F-2, US). — Dept. San Martín: [Prov. Mariscal Cáceres; Dist. Uchiza;] Quebrada Huicte (Río Huallaga), 529 m. alt., in tall forest, *U.C.B.P. (José Schunke V.) 6444* (F). — Dept. Huánuco: [Prov. Leoncio Prado; Dist. Rupa Rupa;] in secondary forest, alt. 700 m., Tingo María, *Woytkowski 5296* (F).

Pubescent phase: Dept. San Martín: Prov. Mariscal Cáceres; Dist. Tocache Nuevo; en bosque alto, desembocadura del Río Mishollo, *José Schunke V. 4708* (F). — Dept. Huánuco: Prov. Huamalies [should be Prov. Leoncio Prado; Dist. Rupa Rupa;] between Supte and Tulumayo Rivers, north of Tingo María, alt. 610 m., *Goodspeed Exped. (Stork & Horton) 9564* (type of var. *pubens* Macbr.; holotype F); [Dist. Rupa Rupa;] in forest, alt. 690

m., Tingo María, *Woytkowski 5321* (F), *5325* (F, MO); Prov. Pachitea; Dist. Honoria; (Bosque Nac. de Iparia: cerca del campamento Miel de Abeja, 1 km. arriba de Tournavista) en monte alto, alt. 300-400 m., *José Schunke V. 1148* (F).

ECUADOR: Prov. Chimborazo: juncture of Provinces of Guayas, Cañar, Chimborazo, and Bolívar, foothills of the western cordillera near the village of Bucay [= General Elizalde], 1,000-1,250 ft. elev., *W. H. Camp 3650* (F, US). — Prov. Guayas: in forest near Pedro Carbo, alt. ca. 100 m., *Haught 3121* (F, US); in forest near Balao, *Eggers 14384* (US). — Prov. Santiago-Zamora: primary rain forest, Taisha, alt. 1,500 ft., *Cazalet & Pennington 7773* (US).

BOLIVIA: Dept. La Paz (?): (Prov. Iturralde?) Maquiqui, *R. S. Williams 689* (US). — Dept. Santa Cruz: Prov. Sara; bosque del Río Palometillas, 400 m., *J. Steinbach 7608a* (F, MO).

3. **Paullinia exalata** Radlk. Bot. Jahrb. 37(1): 150. 1905. Pflanzenreich IV, 165: 244, no. 6. 1931.

Wood composite. Leaves large; petiole not winged, 7-22 cm. long; leaflets 5, (8) 16-22 cm. long by (3.2) 7.5-11 cm. wide, elliptic to obovate, cuspidate with a broad acumen, entire or with a few remote, obtuse or rounded-sinuate teeth; petiolules about 1 cm. long in the specimens and photograph cited below.

Syntypes. — *Ule 5817a* (B) from Brazil, and *Weberbauer 1910* (B) from Peru.

PERU: Dept. Loreto: [Prov. Alto Amazonas; Dist. Yurimaguas;] up river from Yurimaguas, *U.C.B.P. (Mathias & Taylor) 3919* (F-2); Prov. Coronel Portillo; Dist. Yarinacocha; Yarinacocha [near Pucallpa], *Sagastegui & Aldave 5665* (US); vicinity of Pucallpa, southwest bank of Yarinacocha, *U.C.B.P. (Mathias & Taylor) 6023* (F); Dist. Iparia; Bosque Nac. de Iparia, a lo largo del Río Ucayali cerca del pueblo de Iparia, *José Schunke V. 2636* (F). — Dept. Junín: Prov. Tarma; [Dist. Chanchamayo;] La Mercéd in the Chanchamayo Valley, *Weberbauer 1910* (photo ex B: F neg. 5599).

Paullinia elegans Camb. in St. Hil. Fl. Bras. 1: 370, no. 1. 1825. Radlk. Monogr. Paull. 169 no. 9. 1895. Pflanzenreich IV, 165: 255, no. 11. 1931. Not included in "Flora of Peru."

This appears to be a wide-ranging, polymorphous assemblage sparingly found in our area but more common toward the Atlantic and Caribbean coasts of South America. On the basis of the material I have examined there seem to be several regional forms that warrant taxonomic recognition. The most distinctive of these is

found in Paraguay, adjacent parts of Argentina and Brazil (Río Grande do Sul State). It is characterized by relatively small leaflets having reticulate tertiary venation, and broadly marginal teeth. Collections from Bahia State (*Blanchet 1838, 1831, s.n.*; *Glocker 33: Bondar 1665*: all at F) are very near the Paraguayan material, differing if at all, in that the distal leaflets are sessile and often the leaves and leaflets somewhat larger. One herbarium sheet at F (no. 935984) contains fragments of a St. Hilaire collection that seem to belong to this southern element. These fragments are from material at P, and probably the type, and if so that element must be considered typical when assigning epithets to the infraspecific taxa.

It should be noted that although Radlkofer included this species among those of section *Neurotoechus* having composite wood, this characteristic is not so marked as in species such as *P. alata* (R. & P.) G. Don and *P. exalata* Radlk. In *P. elegans* there seems to be, at least in some plants, a growth pattern in which the central bundle develops normally while the peripheral bundles remain small though separate.

4a. subspecies **elegans**. *Plate 1c*.

Syntypes: *St. Hilaire s.n.* from Rio Grande do Sul, and *St. Hilaire s.n.* from Minas Gerais, Brazil.

Distribution (as represented by collections in herbarium F). — Argentina (Provinces or Territories of: Formosa, Chaco, Santa Fé, Misiones, and Corrientes), Paraguay, Brazil (States of Río Grande do Sul, Bahia; Radlk. cites collections from several other states as well).

4b. subspecies **neglecta** (Radlk.) D. Simp. stat. nov. *P. neglecta* Radlk. Monogr. Serjania 42, 71, no. 29. 1875. Monogr. Paull. 167, no. 8. 1895. Pflanzenreich IV, 165: 254, no. 10. 1931. *Semarillaria nitida* Ruiz & Pavón, Fl. Peruv. et Chil. IV: t. 339. 1802.¹ *Plate 1b; plate 11b*.

¹ For the unpublished text intended to accompany the plates of volume IV of the Flora Peruviana et Chilensis, see Anal. Inst. Bot. Cavanilles 12: 157. 1954. Although volume IV was published without text, the illustration is adequate to meet the requirements of the Code (article 44) as an "illustration with analysis showing essential characters." Thus Radlkofer's *Paullinia neglecta*, even though not accompanied by a description, is not a *nomen nudum* since reference to the Ruiz & Pavón illustration fulfills the requirements for validating it as a *nomen novum* replacing *Semarillaria nitida* R. & P. (the epithet *nitida* is preempted in *Paullinia* by *P. nitida* Kunth).

Wood composite. Leaves trifoliolate or an occasional leaf pinnately 5-foliolate; petiole not winged; leaflets elliptic or rotund to obovate, subentire or usually with a few blunt or rounded teeth on the distal half, venation reticulate but occasionally the tertiary veins subclathrate. Inflorescence a spicate or racemose thyrses, the cincinni subsessile. Fruit subglobose, stipitate; the valves sometimes slightly more thick-walled than in subsp. *elegans*.

The occasional presence of pinnately 5-foliolate leaves that Radlkofer mentioned is especially well illustrated in *Schunke-V.* 3877 where a few 5-foliolate leaves are interspersed among the predominantly 3-foliolate leaves! Since even on plants with 5-foliolate leaves, 3-foliolate leaves predominate, this seems to be a "good" (i.e., constant) and, therefore, useful feature for recognizing this taxon.

