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A TAXONOMIC REVISION OF PROTIUM (BURSERACEAE) IN EASTERN
AMAZONIA AND THE GUIANAS. (VOLUMES I AND II)

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A TAXONOMIC REVISION OF PROTIUM (BURSERACEAE)
IN EASTERN AMAZONIA AND THE GUIANAS

by

Douglas Charles de Burgh Daly

A dissertation submitted to the Graduate Faculty in Biology
in partial fulfillment of the requirements
for the degree of Doctor of Philosophy,
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1987

Volume I

This manuscript has been read and accepted for the Graduate Faculty in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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Prof. David Stevenson, NYBG

Philip I. Prance
Dr. Ghilleen Prance, NYBG

Supervisory Committee

Abstract

A TAXONOMIC REVISION OF PROTIUM (BURSERACEAE)

IN EASTERN AMAZONIA AND THE GUIANAS

by

Douglas C. Daly

Adviser: Dr. Ghilleen T. Prance

Protium is a genus of over 100 species, all but eight of them Neotropical, and most occur in Amazonia and the Guianas. Because the subgeneric classification of Protium is still unsatisfactory, the present work is a revision of the genus in a discrete geographic region.

The tribe to which Protium belongs needed to be re-circumscribed and that generic limits in the tribe had to be re-defined. Characters which had been used to separate it from other genera were found to occur with some frequency in Protium, therefore the limits of the genus had to be defined by other characters.

Protium is almost exclusively dioecious, and sexual dimorphism in the genus was examined in some detail. There is a three-stage morphological series in the reduction of the non-functional pistil in staminate flowers; related species within Protium always show the same stage in that series.

A number of hitherto unexploited taxonomically useful characters were identified in the fruit of Protium, involving variation in color, texture, mesocarp thickness, distribution of the arillate structure on the pyrene, and shape and folding of the cotyledons. Many of these characters can be

studied in the herbarium, but further field observations are needed.

Protium is rather homogeneous ecologically. The great majority of the species are small to medium-sized trees of primary lowland moist forest on terra firme. There are almost no edaphic specialists, and very few species occur in secondary forest. Nonetheless, the Burseraceae (most of them Protium) comprise one of the ecologically most important families in Amazonia. This is primarily due to their high relative density.

Despite this ecological homogeneity, up to 13 species of Protium can occur sympatrically on two hectares of Amazonian forest. Ecological displacement by these taxa can be explained only partially by phenology, strata, and inflorescence types (used as an indication of pollinators). More field work is needed to investigate this phenomenon.

Most species of Protium are widespread in Amazonia, but the patterns of distribution shown by some taxa support the existence of discrete centers of endemism (or Pleistocene refuges) in northern South America.

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enthusiasm and hard work in the field, and for perfectionism in the writing-up of results. Dennis Stevenson of Barnard College has been as helpful and encouraging as anyone at NYBG, and he has always had a ready answer from the most recent literature for any question relating to botany.

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This work is dedicated to the people of Bantry, County Cork, Ireland.

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Introduction

The Burseraceae are a pantropical family of trees consisting of approximately 600 species in 17-20 genera. Four large genera-- Protium, Canarium, Commiphora, and Bursera-- account for 77% of the species. The centers of diversity for the family are the Malaysian archipelago, east Africa, and Amazonia, with one of its three tribes dominant in each of these regions.

The tribe which is dominant in the New World, the Protieae, consists of five genera and about 175 species, of which 75% are in the genus Protium. At least 90% of the species in the Protieae are Neotropical, but Garuga (four species) is restricted to the Malaysian archipelago, and there are eight relictual species of Protium scattered through several discrete portions of the Paleotropics.

Despite the efforts of previous specialists in the family, the majority of the New World Burseraceae (with the exception of Bursera, which has been better studied, e.g., McVaugh & Rzedowski, 1965) have languished undetermined or mis-identified in the herbaria. There has been no active specialist for all the Neotropical genera since Cuatrecasas worked on the family in the 1950's and 1960's, and no one has attempted to see the types for all these taxa since Swart in the 1930's. Porter (1970a) treated the family for the Flora of Panama and published several new species and combinations.

The keys developed by Swart and Cuatrecasas depended primarily on such unreliable leaf characters as the number of leaflets, the length of the acumen, and number of secondary veins. Swart's monograph of Protium was

based exclusively on herbarium work.

With the exception of Protium the genera of the Protieae are all rather small except for Dacryodes, which is severely under-collected. Before the research for the present treatment began there was only one small section of Protium (Icicopsis) separated from the mass of species in the New World. Moreover, this section is an unnatural assemblage of species. Therefore, since the subgeneric divisions of Protium were obviously unsatisfactory, it was decided to revise the species of Protium for a limited geographic area and in the process to carry out a wider review of the subgeneric divisions, rather than choose a badly defined and unnatural section of a genus.

Although the type species of the genus, Protium javanicum Burm. f., was described from Indonesia, there are only 8-9 species in the Paleotropics, and the remainder, 120 or so species, are found in the New World. There are pockets of endemism in Cuba, Central America, Pacific coastal Colombia, the Atlantic forests of Brazil, and the middle to upper Rio Negro. The center of diversity for the genus is in Amazonia.

Most of the Amazonian species of Protium are widespread in the region, and a few extend through the Brazilian Planalto to the Atlantic forests. Approximately 15 species are restricted to western Amazonia or the foothills of the Andes, or as noted to the Rio Negro system, and several appear to be restricted to Amapá and French Guiana.

The greatest concentration of species and individuals is in eastern Amazonia and the Guianas, where some 35 taxa occur. Table I lists estimates of the number of species of Protium in each part of its range.

Table I

Approximate species density of *Protium* by geographic region
(N.B. Overlap between some regions of northern S. America)

geographic region	approximate number of species	
Madagascar	2	
Mauritius	1	
Indonesia	1	
Philippines	1	
New Guinea	1	
India, Thailand, Indo-China	1	7 spp. in Paleotropics
Cuba	5	
Hispaniola	1	
Lesser Antilles	1	ca 7 in Antilles
Mexico	4	
Central America (excl. Mexico)	10	ca 14 in Central America
Colombia and Ecuador		
west of the Andes	10	
northern Venezuela	8	
Guayana region	15	
Guianas	25	
rest of northern S. America	10	
Amazonia	70	
Central Brazil	8	
E and SE Brazil	12	
S Brazil	1	
Paraguay	1	ca 115 in South America

Because eastern Amazonia and the Guianas were much more heavily visited than western Amazonia by the earlier botanical explorers, most of the older names in the genus are to be found from there. Therefore, in virtually all cases, should a western species later prove to be a taxonomic synonym the name used in this treatment will remain unaltered.

Subfamilial classification and generic limits in the Protieae

The generic limits of Protium must be determined in the context of the Protieae, the tribe to which the genus belongs. In order to maintain the integrity of the tribe, Trattinnickia, as shown below, should be transferred to the Canarieae. The remaining four genera, with the exception of the small Asian genus Garuga, are difficult to separate. The key characters that have traditionally been used to separate Crepidospermum and Tetragastris from Protium have since been found in Protium, a situation that resulted in the segregation of two additional genera. These taxa are not recognized in the present treatment, because their acceptance would entail a proliferation of weakly characterized segregate genera. Such a classification is unlikely to be an improvement from a phylogenetic or practical standpoint. Final judgment of this conservative stance will have to await completion of a monograph of the entire genus, which is now under way. The taxa from the Paleotropics, Central America, and eastern and southeastern Brazil must be examined more closely, and further data are needed on leaf anatomy and especially on mature fruits with developed embryos.

Since the unification of Marignia Commers. ex Kunth, Icica Aublet, and Protium Burm. f. under the latter name by Marchand (1867-1868), few attempts have been made at a subfamilial classification of the Burseraceae. Marchand, in the same publication, divided the family by a criterion of free or connate petals, although he himself stated that this system was artificial and unsatisfactory. The family consisted of: tribe

Protieae, with convex receptacle, hypogynous stamens, and free petals; tribe Hedwigieae, with convex receptacle, hypogynous stamens, and connate petals; and tribe Garugeae, with concave receptacle, perigynous stamens, and free petals.

Connation of the petals did not figure in the first classification presented by Engler (1874). Crepidospermum stood alone in tribe Crepidospermeae Engl., defined by its U-shaped embryo. The rest of the family, ostensibly with contortuplicate cotyledons, was contained in the Bursereae Benth. & Hook. f., which was divided into two subtribes: Protieae sensu Marchand, with convex receptacle and hypogynous stamens; and Garugeae Marchand, with concave receptacle and perigynous stamens.

Guillaumin (1909a) experimented with several keys to the genera of Burseraceae, each one stressing a different set of characters: anatomy only; fruits, seeds, and germination only; flowers only; and all characters combined. In all of the keys the genera sorted out in almost the same way, what is now considered the Canarieae in one portion of the key and what are now considered the Bursereae and Protieae mixed together in the other portion. In the anatomical key, the latter assemblage uniformly lacked both "abnormal" vascular bundles and a hypodermis in the leaflets. In the fruit-based key these same genera reappeared together because their drupes contain more than one unilocular pyrene, not a single plurilocular one. Further sorting of the genera was confused, however, by erroneous data concerning which genera have dehiscent fruits. In the flower-based key and the general key the Bursereae and Protieae were mixed together in the portions set off by 4-5-merous flowers.

In Engler's (1913) second classification, which he maintained subsequently (Engler 1915, 1931), he divided the family into three tribes based on the degree of concrescence of the pyrenes. The Protieae sensu Engl. have completely free pyrenes which may be in contact, the Boswellieae Engl. (now Bursereae (Engl.) Lam; cf. Lam, 1932a) have the pyrenes partly connate but separable, and the Canarieae sensu Engl. have the pyrenes completely fused.

In this system, Engler referred Trattinnickia and Dacryodes to the Protieae and Canarieae, respectively. However, both morphological and anatomical characters support the placement of Trattinnickia in the Canarieae. First, the pyrenes in a fruit of Trattinnickia are inseparably fused; secondly, the flowers are trimerous; thirdly, the fruits are indehiscent and have an oily-resinous mesocarp around the three fused pyrenes (instead of a sugary pulpy pseudaril enveloping each pyrene); and fourthly the petioles have anomalous vascular bundles in the medulla (Solereider, 1908). These character states predominate in the Canarieae and are completely lacking in the Protieae if Trattinnickia is excluded. To illustrate how well Trattinnickia is accommodated in the Canarieae, two species of Dacryodes, D. cuspidata (Cuatrec.) Daly and D. glabra (Steerm.) Cuatrec., were originally published as species of Trattinnickia.

With Trattinnickia removed, the tribe Protieae consists of Garuga, Crepidospermum, Tetragastris, and Protium. Garuga, an Asian genus of four species (Leenhouts, 1956), is easily separated from the remainder by usually stipulate leaves, by a concave receptacle with perigynous stamens

and disk adnate to the receptacle, and by compound cotyledons.

The remaining genera are not so readily distinguished from each other. Symptomatic of diversity is a wider variation in pollen morphology within Protium than between Protium and some other genera in the tribe (see chapter on pollen).

Crepidospermum was initially separated from Protium by its U-shaped embryo and isostemonous flowers, but this syndrome was weakened by the discovery of C. rhoifolium (Benth.) Tr. & Pl., which has a J-shaped embryo and diplostemonous flowers. Swart (1942b) created the new genus Hemicrepidospermum to accommodate C. rhoifolium, despite the assertion of Triana & Planchon (1872) that its differences were of degree rather than of qualitative differences. Moreover, it was found that while the staminate flowers of C. goudotianum (Tul.) Tr. & Pl. have five stamens, the pistillate flowers may have five or ten staminodes, so the genus is not strictly isostemonous. Hemicrepidospermum is best considered a section of Crepidospermum. The two sections have three and two species, respectively (Daly, 1987).

In most instances Crepidospermum can be separated from Protium by its U- or J-shaped embryo, subserrate leaflets, and the complete lack of pulvinuli on the petiolules, but partial exceptions in Protium call each of these characters into question. In P. trifoliolatum and related species, the cotyledons are entire and essentially plano-convex, but the dorsal cotyledon is distally slightly uncinately incurved. Subserrate or serrate leaflets occur in most individuals of P. subserratum and P. crenatum, and in some individuals of P. unifoliolatum. The leaflet acumen

is subserrate in P. pilosum and often in P. guianense. Pulvinuli are absent from the petiolules of the lateral leaflets of P. subserratum, P. reticulatum, and of some individuals of P. pilosum, although they are present on the petiolules of the terminal leaflet. Pulvinuli are totally lacking in all the Paleotropical species of Protium. An additional character separating Crepidospermum from Protium is the presence of snail-shaped glands (Solereider, 1908; Metcalfe & Chalk, 1950) on all external organs (except the fruits) of all five species of Crepidospermum. Such glands are completely absent from Protium. Guillaumin (1909a) was the first to comment on these glands, which he called "poils en escargot."

The genera Protium Burm. f. and Tetragastris Gaertn. have long been considered closely related; in fact, many specimens of each genus are mistakenly referred to the other. Traditionally the genera have been separated by the corolla and the embryo, Tetragastris having united petals and cotyledons plano-convex and entire, and Protium having free petals and cotyledons which are lobed and contortuplicate. Rigid adherence to this rule, however, led to the segregation of an artificial assemblage of species as a new genus in the Protieae and to the transfer of several Protium species to Tetragastris. The result was an unnatural circumscription of Tetragastris and a rather ambiguous middle ground between it and Protium which called for a re-examination of generic characters in the tribe. Table II summarizes the basic characters associated with the genera and species groups discussed below.

Following publication of the genus Paraprotium by Cuatrecasas (1952), the limits between Protium and Tetragastris became even more blurred. Paraprotium was distinguished by the combination of the free petals of Protium, the plano-convex cotyledons of Tetragastris, and perfect flowers.

Table II. Distribution of basic characters in the Protieae

	petals	cotyledons	pulvinuli	pistillode and disk	anther
<u>Garuga</u>	free	contortuplicate	present	distinct	sagittate
<u>Crepidospermum</u>	free	U- or J-shaped	absent	distinct	sagittate
<u>Tetragastris</u>	partly fused	plano-convex	only on terminal lfllet.	"ovariodisk"	continuous with filament
<u>Protium:</u>					
sects. <u>Protium</u> , <u>Marignia</u>	free	contortuplicate	absent	distinct	sagittate
sect. <u>Icica</u> s.l.	free or partly fused	contortuplicate or plano-convex	present or absent	distinct	sagittate
sect. <u>Icicopsis</u>	free	transversely folded	present	"ovariodisk"	sagittate
<u>P. suberratum</u> group	free	plano-convex	present or absent	distinct	sagittate
<u>P. apiculatum</u> group	free	plano-convex	present	distinct	sagittate
sect. <u>Sarcoprotium</u>	free	contortuplicate	present	distinct	continuous with filament
<u>P. trifoliolatum</u> group	free or partly fused	plano-convex	present or absent	distinct	sagittate
<u>P. opacum</u> group	free or partly fused	contortuplicate	present	distinct	sagittate

To date four species have been described or placed in the genus, but these four species are phylogenetically rather remote. Paraprotium vestitum Cuatrec., the type species, has in fact unisexual flowers essentially like those of Protium. Except for the plano-convex cotyledons-- a character which is discussed below--, there is nothing in the morphology of this species which could be used to exclude it from Protium. Paraprotium amazonicum Cuatrec. (a taxonomic synonym of Protium fimbriatum Swart) and Paraprotium nitidifolium Cuatrec. form a natural group with Protium apiculatum. They are linked to each other and distanced from P. vestitum by a spindle-shaped pistillode, antesepalous stamens which are reflexed at anthesis, branched styles, and ornamented stigmas. Paraprotium ferrugineum (Engl.) Cuatrec., which was transferred from Protium, forms a natural group with Protium subserratum and P. reticulatum. These three species are linked by having milky resin, abaxial leaflet surface papillate, petals densely pubescent adaxially, stamens in two markedly unequal series, style long, and pyrene extremely bony.

In 1961, Cuatrecasas transferred Protium trifoliolatum and P. unifoliolatum to Tetragastris, because their corollas are basally connate and their embryos are plano-convex. However, other aspects of their morphology are characteristic of Protium: lateral petiolules pulvinulate; stamens in two unequal series with essentially terete filaments and distinct anthers; and (in staminate flowers) a reduced ovary complete with locules and non-functional ovules. Tetragastris tomentosa (Porter, 1970b) possesses a comparable syndrome of characters. It is taxonomically synonymous with Protium pittierii (Rose) Engl.

In most cases Tetragastris can be separated from Protium by this suite of characters: no pulvinuli on the lateral petiolules; basally connate petals; in staminate flowers the disk and pistillode fused into a parenchymatous "ovariodisk" (Lam, 1932a); and entire and plano-convex cotyledons. However, these character states are not restricted to Tetragastris. In fact, each occurs sporadically in Protium, and in patterns which indicate that the characters have evolved independently. Thus: a) Lateral pulvinuli are lacking in P. subserratum (Engl.) Engl. and P. reticulatum (Engl.) Engl., but are present in the very closely related P. ferrugineum (Engl.) Engl. Pulvinuli may or may not be present on lateral leaflets of P. pilosum (Cuatrec.) Daly, while they are conspicuous in the closely related P. trifoliolatum and P. unifoliolatum. b) An ovariodisk occurs in Protium tenuifolium (Engl.) Engl., P. sagotianum Marchand, P. robustum Swart, and the other species of Protium sect. Icicopsis sensu Swart, but it is depressed-conical and pubescent, not high-conical and glabrous as that of Tetragastris. c) Entire, plano-convex cotyledons occur in the closely-related P. subserratum, P. reticulatum, and P. ferrugineum, but also independently in distantly species such as P. paniculatum, P. divaricatum, and P. carolense Daly.

Because the occurrence of plano-convex cotyledons in combination with fused petals induced Cuatrecasas to transfer P. trifoliolatum and P. unifoliolatum to Tetragastris, and to describe P. pilosum in Tetragastris, this latter character deserves close examination. The fusion of the petals in these species differs from that in Tetragastris, and probably arose independently. In Tetragastris sensu stricto, prior to the transfers made

by Cuatrecasas in 1961, the flowers are large (usually more than 5 mm long). The calyx is deeply cupular and the lobes irregularly divided. The lobes of the fleshy, tubular corolla are induplicate-valvate in aestivation and at anthesis the lobes are separated for less than half their length by sinuses of equal depth, remaining erect or becoming negligibly inflexed or reflexed.

The situation is quite different among the species which are indicated above as forming most of the middle ground between the two genera: Protium trifoliolatum, P. unifoliolatum, and P. pilosum. All have similar floral morphology and plano-convex cotyledons, and they form a natural group. Here the flowers are small (usually less than 3 mm long). The calyx is uniformly divided and usually shallowly cupular (deeply so in P. pilosum). The corolla is not markedly fleshy, and in aestivation the petals are often imbricate near the base. At anthesis, except in P. pilosum, the separation of the corolla varies from flower to flower on any given inflorescence: they may be fused 2/3 their length or only obscurely so at the base. Sinuses between the corolla lobes may vary in depth even on a single flower.

Protium pittieri (= Tetragastris tomentosa Porter) and the closely-related Protium opacum present a similar case. The calyx is deeply cupular but uniformly divided. The petals are somewhat fleshy, with slightly imbricate aestivation. At anthesis the corolla is variously divided on any given flower, ranging from fusion 1/2 its length to having almost free petals (often completely free in P. opacum). The petal margins are occasionally partially fused to the filament of an antesealous

stamen. In staminate flowers, the disk and pistillode are distinct and the pistillode is provided with locules and reduced ovules. In addition, Protium opacum has a typical Protium-type embryo (fruiting specimens of P. pittierii are not yet known): the testa shows irregular thickenings and is infolded with the lobed, contortuplicate cotyledons.

This independent assortment of characters indicates that connation of the petals may have arisen independently at least three times in the tribe Protieae. All taxa supposedly intermediate between Protium and Tetragastris do not comprise a natural group and therefore cannot be accommodated in a single intermediate genus. Further segregate genera could be defined only by single, non-unique characters.

Tetragastris is defined by a unique suite of characters, but more importantly it possesses at least one character unique in the Protieae. The anthers, which are basifixed on short, broadly laminar filaments, have entire (not sagittate) bases, such that there is no clear distinction between anther and filament and the stamens appear almost laminar. In addition, the stamens are not clearly biseriate and there is a tendency toward basal fusion of the filaments.

A further character which may prove to be useful in separating Protium from Tetragastris is the bark. The three species of Tetragastris which I have observed in the field-- T. altissima (Aublet) Swart, T. panamensis (Engl.) Kuntze, and T. catuaba Soares da Cunha-- have deeply fissured bark which is shed in large irregular plates. In contrast, all of the approximately 25 species of Protium I have observed have a thin, fine-textured, flaky bark.

As can be seen in the morphology chapter of this revision, Protium is a very diverse group of species in which several major characters vary considerably. It may be that the differences between some sections of Protium will turn out to be greater than the those between Protium and Tetragastris as presented here, in which case an argument could be made to submerge Tetragastris in Protium or to raise all the sections of Protium to generic rank. Resolution of this problem will have to await completion of a subgeneric classification of the latter genus. While several natural groups within Protium have been identified and given sectional status, the bulk of the species remain in the artificial conglomeration known as section Icica (published as Eu-Icica Swart, 1942b).

Taxonomic history and infrageneric classification of Protium

Because the history of Protium is so intimately connected with the grouping of species which make up the genus, the two subjects are treated together in this chapter.

As is so often the case in groups which occur on several continents, for many years the species of Protium in Africa, Asia, and America were called by three different generic names, respectively, Marignia, Protium, and Icica. A hundred years passed between the publication of the first species which could be ascribed to Protium and the unification of these three genera under a single name.

Although the taxa published early on under names Marignia, Icica, and Protium all gave rise ultimately to sections of Protium, the characters used to separate them over the years were erroneous. Kunth (1824), who founded the family Burseraceae, stated incorrectly that only Protium had diclinous flowers, that Protium had a three-locular ovary, that Protium and Marignia had indehiscent fruits, and that Marignia had flat cotyledons (observed in immature fruits). With the exception of the latter character, all of these errors were repeated almost verbatim by de Candolle (1825), G. Don (1832), and Endlicher (1840).

The first species which can be ascribed to Protium was originally published by Linnaeus in 1767 as Amyris protium, and it referred to a plant known by the common name "tingulong" in what is now Indonesia (recorded by Rumphius, cited in Burman, 1775). A year later, Burman (1768) published the same species as a new genus and called it Protium javanicum Burm. f. Although somewhat expanded from that of Linnaeus, Burmann's

description of this taxon could be almost any Burseraceae as the family is now circumscribed.

A few years later, on the other side of the world Aublet (1775) published several species in a new genus from French Guiana, Icica, including those currently known as Protium aracouchini, P. decandrum, and P. heptaphyllum. Unfortunately, his description of the genus could refer to any genus in the tribe Protieae (see previous chapter). However, it is possible to redefine his genus more precisely through study of the types and of his illustrations.

Lamarck (1788) described a new species from Mauritius as Bursera obtusifolia, a taxon which later was the basis for the new genus Marignia Commers. ex Kunth (Kunth, 1824). With great foresight, Lamarck observed that if it proved to be impossible to find differences between the bony pyrenes of Amyris (probably referring to A. protium L., now Protium javanicum), Icica, and Bursera (focusing on what is now Protium obtusifolium), these taxa might have to be united in the same genus.

Willdenow (1799) also perceived unity in two of these taxa, because he placed all of Aublet's Icica species in Amyris, which in his work still included Amyris Protium L.

In the meantime, Gaertner (1790) published a taxonomic synonym, Dammara graveolens. Swart (1942b) considered Marignia to be an illegitimate name because below Marignia Kunth wrote "Dammara Gaertn.?", but the question mark indicated Kunth's uncertainty as to whether Gaertner's genus was truly a synonym.

Some confusion was added to the concept of Protium by Wight &

Walker-Arnott (1834), who referred the type species of Balsamodendrum Kunth to Protium. They also published three new species of Protium which were variously placed among several synonyms of Commiphora before being placed in that genus by Engler (1883).

Judging by the earlier tendencies and later consensuses regarding the Burseraceae, Hooker (1862) was uncharacteristically counterproductive in his treatment of the family for Genera plantarum. Although he recognized that Icica and Protium Burm. f. belonged together, he accepted the Protium of Wight and Walker-Arnott (1834) and included Protium Burm. f. in the later-published Icica, Marignia, Icica, Elaphrium Tr. & Pl., and Bursera Jacq. were all made subgenera of Bursera.

Marchand (1867-1868) created the modern concept of Protium Burm. f. when he submerged Marignia and Icica in Protium. He observed that Marignia was 4-merous and Icica was 5-merous, and believed that I. decandrum Aubl. constituted a transition between the two groups because of the occasional meiomery of the ovary, but he did not explicitly recognize any subgeneric taxa.

Triana and Planchon (1872) agreed with Marchand (1867-1868) that the three genera should be united, although they expressed some doubts because Protium javanicum is 5-merous and all the Icica species they knew were 4-merous. They questioned the usefulness of priority in this case and conserved the name Icica over Protium, because many species had already been published in Icica and only one in Protium.

In his treatment of the Burseraceae for Flora brasiliensis, Engler (1874) recognized no infrageneric taxa in Protium, but he published a new

genus, Icicopsis, which he distinguished from Protium by its inconspicuous disk and dehiscent drupes. At that point he still followed the old misconception of Kunth's (1824) that Protium had indehiscent fruits. He also erroneously wrote that the species of Icicopsis have contortuplicate cotyledons, whereas in fact they are all plano-convex. Engler had his doubts about the validity of Icicopsis as a genus. He noted that the petals varied more among the species of Icicopsis than among all the other species of Protium.

In his treatment of the family for de Candolle's Monographie Phanerogamarum, Engler (1883) published sections Icica and Marignia, which were separated on the basis of whether or not a pulvinulus occurs at the base of the leaflet. Section Marignia consisted of the African species of Protium. Section Icica encompassed all the Asian and American taxa, including all the species of his genus Icicopsis, which he submerged in Protium without giving it sectional status.

Icicopsis was resurrected, this time as a section of Protium, by Swart (1942b). Swart recognized four sections of the genus:

- 1) Section Protium (published as sect. Eu-Protium by Swart, 1942b): puberulous vegetative parts, no distal pulvinulus on the petiolules, the leaflet apex acuminate; species from southeast Asia.

- 2) Section Marignia (Commers. ex Kunth) Hook. f. (1862): glabrous vegetative parts, no distal pulvinulus on the petiolules, leaflet apex obtuse to rounded or emarginate (rarely obtusely subacuminate); species from Madagascar and the Mascarenes. This section was published in Genera Plantarum as a subgenus of Bursera, as was Icica.

3) Section Icica (Aublet) Swart (published as sect. Eu-Icica by Swart 1942b): distal pulvinuli on the petiolules, inflorescences thyrsoïd, flowers pedicellate, disc glabrous, in staminate flowers the disk distinct from the pistillode; species of the Neotropics.

4) Section Icicopsis (Engl.) Swart, with pulvinuli on the petiolules, inflorescences pseudospicate (flowers usually sessile), disk and ovary pilose, in staminate flowers the disk and pistillode fused to form an "ovariodisk" (see chapter on flowers); species of the Neotropics.

Clearly the first two sections, from the Paleotropics, are based for the most part on rather weak and unimportant characters, with the exception of the lack of pulvinuli on the petiolules. While these two may be natural groups, the information at hand is insufficient to defend them or reject them. It is worth noting that in their flower structure and pollen morphology, some Asian species are closer to several Neotropical taxa than the latter are to other New World Protium species (see chapters on morphology and pollen). Also, one character which may function at the sectional level is the fleshy and brightly colored (orange or red) pulp enveloping the pyrene in the African species (Capuron, 1968):

Swart's (1942b) section Icicopsis essentially maintained Engler's species composition of the group, with the addition of P. apiculatum and P. fragrans Urban. In the present treatment these two taxa are excluded from the section, as are P. subserratum, P. ferrugineum (Engl.) Engl., and P. reticulatum (Engl.) Engl. The latter three comprise a natural group, and P. apiculatum forms a natural group with P. fimbriatum Swart, P. firmum Swart, P. nitidifolium (Cuatrec.) Daly, P. minutiflorum Cuatrec.,

and two undescribed species. The three groups are compared in Table III. While they share several characters, it can be seen that the P. apiculatum group is particularly distinct from section Icicopsis in the stricter sense. Section Icicopsis is further defined by punctate leaflets and transversely folded cotyledons.

In the New World, I have recognized one further section of the genus in addition to sections Icica and Icicopsis. Section Sarcoprotium (Daly, in review) is set apart from the rest of the genus by the cucullate petals with clawed bases and usually with a dorsal thickening produced vertically as an appendage, staminate inflorescences always with at least some 3-merous flowers, short stout cylindrical filaments, the anthers showing latero-introrse dehiscence, and usually ellipsoid fruits. In eastern Amazonia this section is represented by the two subspecies of Protium polybotryum

Other assemblages of closely-related species can be recognized within the genus. In some cases the data are not adequate to set them apart as sections. In others I feel it is better to wait until the extra-Amazonian species of the genus have been examined more closely, so as to avoid omission of taxa from a section which might help to define it more clearly. Some of these species groups are as follows, with those occurring in eastern Amazonia and/or the Guianas indicated by an asterisk.

Protium opacum & vars.(*), P. klugii Macbr., P. pittieri (Rose) Engl., P. araguense Pittier.

Table III.

Pivotal characters in section Icicopsis and its segregates

	section <u>Icicopsis</u>	subseriatum group	apiculatum group
sap	resin	latex	latex
lateral pulvinuli	conspicuous	often absent	inconspicuous
<u>leaflets</u> basal pair	opposite	sub-opposite	opposite
lamina	punctate	epunctate	epunctate
abaxially	not papillate	papillate	not papillate
flowers	sessile	sessile	pedicellate
<u>petals</u>			
base	saccate	saccate	not saccate
adaxially	papillate	papillate	dense, long hairs
anthers of two series	unequal	unequal	unequal
disk	pubescent	pubescent	sometimes glabrous
disk and pistillode	"ovariodisk"	"ovariodisk"	distinct
style	long, unbranched	long, unbranched	short, branched
stigmas	globose	globose	caudiculate
fruit	glabrous, smooth	pubescent, smooth	pubescent, usually corrugate
pyrene	bony	bony	cartilaginous
cotyledons	transversely folded	plano-convex	plano-convex

Protium giganteum & vars.(*), P. morii(*), P. carolense Daly, P. decandrum(*).

Protium apiculatum(*), Protium nitidifolium (Cuatrec.) Daly, P. fimbriatum Swart, P. minutiflorum Cuatrec.

Protium trifoliolatum(*), P. pilosum(*), P. guianense(*), P. unifoliolatum(*).

Protium pallidum(*), P. cuneatum(*), P. laxiflorum.

Protium aracouchini(*), P. divaricatum & sspp.(*), P. calanense Cuatrec., P. strumosum

Protium subserratum (Engl.) Engl., P. reticulatum (Engl.) Engl., P. ferrugineum (Engl.) Engl.

Protium demerareense(*), P. altsonii(*).

Protium spruceanum(*), P. heptaphyllum(*), P. guianense(*)

Protium decandrum(*), P. morii(*), P. giganteum(*), P. grandifolium(*).

In addition to the genus Paraprotium (see chapter on generic limits), consideration was being given recently to segregating an additional genus from Protium (J. Cuatrecasas, pers. comm.; D. Porter, pers. comm.). This undescribed taxon is closely related to Paraprotium nitidifolium Cuatrec. These in turn are related to Protium apiculatum Swart as well as a very distinct undescribed taxon from western Amazonia. This group of taxa, originally placed by Swart in section Icicopsis (see Table III), is characterized by latex-like resin, inconspicuous or absent pulvinuli, branched styles, ornamented stigmas, usually corrugate fruits, and entire, plano-convex cotyledons.

Morphology

Materials and methods

This section presents the approach taken to sampling for purposes of species descriptions and explains how the various measurements were made.

Although the scope of this revision is only eastern Amazonia, specimens for measurement were selected from throughout the range of each taxon, in order to make the descriptions more broadly useful. Specimens were also selected to represent the morphological range of each taxon. For each description, when sufficient material was available a total of at least 18 specimens were thoroughly measured, consisting of six fruiting specimens, six specimens with staminate flowers, and six with pistillate flowers. Each of these specimens was measured for 53 parameters, with the quantitative range being recorded for each parameter. When the material allowed, three or more flowers were dissected and measured for the relevant parameters. In addition, once examination of the sample group had been completed, all the material at hand was surveyed for quantitative extremes for all the parameters.

The results of the measurements are expressed as follows: for each parameter, extreme values which represent marked discontinuities in the range of variation are expressed in parentheses. Where data are scarce the entire range is expressed. In some cases when more than 20 specimens were measured and discontinuities were present, one or two sub-extreme values were eliminated, and the range that remained is presented between the extreme values (in parentheses). The data from which the ranges and

extremes were derived have been retained if a statistically more rigorous presentation of the data is desired in the future. The ways in which the measurements were made are as follows.

Vesture. Because original anatomical studies were not carried out in this revision, the complement of trichomes cannot be treated as thoroughly as could be desired. Based on experience and on the recommendations of Theobald et al. (1979), it was decided to avoid the inconsistent and confusing terminology used to describe the overall surface appearance (indumentum). A limited number of terms are used in the present work, in order to avoid confusion and in view of the small range of hair types in Protium (see chapter on anatomy). For a given surface, information is provided for trichome density, thickness, orientation, and length.

Papillae occur on the calyx lobes, adaxial surface and margins of the petals, rarely on the adaxial leaflet surface (P. subserratum and relatives), and rarely on the filaments (P. polybotryum and one undescribed species). A surface is described as long-papillate if the papillae exceed 0.05 mm in length.

The remainder of the trichomes in Protium consist of simple hairs, except for two specialized types discussed in the chapter on anatomy. The covering of hairs is described as dense if the surface is obscured or virtually so, sparse if the hairs would contact each other if laid flat, and scattered if they would not contact each other. Orientation of the hairs is described as erect, ascending (inclined in the direction of the axis), or appressed. Most hairs are straight but some are flexuous. Most are acute but in some instances they are blunt. Hairs described as fine

are translucent and needle-like; those described as thick are short enough and broadened enough basally that they are no longer linear. My future anatomical research on Protium will include a focus on the histological descriptions of the several hair types which occur in the genus.

Branchlets. Branchlet diameter was measured at 2 cm below the vegetative apex, so as to quantify how slender or robust the branchlets are. Branchlet pubescence was examined at 2-5 cm below the apex.

Leaves. Only mature leaves were measured, but because these measurements were made from herbarium material they usually reflect the morphology of the leaves occurring on fertile branchlets. Even these may not reflect the true range, because when species with very large leaves are pressed in the field the branchlets with larger leaves are often either rejected or pruned so they can be more easily pressed. Leaves occurring on the branches or on sterile branchlets are usually larger in every dimension. In cases where sterile inventory material was available, these differences were sometimes taken into account.

Total leaf length includes the petiole and the terminal leaflet. Petiole length is from its point of insertion on the branch(let) to the point of insertion of the basal leaflets, or in unifoliate leaves to the beginning of the terminal pulvinulus. Petiole diameter was measured immediately distal to the pulvinus. The interjuga, expressed in some other taxonomic works as "interpinnal segments," are the segments of the rachis between the insertion of each pair of lateral leaflets. Measurement of the lateral petiolules includes the pulvinuli. The terminal petiolule was measured from the insertion of the ultimate pair of leaflets to the base

of the terminal leaflet blade. The acumen of the leaflet apex was measured from the point of inflection of the curve of the leaflet margin, as judged by eye.

Inflorescences. The inflorescence length/ leaf length ratio was obtained using only the leaves subtending the inflorescences. Inflorescence diameter was measured at ca 1 cm from the point of insertion. Secondary axes are those arising at least 1 cm from the point of insertion. Inflorescences with axes arising less than 1 cm from the point of insertion were considered fasciculate, even if there was a more robust central axis. Inflorescence bracts were divided into three categories for purposes of measurements: those subtending the inflorescences, those occurring on the primary axis, and those occurring on the secondary or higher order axes.

Flowers. Measurements for the flowers parts may seem excessively precise, but on the scale of a flower with a total length of 2-3 mm a difference of 0.2 mm is not trivial. These measurements were obtained using a dissecting microscope equipped with a micrometer which was calibrated daily. Except for overall flower size, flower measurements were made using flowers which had been rehydrated in a weak detergent solution and then hardened in a 70% ethanol solution.

Measurement of the calyx overall includes the calyx tube and the calyx lobes. In species with clavate pedicels the pedicel and the calyx were sometimes difficult to distinguish. Petal length reflects the total length from the point of insertion, not just the portion extending beyond the calyx.

Because the stamens and staminodes are in two series, the measurements for the stamens, filaments, and sometimes the anthers (when anisomorphic in the two series) are presented in pairs, those for the antepetalous stamens being presented first. Disk height is the external height of the disk measured from the insertion of the filaments, and was usually obtained from longitudinal sections of flowers. Disk height varies even within a single flowers because of its laterally undulate shape. Disk width is an expression of the thickness of one side of the disk as seen in longitudinal section. This also varies within a single flower because insertion of the two series of stamens yields sulca of two different depths at the periphery of the disk.

Measurement of the pistillode or pistil overall includes the ovary, style, and stigmatic area, and expresses the height from the point of insertion, not from where the structure exceeds the disk. Pistillode or pistil diameter was measured at the broadest point, usually near the base, and was usually obtained from longitudinal sections of the flowers. Pistil length appears especially variable in some taxa because after pollination the ripening ovary may begin to enlarge before the petals abscise. Measurement of the style length was sometimes difficult, because in many taxa the ovary is only gradually contracted into the style. The point of inflection of that curve had to be estimated. Style diameter was measured at the approximate midpoint of the style.

Fruits. Fruit measurements reflect the fruit size when dry. Fruits are regarded as substipitate if the width of the stipe exceeds its length, and as stipitate if the length exceeds the width. Only mature fruits were

measured, and these were determined by the label information and/or by dissection of a fruit to see if mature embryos were present. Only the 2-3 largest fruits of each specimen were measured, because the fruits on a given infructescence do not mature simultaneously. The pyrenes were measured with the pulp (pseudaril) removed. It should be noted that the descriptions of pyrene shape apply to those removed from fruits that had produced a single pyrene, because fruits which develop more than one locule have pyrenes which are much more variable in shape.

Habit and Architecture

As is true of most of the Burseraceae, the vast majority of the species of Protium are trees. Some taxa tend to be shrubs when they occur in relatively open habitats such as river banks, savannas, or secondary forest, but these same taxa (Protium trifoliolatum, P. guianense, P. unifoliolatum, and P. pilosum) usually also occur as small trees in primary forest. It is interesting to note that they are rather closely related.

The remaining taxa show three patterns: 1) consistently small understory trees which rarely exceed 10-15 m in height and 15-20 cm DBH; 2) small to moderate-sized trees which often reach 20 m in height; and 3) moderate- to large-sized trees whose reproductive individuals are usually 20-30 m tall or higher (see chapter on ecology). I know of no species in Protium which manifests the pattern typical of Trattinnickia, in which most individuals reach or exceed the canopy (emergents), and a few small individuals-- reproductive or not-- are infrequently encountered.

Very little work has been done on the architecture of Burseraceae, perhaps because so few of them are important timber trees. Hallé et al. (1978) included several burseraceous genera in their landmark work on tree architecture: Aucoumea, Canarium, Dacryodes, Pachylobus, Tetragastris, Trattinnickia, and Protium. All but one of the genera they surveyed showed Rauh's Model of growth, in which a rhythmically-growing monopodial trunk develops tiers of proleptic branches which are morphogenetic equivalents of the monopodium.

The only exception was Protium, which they indicated as showing

Troll's Model. In this model, all axes are plagiotropic, the architecture being built by "superposition" of arching terminal axes by axillary branches which arise from the tops of the arches.

The rigorous work of Hallé et al. (1978) often presents voucher collections for the taxa surveyed. I have seen the voucher specimen for their "Protium sp. (Oldeman 2146)," and unfortunately it is a sterile specimen which I cannot identify. While the plant is probably a Burseraceae, I doubt that it is a Protium. Moreover, the notes for one collection of P. robustum (Oldeman 3211) indicate that this species shows Rauh's Model.

In the field, I have dissected (cut down large branch systems) and analyzed the architecture of two taxa, Tetragastris panamensis (Engl.) Kuntze and Protium decandrum, and both show Rauh's Model. I have encountered herbarium material of most species of Protium which shows the tiers of branches characteristic of Rauh's Model.

Some of the smaller understory species of Protium which tend to have relatively broad crowns, such as P. aracouchini and P. trifoliolatum, have the general form of Troll's Model, but I have yet to analyze their architecture. The occurrence of this model in Protium cannot be ruled out, but it has yet to be confirmed.

In the field or on herbarium specimens I have occasionally seen branchlets on which the apex had aborted and a tier of lateral branches had arisen proximal to the aborted apex. If this pattern were to continue it would yield something along the lines of Koriba's Model or Leeuwenberg's Model, but the cases I have encountered have been exceptions

to the rule for each species.

The inflorescences in Protium, as in most other Burseraceae, are axillary. They may be subtended by a leaf or only by a small fleshy bract. They may be distributed along the leaf axils of a branch or they may be congested near the apex, often obscuring the apical bud. In the latter case, as often occurs in Rauh's Model, flowering precedes the development of a tier of proleptic subapical axillary branches.

One variation in the architecture of Protium is found in P. javanicum, in which spines have been observed developing from aborted branchlets (Guillaumin, 1912). Lam (1932a) indicated that this is found only in young individuals of the species. The same phenomenon occurs in adults of Commiphora and, to a lesser extent, Bursera, both genera of the tribe Bursereae. In Neotropical Protium, only P. melinonis shows anything of this nature. Protium melinonis, known only from the holotype in Paris, has two thorns or spines on the one branchlet representing the species. The affinities of this species are unknown, and it is considered a doubtful species in this treatment.

Germination

Germination is clearly a difficult evolutionary problem to solve for seeds which are enclosed in a hard endocarp. Some taxa achieve germination via irregular splitting of the pyrene (stone) wall, e.g., Sideroxylon (Sapotaceae). In some Anacardiaceae each locule of the the stone splits in half at the apex. Some taxa develop fenestral openings in the pyrene. In others, including some Anacardiaceae such as Sclerocarya, an opercular structure develops (Hill, 1933, 1937; von Teichman & Robbertse, 1986).

Protium apparently does not have the specialized germination system developed by at least some species of Canarium, where the embryo pushes out a valve which develops in the hitherto intact compound pyrene (Hill, 1933, 1937). Only one account of the germination of Protium seeds appears in the literature. According to Guillaumin (1909a), the pyrene of P. javanicum Burm. f. opens by a longitudinal line, but he did not indicate where this line appears. I have observed the empty pyrenes of Protium species which remained after germination. Based on these observations and on observation of the intact pyrenes of many dissected fruits, it is apparent that at least in the species of Protium with cartilaginous (not bony) pyrenes, there is a zone of weakness at the trigonal apex of the pyrene (Fig. 10a) which most likely corresponds to the site of the micropyle. When pressure is applied to the pyrene-- at least from without-- the pyrene splits from the apex for a short distance along two lateral lines. These ruptures do not occur easily, but a split on either side of less than one-third the length of the pyrene yields an opening probably large enough for the radicle to emerge. It is possible that a

similar zone of weakness develops in the extremely hard and bony pyrenes of some species such as Protium crenatum and P. subserratum.

Seedlings

This section utilizes the terminology employed by Duke (1965).

Seedlings of Burseraceae may be phanerocotylar (Triomma; Guillaumin, 1910; Bursera, Tetragastris, Protium; Duke, 1969) or more commonly cryptocotylar. When phanerocotylar they may be chlorophyllous (Canarium; Guillaumin, 1909a; Triomma; Guillaumin, 1910) or more often achlorophyllous. They may be entire (Triomma, Aucoumea, Scutinanthe, Tetragastris, Crepidospermum; Guillaumin, 1910; Haplolobus; Leenhouts, 1972), lobed (Santiria, Protium; Guillaumin, 1910), or compound (Canarium, Pachylobus, Garuga, Boswellia, Bursera; Guillaumin, 1910). The eophylls may be alternate (Bursera; Duke, 1969) or more often opposite (falsely opposite in the conception of Guillaumin, 1912). In a few cases these characters may vary within a species. The cotyledons in Dacryodes and Canarium may be compound or pinnatifid (Lam, 1932a). In Dacryodes they are cryptocotylar in the America species D. excelsa Vahl, but it appears that the Old World species are all phanerocotylar (pers. obs. from illustrations in the literature and slides generously supplied by T. Plowman and J. Reitsma).

The few sources available indicate that Protium is phanerocotylar with lobed cotyledons (Guillaumin, 1909, 1910; Duke, 1969). In Protium javanicum Burm. f., the cotyledons become chlorophyllous only after they are exposed to sunlight, and the first eophylls are trifoliate (Guillaumin, 1909a). I have observed older seedlings of various Neotropical species of Protium, and the eophylls are simple, entire, and frequently opposite.

Leaves

It is perhaps most useful to begin this chapter with a diagnosis of the leaf characters of Protium, utilizing the terminology of Hickey (1979). The leaves are alternate, exstipulate, once pinnate, imparipinnately compound to pinnately trifoliate (trifoliolate) or unifoliolate. The lateral leaflets are opposite, although sometimes the basal pairs are subopposite. The leaflets vary greatly in shape. The margin is usually entire or in some instances subserrate or very rarely serrate and never lobed or crenate or dentate. Leaf texture may be membranous, chartaceous, coriaceous. The petiole may be semi-terete or canaliculate, then often slightly acutely winged.

Venation throughout the genus is pinnate/ camptodromous/ brochidodromous. The primary veins are moderate in size and straight. The secondary veins are moderately thick, and their angle of divergence is moderately to widely acute and usually nearly uniform. The course of the secondary veins is usually uniformly curved, rarely abruptly curved. They are usually branched. The loop-forming branches of a secondary vein may join the superadjacent secondary at a range of angles from acute to obtuse. The intersecondary veins may be simple or composite.

Intramarginal veins do not occur. The pattern of the tertiary veins may be reticulate or percurrent. When percurrent they are usually convex; relative to the midvein they are oblique and maintain an approximately constant angle to it; and they are predominantly opposite, joining each other smoothly.

In some cases the higher order veins form a reticulum in which vein

orders cannot be distinguished.

In those leaflets which are toothed, the apical termination is simple.

The leaves of Protium are alternate, but the seedlings often have opposite eophylls (see chapter on seedlings). While the leaves are exstipulate, it should be noted that various kinds of stipular structures are found elsewhere in the family, notably in the tribe Canarieae (Lam, 1932b). Leenhouts (1956) doubted whether true stipules occur in Haplolobus, Garuga, and Dacryodes, but asserted that they do occur in Canarium section Canarium. Guillaumin (1912) stated that since 'floral articulations' occur in many Burseraceae, this means that the entire family has stipules, whether they are visible or not.

The lateral leaflets are opposite throughout the family, with some partial exceptions. Lam (1932b) noted that Santiria griffithii (Hook. f.) Engl. has almost alternate leaflets. In most Protium the basal pair or two may be subopposite. This is most pronounced in the closely related species P. subserratum, P. reticulatum, and P. ferrugineum.

The vast majority of taxa in Protium have imparipinnately compound (sometimes trifoliolate) leaves. The eophylls of the seedlings of Protium are consistently unifoliolate, and unifoliolate mature leaves may occur in any taxon but are rare in most.

Unifoliolate leaves are the rule in some taxa. The capacity of P. unifoliolatum to produce trifoliolate leaves on occasion led Engler to describe P. pubescens, a nomen illegitimum which Swart published as P. benthami, based on the same type. The organization of shoot and leaf organogenesis in P. unifoliolatum may be viewed as flexible or plastic,

because on many individuals the majority of the unifoliolate leaves are opposite and are accompanied by a swelling on the branchlet at the point of insertion.

Swart (1942a) described a variety unifoliolatum for P. heptaphyllum, but he noted that it sometimes had trifoliolate leaves. The variety is not recognized in this treatment.

Only two taxa of Protium are consistently unifoliolate at every stage of development (based on my own field observations of individuals of various ages), and both are as yet undescribed. One occurs nears Manaus, Brazil, and is closely related to P. unifoliolatum. The other is found in the higher restinga forests of Bahia and may be a subspecies of P. icicariba (DC.) Marchand.

While the petiole in Protium is often very slightly acutely winged, the leaf rachis is terete or slightly angled in cross-section, with very few exceptions. Capuron (1968) pointed out that the rachis in P. beandou Marchand is sometimes winged ("rebordé-ailé"). This is also true of the western Amazonian species P. klugii Macbr., in which the petiolules can also be slightly winged.

The great majority of the species of Protium have entire leaflets, and even those species which have non-entire leaflets are inconsistently toothed. In the Old World, P. serratum has subserrate leaflets (defined as having teeth less than 1 mm long). In the New World, several species have irregularly subserrate leaflets. P. crenatum has the most consistently subserrate leaflets, but rarely a few leaflets on a branchlet are completely entire. Protium unifoliolatum frequently has subserrate

leaflets, indeed, Engler described a variety of the species, var. subserratum (not recognized in this treatment). He also described a var. subserratum for the southeastern Brazilian species P. brasiliense (Spreng.) Engl., but this species also may show a morphological continuum in which recognition of the variety would confuse the taxonomy. Protium subserratum is the only species in the genus which may have serrate (teeth longer than 1 mm) leaflets. However, most individuals have irregularly serrulate leaflets and the populations of several geographic regions have completely entire leaflets. As is discussed in the taxonomic portion of this treatment, at least some of these groups of populations may deserve taxonomic rank. The leaflets of Protium pilosum and P. guianense almost always have a sparsely serrulate acumen, the rest of the leaflet being entire.

Guillaumin (1909a) observed that in seedlings of Protium javanicum Burm. f. the first leaves have serrate leaflets. Unfortunately, data are lacking on the morphology of the seedlings in New World Protium; it would be interesting to determine which species, if any, show a pattern similar to P. javanicum. It may be that the serr(ul)ate mature leaflets found in some Neotropical species are examples of neoteny, or persistence of a juvenile condition, which in other species is not maintained past the seedling stage.

The petiolules in Protium are usually once- or twice-canaliculate above, and a pulvinulus occurs at the distal end. The pulvinulus is one of the more perplexing and misleading characters in the genus Protium. The taxonomic distribution of this character has affected the generic limits

of Protium and has been a pivotal character in the infrageneric classification of the genus (see chapter on generic limits). It can be useful as a practical character for separating Protium from some genera, but it is not a diagnostic character for the genus.

The pulvinulus in the Burseraceae is evidenced by a swelling at the distal end of the petiolule or at the base of the leaflet blade, as some authors have described it. It is not so versatile nor so dramatic in its effect as some mimosoid legumes, because it does not respond to any tactile stimulus nor does it control the angle of the leaflet blade relative to the sun. I have only observed it functioning in conditions of water stress and in young expanding leaves.

Guillaumin (1909a), who worked extensively on the Burseraceae, studied the anatomy of the pulvinus at the base of the petiole and of the distal pulvinulus on the petiolule, both of which he called "renflements moteurs," or motor swellings. He presented a diagram of the pulvinus of the young leaf of a species of Canarium, indicating that the pulvinus and pulvinulus show the same anatomical pattern. The vascular bundles are scattered throughout the pulvinus, but on either side of it the vascular bundles can be regarded as re-coalescing in a ring or a cylinder. Unlike the anatomical pattern for pulvini described by Esau (1967), the vascular bundles are not compactly grouped in the center and surrounded by a great deal of parenchyma. Neither Solereder (1908) nor Metcalfe & Chalk (1950) examined or reported on the pulvinus or the pulvinulus in Burseraceae. Further anatomical work on this character is needed.

The pulvinulus has been considered a significant character in the

Protieae. Engler (1883) based his two sections of Protium on the presence or absence of pulvinuli. In the New World, Protium and Tetragastris can be distinguished in virtually all cases by the absence of lateral pulvinuli in the latter genus. Some natural groups within Protium may lack lateral pulvinuli.

Lateral and terminal pulvinuli appear to be entirely lacking from the three African species of Protium, although on some specimens of P. obtusifolium (Lam.) Marchand and on the isotype at Kew of P. madagascariense there is a slight distal broadening of the terminal petiolule. Among the Asian species, lateral and terminal pulvinuli are never conspicuous, but both do occur in P. macgregorii (F. M. Bail.) Leenh. and P. connarifolium (Perk.) Merr. Only terminal pulvinuli are occasionally visible on leaves of P. javanicum Burm. f., and pulvinuli are negligible or absent on the dozen or so specimens I have seen of P. serratum (Wall. ex Colebr.) Engl.

Among the New World Protieae, pulvinuli are lacking entirely from Crepidospermum, and Tetragastris has only terminal pulvinuli. Terminal pulvinuli are present in all species of Protium. Lateral terminal pulvinuli are present in virtually all Protium with only three exceptions. They are consistently lacking in P. subserratum, they are negligible or absent in P. reticulatum (Engl.) Engl., and they may be present or absent-- even on a single branchlet-- in P. pilosum.

The number of juga-- pairs of leaflets-- is much less constant and reliable a character than has been assumed by most previous authors. Protium unifoliolatum is an extreme case, but some other species are

similarly misleading. For example, P. trifoliolatum may have anywhere from zero juga (that is, unifoliolate) to three juga in rare instances. For most species there is a minimum and a maximum number of juga one may encounter, as well as a standard range. For this reason the number of pairs of leaflets is expressed in the species descriptions in the same format as the measurements. In the taxonomic portion, unifoliolate leaves are conceived of as having no juga, therefore the leaves of Protium trifoliolatum are described as being 0-3-jugate. The term "interjuga" is a shorter way of referring to what some authors have called the "interpinnal segments" of the imparipinnate leaf.

In the taxonomic portion of this treatment, the morphology of the petiole, rachis, petiolules, pulvinulus, and leaflets is used extensively to define and separate taxa, but not to the extent that previous authors have done. Much greater emphasis is placed on flower and fruit characters to compensate for the neglect of those characters in earlier treatments of Neotropical Burseraceae.

Inflorescences

The inflorescences of Protium appear to be rather varied, but all follow the same structural pattern and it would be difficult to assign different terms to even the extremes of length and complexity (see Fig. 1). Although Lam (1932a) wrote that truly terminal inflorescences occur in Canarium and Dacryodes, all inflorescences of Protium are axillary. All inflorescences are subtended by a single bract. In species with relatively long inflorescences they tend to be congested toward the apex (and so are "subterminal"), and in some of these cases the inflorescences may be subtended only by a bract and not by a leaf as well. The inflorescences branch so close to the base that that it is difficult to say whether or not they are truly fasciculate. Each branch of the inflorescence is subtended by a single bract.

The primary axis of the inflorescence is monopodial and apparently "indeterminate," although use of that term has come into question (see discussion below). On longer inflorescences, the secondary axes are usually alternate (rarely opposite) monopodial branches, especially toward the base. In some species, these may give rise to further monopodial tertiary and even quaternary axes. On more reduced inflorescences and toward the distal end of longer inflorescences, the secondary axes are often simple cymules (simple dichasia, or, "triads," in the terminology of Briggs and Johnson (1979)) or poorly-developed compound dichasia. Often one or both of the lateral flowers may not develop. This apparently depends on the vigor of the inflorescence, because this condition varies

among individuals in a species and even somewhat among branches of a single plant.

All axes other than the monopodial axes, that is, the dichasia, terminate in cymules. Each cymule is subtended by two bracts, and each of the lateral flowers is subtended by two further bracts. These two bracts almost always occur immediately above the bract on that side of the cymule, and each subtends a bud, indicating the potential for further development of the dichasium.

Briggs and Johnson (1979) introduced the term "metaxyphyll" to indicate an empty phyllome (or bract) proximal to the terminal flower of an anthotelic (terminating in a flower) axis, "empty" meaning it lacks an axillary bud or the buds do not develop. The usefulness of the term, at least in the Burseraceae, is questionable, because it is not known to what extent the failure of a bud in the axis of a bract is facultative and due to environmental conditions or the energetics of the individual plant. However, while no species show a fixed length or number of branches or nodes, all do show a definite range in the length and degree of branching in their inflorescences. In their discussion of metaxyphylls, Briggs and Johnson did make the point that it is important to indicate whether or not a pair occurs between the terminal flower of each cymule and the pedicels of the lateral flowers. In Protium this does not occur (Fig. 1).

The region in question, usually referred to as the pedicel of the terminal flower, is problematical because when metaxyphylls do occur there, "pedicel" does not distinguish between the two regions on either side of the node created by the metaxyphylls. Briggs and Johnson

introduced the term anthopodium to refer to the internode between the flower and the ultimate node of the axis it terminates. They prefer to use the new term because, as Schmid (1972) noted, when the anthopodium elongates it is anatomically indistinguishable from the penultimate internode.

There is one instance of that kind of problem in the two subspecies of Protium polybotryum, but it occurs in the lateral flowers of the cymules (see Fig. 1b). In P. polybotryum ssp. blackii, the two metaxyphylls subtending the each lateral flower show the normal condition for the genus, that is, they occur immediately above the bract subtending that side of the cymule. In ssp. polybotryum, however, the metaxyphylls occur part-way between the bract and the flower, such that the "pedicel" is divided in two parts. In the description for that taxon the measurements for the pedicel refer to the portion of the anthopodium distal to the metaxyphylls.

Judging by some of the more commonly consulted sources on inflorescence terminology, the inflorescence of Protium may be considered a panicle or a thyrs. The detailed description given above is necessary because of the ambiguity and contradictions in the terms applied to different inflorescence structures. Table IV lists the terms given to the inflorescences of Burseraceae by various authors.

The simplest concept of the panicle is that of a branched inflorescence with pedicellate flowers (Radford et al., 1974). Lawrence (1951) was a little more specific, considering it to be an indeterminate branching raceme, the branches of the primary axis being racemose and the

Table IV.

Classification of the inflorescences of Burseraceae
by different authors

source	inflorescence type
Burman, 1768	complex paniculate raceme
Lamarck, 1788	highly branched panicles ("grappes")
A. L. de Jussieu, 1789	panicle
de Candolle, 1825	simple raceme
Endlicher, 1840	raceme or panicle
Bentham & Hooker, 1862	racemose or paniculate
Marchand, 1867-1868	panicles with 'bipaired' cymose branches
Engler, 1883	various
Lam, 1932a	paniculate to racemose, rarely spicate
Engler, 1931	panicles ("Rispen") with cymose side-branches, these sometimes shortened, then the inflorescence glomerulose or fasciculate
Swart, 1942b	mixed type: panicles with primary to tertiary branches racemose, but flowers in usually dichasial cymes
Cuatrecasas, 1957	panicle
Capuron, 1968	simple or slightly branched panicles, with (usually uniflorous) cymules

flowers pedicellate. Rickett (1955) essentially rejected the typological dichotomy of determinate versus indeterminate axes-- a concept he traced back to Asa Gray-- because there are too many exceptions. He defined a panicle as a compound raceme, or a raceme of racemes, a raceme being a monopodial inflorescence consisting of a central axis with lateral flowers or flower clusters, usually flowering acropetally, and terminated by a flower or not.

Briggs and Johnson (1979, p. 239) also rejected the notion of indeterminate axes, noting that "so-called open ('indeterminate') shoots may in fact be quite determined (anauxotelic) in their growth possibilities." They defined a panicle as an anthotelic (terminating in a flower) inflorescence in which the main axis and at least some of the lateral axes have nodes distal to prophyllar nodes, and in which the laterals must ultimately bear single flowers at two or more successive nodes.

The thyrses was defined by Radford et al. (1974) as a many-flowered inflorescence with an indeterminate primary axis and many opposite lateral dichasia. Lawrence (1951) only vaguely distinguished thyrses from panicles, calling the former a compact and more or less compound panicle, or a panicle-like cluster with an indeterminate primary axis and determinate lateral branches. Rickett (1955) made it even more difficult to separate the two, as he called a thyrses a compact panicle of more or less cylindrical form.

Briggs and Johnson (1979) described a thyrses as a blastotelic (terminating in an abortive vegetative apex or continuing vegetative

growth beyond the flowering region) inflorescence with a multinodate primary axis that bears lateral cymes. They coined the term "thyrsoid" to describe the same type of inflorescence but with an anthotelic primary axis. They considered a panicle-like inflorescence with lateral branches which do not bear single flowers at two or more successive nodes to be a complex thyrsoid. It is not clear from their discussion whether these single flowers can be the terminal flowers of cymes, the laterals unexpressed in the axils of bracts (and the bracts thus termed metaxyphylls), or whether they must be truly solitary.

As can be seen from the description given above, the inflorescence of Protium is a panicle by the criteria of Lawrence (1951) or Radford et al. (1974). By Rickett's (1955) definitions most Protium have panicles, but the more reduced inflorescences of some species would be called racemes, since Rickett allowed racemes to have lateral flower clusters as well as individual flowers. Following the rather complex definitions of Briggs and Johnson (1979), the inflorescences of Protium are probably complex thyrsoids, since the primary axis appears to be anthotelic. In the present work, for the sake of simplicity the inflorescences in Protium will be referred to as panicles of racemes or racemes, depending on whether the secondary axes are well developed.

Lee (1967) examined the inflorescence structure of several taxa in the Meliaceae, Anacardiaceae, Sapindaceae, and Rutaceae. Except for the Rutaceae, which he said had compound cymes, the taxa he looked at had thyrses, which he defined as a panicle of cymes. This terminology was followed by Styles (1972) in his analysis of the flower biology of the

Meliaceae. Regardless of the name given to them, the inflorescences of Melia azedarach L. (Meliaceae) and of Mangifera indica L. (Anacardiaceae) have the same structure as Protium, with the exception of the position of the metaxyphylls on the lateral flowers of the cymules.

Flowers and sex expression in Protium

While a description of the flowers of Protium appears in the generic description later in this treatment, some aspects of flower morphology merit more detailed discussion, especially those which involve sexual dimorphism. This phenomenon can profitably be discussed in the context of other sapindalean families.

The aestivation of the corolla may show a number of patterns in a few other burseraceous genera such as the Asian Canarium (Lam, 1932b), but in Protium it is induplicate-valvate almost without exception. Leenhouts (1956) noted for the family in general that the petals are sometimes irregularly imbricate in the middle of their length. This occurs in Protium, but the partial overlap of the petal margins almost always occurs in the opening or opened flower. Truly imbricate aestivation-- however slight-- appears to occur in Protium klugii Macbr., and for this reason Macbride (1949) transferred this species to Bursera. However, as Gillett (1980) has pointed out, even in Bursera induplicate-valvate aestivation is the rule, and P. klugii shares no important characters with that genus.

Lam (1932c) asserted that most of the Burseraceae-- including Protium-- are meta-obdiplostemonous, meaning that the stamens occur in one series outside the disk. In fact, virtually all Protium species are simply and visibly diplostemonous, meaning that the antepetalous series is inserted inside the antesepalous series. The only known exceptions are isostemonous, where the antepetalous series is lacking. Protium divaricatum ssp. divaricatum is consistently isostemonous in both sexes, as are some flowers of P. pilosum, all pistillate flowers of P. robustum,

and all flowers on the type specimen of P. mcleodii I. M. Johnston (Johnston 157), a species I have not yet studied in detail.

Several authors, including Bentham & Hooker (1862), have indicated that the filaments may be inserted on the margin of the disk in Protium. This sometimes appears to be so because the base of the disk is undulate, but in fact they are always inserted at the base of the disk.

Although the antesealous stamens are virtually always longer than the antepetalous stamens, in most taxa the anthers are essentially even with each other because the latter series is inserted higher than the former. The difference in length between the stamens of the two series is usually about one millimeter. Consistently pronounced didynamy is present only in section Icicopsis and a group of species including P. apiculatum. This is because the antesealous stamens are usually several millimeters longer than the antepetalous ones.

The anthers of Protium may be dorsifixed or basifixed, but the distinction is often not easy to make. The sterile anthers of staminodes are almost always basifixed. Also, the shape of the anther may change significantly after it dehisces.

The anthers of the two series of stamens can be dimorphic, differing in size, shape, or both. They are dimorphic in Paletropical Protium madagascariense Engl. and P. beandou Marchand (Capuron, 1968) and in several Neotropical species of the genus, including P. pallidum, P. aracouchini, and P. elegans Engl.

Historically there has been some confusion as to the sexuality of burseraceous flowers, probably because, while perfect flowers are rare, in

most taxa there are staminodes in pistillate flowers and a pistillode in staminate flowers. The occurrence of morphologically hermaphrodite unisexual flowers was perceived rather early in systematic botany. By 1742 Linnaeus noted two types of flowers in Acer-- female "hermaphrodite" flowers with indehiscent anthers, and male "hermaphrodite" flowers in which the pistil does not grow-- and by 1754 he had observed the second type of male flower, in which there is a split stigma but no ovules or style (cited and quoted by de Jong, 1976).

Despite this early awareness, G. Don (1832) indicated that the flowers of Burseraceae are hermaphroditic but occasionally unisexual. Endlicher (1840) noted that the flowers are hermaphroditic or usually unisexual by abortion. Bentham (1862) wrote that the flowers are hermaphrodite or polygamo-dioecious. In the Prodromus, de Candolle (1825) separated Icica and Marignia from Protium-- now respectively the Neotropical, African and Asian species of Protium-- by saying that the first two are hermaphroditic and the latter is unisexual. This error was repeated by G. Don (1832).

Engler (1883) wrote that the flowers of Burseraceae are almost always polygamo-dioecious and only rarely hermaphroditic. Unfortunately, Engler's keys to Protium did not reflect this more accurate assessment. In Flora brasiliensis (Engler, 1874) the genus was separated into two major groups on the basis of whether stamens exceed the pistil or vice versa, and in the Monographie Phanerogamarum (Engler, 1883) one of the primary characters in the key is whether or not the ovary is mostly immersed in the disk. These are actually characters which separate most staminate flowers from most pistillate flowers (see below), and Engler's

misunderstanding of this situation led him to describe several redundant taxa, such as Protium nitidum (see discussion in the description of P. paniculatum).

In his treatment of the Burseraceae for the Flora Ilustrada Catarinense, Reitz (1981) called the flowers of Burseraceae hermaphroditic. It is possible that his use of the term refers to morphology and not to function.

Staminate and pistillate flowers of most species of Protium are difficult to distinguish without removal of a petal and examination under at least 10X magnification. Virtually without exception the flowers of both sexes are of the same size, not following the pattern observed in tropical dioecious trees by Bawa and Opler (1975), in which pistillate flowers are larger than staminate ones. Mimicry of staminate flowers by pistillate ones clearly occurs, and may promote pollination by attracting secondary visitors in search of pollen (see chapter on pollination).

Upon examination of the flowers, however, the staminate and pistillate flowers can be distinguished by a number of characters. In the staminate flowers of most species, the pistillode is reduced in size and modified in shape relative to the pistil, and usually only the stylode exceeds the disk. Occasionally the entire pistillode is exceeded by the disk. The stamens greatly exceed the pistillode. Usually there is a stylode present, but its stigmas do not develop on the pistillode. Instead, the stylode is either slightly acutely winged or lobulate, and there is nothing like the globose or compressed-globose to discoid capitate stigmas which characterize fertile pistillate flowers.

In staminate flowers there is a reduction series involving the pistillode. In most species the pistillode is provided with a rudimentary ovary with locules but only reduced ovules which do not fill them (Fig. 2a). This is also true in most Meliaceae (Pennington & Styles, 1975). A limited number of species, including all species of section Sarcoprotium (Fig. 2b), possess a degenerate pistillode which is still distinguishable from the disk but which is a solid parenchymatous structure without ovules or locules. In the final step of this reduction series the pistil in the staminate flowers is altogether obsolete. In most of the species of section Icicopsis, the pistillode is obsolete or ontogenetically fused with the disk, such that they are indistinguishable. The resulting structure-- called the "ovariodisk" by Lam (1932a)-- is a densely pubescent depressed-discoïd to depressed-conical mass (Fig. 2c).

The second and third steps in this reduction series occur in a number of genera in the family. Lam (1932a) noted that in some taxa of Dacryodes and Canarium the pistillode may have the shape of the pistil but be parenchymatous, while in others the pistillode is absent altogether.

In rare instances, a single taxon may show more than one phase of the reduction series. Swart (1940) noted that in the Asian Protium serratum (Wall. ex Colebr.) Engl. staminate flowers can have either a pistillode with reduced ovules and locules, or reduced ovules with one ovule per locule, or a parenchymatous pistillode. In the Neotropics, staminate flowers of P. apiculatum may have a pistillode with apparently empty locules or it may be a solid parenchymatous structure.

As noted above, most species of Acer commonly display two types of

staminate flower, one with a completely aborted ovary and the other with reduced locules and ovules. These two types appear in two distinct staminate phases, one preceding and one following the pistillate phase of these primarily dichogamous plants (de Jong, 1976). In another sapindalean family, the Meliaceae, the staminate flowers may produce an ovary which appears normal in size and shape, but the ovules are brown, reduced in size, and do not fill the locule. Also, the style is longer, and the style head is reduced in size and less glandular (Styles, 1972).

In pistillate flowers of Protium, the style and ovary together greatly exceed the disk. The stamens are level with or more often exceeded by the pistil, except in section Sarcoprotium and in the western Amazonian P. leptostachyum Cuatrec. The filaments may or may not be shorter than those in the staminate flowers, and the filaments are usually strap-shaped, but true stamens also may have strap-shaped filaments. On the staminodes, the anthers (sometimes referred to as antherodes) are sometimes smaller than but virtually always anisomorphic with those of the staminate flowers. As noted above, the anthers of staminodes are almost always basifixed.

The anthers of the staminodes do not of course produce perfect pollen, and dissection of these anthers yields no evidence of pollen whatsoever. In Protium serratum, development of the microspores stops after the development of the tapetum and the endothecium, such that the microspore mother cells degenerate (Narayana, 1960; Davis, 1966). Similarly, pollen is not produced in the staminodes of Acer (de Jong, 1976) and Meliaceae (Styles, 1972).

This morphology can be contrasted with the interesting situation in

Cupania guatemalensis Radlk. (Sapindaceae). In pistillate flowers, the anthers produce pollen which appears viable based on its size, shape, and stainability, but the anthers do not dehisce (Bawa, 1977).

The pistillate flowers of Meliaceae are distinguished from the staminate flowers by some characters different from those found in the Burseraceae. In the Meliaceae the petals are often smaller than those of the staminate flowers; the anthers are smaller; the style is shorter (the opposite is true in the Burseraceae) and is terminated by a thick style-head; and the stigmatic surface has glandular papillae. In the Melioideae, however, the staminate and pistillate flowers are morphologically so similar that according to Styles (1972) they can be distinguished only by field observations.

Staminate and pistillate plants of the Burseraceae may be distinguished in a number of other ways. Lam (1932a) stated that the staminate inflorescences usually are longer and have more flowers. This follows the general pattern observed in other sapindalean families such as the Meliaceae (Pennington & Styles, 1975), Anacardiaceae (J. Mitchell, pers. comm.), and the Simaroubaceae, most dramatically in Picramnia (W. W. Thomas, pers. comm.). In Aglaia (Meliaceae), the staminate inflorescence can be 20-50 cm long while the pistillate may be 2-3 cm long with fewer than ten flowers (Pennington & Styles, 1975).

My own observations of Protium indicate that staminate inflorescences tend to have more flowers, but I have not found them to be longer as a rule. The overall pattern may be obscured by the great variability in inflorescence length. Also, inflorescences are easily damaged during

collection, pressing, and mounting of herbarium specimens, so any quantitative evaluation should be done in the field. Only in section Icicopsis is the difference so marked that it can be quantified based on a limited sample. For example, after selecting for extremes of length in the material of P. robustum at hand and measuring only the longest inflorescence on each specimen, it appears that staminate inflorescences are 12-21 cm long (n=5) and pistillate ones are 5-7.2 cm long (n=5).

One limited field study of this nature has been carried out on a species of Protium (undescribed as yet) occurring on the World Wildlife Fund reserves near Manaus, Brazil. It was found that staminate inflorescences were 10-25 cm long ($\bar{x}=21$, n=9), while pistillate inflorescences were 12-18 cm long ($\bar{x}=15$, n=10). On 17 hectares of forest, there were 83 staminate individuals, with ca 1,375 inflorescences each (n=2) and ca 150 flowers per inflorescence (n=10). There were 49 pistillate individuals, with ca 517 inflorescences each (n=2) and ca 85 flowers per inflorescence (n=10). Therefore, the ratio of the number of flowers on staminate versus pistillate plants was about 4.7 (M. Vinicius, pers. comm.).

Inflorescences with unisexual flowers must be examined with care before a plant is pronounced staminate or pistillate, because monoecious plants show a variety of spatial arrangements of staminate and pistillate flowers. For example, in most Swietenieae (Meliaceae), when flowers of both sexes occur on the same inflorescence only the center flower of each cymule is pistillate (Styles, 1972).

The length of the pedicel can often be used as a differential

character to help separate two taxa, but this character must be used with caution. In some taxa the pedicel of the staminate flowers is consistently longer than that of the pistillate flowers. An example is Protium demerarens, in which the staminate flowers have pedicels (1.2) 2.2-2.9 mm long, while the pistillate flowers have pedicels (1) 1.5-2 mm long. It should also be noted that the pedicel usually lengthens and thickens considerably under the developing fruit.

Number of flower parts is not nearly so variable in Protium as in Bursera, where in section (or subgenus) Bursera the staminate flowers are (3-4) 5-merous while the hermaphrodite flowers are 3-merous exclusively (Gillett, 1980). In Protium it may sometimes be used to help separate taxa, such as the 4-merous P. giganteum and the 5-merous P. decandrum, while in others, such as P. paniculatum, 4- and 5-merous flowers may occur on the same inflorescence (Frôes 25599; Prance et al. 16016). The only instances of sex-linked number occur in section Sarcoprotium, in which some 3-merous flowers always occur on the staminate inflorescences.

The calyx often differs between the sexes (although seldom much), either in length of lobes or in overall length. In Protium altsonii the calyx of staminate flowers is (0.5) 0.6-0.8 (1) mm long overall and that of pistillate flowers is 0.9-1.3 mm long. Another character of the calyx which is useful taxonomically is its level relative to the disk, pistillode, or anthers.

As a rule, Protium is dioecious, although in most of the taxa the organs of one sex are expressed as a non-functional rudiment in the other. Theoretically the further development of the rudimentary stamen

(staminode) or pistil (pistillode) can be derepressed in rare instances, yielding an occasional functionally perfect flower. While there is no doubt that this is possible where the rudimentary ovary persists in staminate flowers (see discussion below), in the course of dissecting ca 2,000 flowers of Protium I have yet to encounter a functionally bisexual flower. The best evidence of a derepressed pistillode (leading to polygamodioecy) is the occasional fruit on a known staminate individual.

I have encountered one case of derepression of the pistillode after anthesis, but this was in sterile flowers. On a collection of P. heptaphyllum (de la Cruz 4558), most of the open flowers are provided with staminodes and pistillodes, but several flowers are at various stages in development of pistillodes into apparently functional pistils, meaning they have increased in size, the ovules fill the locules, and stigmas have begun developing.