Type: *Tafalla s.n.* from Vitoc, Peru.

PERU: Dept. Loreto: [Prov. Coronel Portillo; Dist. Callería] on the shore of the lake, Pau Cocha, Pucallpa, alt. 200 m., *Woytkowski* 6320 (MO). — Dept. San Martín: [Prov. Lamas;] Rumizapa, near Tarapoto, *Ll. Williams* 6752 (F); Prov. San Martín; Tarapoto, *Ll. Williams* 6626 (F); in forest, Juan Guerra, near Tarapoto, *Ll. Williams* 6851 (F), 6911 (F); Prov. Mariscal Cáceres; Dist. Tocache; Fundo Miramár 5 km. abajo de Tocache Nuevo, *José Schunke V.* 3877 (F). — [Dept. Pasco (Dept. Junín on label): Prov. Oxapampa;] low andean woodland, Yunguy, alt. 1,600 m., *Woytkowski* 6573 (MO), 6575 (F, MO, US, WIS). — Dept. Junín: [Prov. Tarma; Dist. Chanchamayo;] along Río Perené [now considered part of Río Chanchamayo], near "Hacienda 3," Colonia Perené, alt. about 600 m., forest [at approximately 75° 15' W, 10° 55' S], *Killip & Smith* 25205 (US); cerca al Puente Herrería [bridge over the Chanchamayo River near the village of Francia between San Ramón and La Mercéd], alt. 809 m., *U.C.B.P. (J. Schunke V.)* 6200 (F-2). [Dist. Vitoc;] ad Vitoc arcem, *Tafalla s.n.*¹ (photo ex B: F neg. 5612). — Dept. Ayacucho: Prov. La Mar; Ayna, between Huanta and Río Apurímac, alt. 750-1,000 m., *Killip & Smith* 22743 (US). — Dept. Puno: Prov. Carabaya; [Dist. Sangabán;] puente Inambari [near mouth of Río Sangabán?], alt. 670 m., *C. Vargas C.* 16076 (US).

BOLIVIA: [Dept. La Paz: Prov. Larecaja;] Guanai, 2,000 ft., *Rusby* 530 (F, US), 626 (F). — [Dept. Bení: Prov. Ballivianes;] San Pedro Hacienda, [near] Reyes, alt. 1,000 ft., *Rusby* 1330 (F, MO). — Dept. Sta. Cruz: Prov. Cercado [= Prov. Ibañez?]; campos del

¹The type has been cited as *Pavón s.n.*, or *Ruiz & Pavón s.n.* but was actually a Tafalla collection (see footnote 1, page 154).

Cúchi, 450 m., *J. Steinbach* 7462 (F); Prov. Ibañez; Sta. Cruz de la Sierra, *Ismael Peredo* (20/XI/1946) (F); Prov. Sara; bosques de Buena Vista, 450 m. alt., *J. Steinbach* 6913 (F, MO) [the specimen at MO has leaves trifoliolate only, that at F has both 3- and 5-foliolate leaves in about equal number, all on the same branch].

I had earlier thought that *P. tarapotensis* Radlk., belonged in subseries Alatae. Although I have seen no type material of *P. tarapotensis*, a photograph of the holotype (bearing flowers but no capsules) is available and in general appearance resembles *P. elegans* var. *neglecta*, differing only in leaflet number. Later, certain specimens were found that fit Radlkofer's description of *P. tarapotensis* but have the capsules of subseries Pinnatae plus other features that separate it from *P. elegans*. This discovery occurred too late to revise the manuscript, instead, *P. tarapotensis* is now deleted but will be treated in Part II of this revision.

Subseries 3. **Pinnatae** D. Simp. subser. nov.

Capsulae stipitatae, 2.5-3.5 mm. longae (stipite 3-12 mm. longo incluso), clavatae vel plerumque pyriformes, interdum prominentis tribus, carinatis vel leviter cuculatis, prope apicem instructis; valvis ca. 2 mm. incrassatis, ad maturitatem rigescentibus vel rigidis.

Capsules stipitate, sometimes markedly so, clavate (especially in *P. pinnata*) or more commonly pyriform (with the part above the stipe usually ellipsoidal), sometimes with 3 carinate or slightly cuculate projections near the apex, mostly 2.5-3.5 cm. long including the 3-12 mm. long stipe; the valves about 2 mm. thick, rigid at maturity.

The species of this subsection found in the regions covered in this work are *P. clavigera* Schlect., *P. hemiptera* D. Simp., *P. pinnata* L., *P. spicata* Benth., and *P. tumbesensis* D. Simp. Other species that probably belong to this subseries include *P. sessiliflora* Radlk. and perhaps *P. fibrifera* Radlk., although I have seen no material of this latter species (the several specimens so labeled in hb. F belong rather to some species in Radlkofer's section III).

Type species: *P. pinnata* L.

5. **Paullinia pinnata** L. Sp. Pl. (ed. 1) 366, no. 7 pro partim. 1753. Radlk. Monogr. Paull. 135, no. 6. 1895. Pflanzenreich IV, 165: 247, no. 8. 1931.

Wood composite, sometimes the peripheral bundles remaining small and indistinct, sometimes becoming simple by loss or sloughing of peripheral bundles. Leaves pinnately 5-foliolate; leaflets remotely rounded-serrate; petiole and rachis winged; stipule acicular, 4-7 mm. long, caducous. Inflorescence spicate, axial or terminal; cincinni sessile or elongating in fruit to 5-8 mm. long, subtended by an acicular bract usually not exceeding the flower buds. Capsule 25-30(35) mm. long, the valve ca. 2 mm. thick.

Said to be in Peru based on a Pavón collection in hb. Boiss. (G) [fide Radlk.]. We have no duplicate of this collection at F, nor am I able to find a photo of it in the "phototype" collection¹. I have not yet seen Peruvian material that definitely belongs to this species. Nor have I seen any Ecuadorean or Bolivian collections of this species, but it may possibly be found in the eastern and southern parts of Santa Cruz Department of Bolivia.

This and the following species may be conspecific but the matter is too complicated to attempt a solution here. There seem to be three main forms of *P. pinnata* in the Western Hemisphere; one with narrow elongate leaflets and narrowly claviform capsules found in the Chaco forests of northern Argentina, Paraguay, and adjacent parts of Brazil; one with leaflets broadly ovate to elliptic, seldom more than 8 cm. long, and capsules pyriform or broadly clavate, found from northeastern Brazil through northern Goiás State, Pará State, the Guianas, and northeastern Venezuela; and the third, a more heterogeneous element with larger leaflets that is found from Mexico to Panama and in the West Indies. This third form seems to intergrade with *P. clavigera* in certain parts of Mexico and Central America. The narrow-leafleted "Chaco" form mentioned above probably occurs in southeastern Bolivia and on that basis the species is included in this treatment.

6. ***Paullinia clavigera*** Schlect. *Linnaea* 10: 239, no. 306. 1836. Radlk. *Monogr. Paull.* 175, no. 16. 1895. *Pflanzenreich* IV, 165: 261, no. 20. 1931. Not included in "Flora of Peru."

This species, although primarily from Central America and Mexico, was said by Radlkofer to include a collection from Amazonian Brazil; *Ule 5954* from Fortaleza, on the lower Río Juruá. I have seen no material of the Ule collection, nor any photograph of it. The abundant material from Mexico and Central America in this herbarium (F) is obviously conspecific with several Peruvian collections previously misidentified and filed under other names. However, these collections do seem to represent two more or less distinct elements which are here recognized as two varieties of this species.

6a. var. ***clavigera***.

Lianas; wood usually composite but the peripheral bundles remaining very small relative to the central bundle, or occasionally simple. Leaves (in South American material) very large, (16) 21-40 cm. long; petiole and rachis winged, petiole (4) 6-14

¹See page 131 above for explanation of "phototype" collection.

cm. long; leaflets not pellucid, mostly from 12 cm. long by 4 cm. wide to 18 cm. by 7 cm., subentire to remotely serrate-dentate, apically acuminate or acutely subcuspidate; stipules elongate, broadly ligulate or lanceolate, striate, 10-15 (25) mm. long. Inflorescence borne singly in the leaf axil; the axis becoming robust at maturity; cincinni sessile, subtended by acicular bracts about 4-6 mm. long; flowers pedicellate. Capsules short stipitate, obovate or turbinate, 22-35 mm. long including the 3-5 mm. stipe.

Type: *Schiede 306* from Mexico (photo ex B: F neg. no. 5592).

PERU: Dept. Loreto: [Prov. Coronel Portillo;] Neshuya, 250 m. alt., *U.C.B.P. (José Schunke V.) 6647 (F-2); José Schunke V. 912 (F)*.

BOLIVIA: [Dept. la Paz: Prov. Iturralde;] Tumupasa, *R. S. Williams 466 (US-2)*.

6b. var. **bullata** D. Simp. var. nov. *Plate IId*.

A varietate typica differt foliis rugosis, stipulis aliquantum grandioribus, capsulis pyriformibus, et stipitibus capsularum 6-12 mm. longis.

Like the typical variety except as follows: leaves rugose; stipules somewhat larger; capsules pyriform; stipe 6-12 mm. long.

Type: *Woytkowski 7149* from Dept. San Martín, Peru.

PERU: Dept. Loreto: [Prov. Maynas;] river bank, San Antonio, Río Momón near Iquitos, *U.C.B.P. (Mathias & Taylor) 3880 (F, US)*; [Prov. Requena;] vicinity of Requena, *U.C.B.P. (Mathias & Taylor) 5530 (F-2)*; [Prov. Coronel Portillo;] southwest bank of Yarina Cocha, vicinity of Pucallpa, *U.C.B.P. (Mathias & Taylor) 6020 (F)*. — Dept. San Martín: [Prov. Mariscal Cáceres;] outskirts of forest, Huinguilla [on Río Huallaga between Campanilla and Juan Jui], alt. 500 m. *Woytkowski 7149* (holotype MO, hb. sheet no. 1,793,213; isotype US, hb. sheet no. 2,453,494). — Dept. Junín: [Prov. Tarma; Dist. Chanchamayo;] in forest, Huatsiroke, alt. 1,800 m. [Río Huatziroqui is a tributary entering the Río Chanchamayo (or Río Perené) on the right bank, about 10 to 15 km. below the confluence of the Río Paucartambo], *Woytkowski 5573 (F, MO-2)*.

7. **Paullinia hemiptera** D. Simp. sp. nov. *Plate IIe; plate III*.

Frutex scandens; ligno simplici; ramis juvenilibus pubescentibus et leviter 3- ad 6-angularibus, deinde glabrescentibus et teretibus. Folium 5-foliolis, pinnatim compositum; petiolo et rache alata; foliolis sessilibus, ellipticis vel oblongis vel obovato-ellipticis, subintegeris vel in dimidio distali remote serrato-dentatis; foliolis, rache, et petiolo tomento molli, velvetino obsiti; stipulis acicularibus, 4-8 mm. longis, ad basim 0.5-1.5 mm. latis. Inflorescentiae condensatae, ad nodos caulium veterum effoliferorum fasciculatae. Capsulae clavatae, pubescentes, ad apicem per cristam supra quoque valvam subalatae.

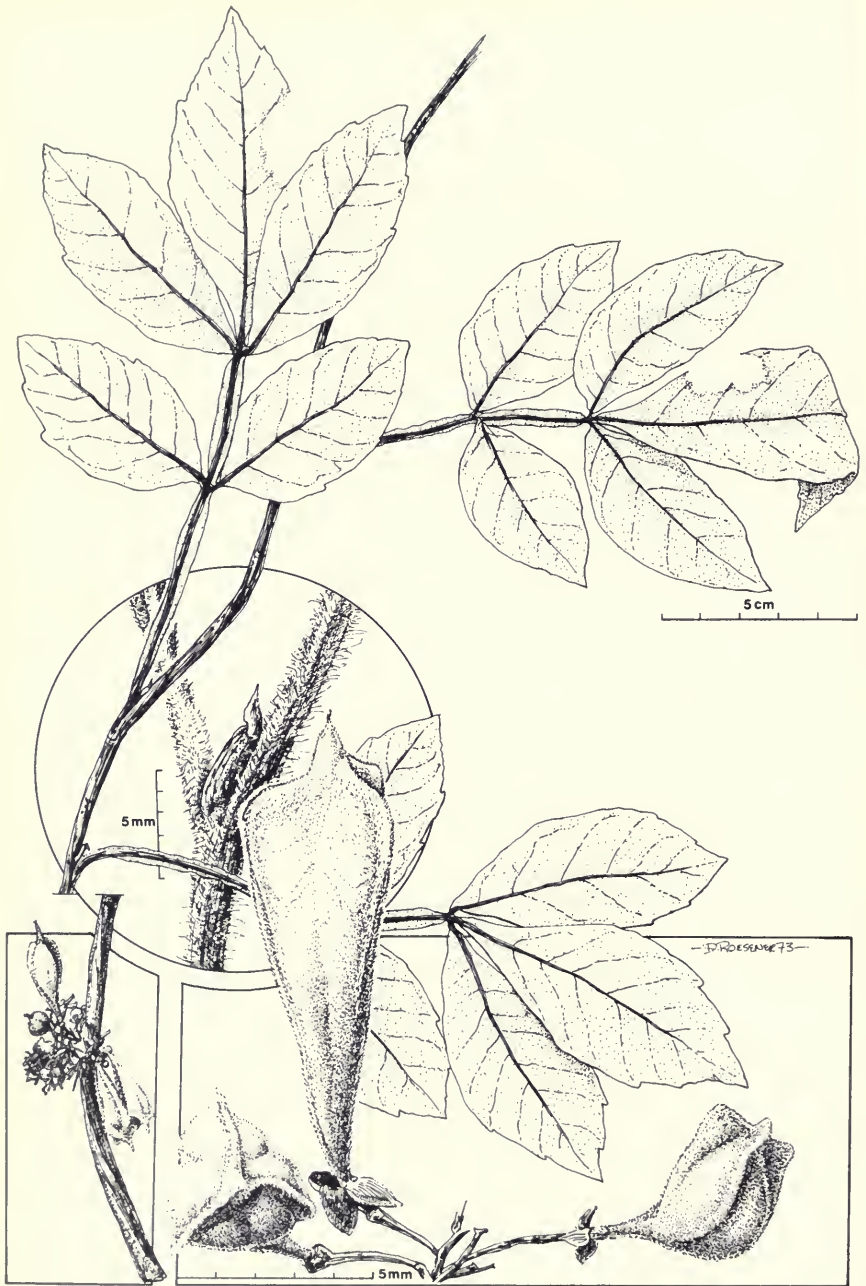


PLATE III. *Paullinia hemiptera*; from holotype, *Ll. Williams* 6517.