I have found only three individuals (collections) of Burseraceae which were truly monoecious. There are a few pistillate flowers on the otherwise staminate inflorescences of one collection of P. opacum ssp. rabelianum (Tillett & Tillett 45585); on one collection of P. paniculatum var. riedelianum (Prance et al. 1475); and on only one individual of one collection of P. brasiliense (Spreng.) Engl. (Prance & N. T. Silva 58446, at GH). In all three cases the pistillate flowers occur as the center flower of a cymule, just as in monoecious Meliaceae (see discussion above).

I have observed only three cases of sex reversal, and only two are certain. One herbarium specimen of P. aracouchini (Aublet) Marchand from

Venezuela (Maguire et al. 36491) has one branchlet on which there is one mature fruit and several staminate inflorescences. One collection of P. robustum (Daly et al. 1166) has several branchlets with staminate inflorescences but at least one with maturing fruits. One collection of P. giganteum var. crassifolium (Sagot 970) has some duplicates with staminate-flowering branchlets and some with fruits.

These three individuals could be said to be sequentially monoecious, or dichogamous. This phenomenon, so common elsewhere in the Sapindales (see discussion below), may occur more frequently in the Burseraceae than I have been able to observe, but it is clearly not the rule.

Another phenomenon which may be encountered on occasion is the occurrence of pistillate and sterile flowers on the same inflorescence, that is, flowers with staminodes and pistillodes, and therefore no functioning sexual organs. In addition to the case of pistillode derepression cited above, there are instances of this in Protium giganteum (Rodrigues (INPA) 2028); P. krukoffii (Krukoff 8108); and P. unifoliolatum (Ducke 7106). Observations of sterile flowers in several species of Acer have been cited by de Jong (1976).

If this phenomenon proves to be more than just an abnormality, there may be some natural selection for it. Large-scale abortion of flowers and of developing fruits occurs commonly in tropical trees (Bawa & Webb, 1984). Granted that resource limitation is a major factor in the abortion of fruits (Lee & Bazzaz, 1982), it is clear that mass-flowering trees like Protium cannot "afford" the energy expenditure to develop every fruit if all the flowers are pollinated. Sterile flowers may serve the function of

attracting pollinators (via nectar production or by serving as decoys) without risking or wasting an initial energy investment on development of an ovary and possibly a fruit doomed to be aborted. However, the occurrence of sterile flowers is apparently very rare in Protium, so the cases which have been documented must be regarded as aberrations.

Most of the species in the Sapindales have unisexual flowers. While dioecy prevails in the Anacardiaceae (J. Mitchell, pers. comm.) and the Burseraceae, judging by the available literature some form of monoecy characterizes much of the rest of the order. Bawa (1980) has suggested that since few or no monoecious taxa are encountered in the Burseraceae, Flacourtiaceae, Lauraceae, Simaroubaceae, and Rutaceae, dioecy in these families may have evolved directly from hermaphroditism via "subdioecy." Monoecy in the Sapindales is almost always accompanied by one of several systems of temporal displacement of the sexes (dichogamy), and andromonoecy appears to be particularly common. Androdioecy is known from at least some taxa in the Sapindales, including Xerospermum intermedium Radlk. (Sapindaceae, Appanah, 1982).

In one breeding system encountered rather frequently, the plants are monoecious but go through an initial staminate phase which is followed by a pistillate phase and finally by a second staminate phase. This has been found in Cupania guatemalensis Radlk. (Sapindaceae; Bawa, 1977), Litchi chinensis Sonn. and Koelreuteria paniculata Laxm. (both Sapindaceae), Dipteronia japonica Oliv. (Aceraceae), and the majority of the species of Acer. A number of sapindaceous genera show simply a staminate phase followed by a pistillate phase. Several species of Aesculus

(Hippocastanaceae) have an initial staminate phase followed by an hermaphrodite phase (de Jong, 1976).

Among the Meliaceae, in monoecious Swietenioideae, when both sexes occur on the same inflorescence the central pistillate flower of each cymule opens before the lateral staminate flowers. In Melia and Azadirachta (both Melioideae) the hermaphrodite central flower opens before the lateral staminate flowers (Styles, 1972).

Further field and herbarium work in the Burseraceae will have to be carried out with an understanding of the various breeding systems in other sapindalean families which may eventually be found in this family. Herbarium specimens can be especially misleading. As Bawa (1977, p. 60) noted regarding herbarium collections of Cupania guatemalensis Radlk. (Sapindaceae), "If the specimens from a population are collected and examined at only one point in time, the same species can be described as monoecious, dioecious, or polygamous."

Pollen

Before this treatment was undertaken there were no scanning electron microscope studies of Protium pollen and very few observations in the literature on the features available via light microscopy. Figures 3-9 constitute an incomplete survey of the pollen of Protium and include pollen from the other genera of the tribe Protieae, with the exception of the Old World genus Garuga. The pollen was taken from recent collections whenever possible and was sputter-coated without other preparations. Because in most cases the collections were recent ones, there was little collapse of the pollen grains.

The pollen of all Burseraceae occurs as monads. They are isopolar, tricolporate, prolate to spheroidal in shape, and the ora is lalongate (Erdtman, 1966; Mitra et al., 1977). Erdtman (1966) commented that the pollen of Burseraceae in general resembles that of the Simaroubaceae more than that of the Meliaceae or Rutaceae.

The pollen surveyed ranged in size from the spheroidal pollen of Protium polybotryum (Fig. 3a), which was ca 14 micrometers in diameter, to the prolate pollen of P. obtusifolium (Fig. 4d), which measured 24.3 x 16.6 micrometers. The majority of the pollen surveyed measured between 18-23 micrometers in their largest dimension. Thus the pollen of Protium and the Protieae as a whole all fall within the category of small pollen grains indicated by Erdtman (i.e., 1966).

The pollen showed a continuum of shapes ranging between spindle-shaped or prolate with rounded to truncate ends, to spheroidal. Only two rather distantly related taxa, Protium robustum (Fig. 3b) and P. polybotryum

(Fig. 3a), proved to have actually spheroidal pollen. Virtually all the taxa surveyed showed protruding pori.

Only a minority of the species show any notable surface sculpturing. Protium polybotryum (Fig. 3a) has spheroidal pollen with a densely baculate sexine and indistinct ectoapertures. P. robustum (Fig. 3b) also has spheroidal pollen, but in this case the sexine is coarse-reticulate, with smooth thick muri intertwining at various levels. Four taxa showed prolate pollen grains with long ectoapertures and irregularly (non-parallel) striate sculpturing; two of them, P. apiculatum (Fig. 3c) and P. fimbriatum (Fig. 4a), are closely related, but the other two are only distantly related to each other and to the first two: P. plagiocarpium (Fig. 4c), and P. obtusifolium (Fig. 4d) from Mauritius.

The remainder of the taxa surveyed have pollen grains which are either smooth or somewhat foveolate. Only a very few taxa are distinctly foveolate, such as Protium paniculatum var. paniculatum (Fig. 5a) and P. sagotianum (Fig. 5b), while several others occupy a place in a continuum from slightly foveolate to almost perfectly smooth. Among these is P. mcgregorii (Fig. 5b) from New Guinea, which has pollen virtually indistinguishable from many of the Neotropical species of the genus.

In general, pollen does not appear to be of great help to the systematics of the tribe or of the genus Protium. The distinctiveness of the surface sculpturing on the pollen of P. robustum (Fig. 3b) can be used to defend its integrity as a species distinct from P. tenuifolium (Fig. 5c). The close morphological relationship between P. apiculatum (Fig. 3c) and P. fimbriatum (Fig. 4a) is confirmed by their very similar pollen.

Three rather closely related species, P. divaricatum (Fig. 5d), P. aracouchini (Fig. 6a), and P. strumosum (Fig. 6b), differ slightly from the rest of the genus by their smooth to foveolate pollen, by their more narrowly ellipsoid shape, and by the fact that their colpi extend almost to the poles. The rest of these taxa-- in fact, the majority of the species of Protium (see Figs. 6b-8d)-- tend to have almost rotund pollen in which the colpi stop well short of the poles.

It is interesting to note, as illustrated in Figures 3 and 9, that there is far greater diversity in the pollen morphology within the genus Protium than between Protium and the other genera in the tribe Protieae. More sampling of species from elsewhere in the Neotropics is necessary before it can be said whether the pollen will be of further use in the infrageneric classification of the genus.

Fruits

The fruit is the most neglected aspect of the morphology of Protium. There is some confusion as to what type of fruit Protium has and there is disagreement as to the homologies of the several layers of the fruit. There has been a misconception about the presentation of the unit of dispersal following dehiscence of the fruit. Several taxonomically useful characters of the fruit have never been previously recognized.

The range of variation in the morphology of the fruit and seed of Protium has been inadequately appreciated; consequently, approaches to compartmentalization of this variation have been poorly developed. Collections of Protium with mature fruits are insufficient, both in quantity and in quality, and extensive field observations for a number of fruit characters are needed. Thus, there are inadequate data for many species regarding fruit color, texture of the mesocarp, color of the mesocarp within, color and texture of the pseudaril, distribution of the pseudaril on the pyrene, presence and distribution of hygroscopic fibers on the pyrene, and testa and cotyledon morphology. Nevertheless, examination of the available material has shown these characters to be extremely significant taxonomically, not only at the rank of species but at the generic level as well (see also the chapter on generic limits).

Historically, the fruit of the genera which comprise the Protieae has been called a drupe (e.g., Lamarck, 1788 (as a drupaceous berry); Kunth, 1824; de Candolle, 1825; Endlicher, 1840; Benthams, 1862; Marchand, 1868; Baillon, 1874; Engler, 1874; Swart, 1942; Cuatrecasas, 1957) or less often a capsule (e.g., de Jussieu, 1789; Corner, 1976). The indurated endocarp

which serves as the unit of dispersal has been called a pyrene, (Endlicher, 1840; Swart, 1942b), a "noyau" (Baillon, 1874; Capuron, 1968), a "nucule" or "nucula" (Triana & Planchon, 1872; Cuatrecasas, 1957), an "ossea nuce" or "ossicula" (de Jussieu, 1789, and Kunth, 1824, respectively), or a "caroço (drupeola)" (Reitz, 1981). The greater number of names for this structure may be because in some instances there is no cognate for the term in some other languages.

While true drupes characterize the entire tribe Canarieae of the Burseraceae, the fruit of Protium and its relatives is not easily accommodated in any of the classical fruit types. Strictly speaking, drupes are indehiscent structures. Undoubtedly the reason some of the earlier authors termed it a drupe was because of the long-lived misconception that the fruits of the Asian (as Protium) and African (as Marignia) species of Protium, as well as some of the Neotropical species (as Icica) are indehiscent (Kunth, 1824; de Candolle, 1825; G. Don, 1832; Endlicher, 1840). On the other hand, Protium fruits do not fit the definition of a capsule in the Encyclopedia of Plant Anatomy as a "pluricarpellate many-seeded dry fruit" (Roth, 1977). While Roth recognizes a sub-category of fleshy capsules which includes such genera as Myristica and Punica, she stresses that "the most characteristic feature of the capsule is certainly that it open to liberate the seeds," a qualification that excludes Protium fruits because what is dispersed is the pyrene, which encloses the seed. In this treatment the fruit is given the awkward but perhaps most accurate name of a "dehiscent drupe," as it was called by Engler (1874) in Flora brasiliensis.

Whatever the most appropriate name for the fruit, it develops as a fleshy structure (sometimes becoming sometimes lignified) of diverse shape, with as many lobes as the number of locules of the ovary which develop pyrenes and seeds. Within the fruit, the pyrenes are separated from each other by tissue of the ovary wall. At maturity the fruit dehisces by as many valves as there are pyrenes. Thus each valve splits acropetally along two sutures. When a valve falls away, it exposes a pyrene, which is partially or entirely enveloped in a sweet, spongy pulp, referred to in this treatment as a pseudaril (see discussion of this structure below). The pyrene usually falls away from the ovary wall but is suspended from the apex of the fruit by a structure which adheres weakly to the pyrene apex (see Fig. 10d). Dispersal of the pyrene either by falling or via an animal vector leaves a columellar structure, plus any intact locules which failed to develop.

While at anthesis the pair of ovules almost fill each locule, after fertilization the fruit and pyrene develop faster than the seed, reaching their full size well before the embryo expands to fill the cavity within the pyrene. This pattern of development occurs in a number of groups with drupaceous fruits, including the Chrysobalanaceae (Prance, pers. comm.) and such anacardiaceous genera as Pistacia (Grundwag, 1976) and Sclerocarya (von Teichman & Robbertse, 1986). Lignification of the pyrene also precedes development of the embryo, although it may not be complete before development of the embryo begins. Differentiation of the sugary pulp which envelops the pyrene occurs just as seed development is completed or shortly thereafter.

In most cases the fruit changes to its mature color just before dehiscence of the mature pyrene and seed, but in some species it consistently changes color prematurely. In Protium unifoliolatum the fruit turns red long before the seed has matured.

These developmental patterns, in which there is tendency for the external appearance of the fruit to indicate maturity before the embryo develops, may well serve the function of confusing and misleading fruit predators and causing them to waste considerable amounts of energy on predation of immature fruits from which they can obtain no nutrition.

The homologies of the various layers of the fruit of the Protieae are unresolved. This uncertainty stems from a fundamental problem in the understanding of fruit development, which is how to interpret the transition from an ovary wall with two layers-- an outer epidermis and an inner epidermis-- to a fruit with a three-layered pericarp-- an exocarp, a mesocarp, and an endocarp. It should be remembered, as Esau (1967, p. 589) noted, that "the terms applied to the different layers of the pericarp have little value for showing the origin of the various tissues of the fruit wall, but they are useful for the description of mature fruits." Richard (1819) conceived of the exocarp as consisting only of the outer epidermis, the endocarp as only the inner epidermis, and everything in between as the sarcocarp. While this definition leaves little room for error, it yields odd interpretations of real fruits; thus the stone of a peach was conceived of as consisting of the endocarp united with an indurated portion of the sarcocarp.

Most authors since Richard have accepted a broader and more flexible

definition of the layers of fruits, but this of course has led to differences of opinion as to where to demarcate the three zones.

If the fruit of the Protieae were a simple drupe such as a peach, there would be little disagreement as to where to draw the lines for the four layers. The outer epidermis and several layers of collenchyma beneath it would comprise the exocarp. The thick layer of parenchyma beneath that would be the mesocarp, and the layer of tightly packed sclereids below that would be the endocarp. Unfortunately, in the Protieae and Bursereae the cell types are not as easily categorized, and the layers are not comparable to those of a peach. There are an outer epidermis; a zone of parenchyma which includes resin canals; a zone of small cells; a zone of large cells which corresponds to the pseudaril; another zone of small cells; and a zone of sclereids or fibers which corresponds to the pyrene.

Oliver (1894) believed that the pseudaril does not constitute a distinct zone of the pericarp, but rather develops from and is a modification of the endocarp. On the other hand, Engler (1931, regarding Bursera and Commiphora) regarded the pseudaril as the mesocarp of the fruit.

Corner (1976) collected and examined the anatomy of mature fruits of Protium unifoliolatum. He interpreted the exocarp as consisting of the outer epidermis plus the zone of parenchyma with resin canals. The pseudaril he called an arilloid mesocarp, and he interpreted the zone of small cells on either side of the pseudaril as marking its interface with the exocarp and the pyrene, which he considered homologous with the endocarp.

Van der Walt (1975) carried out an ontogenetic study of the fruits of several species of Commiphora (Bursereae). While this genus belongs in another tribe, the Bursereae have a fruit very similar to that of the Protieae in most respects, including the manner of dehiscence and the presence of a pseudaril, and for the present it is assumed that the ontogeny of the fruit is essentially the same. He interpreted the exocarp as consisting of the epidermis plus hypodermal layers consisting of collenchymatous cells. He considered the mesocarp to be a zone of large parenchymatous cells where the resin canals and vascular bundles occur. He conceded that there is no sharp demarcation between the exocarp and mesocarp. The outer zone of small cells he called a "separation layer," which has intrusions through the mesocarp to the exocarp. Dehiscence of the fruit (abscission of the valves) is effected by disintegration of the cells of the separation layer.

He noted that after the cells of the inner epidermis have proliferated, hypodermal cells beneath the derivatives of the inner epidermis divide and enlarge to form the cells of the pseudaril. He also pointed out that there is a gradual transition from the cells of the pseudaril to the sclereids of the pyrene. He therefore concluded that the pseudaril is best considered as part of the endocarp.

It is true that Commiphora belongs to the Bursereae, and that the cell types in the two cases are not identical. Also, the transition from the pseudaril to the pyrene (endocarp) appears to be much more abrupt in P. unifoliolatum than in Commiphora. However, van der Walt's (1975) was an ontogenetic study, and his arguments are borne out by the plates that

accompany the paper. Also, I have found that in those species of Protium with a fiber layer on the pyrene, the pseudaril is continuous with the fiber layer and the fiber layer is continuous with the pseudaril (Fig. 10c), which supports van der Walt's interpretation.

Clearly ontogenetic studies of the fruits of Protium are necessary to resolve this disagreement, but the authors agree that the pyrene is homologous with the endocarp and that the sweet pulp enveloping the pyrene is not a true aril. Oliver (1894) was the first to call this structure a "pseudo-aril," a term which Lam (1932a, 1932b) and most later authors (e.g., Gillett, 1980) have contracted to "pseudaril," the term used in this treatment. True arils are associated with the seed, whereas this analogous structure is associated with the pyrene.

In the course of boiling and dissecting mature fruits of Protium for extraction and morphological study of the pyrene, I found that, in a number of species, removal of the pseudaril revealed a layer of matted fibers (Fig. 10b, c). These fibers could be scraped off only with some difficulty. I discovered that when of a drop of water is applied to the base of the pyrene of these species, the fiber layer breaks the surface tension of the water and transports it rapidly by capillarity to the apex of the pyrene. As noted in the chapter on seedlings, the apex is the site of germination in Protium, therefore it is not unreasonable to postulate that once the pseudaril is removed by a dispersal agent (or by insects on the ground) and the germinating seed has forced open the apex of the pyrene, the fiber layer helps to carry water to the growing seedling. The fibers, which may reach 0.4 mm in length, are rooted as it were in the

endocarp by a swollen base (Fig. 10c).

Another structure which has not been previously noted involves attachment to and suspension of the pyrene from the fruit apex. There is of course a funiculus which passes through the pyrene and vascularizes the developing seed. The place where the funiculus passes into the pyrene is easily visible and is surrounded by a usually discoloured area referred to in this treatment as the funicular scar (called a "cicatrice ombilicale" by Perrier de la Bathie (1946). Capuron (1968) implied that in the Madagascan species of Protium the exposed pyrene is attached to the fruit by the funiculus. However, in the Neotropical species of Protium, at least, the exposed pyrene is not suspended by the funiculus-- which apparently disintegrates as the pyrene matures-- but rather by an inverted V-shaped structure at the apex of the columella (Fig. 10d). This rather fragile laminar structure clasps the pyrene dorsally just behind its trigonous apex, which is also the site of the micropyle. The homology and development of this structure are unknown.

At this point it may be useful to review the characters of the fruit which have proven to be taxonomically useful. No use of fruit color in Protium was made by previous specialists in the family, possibly because few of them had any field experience with the genus (J. Cuatrecasas is an obvious exception), and because it was perhaps assumed that the fruits of all the species are red at maturity.

The mature fruits of most species are indeed various shades of red, but there are many distinctive exceptions. The exterior of the mature fruit may also be green (e.g., Protium cuneatum, P. divaricatum, P.

krukoffii, P. pallidum, P. paniculatum); brown to beige (P. demerarensis), gray (P. morii); pale green to almost white (P. pilosum); two-toned, green above and red below (P. aracouchini, P. calanense Cuatrec.) and perhaps other colors which have not yet been observed.

Another part of the fruit for which observations of color are sorely lacking is the inside of the ovary wall once the valves have fallen away, that is to say the columella. The color of this structure is perhaps more important than the exterior in attracting dispersal agents, because the valves are of course not present when the pyrene is exposed. Thus far I have seen the dehiscent fruits only of red-fruited Protium species, and the columella and the inside of the valves were all light red. It is quite possible that those species with rather dull-colored fruits may be brightly-colored within. This is true of two green-fruited species of Tetragastris I have observed: T. breviacuminata Swart and the recently re-discovered T. catuaba Soares da Cunha.

The range in size of Protium fruits is considerable (Fig. 11)-- approximately 1-3.5 cm in their largest dimension-- and while the size of the fruit in any given species can vary significantly, there are often discontinuities between closely-related or similar taxa.

There is also a very broad range of variation in the shape of Protium fruits (Fig. 11). While it is gratifying to have these shapes to use as tools for identification, they are difficult to describe and even more difficult to group into discrete categories. They range from almost globose P. altsonii, Fig. 11, no. 10) to essentially ellipsoid (P. polybotryum, Fig. 11, no. 12) to extremely oblique-ovoid (P. robustum,

Fig. 11, no. 7). Taxa which are clearly closely related as indicated by flower and vegetative characters also have similar fruit morphology. Also, there is considerable parallelism in fruit shape between relatively distantly related groups of species.

In their surface texture, most species of Protium have dull smooth surfaces when fresh, drying wrinkled. Again there are dramatic exceptions. Some species have very glossy fruits (e.g., P. pallidum, P. altsonii), some are rough-textured and lenticillate (P. opacum ssp. rabelianum, P. morii, P. demerarensis), and some are extremely coarsely rugose even fresh (P. fimbriatum). Those species which dry wrinkled have fleshy mesocarps, while those which dry smooth tend to have rather woody mesocarps (P. opacum, P. grandifolium, P. demerarensis, P. morii).

To date, the pseudaril has not been utilized as a taxonomic character in Protium. It has been either ignored or described as a uniform character: a spongy white pulp which envelops the pyrene entirely. Capuron (1968) was the first to give any indication that this is not the case, for when he gave a description of the two Protium species of Madagascar he noted that the pseudaril covers the pyrene except in the area around the funiculus. Dissection of Neotropical Protium fruits-- for those Protium species for which ample fruit material is in the herbaria-- has revealed that the distribution of the pseudaril over the surface of the pyrene follows several distinct patterns. It may cover all but the area immediately around the funiculus, which is the most common case. It may occur only as a lateral peripheral band around the pyrene (e.g., Protium cuneatum, P. pallidum). It may be absent from most of the ventral side of

the pyrene (P. giganteum, P. paniculatum). It may be absent from a portion of the ventral surface with a distinctive shape (P. carolense Daly, P. klugii Macbr., P. krukoffii).

Pseudaril patterns comprise one of the premier characters in the classification of the genera Commiphora and Bursera. Engler (1913) was the first to recognize the importance of this character. In an essay on African Burseraceae, although he organized Commiphora primarily by leaf morphology, the figures he presented were mostly of pyrenes and pseudarils. Later, Wild (1959) developed an infrageneric classification of Commiphora based largely on pyrene characters, with pseudaril patterns figuring prominently in the key to the sections. This approach has been followed, with some revisions and additions, by later authors (e.g., Vollesen, 1985). Rzedowski (i.e., Rzedowski & Kruse, 1979) has found the pseudaril to be a significant character in the classification of Bursera, a New World genus difficult to distinguish from Commiphora (Gillett, 1980).

Gillett (1980) and Rzedowski and Kruse (1979) have both noted that the pseudaril is a difficult character to study. Fully mature fruits are needed, as are thorough field observations regarding the color and texture of the pseudaril. In the herbarium, the proteinaceous pseudarils of Bursera and Commiphora are especially prone to attack by mites (Gillett, 1980). The sugary pseudarils of the Protieae suffer less damage from herbarium pests, but because their pyrenes are less securely fastened to the fruit once the valves have fallen away, it is less common to find intact, exposed pyrenes on herbarium sheets. The morphology and distribution of Protieae pseudarils may be distorted on pyrenes dissected

out of closed mature fruits, therefore field observations of the pseudaril in this group are as crucial as they are in Bursera and Commiphora.

Once a greater base of data for the pseudaril of Protium has been developed, it will be important to examine the constancy of this character within a given species. Gillett (pers. comm.) has warned that in Commiphora pseudaril characters are not so good as Wild (1959) and others have thought, at least in such widespread taxa as C. africana.

Field observations are needed for the texture and color of the pseudaril of Protium. From rehydrated material, the texture appears to vary from aerated and spongy (which I have observed in the field) to dense and fleshy. Once further data are available, it will be important to utilize a consistent vocabulary to account for these differences.

While the pseudaril of Commiphora and Bursera may occur in several bright colors (usually red or yellow or orange), to date no commentary has been made regarding the color of the pseudaril of Protium. In my own experience I have seen only white pseudarils, but recently reports of other colors have come to light. The pseudaril was reported as being yellow on one collection of Protium paniculatum var. paniculatum from Peru (Reyna 22), and light purple on one collection of P. altsonii from Venezuela (H. Clark 7099). Further field work is necessary to determine whether these colors occur consistently or whether they were the result of oxidation of the pseudaril.

One incontestable occurrence of a non-white pseudaril in Protium which has been reported several times-- including independent field observations-- is found in the Madagascan species, P. madagascariense

Engl. and P. beandou Marchand (Perrier de la Bathie, 1946; Aubréville, 1962; Capuron, 1968). In these species the pseudaril covers all but the area around the funiculus, and it is bright red. The same color was reported for the single species found on Mauritius, P. obtusifolium (Lam.) Marchand (Lamarck, 1788). Although Lamarck's observation has not been confirmed by a primary source in recent years, there is no reason to doubt that this closely related species does not share such a distinctive character with its floristic "neighbors."

I have seen no reports of the color of the pseudaril in the Asian species of Protium, but this character will undoubtedly prove to be useful at the sectional level.

The distribution of the fibers on the pyrene appears to follow the distribution of the pseudaril which overlies it. As noted above, the taxonomic occurrence of a hygroscopic fiber layer on the pyrene is discontinuous. The presence or absence of the fiber layer is consistent within natural groups. Thus it is present in all the species related to Protium trifoliolatum, while it is absent in all the species of sections Icicopsis and Sarcoprotium. The occurrence of the hygroscopic fiber layer in the eastern Amazonian species of Protium for which its presence or absence could be confirmed is as follows:

present	absent
<i>P. altsoni</i>	<i>P. apiculatum</i>
<i>P. cuneatum</i>	<i>P. crenatum</i>
<i>P. decandrum</i>	<i>P. divaricatum</i>
<i>P. demerarensense</i>	<i>P. pallidum</i>
<i>P. giganteum</i>	<i>P. plagiocarpium</i>
<i>P. hostmanni</i>	<i>P. polybotryum</i>
<i>P. krukoffii</i>	<i>P. robustum</i>
<i>P. opacum</i>	<i>P. sagotianum</i>
<i>P. paniculatum</i>	<i>P. tenuifolium</i>
<i>P. pilosissimum</i>	
<i>P. pilosum</i>	
<i>P. strumosum</i>	
<i>P. unifoliolatum</i>	

Further characters of the pyrene itself have proven to be taxonomically useful. Like the fruits of Protium, the pyrenes vary considerably in size and shape (Fig. 12). Most observations of the pyrene color report it as being black, but this may vary. On all pyrenes, there is an identifiable zone surrounding the funiculus, referred to in this treatment as the funicular scar (the "cicatrice ombilicale" of Capuron, 1968). This zone is easily distinguished because it is usually discolorous with the surrounding tissue (at least when dry), often distinct in texture (usually smooth while the rest of the pyrene is slightly rugose), and often set in relief from the rest of the pyrene. It is usually not covered

by the pseudaril, and it varies greatly in shape and size. The morphology of the funicular scar is included in the species descriptions of this treatment.

The location of the funiculus itself may vary. The site of the funiculus is recognizable as a round scar set in a depression on the ventral side of the pyrene. The funicular depression (as it is referred to in the species descriptions) may be negligibly shallow or rather deep, and while it is usually situated approximately 2/3 of the distance up the ventral surface, the distance may vary. It is subapical in Protium divaricatum, and located below the middle in section Icicopsis.

The thickness of the pyrene is another character which varies considerably in Protium, and Swart (1942b) included some indication of the its thickness in his monograph of the genus. The pyrene ranges from thinly cartilaginous and flexible (e.g., P. giganteum, P. pilosum, P. krukoffii), thickly cartilaginous and semi-rigid (P. altsonii, P. decandrum), to extremely hard and bony (P. crenatum, P. subserratum), but there is something of a continuum. There is one species, P. divaricatum which has an almost chartaceous pyrene (pers. obs.); in fact, the testa is thicker than the pyrene. The pyrenes of dried herbarium are always more rigid than fresh or rehydrated (boiled and cooled) material. The species descriptions in this treatment refer to pyrenes in the latter condition.

Seeds

The taxonomic distribution of some seed characters in the Protieae, and particularly in Protium, constitutes perhaps the most perplexing problem in the tribe. In the Burseraceae as a whole, the embryo is straight and exalbuminous, the storage tissue being the large cotyledons. In most of the tribe, the testa shows irregular lignified thickenings and is infolded with the lobed (compound in Garuga) and contortuplicate cotyledons (Fig. 13a, b). In a minority of the taxa, however, while the testa may show some irregular thickenings it is not infolded with the cotyledons, and the cotyledons are entire, plano-convex, and either straight or distally uncinately curved. As noted in the chapter on generic limits in the tribe, entire cotyledons occur in Crepidospermum and Tetragastris.

One of the quintessential characters of Protium in all the descriptions of the genus in the literature up to the present time was the occurrence of lobed and contortuplicate cotyledons. As in so many other cases, Triana & Planchon (1872) showed an uncanny prescience when they remarked about Icica macrophylla H.B.K. (now P. macrophyllum (H.B.K.) Engl. that, 'In the only embryo that we have seen (before its complete development) the cotyledons appear to us to be entire.' (my translation). This observation was not pursued by later authors, and until Cuatrecasas (1961) realized that two species assigned to Protium had entire and plano-convex cotyledons, this appeared to be a good character for separating Protium from Tetragastris.

Cuatrecasas transferred the two Protium species to Tetragastris on the

basis of the cotyledons as well as on the basal fusion (inconstant in my observation) of the petals. Then (Cuatrecasas, 1952) he discovered a taxon which has the free petals of Protium and the plano-convex cotyledons of Tetragastris, and he created a new genus, Paraprotium, to accomodate this combination of characters. Later, he added several species to his new genus (Cuatrecasas, 1957).

Since that time, however, entire and plano-convex cotyledons have turned up in other species of Protium which have undeniably and consistently free petals, but which are clearly unrelated to Paraprotium. Furthermore, I am convinced that Cuatrecasas' Paraprotium is an unnatural assemblage of species, based as it was on a single-- and as it turns out, unreliable-- character separating it from either Protium or Tetragastris (see chapter on generic limits). The four species attributed to Paraprotium have been transferred (or returned) to Protium (Daly, in review).

The species of Protium which were found to have entire, essentially plano-convex cotyledons are listed below. Species which are known to be closely related show the same embryo type. For example, all the species of section Sarcoprotium have lobed, contortuplicate cotyledons, while the complex of species which includes Protium trifoliolatum is characterized by entire, essentially plano-convex cotyledons.

<i>P. apiculatum</i>	<i>P. plagiocarpium</i>
<i>P. aracouchini</i>	<i>P. reticulatum</i>
<i>P. divaricatum</i>	<i>P. robustum</i> (*)
<i>P. ferrugineum</i>	<i>P. sagotianum</i> (*)
<i>P. fimbriatum</i>	<i>P. spruceanum</i>
<i>P. guianense</i>	<i>P. subserratum</i>
<i>P. krukoffii</i>	<i>P. tenuifolium</i> (*)
<i>P. pilosum</i>	<i>P. trifoliolatum</i>

The cotyledons of section Icicopsis (starred species in the above list) probably represent a third type of embryo in the genus, because they are consistently transversely folded in an unusual pattern. Both cotyledons are first convexly curved, then concavely curved, such that in cross-section they form two nested double-sigmoid curves. The resulting structure is shallowly concave in the middle and has marginally involute cotyledons. Except in *P. robustum*, which has straight cotyledons, the base (distal end of the cotyledons) is strongly incurved to form in profile a "6"-shaped figure (Fig. 13d).

Given the perplexing distribution of the basic embryo types in Protium and the tribe Protieae, the question naturally arises as to how the lobed, contortuplicate arrangement of the cotyledons came about, both developmentally and evolutionarily. From the developmental perspective, it could be supposed that this arrangement of the cotyledons is the result of a purely mechanical process, in which the expanding cotyledons outgrow the length of the fully-expanded locule (see chapter on fruits) and are forced

by lack of space to repeatedly fold on themselves. Dissection of developing fruits (fresh, rehydrated, and preserved) of species characterized by lobed, contortuplicate cotyledons, however, revealed that the folding process begins long before the space inside the pyrene is fully occupied by the developing embryo (see Fig. 13b).

Since this morphological phenomenon cannot be explained by a passive mechanical process, perhaps it can be explained as an evolutionary response or "strategy." In the course of dissecting the fruits of Protium species, in several instances dissection of the pyrene exposed the seed-cavity completely occupied by the pupa or adult of a hymenopteran, with no vestige of even the testa remaining (Fig. 13c). Clearly at anthesis or early in fruit development a wasp oviposits one or more eggs in one or more locules of the ovary, after which the larva(e) feed(s) on the developing embryo. For some reason the plant does not always respond by aborting the fruit. I would conjecture that probably other locules of the same fruit are developing normally. Upon reaching the adult stage, the insect must be able to chew or digest its way through the thick, lignified tissue of the pyrene.

In the developing embryo of species with lobed, contortuplicate cotyledons, those portions of the testa located along the folds and especially within the folds of the cotyledons thicken and darken in color, becoming markedly crustose and lignified as the seed matures. In the mature seed, the folding is so dense and intricate that only thin regions of cotyledonary tissue can be traversed before more lignified testa is encountered. This morphology may possibly have evolved to hinder the

destructive progress of the hymenopteran larva as it eats the seed. If this is the case, the seed predator has at best been slowed down, because at least some of the pyrenes occupied by hymenopterans were of species with lobed, contortuplicate cotyledons.

This seed type is not at all restricted to the Burseraceae. Van Heel (1970, 1971) examined what he called the "labyrinth-seeds" of taxa from several families, including the Leguminosae, Anacardiaceae, Convolvulaceae, Rhopalocarpaceae, and Hernandiaceae. He noted that in some groups there are gradations in the complexity of the labyrinth-seeds. Most importantly, he pointed out that three species of Mangifera (Anacardiaceae) have labyrinth-seeds, while the rest of the genus has "normal" seeds. This observation may bear on the taxonomic problem at hand in the Protieae, for if such differences may be accepted as occurring within a genus of a closely-related family, they may cause less consternation in Protium.

Anatomy

Anatomical studies were not carried out as part of this revision, but materials for future anatomical work, especially for leaf and petiole anatomy, were collected during the field phase of this research. Much of the field work was carried out in reserves and other protected areas, so it was often not possible to collect wood samples. However, ample material for studies in wood anatomy can be found among the vouchered wood samples at Madison, Wisconsin and Utrecht, The Netherlands. Review of the available literature on the anatomy of the Burseraceae has provided directions and specific questions for future anatomical studies in Protium and the other genera of the Protieae. Future research in the genus will include a focus on leaf anatomy and the histology of the trichome types.

Anatomy in general has not been stressed as an important tool in the systematics of the Burseraceae. Some of the more in-depth studies of the anatomy of the family have been geared toward examining its relationships to other families, notably the Anacardiaceae. Examples of such studies are the works of Webber (1941) and of Kryn (1952). These and other authors have indicated the close similarities in the anatomy of the Burseraceae and Anacardiaceae. They have also commented on the relative uniformity of wood and stem anatomy within the Burseraceae, indicating that other more variable characters are more profitable avenues of research within the family. As Webber (1941, p. 458) wrote, "The basic similarity in the wood structure of all genera of the Burseraceae therefore indicates that in this family specialization in structure of fruits, flowers and leaves has

proceeded at a more rapid rate than in the woods." In their atlas of Amazonian woods, D  tienne and Jacquet (1983) wrote a joint key to the woods of some Burseraceae and Anacardiaceae species (see more about this work below). Guillaumin (1909a), who looked at the anatomy of quite a range of species of Protium, including taxa from all the major natural groups, commented that the anatomy of the genus is rather uniform.

Nevertheless, clues can be found in the literature to several potential differential characters in the wood-- notably in the occurrence, size, and location of silica crystals-- and in the nature of the rays. In their aforementioned work on Amazonian woods, D  tienne and Jacquet (1983) separated several species of Protium based on the presence or absence of silica crystals in the fibers and on whether the rays are uniseriate or biseriate.

Ter Welle (1976), who surveyed a great number of tree species in Surinam and elsewhere in South America for the occurrence of silica, did not draw any significant conclusions regarding the Burseraceae. He noted that the distribution pattern is variable, and that silica grains do not occur in a minority of species of Protium, namely P. altsonii, P. aracouchini, P. giganteum var. crassifolium, and P. guianense (nomenclature updated).

Another survey of the occurrence of silica specifically in the Burseraceae is currently underway at the Laborat  rio de Produtos Florestais (Forest Products Laboratory) of the Brazilian Forestry Institute (Instituto Brasileiro de Desenvolvimento Florestal). They have identified five patterns in the forms of silica and where they occur (V.

T. Rauber Coradin, pers. comm.):

- 1) Present in large concretions in uniseriate portions of the rays, vessels with oval sections, diameters intermediate.
- 2) Large crystals present in uniseriate portions of the rays.
- 3) Present in large concretions, apparently in all ray cells, vessels with oval sections and small diameters.
- 4) Frequent in concretions in the septate fibers, rarely in the marginal strata and axial parenchyma, with crystal occasionally appearing with the silica or in other cells.
- 5) Few crystals present in uniseriate portions of the rays, vessels with oval sections and intermediate diameters.