Liana; wood simple; young stems weakly 3- to 6-angled, pubescent; older stems mostly glabrous and terete. Leaves pinnately 5-foliolate; petiole and rachis winged; petiole 3.5-8.0 cm. long; leaflets elliptic or oblong or obovate-elliptic, sessile, (4) 6-7.5 (10) cm. long by (2.0) 2.7-3.1 (4.7) cm. wide, subtentire to remotely serrate-dentate in the distal half; the leaflets, rachis and petiole pubescent beneath with soft, velvety tomentum; stipules acicular, 4-8 mm. long, 0.5-1.5 mm. wide at base. Inflorescence of 2 - several condensed thyrses clustered at the nodes of mature, leafless stems. Pedicels 4-5 mm. long, subtended by a minute bract, jointed at midlength. Ovary densely appressed pubescent, strongly 3-angled. Capsules clavate, appressed pubescent; the hairs oriented toward the capsule apex; slightly winged in the apical part; the largest capsules to 22 mm. long by about 8 mm. wide (may develop to larger size; none of those seen had dehisced).

Type: *Ll. Williams 6517* from Tarapoto, Peru.

PERU: Dept. San Martín: [Prov. San Martín;] Tarapoto, alt. 360-900 m., *Ll. Williams 6517* (holotype F, hb. no. 626,681; isotype US, hb. no. 1,779,856); Río Mayo near Tarapoto, *Ll. Williams 6273* (F); Juan Guerra near Tarapoto, *Ll. Williams 6856* (F).

This taxon is probably closely related to *P. pinnata* L., rather than to *P. alata* (R. & P.) G. Don which it resembles in several respects. The crest-like ridges near the apex of the capsule occur occasionally in several species of section *Paullinia*, but seldom as strikingly as in this species.

In choosing the epithet for this species I have followed Radlkofer's practice of using the Latin adjective *alata* when referring to winged petioles (e.g., *P. exalata* Radlk.), while retaining the Greek *pteron* to indicate capsule wings (e.g., *P. plagioptera* Radlk., *P. isoptera* Radlk.).

8. *Paullinia tumbesensis* D. Simp. sp. nov. *Plate Id; plate IV.*

Frutex scandens; ligno composito, fasciculis externis inconspicuis; ramulis, foliis (stipulis petiolisque includentibus), inflorescentiis et sepalis puberulis vel tomentosis. Folia 5-foliolato-pinnata; foliolis late ovatis vel ellipticis vel obovato-ellipticis, rigide subcoriaceis, impunctatis; foliolis ca. 52-109 mm. longis, 29-49 mm. latis; rachibus et petiolis anguste alatis, alis 0.5-1.0 mm. latis utroque costarum; petioli plerumque 4-7 cm. longis; stipulis caducis, subulatis, 6-9 mm. longis. Inflorescentia thyrsium spiciformem in axibus foliorum singulariter prodiens; cincinnis sessilibus; bracteis plerumque 2-4 mm. longis, acicularis. Capsulae stipitatae, pyriformes, ad basim in stipitem attenuatae, 25-32 mm. (stipite incluso) longae.

Climbing shrub or vine; wood composite, the peripheral bundles inconspicuous; branchlets, leaves (including stipules and petiole), inflorescence branches, and sepals puberulous or tomentose. Leaves pinnately 5-foliolate, 12-20 (25) cm. long; leaflets broadly ovate or elliptic or obovate-elliptic, rigidly subcoriaceous, not pellucid punctate, puberulous above on the midnerve and secondary veins, tomentose below on the principle veins and sometimes sparsely between the veins; lateral leaflets mostly 52 mm. long by 29 mm. wide to 91 by 49 mm., terminal leaflet 56 by 30 mm.



PLATE IV. *Paullinia tumbesensis*; from holotype, Simpson 407.

to 109 by 49 mm.; rachis and petiole narrowly winged, the wing 0.5-1.0 mm. wide on each side; petiole (2.4) 4.3-7.0 (9.4) cm. long; stipules mostly caducous, subulate, 6-9 mm. long. Inflorescence single, axillary, a spicate thyrse; the cincinni sessile; bracts mostly 2-4 mm. long, acicular. Capsules stipitate, pyriform, attenuate at base into the stipe, 25-32 mm. long including stipe.

Type: *Simpson 407* from Dept. Tumbes, Peru.

PERU: Dept. Tumbes: Prov. Zarumilla; Dist. Matapalo; Bosque Nac. de Tumbes cerca de Campo Verde, alt. 600-800 m., *Simpson 407* (holotype F-2, hb. sheets no. 1,716,731 fruiting specimen; 1,716,730 flowering specimen; isotypes USM, US, G).

ECUADOR: Prov. Guayas; road from Guayaquil to Cuevedo, km. 78, elev. 100 m., *Dodson & Thien 1285* (F-2, WIS).

9. *Paullinia spicata* Benth. in Hook. Journ. Bot. 3: 193. 1851. Radlk. Monogr. Paull. 104, no. 10. 1895. Pflanzenreich IV, 165: 242, no. 12. 1931.

Wood composite, the branchlets strongly angled and the peripheral bundles small but well defined, or the branchlets terete and the peripheral bundles inconspicuous to absent. Leaves pinnately 5-foliolate; rachis and petiole wingless; leaflets elliptic to obovate, remotely obtuse-crenate, acute-apiculate, tertiary nerves mostly clathrate; stipules minute, covering the apical bud, promptly deciduous. Inflorescence a spicate thyrse, borne singly in the leaf axil; cincinni condensed and sessile, each subtended by an acicular bract 1.5-6.0 mm. long. Capsule stipitate, striate, 2.4-3.5 cm. long; stipe 0.6-1.0 cm. long; valves mostly 2-3 mm. thick; columella sometimes persistent.

Type: *Spruce 524* from Pará State, Brazil.

PERU: Dept. Cajamarca: [Prov. Jaén;] in forest, Jaén, alt. 500 m. [the town of Jaén is at an altitude of ca. 3,000 m., this collection was probably made near Bellavista on the Río Marañon], *Woytkowski 5602* (MO, US). — Dept. Loreto: [Prov. Alto Amazonas;] dense forest, between Yurimaguas and Balsa-puerto, alt. 135-150 m., *Killip & Smith 28167* (US). — Dept. San Martín: [Prov. Mariscal Cáceres; Dist. Juanjui;] in the forest, Juanjui, alt. 400 m., *Woytkowski 7075* (MO, US).

ECUADOR: [Prov. Guayas;] Balao, *Eggers 14247* (US). This specimen has flowering inflorescences but no capsules. It varies from typical *P. spicata* in many respects and its assignment here is tentative. A duplicate of *Eggers 15846* at F appears to be markedly different from the *Eggers 14247* duplicate at US, although both were cited by Radlkofer under *P. spicata*.

An excellent photo of the isotype at M is available (F neg. 5998) but I have otherwise seen no type material. The *Killip &*

Smith collection seems to agree well with the specimen in the photograph, especially as to characters of the leaves, twigs, and inflorescence. The two *Woytkowski* collections, though from widely separated localities, are very similar, yet differ in many ways from both the *Killip & Smith* collection and the type. Although their assignment to this species is tentative, their capsules place them definitely in Subseries *Pinnatae*.

Series B. *Obovatae* D. Simp. ser. nov.

Capsulae grandes, usque ad 7 cm. longae, stipitatae, pyriformes vel obovatae vel fusiformes; valvis plerumque 5-8 mm. crassis, mesocarpio fibroso, plus minusve elastico; placenta post dehiscentiam persistenti, longitudinaliter triquetra, per angustam, filiformem basim ad receptaculum affixa.

Capsules large, to as much as 7 cm. long, stipitate, pyriform or obovate or fusiform; valves of mature capsule mostly (3) 5-8 mm. thick, the fibrous mesocarp slightly elastic; the placenta persistent after dehiscence, longitudinally triquetrous, attached to the receptacle by a narrow thread-like base.

10. *Paullinia obovata* (R. & P.) Pers. Syn. Pl. 1: 443, no. 6. 1805. Radlk. Monogr. Paull. 172, no. 13. 1895. Pflanzenreich IV, 165: 259, no. 16. 1931. *Semarillaria obovata* Ruiz at Pavón, Fl. Peruv. et Chil. Prodr. 54. 1794.

Liana; wood simple; branchlets weakly 3- to 5-angled. Leaves pinnately 5-foliolate; rachis and petiole without wings; petiole mostly 4-12 cm. long; leaflets ovate to elliptic to obovate, 6-18 cm. long and 3-9 cm. wide, acuminate, remotely serrate-dentate, the teeth apices of a dense, gland-like tissue, base rounded to acute (rarely cuneate), glabrous above except scabrous to puberulent along the main veins, a tuft of rigid hairs in the axils of secondary veins beneath, sometimes in the axils of tertiary veins as well, otherwise usually glabrous beneath or infrequently uniformly puberulous, densely glandular to eglandular beneath; stipules caducous (no stipules seen on any of the specimens cited). Inflorescence borne singly in the axil of the leaves or sometimes terminal and axial; rachis usually rusty tomentose; cincinni sessile, bracteate, the bract shorter than or rarely exceeding the flower buds; flowers pedicellate. Fruit stipitate or rarely sessile; obovate to pyriform to fusiform; mostly 3-5 (7) cm. long including the 3-18 mm. long stipe; capsule valves 4-8 mm. thick, fibrous, the fibers oriented longitudinally, sometimes very dense and woody, sometimes corky; the valves dehiscent, usually falling away; the 3-angled placenta usually persistent; seeds half enclosed in the aril; immature fruit green or greenish orange (fide J. Schunke V.), red when mature (fide various collectors), the seed shiny black (fide J. Steinbach) or chestnut-colored (fide Ruiz & Pavón) with a fleshy white aril.

10a. var. *obovata*. Plate Ie.

Leaflets markedly serrate-toothed?, the serrations beginning near the base or at least below the middle; at least some of the secondary nerves bifurcating near the margin; a tuft of barbate hairs in the axils of the secondary nerves beneath, and in the secondary nerve bifurcations, barbate hairs none in the axil of tertiary nerves or rarely a few tertiary nerves with a small axillary tuft. Inflorescence mostly less than

8 cm. long; bracts subulate (fide Radlk.) or (in *Woytkowski 7573*) ligulate, broadly acute, and exceeding the cincinni. Capsules mostly 3 (3.5) cm. long or less, obovate or pyriform.

Type: *Ruiz & Pavón s.n.* from Pozuzo, Peru.

PERU: Dept. Loreto: [Prov. Coronel Portillo; Dist. Callería;] on the shores of the lake, Pau Cocha (Pucallpa) alt. 200 m., *Woytkowski 6305* (MO, US); [Dist. Padre Abad;] in forest, Aguaytía, alt. 300 m., *Woytkowski 5375* (F, MO); river bank opposite village of Aguaytía, *U.C.B.P. (Mathias & Taylor) 3585* (F, LA); on bank of stream, Previsto, alt. 420 m., *Woytkowski 7573* (F, MO, US). — Dept. San Martín: Prov. Mariscal Cáceres; Dist. Tocache Nuevo; en bosque alto, fundo Miramár 5 km. abajo de Tocache Nuevo (margin izquierda del Río Huallaga), *J. Schunke V. 3879* (F). — Dept. Huánuco: [Prov. Leoncio Prado;] Camino Jacintillo [a footpath beginning at the airport bridge opposite Tingo María and leading up the left bank of the Río Huallaga under a precipitous mountainside, upstream to near the confluence of the Río Monzón], vicinity of Tingo María, *U.C.B.P. (Mathias & Taylor) 5928* (F); [Prov. Pachitea; Dist. Pozuzo;] “habitat in Peruviae Andium nemoribus Pozuzo,”¹ *Ruiz & Pavón s.n.* (isotype F; photo ex G: F neg. 23,655; photo ex F: F neg. 53,208); Dist. Honoria; al borde del río en bosque bajo, Isla de Pacanase a 5 km. arriba del campamento (el campamento “Miel de Abeja” del Servicio Forestal, a la orilla del Río Pachitea), 1 km. arriba de Tournavista o unos 20 km. arriba de la confluencia con el Río Ucayali, *J. Schunke V. 2333* (F) [distributed as *P. elongata*].

10b. var. **subrotunda** (R. & P.) D. Simp. stat. nov. *Semarillaria subrotunda* Ruiz et Pavón, Fl. Peruv. et Chil. Prodr. 54. 1794. Ruiz, Syst. Veg. 92. 1798. *Paullinia subrotunda* (R. & P.) Pers. Syn. Pl. 1: 443, no. 15. 1805. Radlk. Monogr. Paull. 174, no. 15. 1895. Pflanzenreich IV, 165: 260, no. 19. 1931. *Semarillaria nervosa* Ruiz et Pavón, nomen ined., in scheda collectionis ex Vitoc a Tafalla legit.

Young branches, inflorescences, and flower buds densely ferruginous tomentose. Leaflet margins with very shallow serrations, mostly limited to the apical half of the leaflet; tertiary venation markedly densely clathrate; leaflets densely puberulous beneath. Inflorescences usually 20-25 cm. long; bracts subulate, ca. 6 mm. long, exceeding the flower buds, soon deciduous. Capsules unknown to me (illustrated in Flora Peruv. et Chil., vol. IV, t. 336).

¹ From Anal. Jard. Bot. Madrid 12: 157. 1953.

Lectotype: *Tafalla s.n.* from Peru¹ (lectotype MA, isolectotypes US, fragment at F).

PERU: [Dept. Huánuco: Prov. Huánuco; Dist. Chinchao;] Pampayacu and [San Juan de] Cochero, *Poeppig 1327* (MO; fragment at F). — [Dept. Junín: Prov. Tarma; Dist. Vitoc;] Vitoc, *Tafalla s.n.* (isolectotype US; fragment at F; photo ex B: F neg. 5629).

Macbride commented in the "Flora of Peru" that this taxon "seems too near *P. faginea*," but this and other comments on the affinities of the *Paullinia* species that he treated should be disregarded. While there are superficial resemblances, the two taxa are, in reality, in separate and only distantly related sections of the genus.

¹No collection sites are given by Ruiz and Pavón in the Prodrómus, but in the Syst. Veg. (p. 93) they state: "habitat offatim in Peruviae nemoribus versus Chinchao, Cuchero et Pozuzo vicos." I have seen none of their specimens from any of those three locations, nor apparently had Radlkofer. In the unpublished text for vol. IV of the Flora Peruv. et Chil. (Anal. Jard. Bot. Madrid 12: 154. 1953) the collection data cited above was repeated and to it was added "..., et in Vitoc via prope Collam et Pucara, ubi Johannes Tafalla." It seems likely that the collections from Chinchao, Cuchero, and Pozuzo were lost in the fire at Macora, since Ruiz in his journal lists *S. obovata* and *S. subrotunda* among those that he subsequently "succeeded in describing in Huánuco, of those that were worked in Macora and were burned in that fire." It is clear from his journal that neither he nor Pavón ever entered the Chanchamayo Valley nor the tributary Río Tulumayo Valley where the village of Vitoc was located.