Although their wood samples are vouchered and consist primarily of material from the INPA herbarium in Manaus, they have yet to match their reference numbers with the determinations I have made at INPA.

In another tribe of the Burseraceae, Stevenson (1979) studied three Bahamian species of Bursera and was able to distinguish them anatomically on the basis of average vessel diameter, percentage of biseriate rays, arrangement of resin canals in the secondary phloem, and presence or absence of secondary phloem fibers. It is of interest to note that the species which has secondary phloem fibers belongs to a different section of the genus than two species which do not have them.

The pioneering systematic work on the anatomy of the Burseraceae was carried out by Solereder (1908) and by Guillaumin (1909a), whose results were later cited by Metcalfe and Chalk (1950). A number of their findings

are worth investigating in all genera of the Protieae. Guillaumin (1909a) pointed out a number of anatomical features in Tetragastris which differ from those in Protium; in the latter there is no hypodermis or mucilage cells in the leaflets; there are no sclereids in the cortex; and there is a layer of cork on one side of the petiole. Metcalfe and Chalk (1950) wrote that Tetragastris has stomates on both sides of the leaflets. Guillaumin indicated that in Crepidospermum, there is no hypodermis in the leaflets and that the pith has irregular cells (contrasted with regular cells in Protium).

Within the genus Protium, the taxonomic distribution of a number of leaf characters is worth investigating. Solereder (1908) observed that medullary vascular bundles were present in the leaf rachis of section Icicopsis but not in the rest of Protium (nomenclature updated). Guillaumin (1909a) remarked that some species in the genus have two layers of palisade cells. He also found that mucilage cells do not occur in many of the Neotropical species but they do occur in section Marignia (the African species) and in P. javanicum Burm. f. Papillate abaxial leaflet surfaces were observed in P. reticulatum (Engl.) Engl., and the same character is observable under the dissecting microscope in two closely related species, P. ferrugineum (Engl.) Engl. (also from the upper Rio Negro region) and the widespread Protium suberratum. Solereder (1908) discovered that vertically transcurrent veins occur in the leaflets of P. unifoliolatum and P. spruceanum.

Solereder (1908) reasoned that the large solitary crystals in the palisade layer of P. serratum (Wall. ex Colebr.) Engl. and P. javanicum

give rise to "transparent dots." The nature and taxonomic distribution of punctations in Protium is well worth investigating. When they occur they are usually seen only through young fresh leaflets or in cleared leaflets. Thus far I have seen punctations only in section Icicopsis, where it appears to occur in all the species, but the description of Protium puncticulatum Macbr. from Peru indicates that the character may be more widespread in the genus.

Some distinctive types of trichomes occur in other burseraceous genera, but Protium appears to manifest a limited number of hair types. However, due to the presence of a few intriguing hair types reported in the literature, it will be worthwhile to carry out a survey of trichomes in the genus. Guillaumin (1909a) reported the occurrence of capitate hairs on the leaflets of P. serratum. In P. spruceanum, Solereder (1908) noted the presence of unicellular two-armed hairs as well as glandular hairs which are broadened toward the apex. I have observed an unusual type of trichome on the abaxial leaflet surfaces of P. apiculatum and on various organs of the members of section Icicopsis. These trichomes, which are short, basally thickened, and somewhat twisted, are reminiscent of the snail-shaped glands found in Crepidospermum (see chapter on generic limits), and should be investigated.

Chromosomes

There are no reports of chromosome counts for Protium in the New World. In the Old World, P. serratum (Wall. ex Colebr.) Engl. was reported to have a count of $2n=22$ (Ghosh, 1969), later confirmed by another count of $n=11$ (reported in Goldblatt, 1981). Table V presents the counts available to date for the Burseraceae, and were garnered from Cave (1959, 1961), Moore (1973, 1977), Goldblatt (1981), and Ornduff (1967).

Clearly Canarium has experienced a good deal of polyploidy, while Bursera, which is known to hybridize frequently (McVaugh & Rzedowski, 1965) appears from this limited sampling to maintain a constant number. The base number for Canarium, Aucoumea, Commiphora, and Garuga appears to be $x=13$, while for Bursera it is $x=6$ or $x=12$.

Raven (1975) indicated that the probable base number for the Burseraceae is $x=13$, and that for the Sapindales it is probably $x=7$. Ghosh (1969) maintained that Protium serratum has a primitive karyotype because all the chromosomes are metacentric or submetacentric, and conjectured that perhaps $x=13$ is not the base number for the family, as has been proposed. Because $n=13$ has been obtained for the majority of the taxa examined to date, and because the same count has occurred in all three tribes of the family, it is probable that the base number for the family is indeed $x=13$ and that at least in terms of its karyology Protium is derived.

In the course of the field work for the present treatment, numerous flower buds, vegetative apices, and seedling root tips were fixed in the field for purposes of chromosome counts. The material was fixed either in

Table V.

Chromosome counts for the Burseraceae

Taxon	n=	2n=
Canarieae		
<u>Canarium bengalense</u>	52	
<u>C. sikkimense</u>	39	
<u>C. strictum</u>	13	
<u>Dacryodes deliciosa</u>		46
Bursereae		
<u>Aucoumea klaineana</u>		26
<u>Bursera delpechiana</u>	12	
<u>B. simaruba</u>	12	
<u>B. tomentosa</u>	12	
<u>Commiphora mukul</u>		26
Protieae		
<u>Garuga gamblei</u>	13	
<u>G. pinnata</u>	13	
<u>Protium serratum</u>	11	22

3:1 100% ETOH: glacial acetic acid or in 4:3:1 chloroform: 100% ETOH: glacial acetic acid. In many cases the material was of necessity collected during the middle of the day. Also, it was not possible to refrigerate the material after fixing. Transferral to 70% ETOH was in some cases delayed for several weeks. These factors may have contributed to the lack of success in obtaining counts from this material, which was prepared using the methods presented in Sharma & Sharma (1980).

Ecology

1. The Burseraceae in Amazonia

Considering the relatively short history of botanical exploration in Amazonia, the importance of the Burseraceae in the region has been commented on for some time, at least since the time of Ducke's pioneering research, which was highlighted by his landmark publication with Black (Ducke & Black, 1953). Ducke and Black commented on the importance of the Burseraceae in eastern Amazonia. However, the data which have been accumulating over the past 15 years indicate that the family manifests a strong presence also in the Guianas, the Rio Negro region, the region around Manaus, and some portions of western Amazonia.

Figure 14a is a map of the sites of the quantitative forest inventories which have been carried out in Amazonia and the Guianas. As the legend indicates, analysis of the data for a number of these studies is still in progress. Data on the Burseraceae are of course lacking for most of these; moreover, some of the studies which are published did not break down their results by species or family, depending on the purpose of the project. Figure 14b is a map of some of the data which are available for the Burseraceae from quantitative inventories, and indicates the rank of the family or of the most important species in terms of relative density. These data are expanded on in Table VI.

The Burseraceae may comprise up to 15% of the trees over 10 cm DBH in the forest in Maranhão (Balée, in prep.), in Amapá on the Guiana Shield (Daly et al., in prep.), and near Manaus (Daly, pers. obs.). The family

Table VI. Burseraceae in Neotropical inventories

source	location	area	no. spp.	no. genera	comments
Balée (in prep.)	Monção, Maranhão	1ha	11	3	15.4% of all individuals
Bastos, 1960	Amapá	362ha	---	---	2nd family in frequency class and density; 27th over 55cm dbh
Balslev et al., (in press)	Añangu, Ecuador	1,000 trees	11	4	12th family in FIV; 13th family in rel. density; 5th in no. of species
Black et al., 1950	Belém	1ha	6(?)	2	2nd and 3rd spp. in density
Boom, 1987	Beni, Bolivia	1ha	2	2	family 11th in rel. density, 12th in Family Importance Value
Cain et al., 1953	Belém	2ha	16	3	5 of top 20 spp. in density, basal area, frequency, importance values; family 1st in total importance value
Campbell et al.,	Rio Xingu, Pará	3ha	3	1	17th sp. in IV
Carvalho, 1981	Tapajós, Pará	35ha	4(?)	2(?)	family 5th in rel. freq., 6th sp. in rel. density
Daly et al. (in prep.)	Falsino, Amapá	3ha	12	4	15% of all individuals
Daly (in prep.)	NE of Manaus	100	45	5	8.6-17% of individuals per hectare
Dantas & Müller, 1980	Altamira, Pará	1.5ha	6	4	

Table VI. (contd.) Burseraceae in Neotropical inventories

source	location	area	no. spp.	no. genera	comments
Davis & Richards, 1933, 1934	Moraballi Creek, Guyana	-----	---	---	9th sp. in rel. density in "Mora" forest; 12th in "Morabukea" forest; 15th in "Greenheart" forest
Gentry (ined.)	Yanamono, Peru	1ha	9	3	family 10th in no. of species
Gentry (ined.)	Mishana, Peru	1ha	13	3	family 7th in no. of species
Gentry (ined.)	Cabeza de Mono, Peru	1ha	12	3	family 4th in no. of species
Gentry, 1985	Manu Park, Peru	1ha	1	1	
Glerum & Smit, 1965	Pará	62ha	5(?)	3	2nd sp. in volume
Hartshorn (ined.)	Tambopata, Peru	1ha	4	3	
Hubbel & Foster 1983	Barro Colorado Island, Panama	50ha	2	2	8th and 9th spp. in rel. density
Lechthaler, 1956	Manaus, Amazonas	1ha	2(?)	?	1st family in rel. density
Maas, 1971	western Surinam	5.5ha	8	4	family 7th in overall rel. density
Mori (in press)	Saül, French Guiana	800 trees	13	3	1st family in frequency, 2nd in dominance, 2nd in Family Importance Value; 1st sp. in freq., dens., dom. & IV; 3 of top 8 spp. in freq.
Pires & Koury, 1958	Belém (várzea)	3.8ha	5	2	10th sp. in rel. density, 11th in rel. frequency

Table VI. (contd.) Burseraceae in Neotropical inventories

source	location	area	no. spp.	no. genera	comments
Pires et al., 1953	Castanhal, Pará	3.5ha	8	?	6th sp. in density
Prance et al., 1976	Manaus, Amazonas	1ha	13	2(?)	5th sp. in density, 7th in volume
Ratter (ined.)	northern MT, Brazil	---	--	--	3rd sp. in IV in dense cerradão; 1st species in IV in cerradão/dry forest; 7th sp. in IV in dry forest
Ratter et al., 1973	Xavantina, Brazil		3	1	family 23% of individuals in Swampy Gallery Forest
Ratter et al., 1978	northern MT, Brazil	---	--	--	3 of 8 most important understory trees in evergreen seasonal forest
Rodrigues, 1961	Upper Rio Negro	0.05ha	4	1	4th family in rel. density
Rodrigues, 1963	Amapá	1.1ha	4	1	5th sp. in density, 7th in volume
Rodrigues, 1967	Manaus	27ha	?	?	6th family in rel. density
Rodrigues (ined.)	Manaus (Hotel Tropical)	-----	?	?	family 2nd in no. of species
Saldarriaga (ined.)	San Carlos, Venezuela	---	---	---	"Protium sp." in top 5 IV's in half of stands of 80-year-old secondary forests, also in half of stands of mature forest
Silva & Lopes, 1982	Tapajós, Pará	----	--	--	6th sp. in rel. density, 2nd highest score in Pielou Index (aggregation)

consistently ranks highly in eastern Amazonia. Inventories carried out in the Rio Negro region have indicated a very strong presence of Burseraceae there as well (Saldarriaga, in prep.; Rodrigues, 1961a).

Areas in which the Burseraceae appear to be relatively unimportant are Roraima (Campbell, in prep.), Manu in Peru (Gentry, 1985) and Guyana (Davis & Richards, 1934), although the latter publication examined some rather specialized vegetation types. Inventories of two hectares on the Ilha do Maracá in Roraima yielded Burseraceae densities of 5.3% and 5.7% (Campbell, unpublished data). The results for Guyana are surprising considering the overall importance of the family in the countries which flank it, French Guiana and Suriname. Perhaps the accelerated collecting which is now being carried out in Guyana will reveal some forests with different results.

While the Burseraceae appear to be less important in western Amazonia in terms of relative density and relative importance values, recent inventories have shown that in many regions they maintain rather high relative diversity. The most surprising data have come from the one-hectare studies of Gentry in Peru (in prep.). Based on determinations made by the present author, he found that at Cabeza de Mono, Mishana, and Yanamono, the Burseraceae were among the top ten families in species diversity (see Fig. 14b; Table VI). Data on relative density and other parameters are not yet available. Similarly, Balslev et al. (in press) found in the Napo region of Ecuador that while the Burseraceae ranked 13th in Family Importance Value (relative density + relative dominance + relative diversity, cf. Mori et al., 1982) and 14th in relative density,

it tied for fifth place in relative diversity, that is, in number of species. The relative density of Burseraceae on six hectares of forest in Acre ranged between 1.9% and 5.3%, but in one of the two-hectare inventories there were 19 species of Burseraceae, a figure which rivals the diversity of the family anywhere.

In Suriname, a country which is relatively well collected and where a significant amount of inventory work has been done (Schulz, 1960; Maas, 1971), the importance of the Burseraceae depends very much on the locality. Schulz (1960) noted that in forests with a strong presence of Vouacapoua americana, the Burseraceae are almost absent. He also noted that the soils in these areas tend to be higher in pH and to have more available potassium and magnesium. This information seems to agree with the Gentry's idea (pers. comm.) that there is a negative correlation between soil quality and the importance of Burseraceae in lowland South America. It should be noted that in Amapá on the Guiana Shield, one inventory with a strong presence of V. americana also showed a 15% relative density of Burseraceae (Daly et al., in prep.).

In the few studies which have examined the forests on the periphery of Amazonia, again the Burseraceae appear to be important elements of the flora. The data of Balée (in prep.) from the "pre-Amazon" forests of Maranhão have been mentioned.

In northern Mato Grosso, the Burseraceae figure prominently in some of the vegetation types which form a mosaic in the complex transition zone between Amazonia and the Cerrado of Central Brazil. Ratter and others (Ratter et al., 1973; Ratter et al., 1978) have studied this area

extensively. In the Swampy Gallery Forest they inventoried, three species of Burseraceae showed a relatively density of 23%. In a transect from Tall Dry Forest through Low Dry Forest to Cerradão and Cerrado (their terminology), the Burseraceae showed a strong presence which weakened progressively as the vegetation became more open and xeromorphic (Ratter et al., 1973). Slightly to the northwest of these sites, Ratter et al. (1978) worked in a more robust and less xeromorphic forest that they referred to as Evergreen Seasonal Forest. There they found that burseraceous taxa comprised three of the eight most important understory species. They recognized six species of Burseraceae in this region.

In the Parque Nacional do Araguaia, some 250 km NW of the other sites, the Burseraceae were a more important part of the dryer vegetation types. In dense Cerradão, Protium heptaphyllum was third in Importance Value (IV), while in the Cerradão/Dry Forest interface it had the highest IV. In the Dry Forest itself, Protium unifoliolatum had the seventh highest IV. Five species of Burseraceae were recognized in this region.

Table VII presents lists of the species of Burseraceae which are known to have been collected in the quantitative inventories to which they refer. One of the great dangers of interpreting the results of tropical forest inventories lies in the determinations of the taxa (Campbell et al., 1986; Daly, in prep.). This is especially true of the Burseraceae. For example, Black et al. (1953) noted that the botanists involved in his project near Belém were confident of the separation of taxa in all groups but the Burseraceae and Myristicaceae. In the tables which follow, only those lists of determinations are used which have been evaluated and are

Table VII

Determination lists of Burseraceae from Neotropical Inventories

<u>Altamira, Pará/ Dantas & Muller, 1980</u>	1.5ha
<i>Crepidospermum goudotianum</i> (Tul.) Tr. & Pl.	
<i>Protium robustum</i>	
P. sagotianum	
P. subserratum	
<i>Tetragastris altissima</i> (Aublet) Swart	
<i>Trattinnickia</i> sp.	
<u>Capitão Poço, Pará/ Dantas et al., 1980</u>	1 ha
<i>Protium altsoni</i>	
P. aracouchini	
P. decandrum	
P. giganteum	
P. pallidum	
P. trifoliolatum	
<i>Tetragastris altissima</i> (Aubl.) Swart	
<i>Trattinnickia burserifolia</i> Mart.	
<u>Castanhal, Pará/ Pires et al., 1953</u>	3.5ha
<i>Protium heptaphyllum</i>	
P. guianense	
P. polybotryum	
P. sagotianum	
P. indet. (4 spp.)	
<u>Mocambo Reserve (Belém), Pará/ (pers. obs.)</u>	8 ha (approx.)
<i>Crepidospermum rhoifolium</i> (Benth.) Tr. & Pl.	
<i>Dacryodes belemensis</i> Cuatrec.	
<i>Protium altsoni</i>	
P. aracouchini	
P. decandrum	
P. giganteum	
P. heptaphyllum	
P. guianense	
P. krukoffii	
P. pallidum	
P. polybotryum	
P. sagotianum	
P. subserratum	
P. spruceanum	
P. tenuifolium	
P. trifoliolatum	
<i>Tetragastris altissima</i> (Aublet) Swart	
<i>Tetragastris panamensis</i> (Engl.) O.K.	
<i>Trattinnickia bursersifolia</i> Mart.	

Table VII (contd.)

<u>Monção, Maranhão/ Balée (in prep.)--</u>	1 ha
<i>Protium altsoni</i>	
P. aracouchini	
P. decandrum	
P. giganteum	
P. pallidum	
P. polybotryum	
P. sagotianum	
P. spruceanum	
P. tenuifolium	
P. trifoliolatum	
<i>Tetragastris altissima</i> (Aublet) Swart	
<i>Tetragastris panamensis</i> (Engl.) OK.	
<i>Trattinnickia bursersifolia</i> Mart.	
<u>Manaus/ Prance et al., 1976</u>	1 ha
<i>Protium altsoni</i>	
P. apiculatum	
P. heptaphyllum	
P. insigne	
P. opacum	
P. strumosum	
P. sagotianum	
P. trifoliolatum	
<i>Protium</i> indet. (4 spp.)	
<i>Tetragastris altissima</i> (Aublet) Swart	
<i>Tetragastris panamensis</i>	
<u>Santa Luzia, Acre/ Campbell (in prep.)</u>	2 ha
<i>Protium altsoni</i>	
P. decandrum	
P. divaricatum ssp. divaricatum	
P. ferrugineum (Engl.) Engl.	
P. fimbriatum Swart	
P. cf. giganteum	
P. grandifolium	
P. guianense	
P. nodulosum Swart	
P. paniculatum var. paniculatum	
P. sagotianum	
P. strumosum	
P. trifoliolatum	
<i>Crepidospermum rhoifolium</i> (Benth.) Tr. & Pl.	
<i>Dacryodes</i> sp. 1	
D. sp. 2	
<i>Tetragastris altissima</i> (Aublet) Swart	
T. panamensis (Engl.) O.K.	
<i>Trattinnickia glaziovii</i> Swart	

Table VII (contd.)

<u>Serra do Navio, Amapá/ Rodrigues, 1963</u>	1.1ha
<i>Protium opacum</i>	
P. subserratum	
P. spruceanum	
P. sagotianum	
P. tenuifolium	
<u>Ilha do Bananal, Brazil/ Ratter, 1985</u>	?? trees (point-quarter)
<i>Crepidospermum rhoifolium</i>	
<i>Protium brasiliense</i>	
P. heptaphyllum	
P. unifoliolatum	
"Burseraceae"	
<u>Añangu, Ecuador/ Balslev et al. (in press)</u>	1,000 trees (point-quarter)
<i>Crepidospermum rhoifolium</i>	
<i>Protium divaricatum</i> var. <i>divaricatum</i>	
P. fimbriatum	
P. insigne	
P. nodulosum	
P. unifoliolatum	
P. sp. 1	
P. sp. 2	
<i>Tetragastris altissima</i>	
T. panamensis	
<i>Trattinnickia rhoifolia</i>	
<u>Yanamono, Peru/ Gentry (ined.)--</u>	1 ha
<i>Dacryodes peruviana</i> (Loesn.) Lam	
D. sp.	
<i>Protium nodulosum</i>	
P. cf. <i>polybotryum</i>	
P. robustum	
P. spruceanum	
P. subserratum	
P. sp.	
<i>Tetragastris panamensis</i> (Engl.) Kuntze	
<u>Mishana, Peru/ Gentry (ined.)</u>	1 ha
<i>Crepidospermum rhoifolium</i> (Benth.) Tr. & Pl.	
<i>Protium apiculatum</i>	
P. aracouchini	
P. carnosum A. C. Sm.	
P. cf. <i>crassipetalum</i> Cuatrec.	
P. divaricatum	
P. ferrugineum	
P. grandifolium	
P. opacum	
P. subserratum	
P. sp.	
<i>Trattinnickia rhoifolia</i> Willd.	

Table VII (contd.)

<u>Cabeza de Mono, Peru/ Gentry (ined.)--</u>	1 ha
<i>Dacryodes</i> cf. <i>kukachkana</i>	
<i>D.</i> nitens	
<i>Protium</i> <i>altsoni</i>	
<i>P.</i> apiculatum	
<i>P.</i> carnosum	
<i>P.</i> cf. <i>crassipetalum</i> Cuatrec.	
<i>P.</i> divaricatum	
<i>P.</i> grandifolium	
<i>P.</i> nodulosum	
<i>P.</i> trifoliolatum	
<i>Trattinnickia</i> <i>rhoifolia</i> Willd. var. <i>lancifolia</i> Cuatrec.	
<u>Mishana, Peru/ Gentry (ined.)--</u>	1 ha
<i>Protium</i> <i>tenuifolium</i>	
<u>Saül, French Guiana/ Mori et al. (in press)</u>	1,000 trees (point-quarter)
<i>Crepidospermum</i> <i>rhoifolium</i>	
<i>Dacryodes</i> sp.	
<i>Protium</i> <i>apiculatum</i>	
<i>P.</i> decandrum	
<i>P.</i> divaricatum var. <i>fumarium</i>	
<i>P.</i> heptaphyllum	
<i>P.</i> guianense	
<i>P.</i> morii	
<i>P.</i> opacum var. <i>rabelianum</i>	
<i>P.</i> pallidum	
<i>P.</i> pilosum	
<i>P.</i> plagiocarpium	
<i>P.</i> sagotianum	
<i>P.</i> tenuifolium	
<i>P.</i> trifoliolatum	
<i>Tetragastris</i> <i>altissima</i>	
<i>T.</i> panamensis	
<i>Trattinnickia</i> <i>rhoifolia</i>	

considered reliable.

It can be seen from Table VII that the number of Burseraceae in an Amazonian forest usually ranges from five to twelve per hectare. The number of genera ranges from one to five but is usually three to four. One pattern that will be examined later in this chapter is that the genera other than Protium are never represented by more than two species, while Protium seldom shows fewer than five. Dacryodes is encountered in eastern Amazonia and the Guianas much less often than in western Amazonia.

In their ecological importance, the Burseraceae are on a par with all of the great plant families of Amazonia, but the manner in which this importance is achieved differs from some of those other families. Like the Chrysobalanaceae, the Burseraceae achieve their importance primarily by dint of their great density. In virtually every Amazonian inventory for which such data are available, the Burseraceae score significantly higher in relative density than in relative "dominance" (basal area), and somewhat higher than in relative diversity (number of species). The importance of the Leguminosae is due more to their basal area and especially their great diversity. While the Lecythidaceae may often show high relative density or relative diversity, the importance of that family in inventories is due more to its basal area. A few individuals of the massive Bertholletia excelsa H.B.K. can greatly influence the ranking of the Lecythidaceae in both relative dominance and in Family Importance Value (Campbell et al., 1986).

It may be that in western Amazonia the importance of the Burseraceae is due more to its unexpectedly high diversity than to its relative

density. The results of the study at Añangu in Ecuador (Balslev et al., in press) show that while the family ranked 14th in relative density it ranked 5th in relative diversity. It is probable that similar results will be obtained for the several studies in Peruvian Amazonia where the relative diversity of the Burseraceae was also very high, as noted above.

2. Ecology of the genera, autecology of species

The overall pattern in which the family ranks higher in relative density than in relative dominance is due to the ecology of the group, and each genus has its own ecological range. Crepidospermum never reaches the canopy and has never figured prominently in any inventory, although C. goudotianum (Tul.) Tr. & Pl. is common in the understory of the forest-savanna transition near Macapã, Amapã (pers. obs.). Dacryodes, still a very poorly known genus, can occasionally reach the canopy. Although seven species have entered the inventory of 100 ha of forest made by the World Wildlife Fund near Manaus, all are rare. Tetragastris may also reach the canopy, but most individuals of any given species are of intermediate stature. Only T. altissima (Aublet) Swart is known to be common in any of the forests of Amazonia or the Guianas, but it is interesting to note that in addition to being extremely common in parts of northern Suriname (Schulz, 1960) and near Saül, French Guiana (Mori et al., in press), the same species has also proved to be rather common in some forests of the Peruvian Amazona (based on determinations of inventory material collected by A. Gentry).

Trattinnickia is the only genus of Burseraceae found in Amazonia and

the Guianas that occurs consistently in the canopy. Where it occurs it is represented by a few very tall individuals with large diameters, as on the Mocambo Reserve near Belém (Fig. 15d). This is the pattern shown by Bertholletia excelsa H.B.K.

Protium is much larger and is ecologically more flexible than the other genera represented in Amazonia and the Guianas. Some species may occur as shrubs, such as P. guianense, and P. aracouchini, while others usually reach the canopy where they occur, such as P. pallidum and P. decandrum. Those species which consistently reach the canopy, however, do not show the pattern of Trattinnickia or Bertholletia discussed above. Instead they occupy every stratum leading up to and including the canopy, as can be seen from Fig. 15c.

A distinction should be made between the strata occupied by all individuals of a given taxon and by those occupied by individuals of reproductive age. In the course of his study of the forests of Saül, French Guiana, Mori (pers. comm.) has observed that while discrete strata of the forest as a whole may not be discernible or demonstrable by quantitative methods, there do seem to be strata manifested by the trees of reproductive size, a structural pattern which is obscured by immature individuals.

Figure 15 can be used to illustrate the three basic growth patterns found in the Protium of Amazonia and the Guianas. Some species, such as P. aracouchini (Fig. 15a), are common and never exceed a relatively low height and small diameter. Others, such as P. subserratum (Fig. 15b), reach an intermediate height and diameter with some frequency but never

enter the canopy. The third pattern is exemplified by P. pallidum, which often reaches the canopy where it occurs but is also represented by a number of small and medium-sized individuals. The age and size at which individuals of P. pallidum reach reproductive maturity is uncertain. The fourth pattern in Figure 15-- the Bertholletia pattern-- has not been found in Protium.

The great majority of the species of Protium are understory trees of primary forest on terra firme. This is illustrated by the great differences in all ecological parameters between two forests near Belém, one the terra firme portion of the Mocambo Reserve (e.g., Black et al., 1950), and the other an area of várzea forest nearby (Pires & Koury, 1958). Nineteen species are found in the 8.3 ha of terra firme forest at Mocambo, many of them represented by more than twenty individuals, while the nearby várzea forest yielded only seven individuals in three species on 3.8 ha.

Figure 16 shows ecological preferences or tolerances of three species of Protium at Mocambo, where 8.3 ha of terra firme forest are surrounded by forest on continuously waterlogged soils. Protium trifoliolatum (Fig. 16a) is almost completely restricted to the terra firme area; P. giganteum (Fig. 16b) tends to occur around the periphery of the terra firme area, which is consistent with the observations on herbarium collections that it often is found on riverbanks; and P. decandrum (Fig. 16c) clearly tolerates a great range in soil moisture. Protium never occurs exclusively and only rarely preferentially (i.e., P. krukoffii) in várzea forests or on riverbanks. Even those species which are frequently found on riverbanks

are also found in the adjacent terra firme forests.

The only species of Protium known to occur with any frequency in secondary forests are all relatively closely related, and all occasionally display a shrub habit. Protium trifoliolatum, P. guianense, P. unifoliolatum, P. pilosum and P. heptaphyllum together comprise a rather natural grouping, although sufficient characters have not yet been encountered to justify their designation as a discrete section of the genus. All have been collected more than once in secondary forests, but the majority of the collections for all are from primary habitats. They may be pre-adapted to the intense light regime of disturbed habitats, but neither my own observations of the first three nor the data on any herbarium specimens indicate any preference in primary habitats for light gaps by any of them except P. guianense (ssp. pilosissimum).

Not only are the Burseraceae as a whole marked by a certain range of ecological characteristics, but individual species can be characterized by these similar parameters. These characters include habit, habitat preference, dispersion patterns, height-diameter relationships-- which includes the strata occupied by the species--, phenology, pollination biology, and dispersal biology. Habit and habitat preferences have been discussed above. While caution must be used in applying some aspects of the autecology of species to help in their definition, these characters have been under-utilized in systematics.

It is now widely accepted that, especially in tropical forests, a species which is common in one locality may be rare or absent nearby (Aubréville, 1938, 1961; Richards, 1952). For example, significant

differences were found in the floristic composition of three contiguous 10 x 1000 m transects of terra firme forest near Altamira on the Rio Xingu in Pará, Brazil (Campbell et al., 1986). Another illustration of this point is that while at Mocambo there are 22 individuals of Protium aracouchini over 30 cm circumference in 8.3 ha, only 30 individuals over 10 cm DBH were encountered in the 100 ha inventoried by the World Wildlife Fund near Manaus. Therefore, the commonness of a species in one inventory cannot be validly used as an autecological character for that species.

It is uncertain whether dispersion patterns are consistent for a species. Dispersion (spatial distribution patterns) is one of the most poorly understood aspects of tropical forests, because except for very common species the sample size necessary to draw statistically valid conclusions regarding dispersion requires a prohibitively large sample size. Mapping of the individuals of a species in a parcel of forest as in Figure 16 can be compelling, but statistically they prove nothing. This is a problem that has been commented on by Hubbell and others (Hubbell, 1979; Hubbell & Foster, 1983). The data to date indicate that most tropical trees show aggregation, but only common species have been rigorously tested and logically these are the taxa most likely to show aggregation. Therefore, the dispersion pattern shown by a species in one inventory where it is common may perhaps not hold in another parcel of forest where the species is rare.

Only one species of Burseraceae has been tested statistically for aggregation in Amazonia or the Guianas. An unnamed species of Protium with the common name "breu vermelho" was among eleven common species studied

for dispersion in the Floresta Nacional do Tapajós by Silva & Lopes (1982). In an area of 35 ha, all of the individuals of these eleven species with 15 cm or greater diameter were tested using Pielou's index of non-randomness (Pielou, 1959). "Breu vermelho" had the second highest value, indicating strong aggregation.

For some species of Protium, all the available observations from inventories and general field work indicate that where they occur they are never common and that they appear to have relatively uniform dispersion. Unfortunately, the dispersion pattern for such species have not and perhaps cannot be established quantitatively. It is interesting to note that thus far such is the case for all the species in section Icicopsis as it is circumscribed in this treatment. This may relate to the phenological pattern observed in some members of the section, in which on any given inflorescence during the flowering period only a few flowers are open. This will be commented on further below.

Another aspect of the autecology of a species that may prove to be not only more accessible but more valid is the relationship between height and diameter. Examination of this relationship can provide information about strata, light requirements, and population structure.

One means of presenting height-diameter patterns is by means of the scattergram (e.g., Campbell et al., 1986). Four such scattergrams for species at Mocambo are shown in Figure 15. Protium aracouchini (Fig. 15a) is a shade-tolerant species which reaches only a very modest height and circumference. If the scattergram could be expanded in scale to include several girth classes below 30 cm, it could confirm the field observation

that a greater number of undersize individuals is present. Many of these flower and fruit long before they reach 30 cm circumference. Protium suberratum (Fig. 15b), while tolerating shade, reaches moderate height and circumference and occasionally enters the canopy. P. decandrum (Fig. 15c) also tolerates shade but is more frequently found in the subcanopy and frequently enters the canopy. It shows a much greater range of heights and girths than P. suberratum.

There is a possibility that each species can be characterized by a particular height-diameter scattergram pattern throughout most of its range. It is important therefore to compare the scattergrams for Protium decandrum from Mocambo and from the Rio Falsino. While the left-hand portion of both scattergrams is comparable, at Falsino the species did not show the relatively great heights and diameters it achieved at Mocambo. Unfortunately, the Falsino quadrat was only one hectare, so the results are not easily compared. It is possible that expanding that inventory to eight or more hectares would include the larger individuals missing from the one-hectare sample.

3. Sympatry

Some other aspects of the autecology of the species of Burseraceae can be related to one of the more interesting problems faced in tropical botany, and that is how to explain the frequent occurrence of a large number of congeners in a limited area.

An example of this problem can be found among the Burseraceae at the Mocambo Reserve near Belém, where the challenge is to explain how the 12

species of Protium are ecologically displaced or otherwise reproductively isolated. Since data regarding pollination and regarding breeding systems of Burseraceae in the region are almost non-existent, it is necessary to focus on ecological displacement and to hypothesize differences in pollination systems.

Phenological displacement was the first possibility examined. Figure 17 shows the number of species at Mocambo which have flowered or fruited in a given month, and Table VIII gives the months of peak flowering and fruiting for each species. It is conceivable that there could be continual replacement of one species by another in flowering and in fruiting over the course of a year, considering rainfall in that region is distributed relatively evenly throughout the year (cf. Nimer, 1977). As Figure 17 shows, however, this is far from the case. There are two distinct flowering peaks in October-November and in March, corresponding to the beginning and end of the rainier season, respectively. There is one major fruiting peak in August, usually the driest month, and a lesser fruiting peak in November-December, at the beginning of the rainier season. Thus while there is some phenological displacement at Mocambo, if ecological displacement is to explain the sympatry of a dozen Protium species other factors will have to be considered. It is interesting to note that Mori et al. (in press) encountered a similar situation in trying to explain sympatry of Lecythidaceae in central French Guiana.

Also indicated in Table VIII is the stratum reached by each of the species at Mocambo. Maximum strata A, B, and C correspond roughly to the scattergram patterns in Figures 16c, 16b, and 16a respectively. Stratum C

Table VIII.

Basic partitioning of the species of Protium at Mocambo

species	flowering months	fruiting months	inflorescence type	highest stratum
<i>Protium altsonii</i>	Jul-Sep	sporadic	short	B
P. aracouchini	Jul	Nov	long	C
P. decandrum	Jan	Jan	long	A
P. giganteum	Oct	Oct	long	B
P. heptaphyllum	?	Jan	short	C
P. krukoffii	Nov	Mar	long	B
P. pilosum	Aug-Sep	Mar	short	C
P. pallidum	Jul, Nov	Mar	long	A
P. polybotryum	Jul	Nov	long	B
P. sagotianum	Jan-Feb	Sep	long	
P. spruceanum	Sep	sporadic	short	B
P. subserratum	?	Jul, Nov	short	A
P. tenuifolium	Dec	Nov	short	
P. trifoliolatum	Dec	Mar	short	C

means those species which seldom exceed 15 m in height, stratum B those which seldom exceed 25 m, and stratum those which often exceed 25 m. It is apparent that while most of the taxa show the scattergram pattern of Protium aracouchini (Fig. 16a), there can be said to be at least some displacement by means of the strata occupied by the various species.

Displacement-- and reproductive isolation-- by means of selection for or coevolution with different pollinators cannot easily be deduced in Protium. There are few observations of pollination of Protium in Amazonia and the Guianas (see chapter on pollination and dispersal). It is easy enough to hypothesize quite different pollinators for Tetragastris, Trattinnickia, and Dacryodes. The first two have large fleshy flowers with a relatively long and narrow-tubular corolla, and Trattinnickia usually has red flowers. Dacryodes has minute flowers with a rotate corolla.

The only species of Protium at Mocambo which strongly indicates a different pollinator from the rest is P. subserratum. The petals are free, but they are erect at anthesis, and their adaxial surface is densely covered with long, ascending hairs. It is possible that the two species from section Icicopsis may also have pollinators peculiar to that group, as indicated by their spicate inflorescences and pubescent disks. The species of this group often tend to show a type of "trapline" flowering strategy, in which each inflorescence has relatively few flowers open at a given time. The pistillate plants in this group often have maturing fruits and open flowers on the same branchlet or even the same fascicle of inflorescences.

This still leaves at least nine species of Protium which have small

green to white flowers of similar basic shape and size. Except for chemical repellants or attractants which could effectively select for different pollinators, there is one more gross morphological character which might help in displacement via pollinators. Protium can be roughly grouped into three groups based on the inflorescence. Although there are some intermediates, a given species will show one of these types of inflorescence: 1) long, loosely and profusely branched, and subterminal or congested at the branchlet apices; 2) short, dense, fasciculate, little-branched, arranged in the axils of several nodes leading up to the branchlet apices; 3) (pseudo-)spicate, little-branched, relatively short, with (sub-)sessile flowers. This latter is the type shown by section Icicopsis and the group including Protium subserratum.

At least most of the species of Protium can be separated from each other ecologically on the basis of the basic characters presented in Table VIII. Future field studies may make it possible to increase the sophistication of this rather primitive approach.

Pollination

The vast majority of species in Protium have flowers which are relatively homogeneous in their overall morphology, and when a tree flowers it flowers profusely. This type of syndrome, in which great numbers of small green nectariferous flowers are produced at once, indicates a group which is pollinated by generalists, probably small bees. The available field data support this hypothesis.