The collections from Vitoc and Pucara were made by Tafalla in 1794 six years after Ruiz and Pavón's return to Spain, and Tafalla probably included them in a shipment of specimens that he sent to Madrid in 1795 (see Steele, A. R., *Flowers for the King*, p. 271. 1964). The Ruiz specimens cited by Radlkofer, as also the specimen at US cited above, are undoubtedly duplicates of the Tafalla collection from Vitoc. The US specimen has a label headed "*Herb. Reg. Berolinense*" and on the lower parts of the label are; "Peruvia at Chili." and "Ruiz legit, ex herbario Lamberti." This is perhaps from the Griefswald set sent to US in 1895 (see Taxon 19(4): 540. 1970). Although the label on the specimen at B did not so indicate, it too was probably obtained from the Lambert herbarium. The duplicate at FI (cited as "hb. Webb" by Radlk.) was surely part of the sets of specimens that Webb purchased from Pavón in 1826 (see Steele, p. 314).

It seems probable that all the Ruiz and Pavón collections of this taxon were lost and that of the specimens indicated by Ruiz as belonging to this taxon only the Tafalla collection remains in existence. I, therefore, propose its designation as the lectotype.

On the specimen at US (sheet no. 249,751) the label contains, in addition to the information discussed above, a handwritten binomial which apparently is an unpublished manuscript name. This binomial, "*Semarillaria nervosa*," is in a distinctive hand, almost certainly that of Ruiz. The B specimen as shown in the photograph has two handwritten binomials on the label; the first, "*Semarillaria nervosa* Flor. Per.," by the same hand as that on the US specimen, the second, "*Paullinia subrotunda* Pers., Radlk.," seemingly in Radlkofer's hand. It may be that when first received from Tafalla, Ruiz tentatively wrote this binomial on the label and later, finding it to be the same as his description and illustration of *S. subrotunda* so cited it in the manuscript of the Flora Peruv. et Chil., vol. IV, but neglected to change the specimen labels.

10c. var. **polymorpha** D. Simp. var. nov. *Plate If; plate V.*

Varietas ab aliis varietatibus hujus speciei bracteis minutis vel vestigialibus, capsulis plerumque fusiformibus et usque ad 7 cm. longis differt. A varietate *subrotunda* pube sparsioribus in pagina inferiore foliolorum et in ramulis, alabastris plerumque grandioribus, et ab varietate *obovata* capsulis longioribus, foliolis plerumque grandioribus, et nervis tertiariis magis clathratis differt.

Differing from the other varieties of this species by the minute or vestigial bracts, capsules that are fusiform and up to 7 cm. long, from the variety *subrotunda* by the more sparse pubescence on the lower surface of the leaflets and on the branchlets, the larger flower buds, and from the variety *obovata* by the longer capsules, somewhat larger leaflets, and the more clathrate tertiary nerves.

Type: *José Schunke V. 4580* from Tocache Nuevo, Peru.

PERU: Dept. Amazonas: Prov. Bagua; rainforest along Río Santiago 10-15 km. above mouth, elev. 250 m., *Wurdack 2505* (F, US); above Pongo de Manseriche, left bank of Río Santiago, overflow bank ["Dept. Loreto" on label is error], *Mexia 6297* (F, MO, US). — Dept. Loreto: [Prov. Alto Amazonas; Dist. Yurimaguas;] edge of river, Sapote Yacu, Sta. Rosa [ca. 15 km. linear distance downstream from Yurimaguas], alt. 115-210 m., *Ll. Williams 4928* (F). — Dept. San Martín: Prov. Mariscal Cáceres; Dist. Tocache Nuevo; a orilla del río en bosque alto, Quebrada de Tananta (margin derecha del Río Huallaga), *José Schunke V. 4574* (F-2 [flowers and fruit]; duplicates not yet distributed), *4580* (holotype F-2, hb. sheets no. 1,716,732 and 1,716,733 [fruit only, no flowers]; duplicates not yet distributed).

BOLIVIA: Dept. Sta. Cruz: Prov. Sara; quebrada húmeda, bosque, Buenavista, alt. 450 m., *J. Steinbach 7102* (F, MO); bosque del Río Palometillo, alt. 400 m., *J. Steinbach 6783* (F).

The vegetative morphology of this species seems to be exceptionally variable compared to that of the other species in this section. This was probably not apparent to Macbride when he treated *Paullinia* for the "Flora of Peru," for he cited only four collections in all; two under *P. obovata* (the Ruiz and Pavón type and *José M. Schunke 118*) and two under *P. subrotunda* (the type collection and *Poepig 1327*). For the type of *P. subrotunda* he had only the photograph cited above, a fragmentary part of one leaflet from a specimen at Madrid, and a fragment of the *Poepig* collection. It is now fairly obvious that *Schunke 118* is not *P. obovata* nor even closely related to it, but for the Ruiz and Pavón type he had both a full specimen and a photograph of the duplicate at B.



PLATE V. *Paullinia obovata* var. *polymorpha*; from holotype, J. Schunke V. 4580.

Since Macbride's treatment was published new material has accumulated in the herbarium that clearly demonstrates the mutual affinities of *P. obovata* and *P. subrotunda*. At the same time, these new materials raise problems that were not previously apparent. The principal problem concerns devising a new taxonomic treatment. Clearly *P. obovata* and *P. subrotunda* are conspecific, but to what extent should infraspecific elements be given taxonomic recognition and at what hierarchical levels? Unfortunately, even with the additional collections of the last two decades the total of material now available is still such a scanty sampling of this widespread and complex species that it is not yet possible to devise a satisfactory taxonomic treatment.

Even with these few collections there appear to be evident some meaningful patterns of morphology and distribution, and these I prefer to interpret as reflecting the recent evolutionary history of the species. Some hypotheses concerning that evolutionary history are proposed as follows:

The species, perhaps originally a more homogeneous taxon morphologically similar to *Wurdack 2505* and *Ll. Williams 4928*, was geographically fragmented into three elements probably by no later than the mid-Pleistocene. These three elements, var. *obovata*, var. *subrotunda*, and var. *polymorpha*, evolved some differences in morphology in response to ecological selection.

During the period of isolation and divergence the three elements could have been distributed as follows: The var. *obovata* occupied the middle Ucayali Valley centered around the confluences of the Pachitea and Aguaytía Rivers; var. *subrotunda* was confined to a narrow band of forest at middle elevations on the eastern slopes of the Andes; and var. *polymorpha* was probably endemic to a lowland forest refugium centered around the confluence of the Santiago and Marañon Rivers and extending south to the confluence of the Cainarache and Huallaga Rivers, near present-day Yurimaguas.

Post-Pleistocene shifts in climate have brought these three elements into contact again, with hybridization and considerable gene flow between elements resulting in the blurring of morphological differences.

Among the collections cited under var. *polymorpha*, *Schunke 4574* and *Mexia 6297* suggest a strong infusion of var. *subrotunda* genes as also do the *Steinbach* collections from Bolivia.

11. **Paullinia bracteosa** Radlk. Bull. Herb. Boiss., ser. 2, 5: 321. 1905. Pflanzenreich IV, 165: 264, no. 24. 1931. *Plate Ig*.