As noted in the chapter on ecology, there have been very few reliable observations of pollinators-- or at least flower visitors-- of Protium. The most frequent visitors appear to be small stingless (trigonid or meliponid) bees. This follows the pattern proposed by Bawa and Opler (1975) for tropical dioecious trees.

"Blond" Trigona bees were seen visiting the flowers of P. opacum ssp. rabelianum (fide Mori & Pennington 17975). Dipterans were observed taking nectar from flowers of P. divaricatum ssp. fumarium (fide Mori & Pennington 18034) at Saül, French Guiana. Meliponid bees were observed visiting P. icicariba (DC.) Marchand near Una, Bahia (pers. obs.). Roubik et al. (1986) made quantitative observations of flower visitors of various trees on Barro Colorado Island (Panama), and they found that pollen utilization of P. tenuifolium was heavy by Trigona jatifomis, light by T. barrocoloradensis, and heavy by the invading Apis mellifera. Preliminary observations of an undescribed species of Protium on the World Wildlife Fund reserves near Manaus, Brazil, indicate that the principal insect species visiting the flowers are Ptilotrigona cf. lurida, P. cf. camargoi, Tetragona cf. goettei, Trigona cf. amazonia, Plebeia sp., and several

Vespidae and Lepidoptera (M. Vinicius, unpublished results).

There is little variation in flower color of Protium, and the range in size or overall morphology is not remarkable, with the exception of section Icicopsis. The members of this group have essentially spicate inflorescences, and the flowers have relatively large petals which are in most cases erect at anthesis. In addition, at least some individuals of some species in the section display the phenological pattern which is known as the "trapline" syndrome, in which on any given inflorescence only a few flowers are open at any given time. Open flowers and maturing fruits may be found on the same inflorescence in these taxa.

One group of closely related species consisting of P. subserratum, P. reticulatum (Engl.) Engl., and P. ferrugineum (Engl.) Engl. has petals in which the adaxial surface is densely covered with long ascending hairs. It is hypothesized here that at least that trio of species have rather different pollinators.

As was remarked earlier in this chapter, there are two basic inflorescence types present in Protium: long, loosely-branched and congested near the branchlet apices vs. short, little-branched and distributed along the branchlets. It is possible that these two basic types are indicative of different pollinators.

One morphological syndrome which occurs rarely in Protium indicates that anemophily may be a secondary means of pollination for a few species in the genus. In P. apiculatum, the related P. fimbriatum Swart, P. robustum, and a few other species, after anthesis the filaments of the antesealous stamens are strongly reflexed outward between the petals and

downward.

It is interesting to note that in the pistillate flowers of these species the filaments of the staminodes reflex also. Considering the sterile anthers produce no pollen (see chapter on flowers), this behavior is an example of mimicry of the staminate flowers. Such mimicry is very common in the Sapindales. Bawa (1976) noted the importance of this mimicry in attracting visitors to pistillate flowers of Cupania guatemalensis Radlk. (Sapindaceae), especially considering that the disks of those flowers produced no measurable nectar. He regarded the staminodes (actually stamens with indehiscent anthers) as "decoys" which fooled flower visitors seeking nectar.

Dispersal

The fruit type and phenological characteristics of Protium are indicative of a generalist strategy. As in their flowering, the trees generally fruit profusely. Unlike the tribe Canarieae, in which the mesocarp of their (indehiscent) drupes are resinous and rich in oils-- Dacryodes trinitensis Sandw. is the primary food source of the Oil-bird (Steatornis caripensis) on Trinidad (Snow, 1962)-- the pseudaril which envelops the pyrene of Protium is watery and sugary and probably without much nutritional value.

The only known study of dispersal in the Protieae to date was carried out by Howe (1980) on Tetragastris panamensis (Engl.) Kuntze on Barro Colorado Island (Panama). He observed that a variety of mammals and birds removed the pyrenes from the fruits, but that monkeys were the

primary dispersal agents. Seeds from the feces of the mammals were viable.

It is possible that while the dispersal strategy of Protium is geared to a similar range of arboreal or flying dispersal agents, there may be a secondary strategy of dispersal by terrestrial animals. The rationale for this is as follows: The pyrene, enveloped in a usually white pseudaril, is set apart visually from the rest of the fruit, which is red without and usually within. The pyrene in Protium (and in Tetragastris, for that matter) is suspended from the apex of the fruit by a small, laminar, inverted-V-shaped structure which clasps the pyrene weakly behind its apex. The pyrene is easily dislodged from this structure (pers. obs.); therefore probably only a relatively short time passes before the pyrene falls to the ground. I have observed many instances of fallen pyrenes with the pseudaril intact and not discolored. Therefore pseudarils in good condition are available in quantity to terrestrial animals.

Phytogeography

As it is now defined, Protium shows an interesting overall geographic pattern, with relatively few relictual taxa in the Paleotropics and a great radiation in the Neotropics (Table I). This overall geographic pattern, especially its occurrence in Paleotropical regions known to be centers of archaic floras, confirms its identity as an ancient Gondwanaland genus in the sense of Raven & Axelrod (1974).

In the Neotropics, outside of Amazonia the more important centers of endemism and diversity of Protium are Cuba, the Pacific coast of Colombia and Ecuador, Southeastern Brazil, and the Guianas. These are also regions of archaic Tertiary floras (Kubitzki, 1975; Soderstrom & Calderón, 1974).

While there are ample instances of regional endemism in Protium, the genus shows very few narrow endemics in Amazonia and the Guianas, partly because of the almost total absence of "edaphic specialists" in the group (see chapter on ecology). This is true even of most of the recently described taxa in the genus (Daly, in review).

Within Amazonia and the Guianas, there are only two regions where relatively narrow endemics in the genus are known to occur. Two species-- Protium reticulatum (Engl.) Engl. and P. carolense Daly-- are endemic to a portion of the Rio Negro system. The only other relatively narrow endemics are found in French Guiana, contiguous Surinam, and northern Amapá, Brazil. They are listed in Table IX, and mapped in Figure 18.

In Amazonia and the Guianas, Protium is of much greater interest for its distribution patterns than for its centers of endemism. Table X lists

Table IX

Species of Protium endemic to French Guiana, Amapá, and Surinam

species	known range
<i>Protium divaricatum</i> ssp. <i>funarium</i>	Saül
P. <i>giganteum</i> var. <i>crassifolium</i>	central massif and northern range of French Guiana (with one possible disjunct on Marajó Island)
P. <i>morii</i>	Saül and the Oyapock region in French Guiana; contiguous Surinam; Amapá on the Guiana Shield; disjunct near Santarém
P. <i>plagiocarpium</i>	north-central and central French Guiana; contiguous Surinam

Table X

Distribution patterns of Amazonian Burseraceae
(see figures 18-24)

pattern	examples
widespread in Amazonia	<i>Protium subserratum</i> , <i>P. trifoliolatum</i>
widespread in Amazonia and disjunct to Eastern Brazil	<i>P. aracouchini</i>
widespread in Amazonia and continuous to Eastern Brazil	<i>P. spruceanum</i> , <i>P. unifoliolatum</i>
French Guiana only	<i>P. plagiocarpium</i> , <i>P. giganteum</i> var. <i>crassifolium</i> (possible disjunct on Marajó Island)
French Guiana, Amapá, Surinam	<i>P. morii</i> (disjunct near Santarém), <i>P. plagiocarpium</i>
Guianas and Amapá, skipping Surinam	<i>P. demerarense</i> and <i>P. opacum</i> ssp. <i>rabelianum</i> (both w/ Rio Trombetas disjunct); <i>P. cuneatum</i>
Atlantic coastal region of Amazonia	<i>P. pilosum</i> (w/ Manaus disjunct)
Rio Negro endemics	<i>P. reticulatum</i> , <i>P. carolense</i>
East-West Amazonia pairs	<i>P. paniculatum</i> vars. <i>paniculatum</i> and <i>riedelianum</i> ; <i>P. altsoni</i> var. <i>altsoni</i> and var. nov.
Southwestern Amazonia	<i>P. carnosum</i> , <i>P. puncticulatum</i>
Western Amazonia	<i>P. nodulosum</i>

the distribution patterns known for these regions. Most of the patterns are exemplified in Figures 18 to 25.

One taxon, Protium divaricatum ssp. fumarium, is endemic to French Guiana. It does not occur in the southern peneplain (cf. de Granville, 1982), whose flora is continuous with northern Amapá. Instead, it is restricted to the Camopi-Inini Range and the Central Massif. In addition to this taxon, P. giganteum var. crassifolium is restricted to the Central Massif and perhaps the Northern Range, except for a disjunct distribution on Marajó, the massive island at the mouth of the Amazon with a poorly known flora.

One species, Protium morii, extends south from the Camopi-Inini Range west into contiguous Surinam and south through the Oyapock region and into Amapá, extending down to south-central Amapá without leaving the Guiana Shield. There is one disjunct collection from near Santarém. The other taxa shared by French Guiana and Amapá have broader ranges.

One distribution pattern shown by at least three taxa is Guyana, French Guiana and Amapá, skipping Surinam. Two of the three show disjunctions to the Rio Trombetas. This pattern is perplexing for several reasons. It is probably not an artifact of collecting, because if any country should show great gaps it should be Guyana, which is severely under-collected. Surinam, on the other hand, is relatively well-collected. Also, in addition to the actual specimens, the literature on inventories and floristics of Surinam (e.g., Schulz, 1960; Lindeman & Molenaar, 1959; Maas, 1971) indicates that the Burseraceae have a strong presence in that country, while the admittedly scant literature on Guyana (Davis &

Richards, 1933, 1934) indicates that the forests of Guyana are relatively poor in Burseraceae. There are no readily identifiable features of topography or climate which could help to explain this gap in the range of these three taxa. In fact, the climate of Guyana differs more from that of Surinam and French Guiana than they do from each other, in that there is a more bimodal pattern to the rainfall (cf. charts in Schwerdtfeger, 1976).

Most of the other taxa of Protium which occur in eastern Amazonia and the Guianas show more generalized distributions extending westward to and including the region around Manaus. It is interesting to note that only in rare instances does the Rio Amazonas appear to function as a barrier to extension of a taxon's range. One example is P. opacum ssp. rabelianum (Fig. 19b). In other cases a taxon with an essentially northern or southern distribution extends a very short distance across the main river. Examples are P. paniculatum var. paniculatum (Fig. 20a), P. guianense ssp. pilosissimum (Fig. 21b), and P. giganteum var. giganteum (Fig. 21a), which shows one disjunct locality in Guyana.

Most of the taxa in Protium which are essentially restricted to the Atlantic Coastal phytogeographic subdivision of Amazonia as defined by Prance (1977; Fig. 25d) show disjunctions in one or more of these three regions: 1) the lower Rio Trombetas; and 2) the region around Santarém on both sides of the Rio Amazonas; and 3) the region around Manaus.

These pivotal areas are also zones of overlap of closely-related taxa. The region around Santarém is where both P. giganteum var. giganteum and P. morii occur. Manaus is a zone of overlap for P. guianense ssp. guianense and ssp. pilosissimum, for the two varieties of P. paniculatum,

and for the two varieties of P. polybotryum.

Figure 25 depicts the four major approaches to date to the phytogeographic subdivision of Amazonia. They were developed by Ducke & Black (1953; Fig. 25a); Rizzini (1951; Fig. 25b); Hueck (1972; Hueck & Seibert, 1972; Fig. 25c); and Prance (1977; Fig. 25d). Except for the system of Prance these maps were prepared following the verbal delimitations given in the references cited.

Comparison of the distributions of several species of Protium given in Figures 18 through 24 shows that very few species of the genus are restricted to a single phytogeographic region. As just mentioned, some taxa support Prance's more extensive Atlantic Coastal Sector, but a similar number of taxa are confined to Hueck's (1972) Guyana, French Guiana, Suriname subdivision, which includes northern Amapá (discussed above). The only other subdivision of Amazonia which can be addressed is in the southwest, where the distribution of such species as P. puncticulatum Macbr. and P. carnosum A. C. Sm. tend to lend support for Prance's (1977) broader Southwest Sector.

The distribution patterns of any group of organisms which is widespread in northern South America should be used to examine the refuge theory of species diversity in the tropics. The types of data utilized by Prance (1973, 1982a, 1982b) to defend the existence of Pleistocene forest refuges include congruence of areas of endemism, disjunctions which exist without any perceivable barrier to dispersal, frequency of sympatry of closely-related congeners, and replacement of species over distance by closely-related species.

Thus in a sense the distributions of Protium are most useful where they do not occur. There are species of Protium which are restricted to the following refuges (or centers of endemism, depending on one's point of view) presented on Prance's (1982a) map (Fig. 26): Chocó (Fig. 26, no. 2), Rancho Grande (no. 9), Paria (no. 8), eastern Guiana (no. 11), Imerí (no. 12), Manaus (no. 16), Bahia (no. 24), and Rio-Espírito Santo (no. 25).

Both the disjunctions which occur in the distribution of a single taxon and those which occur between closely-related taxa might be used to defend hypotheses about vicariant events. It is doubtful that the great gap in the distribution of P. crenatum (Fig. 22b) will be filled, since this is such a distinctive taxon. It remains to be seen whether the disjunction between the two varieties of P. altsonii (Fig. 20b) will stand up; this species is sometimes not easily separable from closely-related taxa, and the undescribed variety is not represented by very good collections.

Some of the disjunctions which occur in Protium have been discussed above. Since there is no ready explanation for the distribution of those taxa which skip Surinam, this may be an artifact of a past vicariant event. For the disjunctions which occur between the Guianas and Santarém and/or Manaus, one possible existing barrier is the NNW-SSE swath of terrain cutting through Santarém which experiences greater seasonality and less overall precipitation than the regions to the east or west (Aubréville, 1961; Nimer, 1977). Still, it might be argued that the distributions were once continuous during a period in which the climate was wetter than now. While the Manaus disjuncts are on the far side of

this so-called "Aw belt" (based on the classification of Köppen (1900), it is strange that the Santarém disjuncts lie in the middle of the drier belt.

While there are great gaps in the distributions of species of Protium in western Amazonia which indicate that there may be further disjunctions, the western Amazon is still too poorly collected to put much credence in the distribution maps that are drawn up from the collections available at this time.

The problem of sympatry of many congeners in Protium is addressed in the chapter on ecology. Although it appears that ecological displacement may be able to explain how this portion of the diversity of Amazonian forests is maintained, it does not explain how it originated. One compelling aspect of the distributions of Protium is the partial overlap of closely-related taxa-- including varieties-- which seems to occur in the same areas. From perspective of the refuge theory, these would be areas where the forest has re-coalesced after fragmentation during one of the glacial periods. The only taxa which may have undergone-- or are undergoing-- hybridization in their zone of overlap are P. guianense ssp. guianense and ssp. pilosissimum, which are not well-defined in their zone of overlap.

There are only a few examples in Protium which appear to illustrate the replacement over distance of taxa by close relatives. The complex of species which includes P. giganteum (Fig. 21a) is one of those examples. Protium giganteum var. crassifolium is restricted to northern French Guiana. In central French Guiana it is replaced by P. morii, which ranges

into southern Anapá. There it is replaced by P. giganteum var. giganteum (there is one collection of P. morii recorded from the area around Santarém), which is widespread in southeastern Amazonia and extends west to the lower Rio Negro. Between the region around Manaus and upper Rio Negro there is a gap in the distribution of the species complex, but in an area corresponding to the Imerí refuge in the middle to upper Rio Negro there is another closely-related taxon, P. carolense Daly.

While it is beyond the scope of this chapter to discuss the validity of applying the types of distribution patterns discussed in these pages to a defense of the refuge theory, there is no question that these various patterns do exist and that attempts must be made to explain them.

Chemistry

As is so often the case with exclusively tropical families, the chemistry of the Burseraceae is very poorly known, in spite of its interest as a source of economic resins such as frankincense, myrrh, guggul, and gum elemi. The range of taxa which have been examined-- however superficially-- is rather narrow. Only eight of the fifteen genera recognized here have been studied at all chemically. Three types of compounds have been reported from species of Protium (see below). Most of the chemical studies of the Burseraceae have been concerned with identifying compounds present in the economically important resin-producing trees of the arid Paleotropics.

The most comprehensive and taxonomically rigorous chemical survey of the Burseraceae to date is that of Khalid (1983), who focused on the position of the family in the Rurales sensu stricto. Pernet (1972) published a helpful taxonomically-arranged chemical survey of the family, although the nomenclature was outdated.

Many of the remaining papers have focused on relating the Burseraceae to other plant families. Based on their chemistry, the Burseraceae occupy a basal position in the Rurales, but they also share a number of compounds and classes of compounds with the Anacardiaceae (Khalid, 1983; Hegnauer, 1983; see Table XI).

While the Burseraceae contain many of the compounds which characterize the Rurales, others are conspicuously absent (Table XII; data for these two tables compiled from the sources cited in this chapter), such as

Table XI.

Compounds linking the Burseraceae with the Rutales or the Anacardiaceae
(information on Anacardiaceae incomplete)

(An= Anacardiaceae; Bu= Burserac.; Ru= Rutac.; Me= Meliac.;
Cn= Cneoraceae; Si= Simaroubaceae)

compound	present in:	Bu	An	Ru	Me	Cn	Si
essential oils		+		+			
phenolics: lignans-- A, B, and C types		+		+			(C)
caffeic acid		+			+		+
flavonoids: kaempferol		+			+	+	+
quercetin		+			+	+	+
5, 7-deoxy-		?	+	+			
biflavonoids		+	+				
tannins: procyanidins		+		+			+
ellagic acid		+		+			+
prodelphinidins		+		+			
terpenoids: mono- and sesquiterpenes		+		+	+	+	
3-epilupeol		+		+			
sapelins		+			+		
cyanogenesis		+		+		+	+
arabingalactan gums		+	+	+	+		
mucilages		+		+	+		
seeds with reserve cellulose		+					+
coumarins-- scopoletin		+	+				
high tannin content		+	+				
fraxinellone ("limonoid metabolite")			+		+		

Table XII.

Rutalean compounds absent from the Burseraceae

compound	present in:	Bu	An	Ru	Me	Cn	Si
phenolics: chromones				+		+	+
acetogenins				+	+	+	
prenylated coumarins				+		+	
alkaloids, amines				+			+
terpenoids: bitter nortriterpenoids				+	+	+	+
betulinic acid					+		+
saponins				+	+		+
2, 6-dimethoxybenzoquinone					+		+
anthroquinones				+			+
seed starches				+	+		+

chromones (Gray, 1983). In addition, some of those most characteristic of the Burseraceae do not occur elsewhere in the Rurales.

The Burseraceae are closely linked with the Rutaceae, a family usually placed at or near the base of the Rurales (Meeuse, 1983; Waterman, 1983). O'Sullivan (1983) stressed the importance of the fact that the Burseraceae are the only family in the Rurales with the most primitive class of lignans, the neolignans. Perhaps the most compelling evidence indicating a basal position for the Burseraceae in the Rurales is found among the triterpenes. Khalid (1983) discussed the occurrence in the Burseraceae of precursors for limonoids, which characterize the Meliaceae and Rutaceae, and of quassinoids, which characterize the Simaroubaceae. He also pointed out that the kinds of reactions necessary to complete the biosynthesis of these compounds from the precursors are already known to occur in other burseraceous triterpenoids.

Some of the compounds which are notable in the Burseraceae are absent from the rest of the Rurales s.s., such as sesquiterpene lactones (Khalid, 1983), biflavonoids (Geiger & Quinn, 1982; these are very diverse in the Anacardiaceae) and oleoresins (gums accompanied by water-insoluble resins instead of simple arabinogalactan; Stephen, 1980). In addition, pentacyclic triterpenes are usually alcohols in the Rurales, but are acids in the Burseraceae (Khalid, 1983).

The chemistry of Protium has been investigated only very superficially. Hegnauer (1964) reported the occurrence of the phenolics coumaric acid, caffeic acid, and kaempferol and quercetin and their glycosides (the latter two are flavonoids) from P. guianense and P.

sagotianum. Pernet (1972) cited reports of amyrenol and elemecin from P. sagotianum. Stephen (1980) noted the occurrence of oleoresins in the tropical Asian species P. serratum (Wall. ex Colebr.) Engl. (listed as Bursera serrata). Most recently, Zoghbi et al. (1981) elucidated the structure of a new compound, propacin, from P. opacum. This was only the second coumarinolignoid ever identified; Zoghbi is continuing her work on the chemistry of two other species of Protium (M. G. B. Zoghbi, pers. comm.).

An interesting approach to the use of chemistry in the systematics of the Burseraceae was taken by Mooney & Emboden (1968) on resins extracted from various populations of Bursera microphylla A. Gray in the southwestern United States and Mexico. With a gas chromatograph, they measured the proportions of ten terpenes (four of them unknown) within and among seven populations and, utilizing a statistical method for scoring the relative proportions, they felt they could draw several conclusions about the genetic affinities of the populations. This method could perhaps be used to study variation within some of the more widespread species of Protium.

Future research on the chemistry of the Burseraceae should be expanded to encompass all the genera, especially Neotropical genera other than Bursera. The family should be surveyed more thoroughly for the occurrence of quassinoid or limonoid precursors (or those classes of compounds themselves) and of biflavonoids or other types of flavonoids.

There are at least two basic types of resins within Protium. Most species produce a watery or more often viscous, transparent or translucent

resin which dries translucent and often rather hard. A few species, such as the natural group including P. subserratum, P. ferrugineum (Engl.) Engl., and P. reticulatum (Engl.) Engl., have a latex-like sap which dries gummy and often oxidizes black. These latter species have never been investigated chemically. A chemical comparison of these two types of resins could produce interesting results.

Common names

It appears that the people living in the forests of South America have had as much trouble with the classification of the Burseraceae as taxonomists have had. As a rule, folk generic names in folk botany tend to map onto botanical species (Berlin et al., 1973, 1974), but this is clearly not the case in the Burseraceae. In most regions there is only one collective term used to refer to all Burseraceae. Foresters and ecologists who have relied on local informants for determinations of trees in quantitative inventories have grossly underestimated the number of species in some families such as the Sapotaceae, Lecythidaceae, and Burseraceae (Campbell et al., 1986; Daly, in prep.). Field assistants have been known to invent new "common names" on the spot for their own reference. Where several species of burseraceous trees are recognized, the taxa are separated on the basis of the qualities of their resins or by the color of the sapwood. In eastern Amazonia and the Guianas, there are only two localities where the collections of Burseraceae are accompanied by the systematically-collected common names of indigenous peoples.

Table XIII presents the prevalent folk generic names most frequently used to refer to Burseraceae in different regions of South America. Swart (1942b) carefully indexed the vernacular names available from herbarium labels up to the time of his monograph. One complicating factor is that in one region there can be one name used by people of European descent, a second name used by long-acculturated people of mixed descent, and a third name used by a relatively unacculturated local tribe. Herbarium labels from Surinam or from French Guiana may carry the common names of two or more Indian tribes.

Table XIII.

Most prevalent folk generic names for Burseraceae in South America

<u>region/country</u>	<u>name(s) usually applied to Burseraceae</u>
Colombia	anime, guacharaco, guacamayo
Peru	caraño, caraña, copal
Venezuela	caraña, tacamajaca, tacamahaca, tacamahaco
Surinam	tingie monie, tingi-monnie, tiengi-monnie, salie
French Guiana	encens
eastern Amazonian Brazil	breu
western Amazonian Brazil	breu sicutã, sicutã
Maranhão, Brazil	breu, mescla
Central and Southern Brazil	almesca, almisca, amescla, almiscar, almecegueira, icicariba
Bolivia	isigo, isigale
Guyana	haiowa, kurokai, peraka

At least some of the vernacular names presented in Table XII, such as "isigo," "sicanã," and the suffix of "tacamahaca," may be cognates derived from the Tupi word for resin or sap, "jyhyk" (W. Balee, pers. comm.). "Icica" was recorded by Piso and Marcgrave (1688) as the indigenous name in southern Brazil (probably) for a burseraceous resin. Aublet (1775) adopted this name to publish a new genus of Burseraceae from French Guiana; Icica was the first generic name applied to the Protium of the New World.

Often the epithet on a vernacular name seems to have been added for the benefit of the visiting botanist, although it is conceivable that such Spanish or Portuguese or French modifiers (not Tupi-Guarani or other indigenous modifiers) which mean large, large-leaved, true, and so on are translations of indigenous names or are truly used to refer to local taxa.

An anecdote may serve to illustrate this problem. A few years ago a field assistant told me of seeing a type of "breu" for the first time which he called "breu cinza." I asked him if that was the local name and he said that no, he had just decided to call it that.

In Amazonian Brazil, there are various attributives appended to stem "breu," such as "breu branco" and "breu vermelho." These two terms, which refer to the color of the sapwood, are applied to a large number of burseraceous taxa.

Many collections of Burseraceae from Surinam and especially from French Guiana have the local Indian name for the plant recorded on the herbarium label. However, the only research among the Indian tribes of eastern Amazonia or the Guianas in which there is a component of

indigenous taxonomy is the current project of William Balée among the Ka'apor and several other tribes in Maranhão and Pará, Brazil.

Tables XIII and XIV give the common names applied to nine of the 13 the species of Burseraceae occurring on one hectare of forest near the Ka'apor settlement. Each species is vouchered by at least one herbarium specimen which is deposited at the New York Botanical Garden. It should be noted that Balée has utilized several informants, and that separation by informant of the names used may show that there is more of a one-to-one relationship between taxon and common name than the tables indicate. Another possibility is that in some cases the multiple common names for a taxon are synonyms. (W. Balée, pers. comm.). Even without doing so, tables XIV and XV prove that the Ka'apor at least have a rather sophisticated understanding of the taxa of Burseraceae in their part of Amazonia.

While the term "jyhyk" is a general term for resins and saps, the term "kandei" refers to useful resin or latex. The latter term is not restricted to the Burseraceae; some taxa of Leguminosae, Sapotaceae and Clusiaceae are classified, as it were, as "kandei" as well.

It is interesting to note that the folk generics in Ka'apor for the genus Tetragastris and for the species Protium trifoliolatum are both distinct from kandei, the folk generic for all other Protium species. Protium trifoliolatum belongs to a distinctive natural group of species which has been placed both in Protium and in Tetragastris (see chapter on generic limits). According to Balée (3rd quarterly report to the Edward John Noble Foundation), these two species produce no (or very little) volatile, illuminative aromatic resins. Among the Ka'apor there appears to

Table XIV.

Common names applied to the Burseraceae by the Ka'apor Indians of Maranhão

species	common name(s)	Balée voucher no.
<i>Protium altsoni</i>	arakandei'y	272
	kandei'y pitã	343
	kandei'y	241
P. <i>decandrum</i>	kandei'y pitã	313
	arakandei'y	207
	kandei'y	35
P. <i>giganteum</i>	kandei'y tuwyr,	
	kandei'y	340
P. <i>pallidum</i>	kandei'y tuwyr	81
	kandei'y	---
P. <i>polybotryum</i>	kandei'y pitã	375
	kandei'y rã	252
	arakandei'y	97
P. <i>sagotianum</i>	kandei'y pita	33
	kandei'y rã	212
P. <i>tenuifolium</i>	kandeiape'y	502
	akuximira	157
	kandei'y hu	177
P. <i>trifoliolatum</i>	sekãtã'y	367
<i>Tetragastris altissima</i>	waruwa'y	471

Table XV.

Common names applied to the Burseraceae by the Ka'apor Indians of Maranhão

common name	species	Balée voucher no.
akuximira	<i>Protium tenuifolium</i>	157
arakandei'y	P. polybotryum	97
	P. decandrum	207
kandeiape'y	P. tenuifolium	502
kandei'y	P. altsoni	241
	P. decandrum	35
	P. giganteum	340
	P. pallidum	---
kandei'y hu	P. tenuifolium	177
kandei'y pitã	P. altsoni	343
	P. decandrum	313
	P. polybotryum	375
	P. sagotianum	33
kandei'y rã	P. polybotryum	252
	P. sagotianum	212
kandei'y tuwyr	P. giganteum	340
	P. pallidum	81
sekätã'y	P. trifoliolatum	367
waruwa'y	<i>Tetragastris altissima</i>	471

be a correlation between uses and indigenous classification on the one hand, and chemistry and taxonomy on the other. These correlative patterns will be subjected to more detailed analysis once all the data are in from the Ka'apor (Balée & Daly, in prep.).

Key to the Neotropical genera of Burseraceae

1. Flowers 3-merous, fruit indehiscent, symmetric Canarieae
2. Flowers 3-5 mm long, corolla sympetalous, tubular, petals fleshy,
fruit +/- globose, green to red, endocarp bony, leaflets asperous
at least abaxially Trattinnickia
2. Flowers 1-2 mm long, corolla apopetalous, petals patent,
membranous, fruit ellipsoid (rarely globose), green to yellow or
blue-black, endocarp cartilaginous, leaflets not asperous
Dacryodes
1. Flowers 4- or 5-merous (rarely 3-merous in Bursera and in Protium
sect. Sarcoprotium), fruit dehiscent, asymmetric
3. Plants usually deciduous, all leaflets without a pulvinulus,
carpels 2 or 3, pyrene 1, with fleshy, brightly-colored
pseudaril Bursera
3. Plants usually evergreen, terminal leaflets and usually lateral
leaflets with a pulvinulus, carpels 4 or 5, pyrenes 1-5, with
spongy white pseudaril Protieae
4. Lateral leaflets with a pulvinulus, corolla apopetalous (rarely
partially fused at base) Protium pro maxima parte
4. Lateral leaflets without a pulvinulus, corolla apopetalous or
sympetalous
5. Corolla sympetalous, petals fleshy, leaflets with entire
margin Tetragastris

5. Corolla apopetalous, petals +/- membranous, leaflet margin serrulate

6. Leaflets uniformly serrulate, petals papillate adaxially, at
anthesis strongly reflexed, stamens 5 or 10, pyrene cartilaginous,
resin clear

Crepidospermum

6 Leaflets irregularly serrulate, petals adaxially with dense long
hairs, stamens always 10, pyrene bony, resin white and
opaque

Protium subserratum complex

Description of the genus Protium

Trees or treelets, rarely shrubs, reproductive height 1.5-40 m. Seedlings phanerocotylar, the cotyledons often becoming chlorophyllous after germination, the first eophylls simple and alternate or opposite. Architecture usually displaying Rauh's model (Hallé et al., 1978). Buttresses often but not always present, the buttresses simple or less often branched, plank or less often flying. Bark usually relatively smooth, gray to brown, thin, brittle, usually lenticellate, often hooped; sapwood white to red. Resin present in all taxa, clear and liquid or gummy to opaque and milky, drying white and powdery, to translucent and hard (in globules), to yellowish and gummy, inflammable or not. Branchlets slender to very robust, apices always densely covered with appressed hairs, sometimes glabrescent, apical meristem not protected by bud scales. Leaves exstipulate, imparipinnately compound, lateral leaflets opposite or rarely subopposite, pulvinus virtually always present at base of petiole and at distal end of petiolules, pulvinuli conspicuous or not, petiole canaliculate or less often semi-terete, often very slightly acutely winged, only very rarely petiole or rachis visibly laterally winged, leaflet insertion horizontal to the meridian (very rarely perpendicular), petiolules terete or 1- or 2-canaliculate; leaflets chartaceous to coriaceous, of variable shape, basal pair often smaller than the other pairs, terminal leaflet often different in shape than laterals, base of the lateral leaflets usually asymmetric, leaflet apex usually acuminate, margin rarely somewhat involute, entire (rarely subserrate or in one instance sparsely serrate), leaflets with various patterns of occurrence

of simple hairs or rarely papillate abaxially, venation pinnate/
camptodromous/ brochidodromous, course of secondary veins usually
secondary veins usually uniformly curved, intramarginal veins absent.
Inflorescences axillary, usually either subterminal and longer than the
petiole of the subtending leaf or distributed along the branchlet and
shorter than the subtending leaf, usually fasciculate, always subtended by
a bract and sometimes subtended only by a bract, bracts subtending
inflorescences usually fleshy and small, bracts on inflorescences small,
chartaceous to coriaceous, sometimes semi-clasping, inflorescence a
panicle of racemes, structurally indeterminate, sometimes essentially
divaricately branched, sometimes reduced to little-branched pseudo-spikes
(sect. Icicopsis); pedicel terete or slightly clavate, sometimes absent
(sect. Icicopsis). Flowers small (2-4 mm long when dry), 4- or 5-merous,
rarely (sect. Sarcoprotium) with some 3-merous flowers on staminate
inflorescences; unisexual, staminate flowers with reduced or rarely
obsolete pistillode, pistillate flowers with reduced staminodes which do
not produce pollen; calyx aestivation valvate, synsepalous, evenly
divided, with as many lobes as petals and alternate with them, deeply or
shallowly cupular, sometimes exceeding the disk; lobes usually contiguous
or rarely discrete and separated by a flat sinus, lobes triangular to
depressed-deltate, apex and sometimes margin short-papillate; corolla
aestivation induplicate-valvate, almost always with free petals, rarely
the petals fused up to 2/3 their length but then irregularly divided,
petals membranous to fleshy, lanceolate to broadly ovate, rarely carinate
abaxially, usually slightly saccate, rarely cucullate with a clawed base

(sect. Sarcoprotium), the apex swollen and inflexed in an apiculum of varying length and thickness, petals abaxially glabrous or pubescent, adaxially always short-papillate, sometimes also with several types of pubescence, margin entire and short- or long-papillate, at anthesis erect or slightly to strongly reflexed; stamens arranged such that flowers are diplostemonous (very rarely isostemonous), in two unequal series, inserted at the base of the disk, very rarely the antepetalous series inserted on base of petals, antesepalous series longer than antepetalous series but inserted lower such that except in section Icicopsis the anthers of both series are at essentially the same level, filaments terete or strap-shaped, anthers basi- or dorsifixed, of varying shape, dehiscing latero-introrsely to introrsely by vertical slits (staminodes with indehiscent anthers); nectariferous disk annular, fleshy, usually undulate, laterally sinuate to crenulate due to insertion of the filaments, surrounding the pistil or pistillode, often exceeding the pistillode, rarely the disk and pistillode ontogenetically fused to form a single parenchymatous convex structure (most of sect. Icicopsis), disk glabrous or rarely pubescent; pistillode usually with rudimentary ovary with locules and reduced ovules, otherwise parenchymatous or fused with the disk ("ovariodisk"), stigmas never differentiated, stylode usually distinct, glabrous or pubescent; pistil usually essentially ovoid, sessile or rarely substipitate, usually impressed lengthwise between carpels, style simple, usually short and thick, stigmas distinct, usually sessile, lateral or oriented upward and outward, usually globose to discoid, rarely stigmas contracted at apex in recurved or sigmoid, smooth or

microscopically apiculate spiculate caudicles (P. apiculatum complex; sect. Sarcoprotium), ovary simple, plurilocular, with as many locules as petals and opposite them, placentation axile, each locule with two pendulous, collateral, anatropous, epitropous ovules, at most one ovule per locule developing in fruit. Fruit drupaceous but dehiscent by 1-5 valves (equalling the number of pyrenes developed), when mature usually red but occasionally green or brown, shape variable but usually slightly to markedly oblique-ovoid, slightly to markedly gibbous and ventricose, usually sessile but occasionally substipitate or rarely stipitate, style and stigmas sometimes persistent, external surface smooth or less often lenticillate or rugose, dull or rarely glossy, fruit drying wrinkled or smooth depending on whether mesocarp is fleshy or lignified; pyrene revealed when valves fall away, pyrene suspended by small, membranous, laminar, inverted-V-shaped structure at apex of fruit which clasps pyrene just behind its apex, pyrene partly or completely enveloped in a spongy, sweet, usually white (red in African spp.) arilloid pulp ("pseudaril"), pseudaril often underlain by a hygroscopic layer of matted fibers to 0.4 mm long which are "rooted" in the endocarp, fibers usually with same distribution as pseudaril, pyrene of variable shape, thinly cartilaginous to thick and bony, usually smooth-textured, ventral side with a funicular scar of varying shape and size, often set in relief from rest of surface; seed exalbuminous, embryo large, radicle short and usually concealed between basal lobes of cotyledons, testa papery to slightly fleshy to crustose, usually with irregular thickenings, cotyledons large, lobed and contortuplicate (then with infolded partly lignified testa), or

essentially entire and plano-convex, or transversely folded (sect.
Icicopsis), cotyledons vascularized, resin canals present.

Key to flowering material of Protium
in eastern Amazonia and the Guianas

The following keys are meant to be useful for identification of herbarium specimens. The measurements refer to dry fruits and to rehydrated flowers. Rehydration of flowers is necessary for proper dissection. In most instances dissection of flowers is necessary for access to the taxonomically useful characters.

There are three keys: one to staminate-flowering material, one to pistillate-flowering material, and one to fruiting material. Staminate and pistillate material are separated because of sexual dimorphism in flower structure; the same characters often cannot be used in both sexes to distinguish species. A key to the keys is provided below.

Some species occur twice in the keys, because they may display two character states. For example, Protium aracouchini may have a glabrous or pubescent pistillode, and in P. crenatum the inflorescence sometimes exceeds the pedicel.

Key for the keys to the species

1. Plants with flowers.

2. Flowers with dehiscent anthers that produce pollen and are dehiscent; pistillode (when present) always exceeded by stamens; when locules and ovules present, ovules not filling locule; stigmas not developed, stylode instead with apex rounded, lobulate, or acutely winged; pistillode sometimes obsolete, instead forming with disk a continuous, homogeneous, discoid or depressed-conical structure (staminate flowers).

Key A. (staminate-flowering material).

2. Flowers with anthers that produce no pollen and are indehiscent; true pistil almost always exceeding staminodes (exceeded by them in sect. Sarcoprotium); ovules completely filling locules; stigmas globose to discoid.

Key B. (pistillate-flowering material).

1. Plants with fruits

Key C. (fruiting material).

A. Key to staminate-flowering material

1. Disk pubescent.
 2. Petals adaxially short-papillate, also with dense, long, ascending hairs 0.3-1.1 mm long
1. P. subserratum.
 2. Petals adaxially only short-papillate.
 3. Pistillode and disk distinct; flowers pedicellate.
 4. Flowers 5-merous; petals lanceolate; filaments slender, stamens in 2 very unequal series; anthers 0.55-0.75 mm long.
2. P. apiculatum.
 4. Flowers 4-merous; petals ovate; filaments thick, stamens +/- level, anthers 0.25-0.3 mm long.
3. P. plagiocarpium.
 3. Pistillode and disk not distinct (represented by a discoid or depressed-conical structure; section Icicopsis); flowers sessile.
 5. Stamens exceeding petals; ovariodisk usually flat; leaves 68-110 cm long.
5. P. robustum.
 5. Stamens exceeded by petals; ovariodisk usually depressed-conical; leaves (1.27) 17.5-38.5 (53) cm long
 6. Leaflet apex abruptly and broadly short-acuminate.
6. P. tenuifolium.
 6. Leaflet apex gradually and narrowly long-acuminate.
7. P. sagotianum.

1. Disk glabrous.

7. Inflorescence exceeding petiole.

8. Pistillode glabrous.

9. Flowers 5-merous; stylode markedly acutely 5-winged.

8. P. pallidum.

9. Flowers 4-merous; stylode lobulate or subcylindric.

10. Pistillode greatly exceeding disk, ovoid, gradually contracted to a subcylindric or slightly sulcate stylode; anthers 0.6-0.75 mm long. 19. P. krukoffii.

10. Pistillode slightly exceeding disk, deeply depressed-ovoid, abruptly contracted to a short, distinctly 4-lobulate stylode; anthers 0.15-0.3 mm long.

11. Leaves 25-45 (50) cm long; region between lateral petiolules markedly swollen; branchlets robust and fleshy, 2.3-3.5 (4.5) mm diam at 2 cm from apex, with whitish cast. 10. P. strumosum.

11. Leaves 10-26 cm long; region between lateral petiolules not markedly swollen; branchlets slender and firm, 1-2 (2.6) mm diam at 2 cm from apex, green. 11. P. aracouchini.

8. Pistillode pubescent.

12. Petals cucullate, base clawed; leaflets drying reddish; always some 3-merous flowers present; pistillode without locules (section Sarcoprotium). 4. P. polybotryum.

12. Petals not cucullate, base only slightly narrowed; leaflets drying green or brown; 3-merous flowers never present; pistillode with locules.
13. Anthers in lateral profile usually as broad as tall, 0.15-0.3 mm long.
14. Calyx greatly exceeded by disk; stamens usually 4 (rarely 8); hairs on pistillode appressed. 12. P. divaricatum.
14. Calyx exceeding (rarely level with) disk; stamens always 8; hairs on pistillode ascending. 11. P. aracouchini.
13. Anthers in lateral profile much longer than broad, 0.45-0.75 mm long.
15. Petals adaxially, also pubescent.
16. Calyx greatly exceeding disk, 1.5-2.4 mm long overall. 13. P. opacum p.p..
16. Calyx level with (or exceeded by) disk, 0.9-1.3 mm long.
17. Petals 3-3.3 (4.1) mm long; inflorescence bracts not semi-clasping. 14. P. morii.
17. Petals 2-2.4 (3) mm long; inflorescence bracts semi-clasping. 18. P. paniculatum.
15. Petals adaxially only short-papillate.
18. Calyx exceeding disk; on leaflet abaxial surface, midvein and sometimes secondary veins with dense, flexuous hairs 0.2-0.4 (0.7) mm long. 13. P. opacum p.p.
18. Calyx usually exceeded by (sometimes level with) disk, leaflet abaxial surface without long, flexuous hairs.

19. Flowers 5-merous.
20. Petiole longer than interjuga; leaves (2) 3-5-jugate; calyx lobes usually separated by a flat sinus, 0.05-0.3 mm long; stylode acutely winged. 15. P. grandifolium.
20. Petiole shorter than interjuga; leaves (0) 1-2-jugate; calyx lobes contiguous, (0.3) 0.4-0.6 (0.7) mm long; stylode lobulate. 16. P. decandrum.
19. Flowers 4-merous.
21. Leaflet margin serrulate. 20. P. crenatum.
21. Leaflet margin entire.
22. Stylode apex 4-lobulate; petiole shorter than interjuga; inflorescence slender, 0.4-3 cm x 0.3-1 mm. 21. P. guianense.
22. Stylode apex acutely 4-winged; petiole longer than interjuga; inflorescence robust, (2.5) 3.5-10 (15) cm x (0.8) 1.5-2.3 (3.2) mm. 17. P. giganteum.
7. Inflorescence exceeded by petiole.
23. pistillode glabrous.
24. Flowers 5-merous.
25. Leaflets inserted vertical to the meridian, broadly elliptic to broadly oblong, broadly and abruptly short-acuminate; abaxially glabrous. 9. P. cuneatum.
25. Leaflets inserted horizontal to the meridian, elliptic, gradually long-acuminate; on abaxial surface, midvein and sometimes secondary veins with sparse to dense flexuous hairs 0.2-0.5 (0.7) mm long. 22. P. spruceanum.

24. Flowers 4-merous.

26. Calyx exceeding pistillode; anthers 0.3-0.4 mm long; leaflet

acumen sparsely serrulate.

24. P. pilosum.

26. Calyx greatly exceeded by pistillode; anthers more than 0.5 mm long; leaflet acumen entire.

27. Most flowers with petals basally connate 1/5-3/5 their length.

29. Inflorescence bracts semi-clasping; calyx exceeded by disk; anthers 0.5-0.65 mm long. 25. P. trifoliolatum.

29. Inflorescence bracts not semi-clasping; calyx exceeding disk; anthers (0.6) 0.8-1.1 mm long.

26. P. unifoliolatum.

27. Petals free on all flowers.

29. Leaflets glabrous; stylode distinctly 4-lobulate .

23. P. heptaphyllum.

29. Leaflets with scattered appressed (abaxially) or erect (adaxially) hairs, stylode usually subcylindric.

19. P. krukoffii.

23. Pistillode pubescent.

30. Flowers 5-merous.

31. Petals 3.6-3.8 mm long, margin short-papillate.

27. P. demerarensis.

31. Petals (2.3) 2.5-3 mm long, margin long-papillate.

28. P. altsonii.

30. Flowers 4-merous.

32. Calyx level with top of disk; leaflet margin sparsely
serrulate.

20. P. crenatum.

32. Calyx exceeded by disk; leaflet margin entire.

21. P. guianense.

B. Key to pistillate-flowering material

1. Disk pubescent.
 2. Flowers pedicellate.
 3. Petals adaxially with dense, long, ascending hairs 0.3-1 mm long.
 1. P. subserratum.
 3. Petals adaxially only short-papillate.
 4. Flowers 5-merous; petals lanceolate; staminodes in 2 very unequal series; anthers 0.45-0.6 mm long; hairs on disk dense, to 0.35 mm long.
 2. P. apiculatum.
 4. Flowers 4-merous; petals ovate; staminodes +/- level; anthers 0.25 mm long, hairs on disk sparse, to 0.1 mm long.
 3. P. plagiocarpium.
 2. Flowers sessile.
 5. Leaves 68-110 cm long; staminodes always 5, reaching stigmas; ovary substipitate; stigmas large and globose.
 5. P. robustum.
 5. Leaves (12.7) 17.5-38.5 (53) cm long; staminodes 10 (rarely 5), not reaching stigmas; ovary sessile; stigmas discoid or obdeltoid.
 6. Leaflet acumen 0.3-1.1 cm long; stigmas obdeltoid.
 6. P. tenuifolium.
 6. Leaflet acumen (1.1) 1.3-2 (3) long; stigmas discoid.
 7. P. sagotianum.

1. Disk glabrous.

7. Inflorescence exceeding petiole.

8. Pistil glabrous.

9. Flowers 5-merous; calyx greatly exceeding disk (almost level with stigmas); stigmas stipitate (style with 5 short lateral branches. 8. P. pallidum.)

9. Flowers 4-merous; calyx exceeded by or level with disk; stigmas sessile.

10. Petals (2.1) 2.5-2.7 (3) mm long; anthers (0.25) 0.4-0.55 mm lon. 19. P. krukoffii.)

10. Petals 1.5-2.4 mm long, anthers 0.2-0.35 mm long

11. Leaves 24-45 (50) cm long, region between petiolules markedly swollen; branchlets with whitish cast, robust and fleshy, 2.5-3.5 (4.3) mm diam at 2 cm from apex. 10. P. strumosum.)

11. Leaves 10-26 cm long, region between petiolules not markedly swollen; branchlets green, slender, and firm, 1-2 (2.6) mm diam at 2 cm from apex.

11. P. aracouchini.)

8. Pistil pubescent.

12. Petals cucullate, base clawed; leaflets drying reddish; stigmas abruptly contracted at apex in recurved or sigmoid, smooth or microscopically spiculate caudicules (sect. Sarcoprotium). 4. P. polybotryum.)

12. Petals not cucullate, only slightly narrowed at base; leaflets drying green or brown; stigmas not contracted to caudicules.
13. Anthers small, 0.2-0.35 mm long, in dorsiventral view ovate.
- 14 Hairs on pistil dense, ascending; staminodes usually 4 (rarely 8); calyx exceeding disk. 12. P. divaricatum.
14. Hairs on pistil scattered, appressed; stamens always 8; calyx exceeded by disk. 11. P. aracouchini.
13. Anthers larger, (0.35) 0.5-0.8 mm long, in dorsiventral view lanceolate to obtuse-oblong.
15. Petals abaxially pubescent.
16. Calyx greatly exceeding disk.
- 17 On leaflet abaxial surface, midvein and sometimes secondary veins dense, flexuous hairs 0.2-0.4 (0.7) mm long. 13. P. opacum p.p.
17. Leaflet abaxially only with scattered appressed hairs to 0.1 mm long. 18. P. paniculatum.
16. Calyx exceeded by disk. 14. P. morii.
15. Petals abaxially only short-papillate.
18. On leaflet abaxial surface, midvein and sometimes secondary veins dense, flexuous hairs 0.2-0.4 (0.7) mm long. 13. P. opacum p.p.
18. Leaflets abaxially without long flexuous hairs.
19. Flowers 5-merous.

20. Petiole longer than interjuga, leaves (2) 3-5-jugate.

15. P. grandifolium.

20. Petiole shorter than interjuga, leaves (0) 1-2-jugate.

16. P. decandrum.

19. Flowers 4-merous.

21. Leaflet margin serrulate.

20. P. crenatum.

21. Leaflet margin entire.

22. Petiole shorter than interjuga; inflorescence slender,
0.4-3 cm x 0.3-1 mm; petals ovate; calyx usually exceeded
by disk, lobes 0-0.3 mm long.

21. P. guianense.

22. Petiole longer than interjuga; inflorescence more robust,
(2.5) 3.5-10 (1.5) cm x (0.8) 1.5-2.3 (3.2) mm; calyx
exceeding disk, lobes 0.3-0.6 (0.7) mm long.

17. P. giganteum.

7. Inflorescence exceeded by petiole.

23. Pistil glabrous.

24. Flowers 5-merous.

25. Leaflet insertion vertical to the meridian, broadly
elliptic to broadly oblong, broadly and abruptly
short-acuminate; stigmas stipitate (style laterally
5-branched).

9. P. cuneatum.

25. Leaflet insertion horizontal to the meridian, elliptic,
gradually long-acuminate; stigmas sessile.

26. Leaflet midvein abaxially with sparse to dense, flexuous hairs
0.2-0.5 (0.7) mm long; pedicel (0.8) 1.7-2.2 (3) mm long; calyx
lobes 0.3-0.6 mm long; staminodes 1-1.3 and 1.1-1.4 mm long,
anthers 0.5-0.6 mm long; pistil 1.25-1.5 mm long.

22. P. spruceanum.

26. Leaflet midvein abaxially without long, flexuous hairs; pedicel
(3) 3.5-4 (5) mm long; calyx lobes (0) 0.15-0.25 mm long; stamens
1.65-1.7 and 1.75-1.8 mm long, anthers 0.75-0.8 mm long; pistil
1.6-1.9 mm long.

27. P. demerarens.

24. Flowers 4-merous.

27. Most flowers with petals basally connate 1/5-3/5 their length

28. Pulvinuli inconspicuous or absent, leaflet acumen sparsely
serrulate.

24. P. pilosum.

28. Pulvinuli conspicuous, leaflet margin entire or all of leaflet
margin coarsely serr(ul)ate.

29. Inflorescence bracts semi-clasping; style (0.15) 0.25-0.3
(0.4) mm long; petiole and rachis with sparse stiff erect
hairs 0.3-1 (1.3) mm long.

25. P. trifoliolatum.

29. Inflorescence bracts not semi-clasping; style 0.6-1.2 mm
long; petiole with dense to sparse fine erect hairs to 0.1
mm long.

26. P. unifoliolatum.

27. Petals always free.

30. Leaflets glabrous; style (0.25) 0.4-0.55 mm long; ovary
substipitate. 23. P. heptaphyllum.
30. Leaflet midvein with scattered appressed (abaxially) or erect
(adaxially) hairs, style (0.55) 0.8-1.1 mm long, ovary
sessile. 19. P. krukoffii.
23. Pistil pubescent.
31. Flowers 5-merous. 28. P. altsonii.
31. Flowers 4-merous.
32. Leaflet margin sparsely serrulate. 20. P. crenatum.
32. Leaflet margin entire. 21. P. guianense.

C. Key to fruiting material

1. Fruits subsymmetric, globose or elliptic, sometimes acuminate
2. Inflorescence shorter than petiole.
 3. Fruit smooth, green, glossy.
 4. Fruit (sub)stipitate; leaflet insertion vertical to the meridian; leaflets coriaceous, abruptly and broadly short-acuminate, acumen rounded. 9. P. cuneatum.
 4. Fruit sessile; leaflet insertion horizontal to the meridian; leaflets characeous, gradually and narrowly long-acuminate. 28. P. altsonii.
 3. Fruit gray, rough-textured, dull, lenticellate. 27. P. demerarensis.
2. Inflorescence longer than petiole.
 5. Fruit elliptic.
 6. Fruit not greater than 2 cm long; leaflet margin serrulate. 20. P. crenatum.
 6. Fruit greater than 2 cm long; leaflet margin entire. 4. P. polybotryum.
 5. Fruit essentially globose, sometimes acuminate.
 7. Fruit greater than 2 cm long.
 8. Fruit gray and lenticellate, calyx forming a cupule at base; petiolules inconspicuous. 13. P. opacum.
 8. Fruit green, smooth, glossy; petiolules conspicuous.

- 9. Leaflet pallid abaxially, petiolule adaxially 1-canaliculate;
acumen short, broad, obtuse; pseudaril occurring as a band 0.5
cm wide around periphery of pyrene. 8. P. pallidum.
- 9. Leaflet green abaxially; petiolule adaxially 2-canaliculate;
acumen long, narrow, acute; pseudaril covering all of pyrene.
10. P. strumosum.
- 7. Fruit never greater than 2 cm long.
10. Fruit lenticellate. 15. P. grandifolium.
10. Fruit not lenticellate.
11. Fruit sessile, leaflet margin serrulate. 20. P. crenatum.
11. Fruit substipitate, leaflet margin entire.
12. Inflorescence lax (secondary axes to 11. (20.5) cm
long), (0.4) 0.7-1.3 times length of subtending leaf;
pedicel much thicker than proximal inflorescence axis.
18. P. paniculatum.
12. Inflorescence compact (secondary axes to 5 (7.8) cm
long), 0.2-0.5 (0.6) times length of subtending leaf;
pedicel +/- same diam as proximal inflorescence axis.
17. P. giganteum.
- 1. Fruit markedly oblique, gibbous.
13. Inflorescences paniculate.
14. Inflorescence exceeding petiole.
15. Fruit stipitate, base lobate. 3. P. plagiocarpium.
15. Fruit substipitate or sessile, base truncate or acute.

16. Fruit sessile.

17. Fruit greater than 2 cm long; inflorescence and branchlets robust.

2. P. apiculatum.

17. Fruit less than 2 cm long; inflorescence and branchlets slender.

18. Fruit bicolored, red above and green below; inflorescence usually greatly exceeding pedicel.

11. P. aracouchini.

18. Fruit red only; inflorescence usually shorter than pedicel.

21. P. guianense.

16. Fruit substipitate.

19. Fruit with apex abruptly acute or rounded, usually drying smooth; pyrene thickly cartilaginous.

20. Leaves 0-2-jugate, petiole with fine erect hairs; fruit maturing red and smooth.

16. P. decandrum.

20. Leaves 3-5-jugate, petiole without fine erect hairs; fruit usually maturing gray, lenticellate, rough-textured.

14. P. morii.

19. Fruit with apex long-acuminate, drying wrinkled; pyrene thin-cartilaginous or papery.

21. Inflorescence slightly exceeding petiole; leaflets gradually acuminate; pyrene thinly cartilaginous, with dense layer of matted fibers.

19. P. krukoffii.

21. Inflorescence greatly exceeding petiole; leaflets gradually
acuminate; pyrene papery, glabrous. 12. P. divaricatum.
14. Inflorescence shorter than petiole.
22. Fruit greater than 2 cm long, substipitate, long-acuminate.
19. P. krukoffii.
22. Fruit less than 2 cm long, sessile, apex acute.
23. Pulvinuli lacking on lateral petiolules; plant lactiferous;
leaflets abaxially papillate. 1. P. subserratum.
23. Pulvinuli present on all petiolules; plant resiniferous;
leaflets abaxially without papillae.
24. Fruit pale green to white at maturity, markedly trigonous;
leaflet acumen sparsely serrulate. 24. P. pilosum.
24. Fruit red at maturity, not trigonous; leaflet acumen
entire.
25. Most leaves on all branchlets unifoliolate, rarely
trifoliolate, leaflet margin often serrulate.
26. P. unifoliolatum.
25. Most leaves on all branchlets 1-4-jugate, leaflet
margin always entire.
26. On leaflet, midvein abaxially with sparse to dense
flexuous hairs 0.2-0.5 (0.7) mm long.
22. P. spruceanum.
26. On leaflet, midvein abaxially without long
flexuous hairs.

27. Leaflets glabrous. 23. P. heptaphyllum.
27. Leaflet pubescent.
28. Fruit with short appressed hairs persisting at least at base and apex; petiole and rachis with scattered to dense flexuous hairs 0.1-0.6 (0.8), often also with sparse fine erect hairs to 0.1 mm long. 21. P. guianense.
28. Fruit glabrous; petiole and rachis with sparse, stiff, erect hairs 0.3-1 (1.3) mm long. 25. P. trifoliolatum.
13. Inflorescence pseudospicate; pyrene with site of funicle below middle; cotyledons transversely folded (sect. Icicopsis).
29. Fruit, strongly oblique, apex perpendicular to axes; leaves 68-110 cm long; branchlets (5) 7-12 mm diam at 2 cm from apex; cotyledons not basally incurved. 5. P. robustum.
29. Fruit only slightly oblique; leaves (12.7) 17.5-38.5 (53) cm long; cotyledons basally incurved to form in profile a "6"-shaped figure.
30. Leaflets abruptly and narrowly long-acuminate. 7. P. sagotianum.
30. Leaflets gradually and broadly short-acuminate. 6. P. tenuifolium.

A TAXONOMIC REVISION OF PROTIUM (BURSERACEAE)
IN EASTERN AMAZONIA AND THE GUIANAS

by

Douglas Charles de Burgh Daly

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Volume II

1. *Protium subserratum* (Engler) Engler, DC. Mon. Phan. 4: 89. 1883. Type.
Amazonas: Rio Uaupés, near Panurê, Oct. 1852 (f fl and young fr),
Spruce 2620 (lectotype (designated by Swart, 1942b): P; isoelectotypes:
BM, BR, C, G, GH, K, LE, MO, NY, W).

Icicopsis subserrata Engl. in Mart. Fl. bras. 12(2): 259. 1874. Tingulunga
subserrata (Engl.) Kuntze, Rev. Gen. Pl. 1: 108. 1891.

Trees, reproductive height (5) 10-18 (25) m; often with low plank buttresses, trunk often angled; bark thin, rough, with horizontal lenticels, brittle, pitted, shed in irregular plates; latex white, gummy, produced in all vascularized organs; branchlets usually robust, (2.6) 3.5-8 mm diam, usually with dense suberect to appressed lanate hairs 0.1-0.3 (0.5) mm long. Leaves (3) 4-12-jugate, (22) 27-44 (76) cm long; petiole long and usually slender, (4) 7-14.5 (18) cm x (1.4) 1.7-3.5 (4) mm, much longer than interjuga, semi-terete, usually slightly acutely winged, with sparse to scattered fine erect hairs to 0.05 mm long, usually also with dense to sparse suberect lanate hairs 0.1-0.3 (0.5) mm long, sometimes also with sparse to scattered appressed hairs 0.05-0.15 (latter often absent from upper surface); interjuga (1.3) 2-4.2 (5.8) cm long; petiolules short, shallowly 2-canalicate, distal pulvinuli lacking on lateral petiolules, laterals 0.2-0.6 (0.8) cm long, terminal shorter than interjuga, (0.6) 1.2-2 (2.9) cm long; leaflets chartaceous to coriaceous, basal pair lanceolate to oblong, (5.8) 6.5-10.4 (11.5) x (1.8) 2.2-3.9 (4.3) cm, rest of laterals narrow-oblong to elliptic, longer, ultimate

pair (6) 7.3-10.6 (15) x 2.2-3.6 (3.9) cm, base oblique, proximal side acute to obtuse, distal side obtuse to truncate, terminal lanceolate, (4.8) 5.6-10.5 (13) x (1.8) 2.3-3.8 (4.8) cm, base acute to obtuse, all with apex acuminate, acumen variable in length and breadth, (0.5) 0.7-1.5 (1.8) cm long, margin serrulate (teeth less than 1 mm long) to rarely serrate (western Amazonia), often some leaflets entire, less often all leaflets entire (Brazil: northern Pará except Rio Trombetas basin, Amapá, Maranhão, Rio Japurá basin in Amazonas; French Guiana; Amazonas in Venezuela), teeth (when present) irregularly spaced, to 2.5 mm long, basal side convex, apical side concave, apex obtuse or less often acute, abaxial leaflet surface with midvein prominent, secondary veins prominulous, rest of veins prominulous to impressed, midvein and sometimes secondary veins with scattered suberect flexuous hairs to 0.3 mm long, sometimes abaxial surface glabrous or midvein flanked by scattered appressed hairs 0.05-0.2 mm long, blade papillate, adaxial surface with midvein narrowly prominulous but partly sunk in a groove, secondary veins prominulous to impressed, rest of veins flat to impressed, adaxial surface glabrous.

Inflorescences usually congested near apex, pseudospicate, long and slender, (2.2) 3.5-14 cm x 1-2.2 (2.5) mm (in fruit (1.8) 2.3-11.5 (27.5) cm x (1.5) 1.7-3.5 (3.7) mm, secondary axes poorly developed, 0.4-2.5 cm long (3.8 cm long in fruit), axes with dense suberect to appressed flexuous hairs to 0.3 (0.4) mm long; inflorescence bracts ovate, those subtending inflorescences ovate, fleshy, 1.5-1.8 mm long, those on primary axes (0.8) 1-2 (3) mm long, those on secondary axes 0.3-1.2 mm long; pedicel subcylindric, shorter than flower, stout, sessile or 0.4-1.2

(1.5) x 0.45-0.6 (0.8) mm, with hairs as on axes. Flowers 5-merous, rarely some flowers 4-merous, large, 3-4 (5) mm long when dry; in staminate flowers calyx 1.2-1.6 x 2.3-2.6 (3) mm overall, level with or exceeding pistillode, with hairs as on inflorescence but sparse, less often with dense to sparse appressed hairs 0.1-0.25 mm long, lobes (narrowly) triangular, somewhat saccate, 0.7-1 mm long, apex acute; petals long, narrowly lanceolate, markedly saccate, (4) 4.3-5.7 (6.4) x (0.8) 1-1.4 (1.7) mm, membranous, apiculum markedly thickened and strongly inflexed, abaxially with hairs as on calyx, adaxially with dense, ascending, flexuous hairs 0.3-1 mm long, the shorter hairs toward the apex, margin long-papillate, at base also with sparse to dense erect hairs 0.1-0.35 mm long, at anthesis petals erect or more often reflexed the upper 1/3 their length; stamens long, greatly exceeding pistillode, (1.5) 2.25-2.4 and (2.4) 3-3.5 (4.6) mm long, filaments slender, terete to slightly compressed, (0.95) 1.55-1.75 and (1.8) 2.3-3.1 mm long, anthers dorsifixed, dimorphic, in dorsiventral view antepetalous anthers ovate, 0.5-0.7 mm long, antesealous anthers lanceolate, 0.55-0.75 mm long, base lobulate, apex usually mucronate, in lateral profile all obliquely acute-oblong to broadly so; disk 0.2-0.35 x 0.25-0.55, usually with dense to sparse suberect lanate hairs 0.1-0.25 mm long (hairs absent in Krukoff 5083); pistillode exceeding disk, 0.55-0.75 x 0.45-0.6 mm overall, globose to ovoid, with dense ascending lanate hairs 0.1-0.5 mm long, provided with locules and reduced ovules, gradually contracted to a short thick 5 (4-) lobate stylode 0.2-0.4 x 0.2-0.3 mm; in pistillate flowers calyx 1.5-1.8 (2) x 2.5-3 (3.2) mm overall, greatly exceeding disk and approximately

level base of style, lobes 1-1.3 mm long; staminodes 1.35-1.9 and (1.7) 2-2.3 (2.8) mm long; filaments slender, slightly compressed, (0.85) 1-1.4 and (1.1) 1.6-1.7 (1.9) mm long, anthers 0.45-0.5 (0.65) mm long, dimorphic as in fertile anthers, antepetalous anthers (0.35) 0.5 mm long and antesepalous (0.4) 0.6 mm long; disk shallow and broad, 0.2-0.4 x (0.3) 0.5-0.7 mm, hairs as in staminate flowers; pistil 2.5-3.6 x 1-1.5 mm overall, ovary sessile, ovoid, gradually contracted into a long slender 5-sulcate style 1.4-2 (2.35) x 0.35-0.5 mm, ovary and most of style with dense flexuous ascending hairs 0.3-0.7 mm long, stigmatal region 0.3-0.35 (0.5) mm high, stigmas sessile, lateral, compressed-ellipsoid (less often compressed-globose). In fruit pedicel terete, (0.7) 1.5-2.5 (3.3) x 1.5-2.1 (2.8) mm; fruit sessile or less often substipitate, slightly or less often markedly obliquely ovoid, gibbous, (1.1) 1.3-1.9 (2.1) x (0.6) 1.1-4 cm (to 1.8 cm diam when more than one 1 pyrene), base truncate, apex acute or acuminate, style and stigmas usually persistent, surface incompletely glabrescent, at maturity with appressed hairs 0.1-0.2 mm long scattered on most of surface but dense at apex, smooth, not drying wrinkled, mesocarp relatively thin, fleshy; pseudaril apparently covering all of pyrene; pyrene 0.9-1.2 x 0.6-1 cm, variable in shape, in dorsiventral view (broadly) ovate to depressed ovate or less often broadly lanceolate, base truncate or less often obtuse, apex usually broadly short-acuminate, less often narrowly acuminate, in lateral profile on dorsal side semi-ovate with obtuse base and acute to acuminate apex, on ventral side essentially ovate to lanceolate, funicular scar 1/2 to 3/5 distance to apex, laterally elliptic to rounded-deltate, funicular

depression usually deep; testa with irregular thickenings but not infolded with cotyledons, cotyledons entire and plano-convex.

Distribution. Widespread in Amazonia, also occurring in Guyana, French Guiana, and in Colombia in Antioquia. In Amazonia the species is known from Brazil (Amapá, Amazonas, Maranhão, Pará, Rondônia), Ecuador (Napó, Santiago-Zamora), Peru (Loreto), and Venezuela (Amazonas). Protium suberratum is usually a medium-sized to large, understory or canopy tree of primary moist forests on terra firme. It is most common in areas characterized by sandy soils. It has been reported twice from old secondary forest (Daly et al. 3970; M. Silva 500), and once from várzea forest (Pires & Silva 10688). In eastern Amazonia P. suberratum flowers approximately in June and fruits from Oct-Mar.

Specimens examined. Brazil. Amapá: Municíp. Mazagão, BR-156, incomplete road toward Monte Dourado, 70 km WSW of Macapá, ca 0°08'S, 51°48'W, 22 Dec 1984 (fr), Daly et al. 3970 (HAMAB, NY); Municíp. Mazagão, Camaipi, EMBRAPA reserve and vicinity, 30 km NW of Mazagão, ca 0°10'S, 51°37'W, 22 Dec 1984 (fr), Mori et al. 17489 (HAMAB, NY). Maranhão: Rio Gurupi, 17 Mar 1958 (fr), Frões 34427 (IAN, US); Municíp. Turiaçu, Maracaçumê-Sta. Helena road, 3 Dec 1978 (sterile), N. A. Rosa & Vilar 3145 (MG). Pará: Municíp. Oriximiná, Rio Trombetas, right side, Porto Trombetas, km 60 of Mineração road, behind bauxite mine, near Igarapé Saracazinha, 4 Sep 1980 (sterile), Cid et al. 2087 (NY); Belém, EMBRAPA, Mocambo Reserve, ca 1°23'S, 48°27'W, 10-17 Nov 1984 (fr), Daly et al. 3762 (IAN, NY), 10-17 Nov 1984 (fr), Daly et al. 3764 (IAN, NY); Belém-Brasília Highway km 33, 2 Dec 1959 (sterile), Oliveira 206 (IAN); Rio Jarí, Serra

de Monte Dourado, 3 km from edge, 13 Nov 1967 (fr), Oliveira 3511 (IAN, NY), 8 Nov 1967 (fr), Oliveira 3688 (IAN, NY), Planalto de Monte Dourado, 21 Jan 1968 (fr), Oliveira 3990 (IAN, NY), Monte Dourado, 28 Jan 1968 (fr), Oliveira 4027 (IAN, NY); Monte Dourado, planalto, 4 Feb 1968 (fr), Oliveira 4104 (IAN, NY); Ilha do Mosqueiro, 19 Jul 1971 (sterile), Oliveira 5820 (IAN), next to Fazenda Agro Pastoril, 20 Oct 1971 (fr), Oliveira 5915 (IAN); Colônia 3 de Outubro, between km 100 of Bragança railway and the Rio Guamã, 23 Aug 1952 (fr), Pires et al. 4121 (IAN); Belém, IPEAN, Reserva Mocambo, Jan 1956 (fr), Pires & Silva 6725 (IAN), 2 Jun 1967 (young fr), Pires & Silva 10549 (IAN), Reserva APEG, 14 Aug 1967 (fr), Pires & Silva 10688 (IAN), Reserva Mocambo, 12 Sep 1967 (fr), Pires & Silva 10930 (IAN); Belém-Mosqueiro road, 21 Mar 1968 (fr), Pires & Silva 11471 (IAN); Belém, Reserva Aurã, 2 Feb 1968 (fr), Pires & Silva 11490 (IAN); BR-22, Capanema to Maranhão, 3 Nov 1965 (fr), Prance & Pennington 1928 (IAN, NY, US); BR-163, km 1225, 21 Nov 1972 (fr), Prance et al. 25619 (NY); Acará, Jacarequara, Tapera, 2 Feb 1966 (fr), M. Silva 200 (MG); Portel, Oct 1955 (fr), L. O. Williams & Silva 18200a (IAN).

Guyana: 75 mi Bartica-Potaro road, 23 Nov 1947 (fr), For. Dept. Br. Gui. Rec. No. 5577 (MO, NY, U, US); 83 mi Bartica-Potaro road, 22 Jun 1933 (f fl), Tutin 231 (BM, RB, U, US).

Protium suberratum shows pronounced geographic variation, but because there are so few collections with flowers or mature fruits, it is impossible to say at this time whether these variants deserve taxonomic rank. In this treatment the species is considered to be a widespread and variable taxon and any future assessment of the infraspecific taxonomy

must take into consideration the variation that can be observed even within a single collection. For example, on the several duplicates of Krukoff 7063 the leaflet size varies greatly from one duplicate to another and the leaflet margin ranges from markedly serrate to completely entire. The geographical variants are as follows:

1) Brazil: Amapá, Maranhão, and in northern Pará except the Rio Trombetas basin; French Guiana. The leaflets have consistently entire margins. On the glabrous abaxial surface the secondary veins are impressed, and the adaxial surface is glossy and has impressed tertiary veins. As yet there are no flowering collections from these populations.

2) Brazil: Rondônia, and Amazonas except the Rio Japurá basin; Peru: Maynas; Colombia: Antioquia. The leaves are large. The leaflets are usually large and coriaceous, and the teeth are usually present although they vary in size. The inflorescence is usually long. This is the morphology of the type collection.

3) Peru: San Martín. There are only a few collections from this area. These specimens resemble the preceding group except that the teeth on the leaflet margins are the largest of any population.

4) Guyana. These collections are also similar to those from central Amazonia except that the fruits are larger and the leaflet margins generally have few large teeth.

5) Ecuador: Napo, Santiago-Zamora. These differ from the central Amazon collections by their chartaceous leaflets with rather small teeth on the margins.

6) Colombia: Amazonas; Venezuela: Río Guainia. The collections from

these regions have small, coriaceous leaflets which are broadly short-acuminate and have visibly papillate abaxial surfaces. The inflorescences are long, with the secondary axes not or negligibly developed, and very dense long (0.1-0.4 mm) hairs on the inflorescence which give it a shaggy appearance.

7) Venezuela: southern Amazonas (near Cerro de Neblina); Brazil: Rio Japurá (Rio Xiê). These populations differ in enough qualitative characters to deserve taxonomic rank, but I will reserve judgment as there are not yet any flowering collections. These specimens have slender branchlets. The small and thinly chartaceous leaflets have entire or subentire margins. The inflorescences are consistently very short (to 3 cm long in fruit), and the inflorescence bracts persist in fruit. The staminodes are longer than in other populations. The fruits are small, sessile, and sharply long-acuminate, with scattered hairs persisting.

Protium subserratum constitutes a natural group with P. ferrugineum (Engl.) Engl. and P. reticulatum (Engl.) Engl. (see chapter on infrageneric classification, Table III). Protium subserratum is distinguished from P. ferrugineum (i.e., Vieira et al. 288; Huashikat 2014), a species of the upper Rio Negro basin, by a number of important characters. In the latter species the lateral petiolules are long and slender and are provided with pulvinuli; the disk is glabrous and the shape of the disk and receptacle are such that a hypanthium is formed and the insertion of the perianth is perigynous relative to the tiny pistillode (0.1-0.15 mm long). The anthers are basifixed and have truncate bases such that the anthers are not easily distinguished from the

filaments. In contrast, P. subserratum has short stout lateral petiolules without pulvinuli; the pistillode is superior and exceeds the usually densely pubescent disk; and the anthers are dorsifixed and have lobulate bases.

Protium reticulatum (Engl.) Engl. is known only from a restricted portion of the upper Rio Negro in Brazil and contiguous Venezuela. No flowering collections are known. It has slender branchlets, and long, slender petiolules (without distal pulvinuli); the lateral leaflets are small and ovate, with truncate to slightly cordate bases and abruptly long-acuminate apices; the inflorescence is very short (less than 5 cm long); and the fruits are relatively small and have obtuse or usually depressed apices. Protium subserratum has robust branchlets and elliptic to oblong lateral leaflets with acute to obtuse bases and gradually acuminate apices; the inflorescence is usually quite long; and the fruits are larger with acute to acuminate apices.

One curious aspect of this group is that all three species appear to be sympatric near San Carlos de Río Negro in southern Venezuelan Amazonas. From the collections at hand there are no basic habitat differences separating them. Moreover, they show comparable phenologies:

subserratum:	10.8 km NE of San Carlos, frt Apr (<u>Clark 6619</u>)
	4.3 km NE of San Carlos, frt Sep (<u>Clark 6771</u>)
reticulatum:	4.3 km NNE of San Carlos, frt May (<u>Clark 7190</u>)
	4.3 km NNE of San Carlos, frt Aug (<u>Clark 8103</u>)
ferrugineum:	near San Carlos, frt May (<u>Spruce 3494</u> (type))

2. *Protium apiculatum* Swart, Recueil Trav. Bot. Néerl. 39: 201. 1942.

Type. Surinam: Suriname River near Goddo, 28 Jan 1926 (f fl), Stahel 125 (holotype: U; isotype: MO).

Protium firmum Swart, Acta Bot. Néerl. 15: 49. 1966. Type. Brazil.

Amazonas: Basin of Rio Madeira, Mun. Humaitá, on plateau between Rio Livramento and Rio Ipixuna, 7-18 Nov 1934 (fr), Krukoff 7142 (holotype: NY; isotypes: F, GH, MO).