The branches markedly 3-6-angled and sulcate, stout; wood composite but inconspicuously so,¹ the peripheral bundles remaining very small though distinct. Leaves 5-foliolate pinnate; rachis and petiole broadly winged; leaflets oblong to elliptic to obovate, remotely crenate to obtusely serrate, mostly 12-28 cm. long, (4) 7-12 cm. wide, secondary nerves often plicate-sunken above; petiole (5) 10-26 cm. long; stipules mostly 3-6 cm. long by 5-12 mm. wide, longitudinally striate, oblong or narrowly elliptic, obtuse, usually persistent. Inflorescence stout, usually pubescent throughout, borne singly in the leaf axil; bracts usually exceeding the cincinni, oblong to elliptic, obtuse or broadly acute, 8-20 mm. long, mostly 4-8 mm. wide. Capsules pyriform to broadly obovate, 3-7 cm. long; valves 3-8 mm. thick.

Type: *Tonduz 11416* from Costa Rica.

PERU: Dept. Amazonas: [Prov. Bagua; Dist. Aramango;] in forest at 300 m., Aramango, *Woytkowski 5622* (US). — Dept. Loreto: [Prov. Requena; Dist. Requena;] dense forest on high sandy ground north of Requena, Chacra Canamá [Camaná?], e. side of river, *U.C.B.P. (Mathias & Taylor) 5545* (F); [Prov. Ucayali;] Quebrada de Maquía (Contamana), in tall forest, 220 m. alt., *U.C.B.P. (J. Schunke V.) 6677* (F-2); *J. Schunke V. 938* (F); [Prov. Coronel Portillo; Dist. Padre Abad;] woods near the house of Don Diógenes del Aguila, east of Aguaytía between Pucallpa road and Río Aguaytía, *U.C.B.P. (Mathias & Taylor) 3545* (F), *5066* (F), *5358* (F), *5986* (F). — Dept. San Martín: [Prov. Huallaga; Dist. Saposoa;] in purma [= secondary vegetation], Saposoa, 400 m., *Woytkowski 5070* (F, MO, US), *5404* (F, MO), *5487a* (MO-2); in forest, Gramalote to Saposoa, alt. 450 m., *Woytkowski 5424* (MO); Prov. Mariscal Cáceres; Dist. Tocache; a orilla del río en bosque alto, Fundo Porvenir (margín derecha del Río Huallaga), *J. Schunke V. 4335* (F); [Dist. Campanilla;] in tall forest, 320 m. alt., at Campanilla, *U.C.B.P. (J. Schunke V.) 6314* (F-2). — Dept. Huánuco: [Prov. Leoncio Prado;] at Monzón-Huallaga junction, *U.C.B.P. (Mathias & Taylor) 5339* (F).

BOLIVIA: Dept. La Paz: Prov. Larecaja; Tuirí (near Mapiquí, on left bank of Río Mapiquí), alt. 490-750 m., *Krukoff 10756* (F, MO, US) [distributed as *P. ingaeifolia* Rusby].

The considerable number of collections of this species now in herbaria convincingly demonstrate that the Central American

¹Although the isotype at F seems to lack peripheral bundles, all the other Central American collections (two from Costa Rica and 11 from Panama) have inconspicuously composite wood in which the peripheral bundles seem to remain very small but distinct, as is also the case in the Amazonian materials.

plants, though well separated from the Amazonian ones by geography, differ to no significant degree in any of the critical morphological features. It now seems that the Central American plants are distributed throughout the rain forest of areas below 800 m. alt., from the Caribbean lowlands of Costa Rica and from the Osa Peninsula on the Pacific side of Costa Rica southward, through Panama into the Chocó of Colombia. The Andean highland separates that part of the distribution from the Amazonian populations which occur principally in the western and south-central parts of the Basin. *Krukoff 6522* from Huamaytá on the Rio Madeira, Amazonas State, Brazil, represents the eastern edge of the range as known to me at this time. I have seen no specimens from Colombian Amazonia nor from any part of the Basin north of the Marañon-Amazonas-Solimoes. *P. naiguatensis* Steyermark may prove to be conspecific with *P. bracteosa* and, if so, would considerably extend the range of the latter, for, in addition to the type locality as cited by Steyermark (humid forest in the coastal mountains of the Federal District, Venezuela), there are collections identified by Steyermark as *P. naiguatensis* from Território do Roraima, Brazil (*Prance, et al. 4060*) and an adjacent part of Amazonas State (*Prance et al. 10295*).

12. *Paullinia imberbis* Radlk. Monogr. Paull. 177, no. 18. 1895. Pflanzenreich IV, 165: 263, no. 23. 1931.

Branches 3-6-ridged and sulcate; wood simple. Leaves 5-foliolate pinnate; petiole and rachis winged; leaflets oblong to elliptic to obovate or oblanceolate, remotely serrate. Inflorescence single, axillary or terminal, spicate; cincinni sessile; bracts small, subulate, 2-4 mm. long. Capsules pyriform or [fide Radlk.] ellipsoidal, 2-3 (-4?) cm. long.

Syntypes: *Martius s.n.* from Barra [= Manaus] and Coara on the Rio Negro, and at Pará [Belém]; *Mélinon 59* from French Guiana.

PERU: Dept. Loreto: [Prov. Maynas; Dist. Ramón Castilla;] in forest at Caballo Cocha on the Amazon River [ca. 65 km. east of Leticia, Colombia] *Ll. Williams 2363* (F-2).

There are two collections from Venezuela originally distributed as *P. pinnata* but which are probably *P. imberbis*. These are *Ll. Williams 15242 & 16160*, both from Tatama on the upper Orinoco, in Fed. Terr. Amazonas.

Aside from the three collections cited above I have seen no other material belonging to this species and lacking any photograph of type material must depend on Radlkofer's description alone.

Series C. **Eriocarpae** D. Simp. ser. nov.

Capsulae sessiles (estipitatae) vel subsessiles (tum stipites 5 mm. longae minores), ovoidea vel ellipsoidea vel fusiformes, plerumque pubescentes; valvis 1-5 mm. crassis. Lignum compositum. Folia 5-foliolato-pinnata; rachibus et petiolis alatis.

Capsules sessile (non-stipitate) or subsessile (then the stipe less than 5 mm. long), ovoid to ellipsoid to fusiform, usually pubescent; the valves 1-5 mm. thick. Wood composite. Leaves 5-foliolate pinnate; rachis and petiole winged.

This rather distinctive series includes *P. eriocarpa* Tr. & Pl. (treated below), and *P. leiocarpa* Griseb., a species of the West Indies and the Caribbean Coast of South America, extending eastward through the Guianas to Brazil.

Type species: *P. eriocarpa* Triana & Planchon.

13. **Paullinia eriocarpa** Tr. & Pl. Ann. Sci. Nat. Bot., ser. 4, 18: 353. 1862. Radlk., Monogr. Paull. 179, no. 20. 1895. Pflanzenreich IV, 165: 265, no. 26. 1931. *P. eriantha* Benth. ex Radlk., Monogr. Paull. 179, no. 20. 1895 (*P. eriantha* Benth. was a manuscript name until Radlkofer's monograph provided an accompanying description). *Plate Ih; plate IIc.*

Liana; wood composite, peripheral bundles smaller than the central although remaining noticeably distinct into the older stems; young branches 5-6-angled, densely pilose to lanate with golden yellow to tawny-colored hairs. Leaves pinnately 5- (rarely 3-) foliolate; rachis and petiole broadly winged; leaflets sessile, 7.5-20 cm. long, 3.8-10 cm. wide, usually soft pubescent beneath, subcoriaceous, the tip broadly acute or rounded and with an apiculus, the margin revolute, entire or few toothed, thickened-cartilaginous and straw-colored; petiole 5 to 17 cm. long; stipules lanceolate to narrowly ovate or elliptic, acute or short acuminate, 8-15 mm. long, mostly about 3 mm. wide at base, sometimes to 9 mm. wide by 12 mm. long. Inflorescence densely lanate pubescent, solitary and axial; cincinni sessile; flower buds mostly 7-9 mm. diameter; bracts ovate or suborbicular, sometimes more narrow near the inflorescence apex, broadly acute to rounded at the tip; capsules sessile, fusiform or ellipsoid-fusiform, densely lanate pubescent; the hairs stiff, brittle, and irritating to the skin.