Trees, reproductive height 5-30 m, maximum recorded diameter 41 cm; often with simple, spreading plank buttresses to 50 cm high; bark smooth, gray, scaly; sap white, milky, gummy; branchlets robust, 3.3-7.8 (11) mm diam, with dense ascending to appressed flexuous hairs to 0.4 mm long. Leaves 3-5 (8)-jugate, 21.5-73.3 (92) cm long; petiole semi-terete to subterete, rarely acutely winged, 8.5-28 cm x 1.9-5 (6) mm, longer than the interjuga, interjuga 2.8-8.4 (17) cm long, rachis with scattered fine erect hairs to 0.1 mm long, also with sparse to scattered (rarely dense), ascending to appressed, flexuous hairs to 0.2 (0.3) mm long; petiolules 1-canaliculate (often deeply so), usually long and slender, pulvinuli inconspicuous, laterals 0.6-1.8 (2.6) cm long, terminal shorter than interjuga, (1) 1.7-5.2 cm long; leaflets coriaceous (central Amazonia) to chartaceous (eastern Amazonia), laterals (broadly) elliptic or less often oblong or lanceolate, base subequal, obtuse or rarely acute or truncate, basal pair 8.3-15.8 (19) x (2.4) 3.8-7.8 cm, ultimate pair 10.7-22.5 (26) x 3.7-7.4 (8.9) cm, terminal obovate or less often broadly elliptic, base

obtuse, (7) 9.8-16.6 x 3.1-7 cm, leaflet apex usually gradually acuminate, acumen variable in length and width, often mucronate but sometimes rounded or slightly retuse, 0.5-2.1 cm long, abaxial surface with midvein narrowly prominulous but usually sunk in a groove, rest of veins prominent, midvein and usually secondary veins with scattered appressed (often flexuous) hairs to 0.2 mm long, also with sparse to scattered fine erect hairs to 0.1, rest of surface with scattered, thick, often curved, apparently glandular hairs to 0.05 mm long, adaxial surface with midvein markedly obtusely prominent, secondary veins prominent, rest of veins prominulous, surface glabrous or with scattered appressed hairs to 0.1 mm long.

Inflorescences often congested near apex, fasciculate, long and usually robust, 5-40 cm x 0.9-3.3 (5) mm, 0.3-0.4 (1) times as long as subtending leaf, secondary axes usually well-developed, 0.5-14 cm long, axes with dense ascending to appressed hairs to 0.3 mm long, sometimes also with sparse fine erect hairs to 0.1 mm long; inflorescence bracts (broadly) ovate, those subtending inflorescences rarely seen, to 2.5 mm long, those on primary axes 0.7-3.4 (4) mm long, those on secondary axes 0.3-1.5 (2.2) mm long; pedicel subcylindric, shorter than flowers, (0.3) 0.6-2 (2.7) mm long, 0.25-0.35 (0.4) mm diam in staminate flowers, 0.35-0.65 mm diam in pistillate flowers, with dense to sparse, ascending to appressed hairs to 0.2 mm long, sometimes also with sparse fine erect hairs to 0.1 mm long.

Flowers all 5-merous, small; staminate flowers 2.1-2.7 mm long; calyx variable in depth but exceeded by the disk, (0.3) 0.4-0.8 x (1.2)-2.2 mm, hairs as on pedicel, lobes (depressed-) deltate, acute to acuminate, 0.1-0.3 mm long; petals white, yellow, or cream to yellowish-green,

lanceolate, fleshy, carinate, (1.6) 2-2.5 x 0.8-1.1 (1.5) mm, base often abruptly attenuate, apiculum conspicuous and strongly inflexed, abaxially with sparse to scattered or dense, appressed to ascending hairs to 0.15 mm long, margin short- or long-papillate, at anthesis petals straight or slightly inflexed or reflexed; stamens of two markedly unequal series, greatly exceeding pistillode, 1.55-2 and 1.75-2.3 mm long, filaments slender, +/- terete, 1.05-1.4 and 1.3-1.75 mm long, antepetalous ones often inserted on base of petals, at anthesis antesepalous ones strongly reflexed out between petals, anthers basifixed, in dorsiventral view lanceolate with lobulate base and obtuse to acute apex, in lateral profile elliptic, variable in length, 0.55-0.75 mm long; disk relatively deep and narrow, 0.3-0.6 x (0.15) 0.25-0.4 (0.5) mm, with dense, erect or flexuous hairs to 0.15 (0.35) mm long; pistillode 0.5-0.85 (1.3) x 0.25-0.35 mm overall, usually only slightly exceeding the disk, ovoid, usually substipitate, provided with locules but these apparently without reduced ovules, surface with dense erect or flexuous hairs to 0.25 (0.35) mm long, apex usually gradually contracted to a slightly lobulate or obtusely winged stylode 0.1-0.25 x 0.2-0.3 mm; in pistillate flowers calyx usually level with top of disk, (0.5) 0.8-1.2 x 1.8-2.4 mm, lobes (0.2) 0.3-0.4 (0.5) mm long; staminodes 1.4-1.7 and 1.55-2 mm long, level with or slightly exceeding the stigmas, filaments slender and strap-shaped, 0.95-1.1 and 1.1-1.5, anthers basifixed, in dorsiventral view (broadly) lanceolate with lobulate base and rounded to slightly retuse apex, in lateral profile obliquely obtuse-oblong, 0.45-0.6 mm long; disk deep and relatively narrow, (0.3) 0.5-0.75 x 0.2-0.4 mm, above and often inside

with dense erect or ascending hairs to 0.2 mm long; pistil 1.2-1.3 (1.6) x 0.7-1.05 mm overall, ovary sessile, (deeply) depressed-ovoid, with dense ascending to appressed hairs to 0.2-0.35 mm long, gradually contracted to a very short (or obsolete) thick style 0-0.1 (0.2) x 0.4-0.55 mm, rarely (Stahel 144) appearing slightly branched; stigmatal region 0.2-0.35 mm high, stigmas lateral, subglobose, abruptly contracted in incurved, smooth or microscopically spiculate caudicles, 0.1-0.15 mm long. In fruit pedicel 2-4 (5.5) x 1.9-2.7 mm, fruit red at maturity, oblique-ovoid, gibbous and slightly ventricose, 1.7-2.5 x 1.2-1.9 cm, sessile, apex acute or often (western Amazonia) somewhat acuminate with apex slightly recurved, surface glabrous except a few hairs persisting at base and apex, smooth, drying wrinkled; pseudaril fleshy; pyrene thinly cartilaginous, glabrous, 1.4-2 x 1-1.2 cm, in dorsiventral view elliptic with rounded to acute base and apex, in lateral profile essentially oblong to broadly ovoid with truncate base and acuminate apex, site of funicle 4/5 of distance to apex, funicular scar rounded-deltate to slightly lunate, covering 1/10 of ventral surface; testa papery, without irregular thickenings; cotyledons entire and plano-convex, anterior one thicker than posterior one.

Distribution. Widespread in Amazonia and the Guianas, with one disjunct collection from Costa Rica. Protium apiculatum is a medium-sized to large tree of terra firme primary forests. It is often found in sandy soils and in hilly terrain. In eastern Amazonia and the Guianas the species flowers in October to January and fruits from November to April (July).

Specimens examined. Brazil. Amapá: Municip. Macapá, vicinity of Serra do Navio, next to village, approx. 1°03'N, 52°54'W, 3 Jan 1985 (f fl and young fr), Rabelo & Cardoso 3149 (HAMAB, NY), 3 Jan 1985 (buds), Rabelo & Cardoso 3154 (HAMAB, NY); Porto Grande, Picadão Matapi, 24 Nov 1976 (m fl), Rosa 1039 (MG); Municip. Macapá, margin of Rio Dois Irmãos, 12 km from Cupixi, 20 Apr 1977 (fr), Rosa & Santos 1787 (MO). Pará: Municip. de Faro, Rio Jamundá, São Jorge, Empresa Sta. Terezinha, 12 Nov 1950 (young fr), Black & Ledoux 50-10770 (IAN); Santarém, km 73 of road to Cachoeira do Palhão, on Rio Curuá Una, 3 Dec 1966 (buds), Cavalcante & Silva 1541 (IAN, MG); 45 km from Tucuruí, SSW on new BR 422 and onto logging road, approx. 4°03'S, 49°47'W, 3 Nov 1981 (buds), Daly et al. 1199 (MG, NY); near Rio Itacaiunas: 80 km from Marabá, 37 km S on PA-150 and 50 km WNW on service road, 3 Dec 1981 (fr), Daly et al. 1654 (MG, NY); Serra do Carajás, "Azul," near camp at Serra Norte (22km NW, then 10-15 km SW), 8-12 Dec 1981 (fr), Daly et al. 1881 (MG, NY); castanhais of Lago de Castanha, 25 Nov 1907 (buds), Ducke 8901 (MG); Faro, (without date) (m fl), Ducke RB 11385; Acampamento Poção, planalto of Santarém, 7 Jul 1954 (young fr), Frões 30905 (IAN, U); Rio Acaraí, tributary of Rio Xingu, 12 Dec 1955 (m fl), Frões 32514 (IAN, NY, U, US); Santa Julia, Serra de Parintin, 18 Mar 1924 (fr), J. G. Kuhlmann 1674 (NY, RB); Cuiabá-Santarém Highway, km 1135, vicinity of Igarapé Natal, 16 Nov 1977 (young fr), Prance et al. 25507 (NY); Basin of Rio Xingu, Gleba Bacajá, just below mouth of Rio Bacajá, 3°22'S, 50°47'W, 23 Nov 1980 (buds), Prance et al. 26407 (NY), 23 Nov 1980 (young fr), Prance et al. 26418 (NY), 27 Nov (buds), Prance et al. 26498 (NY); Tucuruí, PA-263, 7 Nov 1983 (buds) J.

Ramos 1027 (INPA, NY); road to Marabá, 25 Jan 1971 (young fr), Ribeiro & Nascimento 69 (IAN, NY); Altamira, EMBRAPA experimental station, Transamazon Highway, km 23 Altamira-Itaibuta road, 30 Oct 1977 (m fl), A. S. Silva 190 (NY); Jarí region, road between Pilão and Repatimento, km 52, 9 Dec 1969 (buds), N. T. Silva 2863 (IAN), Santa Patrícia, left bank of Rio Jarí, 10 Mar 1970 (fr), N. T. Silva 2944 (IAN).

French Guiana: Route de Mana, 17 Dec 1955 (m fl), BAFOG 7100 (NY), 6 Jan 1956 9f fl), BAFOG 7132 (NY, U); near St Laurent, 1955 (f fl), BAFOG 7140 (U); Route de Mana, 25 Feb 1956 (fr), BAFOG 7307 (NY), 15 Mar 1956 (fr), BAFOG 7371 (NY, P); Route de Cayenne, km 9050, 28 Mar 1956 (fr), BAFOG 7424 (NY); Saül, Mont La Fumée, 3°37'N, 53°12'W, 25 Sep 1982 (sterile), Boom & Mori 1847 (NY), 8 Oct 1982 (sterile), Boom & Mori 1921 (NY); Trois Suats, Abattir Alasuka, 23 Jul 1975 (seedling), Haxaire 424 (CAY); margin of Maroni River, 1862 (m fl), Mélinon 252 (P); Saül, Petite Circuit Boeuf Mort, 7 Dec 1976 (buds), Mori et al. 8703 (NY); Saül, Mont La Fumée, 3°37'N, 53°12'W, 4 Dec 1982 (buds), Mori & Boom 15321 (NY), 13 Apr 1983 (fr), Mori & Pipoly 15610 (NY), 8 Apr 1983 (fr), Mori & Pipoly 15547 (NY); left bank of Yaroupi, Saut Tainoua, 16 Apr 1970 (fr), Oldeman T-497 (CAY); Mariaflor Trail, 460 m from the Oyapock, 8 Dec 1965 (m fl), Oldeman 1862 (CAY); Saül, 1 Mar 1966 (fr), Oldeman 2106 (NY); right bank of the Yaroupi, 700m after Saut Tainoua, 16 Apr 1970 (fr), Oldeman B-2990 (CAY, NY); Mont Gauthiot, left bank of the Yaroupi, 20 Apr 1970 (fr), Oldeman B-3032 (CAY); (without locality), (without date) (buds), Poiteau s.n. (P); forestry trail 2 km toward Cayenne from St. Laurent-Mana intersection, 23 Mar 1968 (fr), Sastre 237 (CAY, NY, P).

Surinam: Jodensavanne-Mapanekreek area, 2 Feb 1963 (fr), J. Elburg LBB 9422 (NY); Base camp Winannakreek (Corantijn), 11 Apr 1965 (sterile), Maas LBB 10693 (U); Mapane Creek area, 4 Jun 1971 (sterile), Elburg LBB 13507 (U); Fallawatra, 8 Oct 1971 (sterile), Jimenez-Saa LBB 14306 (U); Jodensavanne-Mapanekreek area (Suriname River), 22 Aug 1953 (sterile), Lindeman 4671 (U), 10 Dec 1954 (sterile), Lindeman 6760 (U); Jodensavanne-Mapanekreek area (Suriname River), 20 Dec 1954 (seedling), Lindeman 6924 (U), 3 Dec 1955 (seedling), Lindeman 7461 (U), 2 Nov 1960 (buds), Schulz 8463 (GH).

Common names and economic uses. Brazil: breu andirobinha (Pará).

French Guiana: waluwa-i (Wayampi).

Protium apiculatum belongs to a distinct group of closely-related species which includes P. minutiflorum Cuatrec., P. fimbriatum Swart, and at least three undescribed species. While P. apiculatum was placed in section Icicopsis by Swart (1942b), it differs from the other two natural groups contained therein by a number of key characters (see chapter on generic limits: Table III).

Among the other species in its group, P. apiculatum is most closely related to P. minutiflorum, the latter as represented by Schultes & Cabrera 14953a (the type collection) and García-Barriga 13898.

Vegetatively, they are indistinguishable, but P. apiculatum differs by its pubescent disk, larger flowers, longer stamens, and larger lanceolate (not ovate) anthers. I have seen no fruiting specimens that can be identified with P. minutiflorum. From the rest of the group P. apiculatum differs most notably by its subglabrous and smooth-surfaced fruits, while the

others (except for a rare new taxon from Peru) have densely pubescent fruits with corrugate surfaces.

In addition to the fruit characters, P. apiculatum differs from another closely-related species, P. fimbriatum, by its acute to obtuse (not cordate to truncate) leaflet base; calyx exceeded by the pubescent (not glabrous) disk; apiculum on the petals much shorter (0.1-0.2 mm long vs. 0.5-0.6 mm in P. fimbriatum); pistillode shorter and provided with locules (not a solid parenchymatous structure); staminodes exceeding the pistil; and hairs on the ovary shorter and appressed (not erect to ascending).

Although there are differential characters which in most cases easily separate P. apiculatum from its relatives, an appreciable number of collections show anomalous and intermediate characters: leaflet acumen very short, broad, and retuse (i.e., N. T. Silva 2944; Daly 1654); fruits sparsely pubescent but not corrugate (i.e., D. Simpson 729); or corrugate and pubescent fruits but acute to obtuse leaflet bases (i.e., Prance et al. 3279), the latter collection considered here to be P. fimbriatum.

One character in this group which needs to be investigated is the type of hair which occurs on the abaxial leaflet surface. Under the dissecting microscope (up to 70X), these strongly resemble the "snail-shaped glands" which have hitherto been regarded as unique to Crepidospermum in the Protieae (see section on generic limits).

3. *Protium plagiocarpium* B  noist, Bull. Soc. Bot. France 66: 359. 1919.

Type. French Guiana: near Charvein, Dec 1913 (fr), B  noist 368
(holotype: P).

Trees, reproductive height 9-21 m; branchlets slender, glabrous or with scattered appressed hairs to 0.1 mm long. Leaves (0) 1-2-jugate, 6-12.6 cm long; petiole semi-terete to slightly canaliculate, usually longer than interjuga, (1.5) 2-3.9 (4.3) cm x 0.7-1.1 mm, glabrous, interjuga 1.8-3.3 cm long; petiolules 1-canaliculate, laterals 0.3-1 cm long, terminal 1.1-3.2 cm long, pulvinuli inconspicuous; leaflets chartaceous, reddish when dry, laterals elliptic or less often (broadly) ovate, base subequal, obtuse to truncate, basal pair (4) 5-9.1 x 1.8-9.2, ultimate pair 5.2-10.3 cm x 2.2-3.4 cm, terminal (broadly) elliptic, base acute, 5.4-9.5 x 2-4.1 cm, leaflet apex abruptly and broadly long-acuminate, acumen 0.5-1.1 cm long; abaxial surface (when dry) with midvein narrowly prominulous, secondary veins slightly prominulous to flat, rest of veins flat to impressed, adaxial surface with all veins impressed, both surfaces glabrous. Inflorescences distributed along branchlets, fasciculate, relatively long and slender, 1-7 cm x 0.4-0.6 mm, 0.4-0.7 times length of subtending leaf, secondary axes poorly developed, 0.5-1.8 cm long, axes glabrous; inflorescence bracts lanceolate, chartaceous, caducous, those subtending inflorescences 0.7-0.9 mm long, those on primary axes 0.4-0.7 mm long, those on secondary axes 0.3-0.6 mm long; pedicel clavate, shorter than flowers, in staminate flowers 1-1.5 x 0.3-0.35 mm, in pistillate flowers 0.8-1 x 0.4-0.5 mm, glabrous or with

scattered ascending hairs to 0.1 mm long at base. Flowers all 4-merous, 1.8-2.2 mm long; calyx shallowly cupular, exceeded by disk in both sexes, 0.5-0.7 x 1.2-1.5 mm, lobes rounded depressed-deltate, apex obtuse, margin papillate; petals yellow, (broadly) ovate, fleshy, slightly cucullate, 1.5-1.7 x 1-1.25 mm, clawed at base, apiculum conspicuous and strongly inflexed, abaxially glabrous or with sparse to scattered, thick, appressed, blunt hairs to 0.05 mm long; in staminate flowers stamens greatly exceeding pistillode, 1-1.2 and 1.1-1.3 mm long, filaments terete, fleshy, 0.75-0.9 and 0.85-1 mm long, anthers apparently dorsifixed, in dorsiventral view ovate with lobulate base and slightly retuse apex, in lateral profile obtuse-oblong to elliptic, 0.25-0.3 mm long, dehiscence latero-introrse; disk 0.25-0.35 x 0.2-0.25 mm, with sparse ascending hairs to 0.15 mm long; pistillode 0.35-0.4 x 0.3-0.4 mm overall, only slightly exceeding disk, sessile, depressed-ovoid, provided with locules and reduced ovules (Mori & Boom 14768) or more often a solid parenchymatous mass, surface with sparse to dense ascending hairs to 0.2 mm long, gradually contracted to a short, rounded, thick stylode 0.1-0.15 x 0.1-0.15 mm; in pistillate flowers staminodes 1 and 1.1 mm long, usually slightly exceeding pistil, filaments slender, terete, 0.75 and 0.85 mm long, anthers dorsifixed, in dorsiventral view lanceolate to ovate, with lobulate base and retuse apex, 0.25 mm long; disk narrow, 0.3-0.35 x 0.1-0.15 mm, with sparse ascending hairs to 0.1 mm long; pistil 0.85 x 0.6 mm overall, broadly ovoid, with dense appressed hairs to 0.2 mm long, gradually contracted to a short thick style 0.3 x 0.3 mm, stigmatal region 0.15 mm high, stigmas lateral, short, +/- triangular, recurved,

microspically spiculate. In fruit inflorescence 3.5-10 cm x 0.7-0.9 (1.3) mm, pedicel subcylindric, 0.8-1.6 x 0.7-1.6 mm, fruit maturing red, stipitate, in dorsiventral view essentially lanceolate, in lateral profile semi-lanceolate, base lobate, with as many lobes as developing pyrenes, apex long-acuminate, 2.1-2.8 x 0.7-1.3 cm (to 1.6 mm diam when more than one pyrene), surface glabrous, smooth, drying wrinkled; pyrene cartilaginous, in dorsiventral view ovate with truncate base and abruptly short-acuminate apex, in lateral profile essentially oblong, with truncate base and acuminate apex, 1.8-2 x 0.8-1.1 cm, glabrous, site of funicle 6/7 distance to apex; cotyledons unknown.

Distribution. French Guiana and Surinam. Protium plagiocarpium is a rare species found as a small understory tree in primary terra firme forest in hilly terrain. It flowers in August to October and fruits in October to March.

Specimens examined. French Guiana: Route de Mana, 9 Feb 1956 (fr), BAFOG 7263 (CAY, NY, U); Route de L'Aracouany, 23 Jan 1957 (sterile), BAFOG 7653 (NY); Saül, Mont La Fumée, 3°37'N, 53°12'W, 12 Sep 1982 (f fl), Boom & Mori 1632 (NY), 12 Oct 1982 (young fr), Boom & Mori 1993 (NY), 12 Oct 1982 (young fr), Boom & Mori 2000 (NY), 25 Oct 1982 (fr), Boom & Mori 2363 (NY); Route de Ste. Elie, 20 Oct 1977 (m fl), Jacquemin 2148 (CAY); Piste de Ste. Elie, 19 Oct 1977 (m fl), Lescure 737 (NY); SW of Sinnamary, piste de Ste. Eli Mar 1980 (fr), Lescure 936 (NY); (without locality), 1864 (sterile), Mélinon s.n. (BM, F); Saül, Mont La Fumée, 3°37'N,

53°12'W, 16 Aug 1982 (m fl), Mori & Boom 14710 (NY), 31 Mar 1983 (fr), Mori & Pipoly 15468 (NY); Cayenne, (without date) (young fr), Poiteau s.n. (W).

Surinam: Sectie O, 2 Mar 1905 (sterile), van Asbeck 4 (U); 8 km ESE of Brownsweeg, 12 Nov 1964 (sterile), van Donselaar 1861 (U); Jodensavanne-Mapanekreek area (Suriname R.), 4 Oct 1953 (sterile), Lindeman 5027 (U); Sipaliwini savanna area on Brazilian frontier, Jan 1970 (sterile), Oldenburger et al. 1186 (U).

Local names and economic uses. French Guiana: sip-i-laānga, sip-i-la (Wayampi). No uses reported.

Protium plagiocarpium bears a strong superficial resemblance to P. aracouchini, but the former is easily distinguished by its broadly and obtusely acuminate leaflets which dry reddish; inflorescence bracts lanceolate (not ovate) and caducous; petals fleshy, slightly cucullate, inflexed, clawed at base, with conspicuous apiculum; filaments markedly fleshy; anthers with latero-introrse dehiscence; pubescent disk which is much narrower in pistillate flowers; stigmas triangular, recurved, and spiculate; and fruit red only, stipitate, basally lobate, and acuminate.

The above characters of the petals, stamens, disk shape, and stigmas, in addition to the usually parenchymatous pistillode, place P. plagiocarpium in or at least very near section Sarcoprotium. The species is distinguished from the members of that section by its lanceolate (not ellipsoid) fruit, apparent absence of 3-merous staminate flowers, pubescent disk, and short stigmas.

4. *Protium polybotryum* (Turczaninow) Engler, Mart. Fl. bras. 12(2): 278. 1874.

Trees, reproductive size 6-26 m x 10-41 cm diam, usually with apparently plagiotropic branches congested toward the crown; trunk often angular; low or no buttresses; bark thin, gray, fine-textured but rough, with raised lenticels, flaky, shed in small irregular plates; branchlets slender to moderately robust, (2) 2.5-3.7 (5) mm in flowering specimens, (1.8) 2.6-4.5 (5.5) mm diam in fruiting specimens, hairs near apex dense, ascending to appressed, of variable length, 0.05-0.35 (0.5) mm long, sparse to scattered on branchlets, usually only the shorter appressed hairs persisting for a time. Leaves (1) 2-5 (6)-jugate, 19-39.3 (56.5) cm long, (to at least 84 cm in sterile specimens, i.e., Gentry 49114); petioles longer than interjuga, slender, (4) 6-10.2 (16.7) cm x (1) 1.5-2.2 (3) mm, terete or less often semi-terete or broadly and shallowly canaliculate, with scattered appressed hairs to 0.05 mm long, sometimes basally with dense erect to ascending hairs to 0.25 mm long, often with exfoliating epidermis (black when dry); interjugae (1.7) 2.3-4.1 (6) cm long, glabrous; petiolules long and slender, 1-canaliculate (rarely 2-canaliculate), laterals (0.3) 0.6-1.5 (2.3) cm long, terminal (1) 1.5-3.9 cm long (to 6.8 cm long in sterile specimens); leaflets coriaceous, elliptic to lanceolate, rarely narrow-lanceolate or oblanceolate, base slightly to strongly oblique, obtuse to acute or truncate, basal pair shorter and more ovate than the rest, (6) 7.4-11 (13.5) x (1.9) 2.3-3.5 (6.2) cm, ultimate pair (7.7) 8.5-14 (15.3) x (2)

2.7-3.8 (5.4) cm (laterals reaching 20 x 6 cm in sterile specimens), terminal (7) 9.8-11.1 (15.3) x (2.1) 2.8-4.3 (5.6) cm, apex long-acuminate often abruptly so, acumen (5) 8-12 (18) mm long, abaxial surface with midvein acutely prominent, secondary veins prominulous or inconspicuous, rest of veins inconspicuous, veins pallid when dry, blade glabrous or midvein with scattered appressed hairs to 0.1 mm long, adaxial surface with midvein obtusely prominulous but sunk in a groove, rest of veins flat or impressed when dry, secondary veins pallid. Inflorescences congested near the apex, long and slender but rarely much reduced, (4) 7-20 (24) cm x (0.6) 0.7-1.8 mm, 0.3-0.8 times length of subtending leaf, stouter and shorter in fruit, (1.5) 5.5-9.8 (16) cm x (1) 1.2-2.3 (2.7) mm, secondary axes usually well-developed, 0.5-11.1 (15.2) cm long, axes compressed, usually terete only near the base, with sparse to scattered or dense ascending (rarely suberect) hairs to 0.3 mm long; inflorescence bracts (narrow-) lanceolate, those subtending inflorescences fleshy, (0.9) 1.25-2.5 (3.5) mm long, those on primary axes 0.5-1.1 (1.5) mm long, those on secondary axes (0.2) 0.3-0.6 (0.75), bracts and base of pedicels with dense ascending hairs 0.05-0.15 (0.2) mm long; pedicel terete, 0.4-2.2 (3) x 0.2-0.35 (0.5) mm, thickened in fruit, (0.7) 1-2.2 (2.6) x 1.3-2 (3) mm, with dense erect to ascending hairs to 0.15 mm long, otherwise with sparse to scattered, ascending to appressed hairs to 0.15 mm long. Flowers 3-4-merous, (1.2) 1.3-2 (2.6) mm long at anthesis; calyx deeply cupular, (0.3) 0.4-0.6 (0.7) x (0.7) 1-1.35 (1.8) mm, with hairs as on pedicel except (sub-)glabrous distally, lobes depressed-deltate, apex acute to acuminate to slightly apiculate, not papillate, 0.1-0.3 (0.5) mm; petals

fleshy, slightly cucullate, ovate to broadly oblong, (1.25) 1.5-1.85 (2.2) mm, moderately reflexed at anthesis, apex obtuse to acute, (0.15) 0.2-0.25 (0.35) mm thick at midpoint, apiculum strongly inflexed, (0.2) 0.35-0.5 mm long, base clawed, (0.25) 0.35-0.5 (0.65) mm wide, abaxially sometimes rugose when dry, with hairs dense to scattered or sparse, ascending to appressed hairs to 0.15 mm long, denser and to 0.25 mm long near the apex, rarely glabrous, also often with scattered appressed blunt hairs to 0.05 mm long, adaxial surface and margin and apiculum long-papillate; in staminate flowers calyx occasionally reaching top of disk with stamens six or eight (when sepals and petals three and four, respectively, (0.7) 0.9-1.1 and (0.9) 1.05-1.2 mm long, filaments subcylindric, markedly fleshy, papillate, (0.4) 0.5-0.6 (0.7) mm long, anthers dorsifixed, in dorsiventral view oblong with markedly retuse apex, in lateral profile elliptic, base lobate, (0.2) 0.4-0.5 mm long; disk tall and narrow, undulate, deeply sulcate, 0.2-0.5 (0.6) mm x 0.05-0.3 mm; pistillode slightly to markedly exceeding disk, columnar, sometimes dilate at both ends or less often spindle-shaped, (0.3) 0.5-0.8 (0.95) x 0.1-0.25 (0.5) mm overall, solid and parenchymatous, lacking locules and reduced ovules, with dense ascending hairs 0.1-0.15 mm long, or sometimes glabrous; apex 3- or 4-sulcate depending on number of flower parts; in pistillate flowers calyx exceeded by disk; staminodes 8 (3-merous pistillate flowers very rare), 0.8-1.2 (1.3) and 1.05-1.4 mm long, exceeding pistil or less often only level with base of the style, filaments thin, somewhat fleshy, compressed-columnar, 0.5-0.6 and (0.65) 0.8-0.9 mm long, otherwise 0.8-1 mm (var. blackii), anthers dorsifixed, in dorsiventral view broadly

lanceolate, apex slightly retuse, in lateral profile narrowly elliptic, 0.3-0.4 (0.5) mm long; disk taller than in staminate flowers and very narrow, 0.35-0.55 x 0.05-0.1 (0.15) mm; pistil (0.7) 0.75-1.35 (2) x 0.4-0.85 (1) mm overall, ovary ovoid to rarely globose or slightly obovoid, sessile, with dense ascending hairs 0.1-0.25 mm long, ovary contracted to a short thick style 0.15-0.25 mm long, stigmatal region 0.1-0.25 high, stigmas lateral, subglobose, abruptly contracted at apex in recurved or sigmoid, smooth or microscopically spiculate caudicules, 0.1-0.15 mm long. Immature fruits stipitate, spindle-shaped, glabrescent, mature fruits sessile, ellipsoid to compressed-ellipsoid, (1.8) 2.3-2.6 (3.2) x (1.2) 1.4-1.6 (2) cm, apex slightly apiculate due to persistence of the only slightly excentric style; pyrene glabrous, bony, in dorsiventral view essentially oblong, sometimes slightly obovate, base truncate to slightly retuse, apex rounded to broadly acute, in lateral profile slightly asymmetric, (broadly) elliptic, slightly acuminate, so pyrene is slightly concave dorsally and ventrally, 1.6-1.7 x 1-1.1 cm, site of funicle subapical, funicular depression shallow, funicular scar rounded-deltate, covering 1/6 ventral face; testa with irregular thickenings, infolded with lobed, contortuplicate cotyledons.

Distribution. As defined here, P. polybotryum is widespread in Amazonia and the Guianas. It is known from French Guiana, Surinam, and Venezuela, and in Brazil from northern and southern Pará, Amapá, Amazonas, Mato Grosso, and Rondônia.

Protium polybotryum, while primarily a terra firme species on undulating terrain, is ecologically rather versatile, occurring in terra

firme forest on clay soil, savanna forest (Rio Cuieras), igapó (near Belém), terra firme forest-savanna transition on humus sand with clay; on hilltops and slopes; or in low-lying areas.

The species of section Sarcoprotium are in some instances not easily separable, especially in fruit. Two related species, P. macrocarpum Cuatrec. and P. pedicellatum Swart, are known only in fruit. The latter is remarkable only for its glossy leaflets, and may prove to be a taxonomic synonym of P. crassipetalum Cuatrec. Protium polybotryum has smaller fruits than P. macrocarpum. In flower, P. polybotryum is distinguishable from P. carnosum A. C. Sm. and P. crassipetalum Cuatrec. by its much smaller flowers with notably less fleshy petals. From P. crassipetalum it is further distinguished by its shorter pedicel, and from P. carnosum by its obtuse to rounded (not acuminate) petals; leaflets less coriaceous; leaflet bases obtuse to truncate (not acute); pedicels after anthesis terete (not compressed) and straight or pendent (not rigidly recurved); and more slender branchlets, petiolules, inflorescences axis, and pedicel.

Protium polybotryum is subdivided here into two subspecies, which are distinguished in the following key:

Key to subspecies of Protium polybotryum

1. Leaflet base usually truncate; pedicel short, 0.4-0.6 (0.8) mm long in flower, (0.7) 1-1.5 (2) mm in fruit; abaxial hairs on petals dense, ascending, 0.1-0.2 (0.25) mm long. Surinam, French Guiana, Amapá, northern Pará. ssp. polybotryum
1. Leaflet base usually obtuse; pedicel longer, (1) 1.2-2.2 (3) mm long in flower, (1.3) 1.6-2.2 (2.6) mm in fruit; abaxial hairs on petals sparse to scattered, appressed, 0.05-0.15 mm long. Central and southern Pará, Amazonas, Mato Grosso, Rondônia. ssp. blackii

4a. Protium polybotryum (Turcz.) Engl. ssp. polybotryum Type. Surinam (without locality), 1843 (m fl), Hostmann & Kappler 1268 (lectotype (designated by Swart, 1942b): U; isoelectotypes: F, G (2), GH, K, NY, OXF, US, W).

Icica polybotrya Turcz., Bull. Soc. Imp. Naturalistes Moscou 31(1): 473.

1858. Tingulunga polybotrya (Turcz.) Kuntze, Rev. Gen. Pl. 1: 108.
1891.

Protium divaricatum Engl. var. trijugum Swart, Acta Bot. Neerl. 15: 47.

1966. Type. Brazil. Amazonas: Tefé, 24 Sep 1947 (m fl), Black 47-1507
(holotype: IAN)

Leaflet base usually truncate; pedicel short, 0.4-0.6 (0.8) mm long in flower, (0.7) 1-1.5 (2) mm in fruit; petals usually fleshy, abaxial hairs

on petals dense, ascending, 1-1.5 mm long.

Distribution. Surinam, French Guiana, northern Pará. Flowering from (May) August to October (December) and fruiting from November to June. This subspecies usually occurs as a medium-size canopy or understory tree in primary moist terra firme forest on clay soils, but it has also been collected at riversides (Rabelo 2178, Fr. Gui. For. Svc. 6249), secondary forest (van Donselaar 1420), "savanna forest" (Elburg 9814), and in transition from rain forest to high savanna forest (Schulz 8943).

Specimens examined. BRAZIL. Amapá: Alto Rio Maracá, margin of black-water river, 14 May 1983 (fr), Rabelo et al. 2178 (HAMAB, NY). Maranhão: basin of Rio Turaçu, Municip. Monção, Ka'apor Indian reserve, 4 km NW of settlement of Urutawy, 30 Jan 1985 (fr), Balée & Ribeiro 98 (NY), 15 Apr 1985 (fr), Balée & Ribeiro 503 (NY). Pará: Tucuruí, PA-149, right side, 18 Oct 1983 (f fl), Lima & Silva 44 (NY); Tomé Açu, going toward fazenda Borba Gato, 4 km from fazenda Curimã, 29 Dec 1972 (fr), Nascimento 346 (MG, NY, US); Rio Jarí, Serra de Monte Dourado, 3 km from margin, 16 Nov 1967 (fr), Oliveira 3547 (IAN, NY); Rio Jarí, Planalto de Monte Dourado, 16 Jun 1968 (fr), Oliveira 4546 (NY); Belém-Brasília highway, km 100, 14 Aug 1964 (m fl), Prance & Silva 58728 (NY); Rio Jarí, Monte Dourado, Planalto A, 17 Sep 1968 (m fl), N. T. Silva 1002 (K, NY, US); 17 Sep 1968 (f fl), N. T. Silva 1021 (IAN, K, NY, US); Rio Jarí, road between Monte Dourado and Munguba, 5 Dec 1968 (fr), N. T. Silva 1501 (K, MO, NY(2), US). FRENCH GUIANA: Crique Serpent, going upstream on Dégrad Vally, left bank (Maroni), 25 Mar 1953 (fr), BAFOG No. 6249 (CAY); Route de l'Acarouany, km 1,970, right side, 20 Mar 1956 (fr), BAFOG No. 7390 (NY).

Surinam: Watramiri Forest Reserve, Section 0, (without date) (young fr), BW (Bureau v. h. Boswezen) 1135 (GH, NY); Zanderij I, 6 Oct 1915 (sterile), BW 1208 (U); Watramiri Forest Reserve, Section 0, 6 May 1916 (fr), BW 1817 (U), 24 May 1916 (sterile), BW 1859 (U); Brownsberg Forest Reserve, 9 Sep 1917 (buds), BW 3229 (BR, NY, WIS); Watramiri Forest Reserve, Section 0, 31 Oct 1917 (fr), BW 3364 (BR, NY); Raleighvallen, Coppename R., 29 Jul 1923 (buds), BW 6176 (IAN); Vkosberg, Coronie, 23 Jan 1947 (fr), D. Burger 12 (U); 1.5 km W of Gansee, 27 May 1964 (sterile), van Donselaar 1420 (U); Mapane Creek area, 9 Dec 1963 (m fl), Elburg (L. B. B. no.) 9814 (NY, VEN); Nickerie District, area of Kabalebo Dam project, 2 km S of road camp, ca. 20 km SW of Avanavero dam site, 13 Nov 1976 (young fr), N. M. Heyde & Lindeman 40 (NY); Fallawatra, 6 Nov 1971 (f fl), Jimenez-Saa 1562 (U); Raleighvallen/ Voltzberg Nature Reserve, 11 Sep 1976 (f fl), de Jong & Holthuyzen 15777 (NY); foot of Voltzberg, 20 Sep 1933 (fr), Lanjouw 905 (MO); forest along Rijsdijk road, Lelydorp Project, 23 Apr 1954 (sterile), J. Lindeman 5757 (U); 50 m W of Winannakreek base camp, Corantijn R., 15 Apr 1965 (sterile), Maas & Tawjoeran (LBB no.) 100723 (U); Raleighvallen-Voltzberg Nature Reserve on the Coppename River, 145 km S of Paramaribo, 21 Nov 1976 (fr), Mori & Bolten 8674 (NY); Kabo, Oct 1978 (fr), Procter 4750 (NY); Raleighvallen-Voltzberg, Aug 1971 9m fl), Roberts (LBB no.) 14045 (U); Mapane Territory, camp 8, 17 Feb 1969 (fr), Sabajo & Roberts (LBB no.) 12411 (U); Jodensavanne-Mapane Creek area, 21 Jan 1956 (fr), Schulz 7547 (U); Jodensavanne-Mapane Creek area (Suriname R.), along road at km 15, 9 May 1961 (m buds), Schulz 8943 (GH, US); Zanderij I, Sep 1942 (buds), Stahel 11 (B, GH, IAN, WIS).