Type: *Triana 3452* from Villavicencio, Colombia.

PERU: Dept. Amazonas: [Prov. Bagua;] forest at Aramango, elev. 300 m., *Woytkowski 5634* (MO). — Dept. Loreto: [Prov. Alto Amazonas;] edge of forest, Fortaleza, Yurimaguas, *Ll. Williams 4302* (F). — Dept. San Martín: [Prov. Lamas;] Rumizapa, near Tarapoto, *Ll. Williams 6770* (F); [Prov. San Martín;] Tarapoto, *Ll. Williams 5849* (F); [Prov. Huallaga;] secondary forest, Saposoa, alt. 400 m., *Woytkowski 5069* (F, MO, US), *7260* (MO, US).

COLOMBIA: Comisaría del Putumayo: forest, Umbria, 0° 54' N, 76° 10' W, alt. 325 m., *Klug 1843* (F, US).

Ll. Williams 4302 from Fortaleza near Yurimaguas is a variant form. It has very broad stipules, flower buds that are pedicellate and smaller than usual in this species; the inflorescence bracts exceed the buds, are only sparsely pubescent, and dark reddish-brown in the dried specimen; the leaflets are nearly glabrous, the apices are subcuspidate and bases are auriculate; the stipules are broadly ovate, ca. 20 mm. wide by 22 mm. long. In all of these features it contrasts with the other Peruvian collections and because there are no fruits, its disposition is tentative.

The other material here cited agrees well with the photograph of the type of *P. eriantha* Benth. ex Radlk., *Spruce 4415* (photo ex B: F neg. 5598) from near Tarapoto. I have seen neither a specimen nor photograph of the type of *P. eriocarpa* Tr. & Pl.

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ADDENDUM

Subsequent to writing the manuscript for this revision I realized that some of Rusby's Bolivian species probably belonged to section *Paullinia*. A loan from the New York Botanical Garden herbarium enabled me to examine type specimens of those species. Four of them proved to be members of this section and synonyms of earlier names as listed here.

Paullinia ingaefolia Rusby, Mem. N. Y. Bot. Gard. 7 (3): 291. 1927.

Type: *O. E. White 1275* from Rurrenabaque, Bolivia. = **P.**

imberbis Radlk.

P. pendulifolia Rusby, *l.c.*, p. 291-2. Type: *Rusby 1622* from pampas near Lake Rogagua, Bolivia. = **P. pinnata** L.

P. ribesiaecarpa Rusby, *l.c.*, p. 293. Type: *Rusby 1730* from Reyes, Bolivia. = **P. elegans** Camb. subsp. **elegans**.

P. tatei Rusby, Phytologia 1 (2): 64. 1934. Type: *G. H. H. Tate 553* from Guanai, Bolivia. = **P. elegans** Camb. subsp. **neglecta** (Radlk.) D. Simpson.

In the "Flora of Peru," Macbride (p. 343) commented under *P. imberbis* Radlk. that *P. ingaefolia* Rusby "is apparently similar but larger in all parts." Before seeing the type of *P. ingaefolia* Rusby, I was inclined to treat it as probably conspecific with *P. bracteosa* Radlk. However, the type specimen has not the distinctive large, obtuse inflorescence bracts of *P. bracteosa*, but shows small, acircular inflorescence bracts like those described by Radlkofer for *P. imberbis*. Even though it seems to fit the description of *P. imberbis*, having neither type material nor "phototype" of the latter, the disposition of *P. ingaefolia* Rusby as a synonym of *P. imberbis* Radlk. must be considered tentative.

VI. INDEX TO EXSICCATAE

Collection		Page	Collection	Page
Blanchet, J. S.	s.n.	143		4574 155, 157
	1831	143		4580 155
	1936	143		4708 141
Bondar, G.	1665	143	Simpson, D. R.	407 151
Camp, W. H.	3650	142	Spruce, R.	524 151
Cardenas, M.	1257	141		4415 161
Cazalet, P.C.D.			Steinbach, J.	6783 155
& T. D.	7773	142		6913 145
Pennington				7102 155
Dodson & Thein	1285	151		7462 145
Eggers, H.F.A.	14247	151	Tafalla, J.	7608A 142
	14384	142		s.n. 140
	15846	151		s.n. 144
Glocker, E. F.	33	143		s.n. 144
Goodspeed Exped.			Tate, G. H. H.	553 162
(Stork & Horton)	9564	141	Tonduz, A.	11416 158
(Stork, Horton, & Vargas)	10454	140	Triana, J. J.	3452 160
Haight, O.	3121	142	U.C.B.P.	
Kanehira, R.	46	140	(Mathias & Taylor)	3545 158
Killip & Smith	22743	144		3585 153
	25205	144		3880 147
	27421	141		3909 141
	28167	151		3919 142
Klug, G.	1034	140		5066 158
	1843	160		5339 158
	1993	141		5358 158
	2879	141		5530 147
	3263	140		5545 158
Krukoff, B. A.	6522	159		5928 153
	10756	158		5986 158
Martius	s.n.	159		6020 147
	59	159		6023 142
Mexia, Y.	6297	155, 157	(J. Schunke V.)	6200 144
Peredo, I.	s.n.	145		6314 158
Poeppig, E. F.	1327	154		6444 141
	2239	139, 140		6647 147
Prance, et al.	4060	159		6677 158
	10295	159	Ule, E.	5816 138
Rimbach, A.	196	140		5817A 142
Ruiz & Pavón	s.n.	153		5954 146
(also see Tafalla)			Vargas, C.	16076 144
Rusby, H. H.	530	144	Weberbauer, A.	1910 142
	626	144	White, O. E.	1275 162
	1330	144	Williams, L.	2339 141
	1622	162		2363 159
	1730	162		4302 160, 161
Sagastegui, A.	5665	142		4317 138
St. Hilaire, A. de	s.n.	143		4928 155, 157
Schiede, C.J.W.	306	147		5849 160
Schunke, J. M.	118	155		6092 140
Schunke V., J.	912	147		6273 149
	938	158		6517 149
	1148	142		6626 144
	2333	153		6752 144
	2636	142		6770 160
	3677	144		6851 144
	3879	153		6856 149
	4335	158		6911 144
				7262 140
				15242 159

	16160	159
Williams, R. S.	466	147
	689	142
Woytkowski, F.	5069	160
	5070	158
	5213	140
	5296	141
	5321	142
	5325	142
	5364	141
	5375	153
	5404	158
	5424	158
	5487A	158
	5573	147
	5602	151
	5622	158
	5634	160
	6299	141
	6305	153
	6320	144
	6573	144
	6575	144
	7075	151
	7149	147
	7573	153
	7888	140
Wurdack, J. J.	1977	141
	2505	155, 157



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