Protium divaricatum var. trijugum possesses all the characters associated with section Sarcoprotium. While the type (Black 47-1507) shows a very pubescent inflorescence with somewhat erect hairs, relatively large leaflets, the base of the inflorescence is subglabrescent and all its characters fall within the range of variation of P. polybotryum ssp. polybotryum.

Local names and uses. Brazil. Amapá: breu; Maranhão: akakandei'y, kandeiape'y (Ka'apor, Balée & Ribeiro 98, 503). Pará: breu branco. French Guiana: wet-sali, encens blanc, moni (Paramaka). Suriname: joriebolli bolero (Arawak), joelliballi beleroe (Arawak), ajawabali (Arawak), Peraka (Carib), tamoene poeleka (Carib), rode bast tingimoni. In Maranhão, the Ka'apor inhale the resin for sinusitis (Balée & Ribeiro 503).

4b. Protium polybotryum (Turcz.) Engl. ssp. blackii (Swart) Daly
(submitted for publication in Brittonia).

Protium polybotryum (Turcz.) Engl. var. blackii Swart. Type. Brazil. Pará: Belém, IAN, Mocambo, 22 Jul 1949 (f fl), Black 49-8085 (holotype: IAN; isotypes: GH, NY).

Protium rubrum Cuatrec., Webbia 12(2): 404. 1957. Type. Colombia.

Amazonas: Río Apaporís, Soratama (above the mouth of río Cananarí),
Schultes & Cabrera 19833 (holotype, US; isotype, NY).

Leaflet base usually obtuse; pedicel relatively long, (1) 1.2-2.2 (3) mm long in flower, (1.3) 1.6-2.2 (2.6) mm in fruit; petals usually

membranous, abaxial hairs on petals sparse to scattered, appressed, 0.05-0.1 mm long.

Distribution. Southern Pará, Amazonas, Rondônia, Mato Grosso. This taxon, like the type subspecies, is a medium-size canopy or understory tree of terra firme forest on clay soils, though there is one collection from igapô vegetation (Pires 7109). This subspecies flowers from June to October (January) and fruits from July to November.

Specimens examined. Brazil. Amapá: Municip. Macapá, road from Cupixi to Vila Nova, 18 km SSW of Cupixi, ca. 0°32'N, 51°42'W, 5 Jan 1985 (m fl), Rabelo et al. 3204 (HAMAB, NY). Pará: Belém, EMBRAPA, Mocambo Reserve, ca. 1°23' S, 48°27' W, 10-17 Nov 1984 (fr), Daly et al. 3756 (IAN, NY), 10-17 Nov 1984 (m fl), Daly et al. 3761 (IAN, NY), 10-17 Nov 1984 (fr), Daly et al. 3768 (IAN, NY); 8 Jan 1985 (m fl), Daly et al. 4059 (IAN, NY); Belém-Brasília highway km 98, 6 Aug 1963 (young fr), Maguire et al. 56034 (NY); Ilha do Mosqueiro, 13 Apr 1971 (sterile), Oliveira 5650 (IAN); Belém, Utinga, 29 Nov 1945 (fr), Pires & Black 662 (US); Colonia 3 Outubro, between km 100 of road to Bragança and Rio Guamã, 23 Aug 1952 (m fl), Pires et al. 4120 (IAN, NY); forest of Cia. Pirelli, Fazenda Uriboça, Jun 1958 (buds), Pires 6794 (US), Aug 1958 (buds), Pires 7109 (US); Belém, IPEAN, Mocambo Reserve, 20 Jul 1966 (fr), Pires & Silva 10292 (IAN, NY), 7 Oct 1966 (buds), Pires & Silva 10293 (IAN), 19 Jul 1967 (galled fl), Pires & Silva 10616 (NY), 18 Jul 1967 (m fl), Pires & Silva 10617 (NY), 20 Jul 1967 (galled fl) Pires & Silva 10619 (IAN, NY), 1 Sep 1967 (m fl), Pires & Silva 10804 (IAN), 5 Feb 1968 (fr), Pires & Silva 11575 (IAN), 27 Jul 1971 (aborted fr), Pires 12195 (IAN); Jari, road between Planalto A and

Tinguelim, km 16, 11 Jul 1969 (f fl), N. T. Silva 2395 (IAN, NY); Rio Tajapuru, km 4 of Gurupá road, 9 Feb 1979 (NY).

Local names and uses. Brazil. Pará: breu.

Protium polybotryum (Turcz.) Engl. var. robustum Swart appears to be a taxonomic synonym of P. crassipetalum Cuatrec. The type collection (Br. Gui. For. Rec. No. 3140) has immature with long pedicels (4.5-6 mm long), which falls in the range shown by the latter species. Another collection from Guyana (Mori et al. 8122) with staminate flowers may also belong to P. crassipetalum, as might one collection from Surinam (Lindeman & de Roon 745). Further material from the localities of these collections is needed to confirm these identifications.

The species of section Sarcoprotium are difficult to separate in fruit. Exhaustive measurement of all the material at hand has shown that the type of P. polybotryum ssp. blackii (Black 49-8085) and other collections from that population match well with the type of P. rubrum and specimens from various parts of the Rio Negro system. The type at first appears glabrous, but discrete portions of the inflorescences show the same pubescence type and length as ssp. blackii. The inflorescences of all species of section Sarcoprotium are glabrescent to varying degrees as the fruits develop. Still, P. rubrum is known only from fruiting collections, so final judgment on this possible synonymy will have to await flowering material from this region.

The characters separating the two varieties are not striking but they are consistent (see Table XVI). The geographical component is compelling but not unambiguous. Anomalous collections of ssp. polybotryum are found

from Tucuruí (Lima & A. Silva 44) and Tomé Açu (Nascimento 346) in north-central Pará, and from the Rio Uatunã (Cid et al. 729) in eastern Amazonas. Unexpected distributions for ssp. blackii are 18 km SSW of Cupixi in Amapá (Rabelo et al. 3204) and in the Jari region near Tinguelim in NW Pará (N. T. Silva 2395).

The distributions of the two varieties apparently overlap in at least three regions. One flowering collection of ssp. polybotryum is from km 100 of the Belém-Brasília highway in central Pará (Maguire et al. 56034), and a collection with young fruits of ssp. blackii was made near km 98 (Prance & Silva 58728). In the Jarí region of Pará, N. T. Silva 2395 is the only collection of ssp. blackii among several of the typical subspecies (i.e., N. T. Silva 1002, 1021). Recently, flowering collections of both varieties have been made near Manaus during inventories on the reserves of the World Wildlife Fund-U.S. It should be noted that the subspecies are more difficult to distinguish in fruit.

The overall distributions for the two subspecies do not fit Prance's (1977) phytogeographic subdivisions of Amazonia. However, all collections of ssp. polybotryum appear to be from forests on either the Guiana or Brazilian Shield and those of ssp. blackii from forests in the Amazon Valley-- that is, on Quaternary and Tertiary sediments-- or in the Rio Negro system. Further collections from the borderline areas noted above are needed to confirm this hypothesis.

Table XVI

Characters separating the subspecies of Protium polybotryum

character	ssp. polybotryum	ssp. blackii
distribution (see discussion)	Suriname, French Guiana, northern Pará	southern Pará, Amazonas, Rondônia, Mato Grosso
pedicel (flowers)	0.4-0.6 (0.8) x 0.2-0.35 mm	(1) 1.2-2.2 (3) x 0.2-0.35 (0.5) mm
(fruits)	(0.7) 1-1.5 (2) x 1.1-2 mm	(1.3) 1.6-2.2 (2.6) x 1.3-2 (3) mm
hairs on petals	dense, ascending, 0.1-0.2 (0.25) mm	sparse/scattered, appressed, 0.05-0.15 mm
staminodes	0.8-0.9 and 1.05-1.2 mm	1-1.2 and (1.15) 1.25-1.4 mm
disk (staminate)	0.25-0.35 (0.4) x 0.05-0.15 (0.25) mm	(0.2) 0.3-0.5 (0.6) x (0.05) 0.1-0.0.3 mm
(pistillate)	0.35-0.45 (0.5) x 0.05-0.1 (0.15) mm	0.4-0.55 x 0.05-0.1 (0.15) mm
pistillode	0.6-0.8 (0.95) x 0.1-0.25 (0.5) mm	0.3-0.6 (0.8) x 0.15-0.25 (0.35) mm
pistil	(0.7-0.9 (1) x 0.4-0.55	0.9-1.35 (2) x (0.65) 0.75-0.85 (1) mm

5. *Protium robustum* (Swart) Porter, Ann. Missouri Bot. Gard. 56: 476.
1970.

Protium neglectum var. *robustum* Swart, Rec. Trav. Bot. Néerl. 39: 204.

1942. Type. Surinam: Surinam River by Goddo, Jan 1939 (f fl and fr),
Stahel 144 (holotype: U).

Protium neglectum var. *robustum* f. *intermedium* Swart, A monograph of the
genus *Protium* and some allied genera (Burseraceae): 384. 1942. Type.
Surinam: Saramacca River, sectie 0, 12 Jan 1917 (m fl), BW 2597
(holotype: U).

Trees, reproductive height 5-15 (25) m; white latex reported in some cases; branchlets robust, (5) 7-12 mm diam, with dense appressed flexuous hairs to 0.3 mm long. Leaves 3-5-jugate, 68-110 cm long; petiole canaliculate, often narrowly and deeply so, rarely semi-terete, rarely slightly acutely winged, much longer than interjuga, (15.4) 25-45 cm x 4.9-7.6 mm, with hairs as on branchlets but usually glabrescent; interjuga 5.2-12.6 cm long; petiolules +/- terete, relatively long and thick, laterals (0.8) 1.4-3.4 cm long, terminal 5-9.6 cm long, pulvinuli inconspicuous or somewhat conspicuous; leaflets coriaceous to chartaceous, usually drying green, laterals oblong to broadly elliptic, rarely broadly lanceolate, base slightly revolute, oblique, proximal side truncate to slightly cordate, distal side acute to truncate (rarely cordate), basal pair (19.2) 28-50 x (7.9) 11.8-19.8 cm, ultimate pair 26-50 x 9.6-15.1 (19.2) cm; terminal obovate to broadly elliptic, base obtuse to truncate, 24-31.8 x 10.3-12.8 (14.2) cm, leaflet apex abruptly and narrowly

long-acuminate, acumen 1-3.5 cm long; veins discolorous, abaxial surface with midvein and secondary veins obtusely prominent, rest of veins prominulous, midvein with scattered appressed hairs to 0.2 mm long, rest of surface glabrous; adaxial surface with midvein obtusely prominent but sunk in a groove, rest of veins prominulous, surface glabrous.

Inflorescences distributed along branchlets, pseudospicate, robust, dimorphic, staminate inflorescences 12-21 cm x 2.6-3.5 mm, secondary axes 3-5.7 (16) cm long, pistillate inflorescences 5-7.2 cm x 2.4-3.9 (5) mm, secondary axes to 1-1.8 cm long, no inflorescences exceeding 0.15 times length of subtending leaf, axes with hairs as on branchlets; inflorescence bracts fleshy, broadly ovate, those on primary axes 0.7-2 mm long, those on secondary axes 0.3-1.7 mm long. Flowers sessile, all 5-merous, staminate flowers at anthesis 1.8-2.4 mm long; calyx deeply cupular, exceeding the disk, (0.9) 1.1-1.7 x 1.3-1.8 mm, hairs as on branchlets, lobes triangular with acute apex, 0.4-0.7 mm long; petals pale green to white or cream, membranous, linear or slightly lanceolate or oblanceolate, sometimes carinate, 2.4-2.9 x 0.7-1.1 mm, glabrous adaxially, margin short-papillate, strongly reflexed at anthesis; two series of stamens markedly unequal, 1.9-2.7 and 2.3-3.7 mm long, antesealous series exserted, filaments slender, terete, 1.3-2.2 and 1.8-3.3 mm long, anthers basifixed, often thecae apparently completely separated by connective, in dorsiventral view lanceolate to obtuse-oblong, with lobulate base and retuse apex, in lateral profile obliquely and broadly obtuse-oblong, with retuse apex, 0.4-0.5 (0.6) mm long; ovariodisk usually essentially flat, 0.25-0.6 x 0.75-1 mm, with dense flexuous hairs to 0.4 mm long; pistillate flowers 2.2-3 mm long at anthesis; calyx 1-1.7 x 1.5-2 mm, lobes 0.5-0.7

mm long; staminodes 5 (antepetalous series lacking), reaching stigmas, 1.5-2 mm long, filaments slender, +/- terete, 1.2-1.7 mm long, anthers in dorsiventral view ovate to broadly elliptic, with truncate base and retuse apex, in lateral profile narrow-elliptic, sometimes apex recurved, 0.3-0.35 mm long; disk narrow, (0.2) 0.3-0.4 x 0.1-0.15 mm, with dense erect hairs to 0.25 mm long; pistil 1.7-2.1 x 0.8-1 mm overall, ovary substipitate, ovoid, with dense ascending flexuous hairs to 0.25 mm long, gradually contracted to a thick style 0.4-0.65 (0.8) x 0.35-0.6 mm, stigmatal region 0.3-0.4 mm high, stigmas sessile, lateral, conspicuous, globose, papillate. In fruit inflorescence 3-6.2 cm x 4-4.4 mm, fruit maturing red, sessile, markedly oblique-ovoid, gibbous, ventricose, 2-2.2 x 0.9-1.3 cm (to 2.2 cm diam when more than one pyrene), apex almost perpendicular to axis, apex acute, surface glabrous, smooth, drying wrinkled; pyrene glabrous, thickly cartilaginous to bony, in dorsiventral view broadly elliptic to slightly ovate, base obtuse, apex slightly acuminate, in lateral profile elliptic to lanceolate, 1.6-1.7 x 0.9-1 cm, funicular depression shallow, site of funicle slightly below middle, funicular scar rounded-deltate to almost orbicular, covering 1/3-1/2 ventral face; cotyledons entire, first convexly curved, then concavely curved (in cross-section forming two nested double-sigmoid curves), such that cotyledons are marginally involute and have a vertical dorsal sulcus.

Distribution. Widespread in Amazonia and the Guianas. Protium robustum is a small to medium-sized tree of primary terra firme forests. It is often found on slopes, but it occurs on a variety of soils. The species is only rarely found in secondary forests or in waterlogged conditions. In eastern Amazonia and the Guianas it flowers from July to December and

fruits from October to May.

Specimens examined. Brazil. Amapá: Municip. Mazagã, BR-156, road which will connect Macapá with Monte Dourado, 81 km WSW of Macapá, 11 km SW of Rio Preto, 0°08'S, 51°48'W, 20 Dec 1984 (fr), Mori & Cardoso 17462 (HAMAB, NY), 20 Dec 1984 (fr), Mori & Cardoso 17470 (HAMAB, NY), 20 Dec 1984 (fr), Rabelo et al. 3044 (HAMAB, NY). Pará: Transamazon Highway, Altamira-Itaituba, km 23, EMBRAPA experimental station, 14 Aug 1978 (m fl), Bahia 28 (F, MG, NY); Santarém, end of road to Cachoeira do Palhão on Rio Curuá Una, 5 Dec 1966 (young fr), Cavalcante & Silva 1590 (MG); Municip. Oriximiná, Rio Trombetas, left bank of Lago Erepecu, 16 Jul 1980 (m fl), Cid et al. 1538 (INPA, MG, NY), left bank of Lago Muçura, 30 km from Porto Trombetas, 23 July 1980 (buds), Cid et al. 1752 (INPA, MG, NY); Boa Vista, Rio Tapajós, 1931 (m fl), da Costa 58 (F); Aramaná Plateau, Jan 1932 (sterile), da Costa 287 (F, US); Igarapé Cagancho, 1 km E of Tucurui dam, approx. 3°50'S, 49°37'W, 29 Oct 1981 (f fl and young fr), Daly et al. 1039 (MG, NY); 18 km from Tucurui, 16 km S on BR 422, then 2 km W on old logging road, approx. 3°53'S, 49°41'W, 1 Nov 1981 (m fl and fr), Daly et al. 1166 (MG, NY); 20 km from Tucurui, 12 km S on old BR-422, 8 km SSW on new BR-422, then 1 km W on logging road, approx 3°54'S, 49°42'W, 7 Nov 1981 (m fl), Daly et al. 1252 (INPA, MG, NY); Almeirim, 9 Dec 1902 (buds), Ducke 3036 (MG); Rio Branco do Obidos, (without date) (fr), Ducke 11427 (RB); Rio Cuminá-Mirim, Castanhal de Pedras, 12 Oct 1913 (m fl), Ducke 14970 (MG); Rio Tapajós, 30 Sep 1922 (m fl), Ducke 18406 (NY); Rio Curuá Una, Oct 1954 (m fl), Frões 31325 (IAN, U, US); Municip. Porto de Moz, Rio Xingu, across from Souzel, 18 Nov 1955 (fr), Frões 32404 (U); upper Cupari River, plateau between Xingu and Tapajós rivers, Sep

1931 (m fl), Krukoff 1126 (BM, NY); Tukurui, km 13 of Transamazon Highway, 11 Nov 1980 (fr), Lisboa et al. 1554 (MG, NY); Rio Jarí, road from Monte Dourado to Caracurú, 12 Nov 1967 (buds), Oliveira 3733 (NY); rios Pacajá and Muirapiranga, 2°33'-2°50'S, 50°38'-50°50'W, 5 Oct 1965 (m fl), Prance et al. 1542 (C, K, MO, NY, US); Transamazon Highway, 5-10 km W of Ruropolis, Presidente Medici towards Itaituba, 29 Nov 1977 (m fl), Prance 25864 (NY), 29 Nov 1977 (fr), Prance et al. 25880 (NY); Basin of Rio Xingu, Gleba Bacajá, just below mouth of Rio Bacajá, 3°22'S, 50°47'W, 23 Nov 1980 (fr), Prance et al. 26409 (NY); Nov-Dec 1980 (sterile), Prance et al. 26959 (NY); Santarém, km 35 of road to Palhão, 31 Aug 1969 (m fl), M. G. Silva 2454 (F, K, MG, MO, NY); Altamira, km 23 of Transamazon Highway, Experimental Center of EMBRAPA, 21 Oct 1977 (fr), M. G. Silva 3462 (MG, NY); Monte Dourado, Planalto A, 9 Sep 1968 (m fl), N. T. Silva 1152 (NY); Rio Jarí, Pico do Igarapé Pacanarí, 11 Jan 1969 (fr), N. T. Silva 1606 (IAN, NY); Jarí region, road to Munguba, km 15, 21 May 1970 (frt), N. T. Silva 3153 (IAN); Portel, 26 Oct 1955 (m fl), L. O. Williams 18244 (IAN).

French Guiana: Route de Mana, 2 Feb 1956 (fr), BAFOG 7274 (NY); Tumuc Humac, frontier with Surinam, top of Kassabatiki, 6 Sep 1972 (buds), de Granville 1497 (CAY); Upper Oyapock, 18 Mar 1975 (fr), de Granville B-5237 (CAY); confluence of the Tampoc and Crique Alice, 2 Apr 1977 (fr), Moretti 683 (CAY); Rivière Camopi, roche José, 7 Dec 1967 (sterile), Oldeman 2581 (NY); Mont Gauthiot, left bank of the Yaroupi, 20 Apr 1970 (fr), Oldeman B-3044 (CAY, NY); Plateau de la Douane (beginning of Tracé Saül-Carbet-Maï's), 29 Jan 1971 (sterile), Oldeman 3211 (CAY).

Surinam: Sectie 0, 20 Feb 1918 (fr), BW 3655 (BR, GH); Tapanakoni

River, 12 Nov 1918 (m fl), BW 4131 (BR, GH, US); Sectie 0, 18 Dec 1919 (fr), BW 4519 (BM, NY), 19 Feb 1923 (fr), BW 6105 (NY); district Brokopondo, between Aboutjeman and Adjama, along Sara Creek, 12 Mar 1964 (sterile), van Donselaar 1007 (U); 1.5 km W of Gansee, 27 May 1964 (sterile), van Donselaar 1416 (U); Boven-Tapanahony, Awalapê-kreek, Jan-Feb 1961 (sterile), Elburg LBB 8889 (U); Jodensavanne-Mapanekreek area, 2 Mar 1963 (sterile), Elburg LBB 9422a (U); Zuid River, 3°30'N, 56°49'W-3°10'N, 56°29'W, 3 km above confluence with Luci River, 20 Sep 1963 (m fl), Irwin et al. 55888 (B, MICH, NY); Jodensavanne-Mapane Kreek (Surinam R.), 25 Mar 1953 (sterile), Lindeman 3573 (U); Maratakka R.-Snake Creek, 21 May 1965 (sterile), Maas & Tawjoeran LBB 10842 (U); Sipaliwini savanna area on Brazilian border, near S headwater of Sipaliwini River, 22 Jan 1970 (sterile), Oldenburger et al. 1106 (U); Wayombo River, E of Donderkreek, 23 Sep 1955 (sterile), Schulz 7369 (U); Saramacca River, W of Poika forest, 5 May 1956 (sterile), Schulz 7634 (U); Sectie 0, Nov 1944 (m fl), Stahel 262 (B, GH, NY, U); Upper Suriname River, 1 Sep 1908 (buds), Tresling 397 (U).

Ironically, although P. robustum was originally published as a variety of another species, it is the most distinct species in section Icicopsis, even on the basis of pollen morphology (see chapter on pollen). It can be distinguished from P. sagotianum and P. tenuifolium by its more robust branchlets; larger leaves and leaflets (possibly the largest in the genus); stamens exserted; ovariodisk usually flat; stigmas large and globose; fruit with apex almost perpendicular to the axis; and cotyledons only transversely folded (not basally incurved as well).

6. *Protium tenuifolium* (Engler) Engler in DC. Mon. Phan. 4: 76. 1883.

Icicopsis tenuifolia Engl. in Mart. Fl. bras. 12(2): 255. 1874. Type.

Peru. Loreto: near Tarapoto, 1855-1856 (m fl), Spruce 4194 (lectotype (designated by Swart, 1942b): BR; isoelectotypes: BM, K). *Tingulunga tenuifolia* (Engl.) Kuntze, Rev. Gen. Pl. 1: 108. 1891.

Protium neglectum Swart, Rec. Trav. Bot. Néerl. 39: 203. 1942. Type.

Surinam: Corantyne River, Kaboeri, Jul 1922 (m fl), BW 5920 (holotype: U; isotype: MO).

Trees, reproductive height (5) 10-34 m; often with simple or branched, spreading plank buttresses to 140 cm high; bark thin, pitted, somewhat fissured, shed in small plates, resin reported white; branchlets robust, 1.9-4.4 mm diam, with scattered (rarely sparse) thick, blunt, appressed or twisted hairs to 0.1 mm long. Leaves 2-4 (5)-jugate, (12.7) 17.5-36.2 (53) cm long; petiole semi-terete to slightly canaliculate, often slightly acutely winged, longer than interjuga, (2.2) 4.2-10.4 (13) cm x 1.5-2.6 (3.9) mm, with hairs as on branchlets; petiolules terete or shallowly 1-canaliculate, robust, laterals 0.4-1.4 (1.9) mm long, terminal 1.1-2.3 (3.4) mm long, pulvinulus conspicuous; leaflets coriaceous or less often chartaceous, laterals with oblique base, proximal side obtuse, distal side truncate, basal pair oblong to broadly elliptic, 5.1-16 x 2.3-4.8 (7) cm, ultimate pair 7-17.5 x 3-5.9 cm, terminal broadly elliptic with obtuse base, 6.8-14 x 2.8-5.7 cm, leaflet apex gradually and broadly short-acuminate, acumen 0.3-1.1 cm long, abaxial surface with midvein and

secondary veins obtusely prominent, rest of veins prominulous, surface with scattered hairs as on branchlets, adaxial surface with midvein prominulous but sunk in a groove, rest of veins prominulous, surface glabrous or with scattered hairs as on branchlets. Inflorescences arranged along branchlets, pseudospicate, robust or less often slender, occasionally exceeding petiole, 4.5-17.8 cm x 0.8-2 (3) mm, secondary axes often well-developed, to 1.8-6 cm long, axes with scattered to dense hairs as on branchlets, sometimes also with sparse to scattered acute appressed hairs to 0.15 mm long; inflorescence bracts coriaceous, ovate, apex acute, those subtending inflorescences 1.2-1.5 mm long, those on primary axes 0.5-1.7 mm long, those on secondary axes 0.3-1 mm long. Flowers all 5-merous, variable in size, 2.5-4.4 mm long; calyx +/- deeply cupular, in staminate flowers calyx 1-1.6 x 1.7-2 mm, level with top of ovariodisk, glabrous or with scattered to sparse hairs as on branchlets, lobes triangular to deltate, 0.4-0.6 (1) mm long; petals greenish to whitish or cream, membranous, lanceolate, 2.4-4.1 x 0.8-1.1 mm, carinate, base slightly saccate, apiculum usually inconspicuous, glabrous or with scattered hairs as on branchlets, margin short-papillate, at anthesis erect or slightly inflexed or reflexed; stamens in two markedly unequal series, 1.5-2.1 (2.25) and 2.1-2.8 (3) mm long, filaments white to greenish-white, slender, terete to somewhat strap-shaped, 1-1.65 and 1.6-2.4 mm long, anthers yellow, dorsifixed, in dorsiventral view lanceolate or more often ovate (especially after dehiscence), base lobulate, apex acute (rarely apiculate), in lateral profile broadly elliptic, (0.4) 0.5-0.6 mm long; ovariodisk usually depressed-conical, rim

0.2-0.45 (0.6) mm high, cone 0.6-0.8 mm high, 0.85-1.6 mm diam, with dense flexuous hairs to 0.4 mm long; in pistillate flowers calyx (1.2) 1.4-1.7 x 2-2.5 mm, lobes 0.3-0.7 (1.1) mm long; staminodes exceeding ovary and rarely reaching stigmas, 1.1-1.25 and 1.4-1.8 mm long, often antepetalous series lacking, filaments usually strap-shaped, 0.7-0.85 and 1-1.3 (1.65) mm long, anthers dorsifixed, dimorphic when two series present, antepetalous ones in dorsiventral view ovate with lobulate base and rounded apex, in lateral profile lanceolate, antesepalous ones in dorsiventral view obtuse-oblong with lobulate base and broadened apex, 0.4-0.65 mm long, antesepalous ones sometimes 0.05-0.1 mm longer than antepetalous ones; disk deep and narrow, (0.3) 0.5-0.7 x 0.2-0.25 (0.35) mm, with dense ascending flexuous hairs to 0.3 mm long; pistil (1.5) 1.9-2.5 x (0.7) 0.85-1.1 (1.25) mm overall, ovary ovoid to depressed-ovoid, with hairs as on disk, usually abruptly contracted to a thick style of variable length, (0.25) 0.4-1 x 0.45-0.5 (0.7) mm, stigmatal region 0.3-0.35 mm high, stigmas lateral, obdeltoid, slightly recurved. In fruit inflorescence 1.5-4 mm diam, fruit maturing red, sessile, oblique-ovoid, gibbous, ventricose, apex acute, 1.7-2.4 x 1.3-1.7 (2) cm (to 3 cm diam when more than one pyrene), surface glabrous, smooth, drying wrinkled; pseudaril pulpy; pyrene glabrous, bony, in dorsiventral view (broadly) ovate to almost obtuse-oblong, base obtuse to truncate, apex rounded, in lateral profile essentially lanceolate to ovate, (1.1) 1.4-1.8 x 0.8-1.1 cm, site of funicle below middle, funicular depression shallow, funicular scar large, essentially ovate, covering 2/3-3/4 ventral side; testa papery, irregularly thickened on ventral side, cotyledons

entire, convexly curved, then concavely curved (in cross-section forming two nested double-sigmoid curves; see chapter on seeds), then base (distal end of cotyledons) strongly incurved to form in profile a "6"-shaped figure.

Distribution. Widespread in northern South America and Central America. Protium tenuifolium is a small to large tree of primary terra firme forests. In eastern Amazonia and the Guianas it appears to flower sporadically.

Specimens examined. Brazil. Amapá: Municip. Macapá, Camaipi, EMBRAPA reserve, Sept 1983 (buds), Daly et al. 3749 (HAMAB, NY); Oiapoque, 13 Oct 1950 (buds), Frões 26604 (IAN); Municip. Mazagão, BR-156, road which will connect Macapá with Monte Dourado, 81 km WSW of Macapá, 0°08'S, 51°48'W, 19 Dec 1984 (young fr), Mori & Cardoso 17445 (HAMAB, NY); ICOMI, 4 km N of Dinning, 3 Sep 1961 (m fl), Pires et al. 50691 (F, IAN, MG, NY); Municip. Calçoene, BR-156, 17 NW of Calçoene, approx 2°28'N, 51°01'W, 8 Dec 1984 (buds), Rabelo & Souza 2936 (HAMAB, NY); Mazagão, Ramal do Camaipi, 20 Nov 1985 (buds), Rabelo et al. 3282 (HAMAB, NY); road to Camaipi, 21 Oct 1985 (m fl), Rabelo et al. 3317 (NY). Marnanhão: Fazenda Bacaba, 5 km S of MA-119, from entrance 3 km NW of Lago do Junco, 4 Oct 1980 (fr), Daly et al. 460 (NY); 17 km N of Tuntum on MA-259 toward Barra do Corda, 11 Oct 1980 (fr), Daly et al. 597 (MG, NY); Municip. Barra do Corda, 30 km NE of town between Rio Mearim and main road to Presidente Dutra, 5°25'S, 45°07'W, 8 Mar 1983 (fr), Schatz et al. 895 (NY); Belém, EMBRAPA, Mocambo Reserve, 10-17 Nov 1984 (f fl), Daly et al. 3772 (NY); Rio Maicuru-Alenquer road, 12 Nov 1953 (fr), Frões 30191 (IANRio Curuatinga,

Planalto de Santarém, Feb 1955 (fr), Frões 31593 (IAN); Belém-Brasília Highway, km 98, 6 Aug 1963 (buds), Maguire et al. 56036 (NY); Tomé Açu, right side of road to Fazenda Curiman, 30 Dec 1977 (f fl), Nascimento 360 (MG, NY); Lago Preto de Juruti, 20 Jan 1957 (fr), Oliveira 45 (IAN); Belém-Brasília Highway, km 249-254, 7 Jul 1980 (f fl), Oliveira 864 (IAN); Rio Jarí, road which links Monte Dourado to Munguba, 14 Apr 1967 (fr), Oliveira 4239 (IAN); Mata da Cia. Pirelli, Fazenda Uriboça, Jul 1958 (buds), Pires 6855, 6948 (US); Serra Buritirama (B%), 5°30'S, 50°00'W, 20 Mar 1970 (f fl), Pires & Belém 12279 (NY), 3 Jul 1970 (m fl), Pires & Belém 12374 (IAN, NY, US), 5 Jul 1970 (m fl), Pires & Belém 12404 (US); Municip. Paragominas, Belém-Brasília Highway, 17 km S of Ligação do Pará, near km marker 1509, 4°17'S, 47°32'W, 1 Mar 1980 (fr), Plowman et al. 9425 (NY); Tucuruí, PA-263, 7 Nov 1983 (f fl), Ramos 1050 (NY); Tucuruí, Rio Cagancho, 29 Sep 1980 (young fr), Rosário 109 (MG); Serra dos Carajás, 1-4 km along road from camp AZUL toward AMZA camp N-1, 6°06', 50°17', elev. 550-600 m, 28 May 1982 (f fl), Sperling et al. 5859 (NY), 10 km E of AMZA camp N-1 and 3 km along entrance road to AZUL, 6°04'S, 50°14'W, 18 Jun 1982 (m fl), Sperling et al. 6219 (NY).

French Guiana: Route de Cayenne, km 9250, 21 Jan 1956 (fr), BAFOG 7199 (NY); Saül, Mont La Fumée, 3°37'N, 53°12'W, 12 Oct 1982 (buds), Boom & Mori 2007 (NY), 20 Oct 1982 (sterile), Boom & Mori 2190 (NY), Saül, Grand Circuit ORSTOM de Boeuf Mort, 8 Dec 1976 (buds), de Granville B-5394 (CAY); (without locality), 1819-1821 (buds), Poiteau s.n. (G).

Guyana: Basin of Kuyuwine River (Essequibo tributary), 21-26 Nov 1937 (buds), For. Dep. Br. Gui. 2582 (NY); Mazaruni Station 12 Jan 1910 (f fl),

For. Dep. Br. Gui. 3078 (NY); Berabara Creek, Lower Essequibo River, 28 Nov 1942. (f fl), For. Dep. Br. Gui. 3681 (NY); Mazaruni Station, 18 Jan 1944 (young fr), For. Dep. Br. Gui. 4283 (NY); Matthews Ridge, Barima River, 23 Jan 1955 (fr), Maguire et al. 39328 (GH, NY), 18 Jan 1955 (buds), Maguire et al. 40529 (GH, NY); west extremity of Kanuku Mts., in drainage of Takutu River, 4-22 Mar 1938 (buds), A. C. Smith 3223 (B, G, GH, NY, W); NW slope of Kanuku Mts., 31 Mar-16 Apr 1938 (fr), A. C. Smith 3531 (B, G, GH, NY, W); Kaboeri, 2 Oct 1980 (buds), BW 5009 (BM, GH, IAN, NY); (without locality), (without date) (buds), Hostmann 1039 (NY, P); Raleighvallen, 6 Jan 1968 (m fl), Tawjoeran LBB 11963 (NY).

Engler (1874) published two varieties of Icicopsis tenuifolium, which he later transferred to Protium (Engler, 1883). Taxonomic placement of these varieties, the types of which are from Colombia and Peru, will have to await further work on this widespread and variable taxon. Swart (1942b) based P. peruvianum on the type of var. brevicalyx (Spruce 4473), thus making the former a nomen illegitimum. He considered var. multijugum to be a form of P. insigne (Tr. & Pl.) Engl.

Protium tenuifolium is most closely related to P. robustum and P. sagotianum. From the former it is distinguished by its more slender branchlets, smaller leaves and leaflets, larger flowers, included stamens, usually depressed-conical (not usually discoid) disk, obdeltoid (not globose) stigmas, oblique (not perpendicular) fruit apex, and basally incurved cotyledons. Although the discontinuities with P. sagotianum are often not sharp, in most instances P. tenuifolium has: leaflet acumen shorter and broader; pistillate inflorescence not markedly shorter than

staminate ones; calyx deeper; stamens and staminodes shorter; pistillate flowers often isostemonous; disk in pistillate flowers deeper; and stigmas obdeltoid (not discoid).

Swart (1942b) recognized an additional species, P. neglectum, which he distinguished from P. tenuifolium by its fasciculate (not solitary) inflorescences. However, as Cuatrecasas (1957) pointed out, the distinction between fasciculate and basally branched inflorescences is not easy to make, and both types can occur on a single branch. Swart also published a number of varieties within P. neglectum, but when he published Icica sessiliflora Rose (= P. sessiliflorum (Rose) Engl.) as a variety of P. neglectum, he made the latter species a nomen illegitimum, as Cuatrecasas noted.

Cuatrecasas (1957) considered all the taxa published under P. neglectum to be varieties of P. tenuifolium. In the present treatment, the two species are considered taxonomic synonyms, but since most of the taxa published in this complex occur in Central America and western Amazonia, the infraspecific division of P. tenuifolium is left for the upcoming monograph of the genus.

7. *Protium sagotianum* Marchand, *Adansonia* 8: t. 1. 1867-1868. Type. French Guiana: Aracouany, Aug 1858 (f fl), Sagot 1191 (lectotype (designated by Swart, 1942b): P; isoelectotypes: K, W).

Bursera caudata Turcz., Bull. Soc. Imp. Naturalistes Moscou 1: 613. 1863, nom. confusum. Icicopsis caudata (Turcz.) Engl. in Mart. Fl. bras 12(2): 257. 1874. (pro parte). Tingulunga caudata (Turcz.) Kuntze, Rev. Gen. Pl. I: 107. 1891 quoad syn. P. sagotianum.

Protium insigne (Tr. & Pl.) Engl. in DC. Mon. Phan. 4: 77. 1883. Icica insignis Tr. & Pl., Ann. Sci. Nat., Ser. 5, 14: 299. 1872. Type. Colombia: Llano de San Martín, 1856 (fr), Triana 5932 (holotype: BM). Icicopsis insignis (Tr. & Pl.) Engl. in Mart. Fl. bras. 12(2): 256. 1874. Tingulunga insignis (Tr. & Pl.) Kuntze, Rev. Gen. Pl. 1: 108. 1891. Icicopsis caudata (Turcz.) Engl. in Mart. Fl. bras 12(2): 257. 1874. (pro parte). Tingulunga caudata (Turcz.) Kuntze, Rev. Gen. Pl. 1: 107. 1891 quoad syn. Bursera caudata Turcz.

Trees, reproductive height 4-15 (25) m; often with simple plank buttresses to 80 cm high; resin whitish, sticky; branchlets slender to robust, 2.1-4 mm diam, with dense, thick, ascending or flexuous hairs to 0.15 mm long. Leaves 3-4 (5)-jugate, 19-38.5 cm long; petiole semi-terete to terete, often acutely winged, longer than interjuga, (4.2) 5.7-14.6 cm x 1.2-2.8 mm, with hairs as on branchlets but often sub-glabrescent, interjuga 1.5-4 (5.6) cm long; petiolules terete or sometimes slightly 1-canaliculate, long and slender, laterals (0.4) 0.9-2.6 cm long, terminal

1.2-3.3 (4.2) cm long, pulvinuli conspicuous; leaflets chartaceous to coriaceous, variable in size, basal pair (broadly) elliptic or rarely oblanceolate, 6-14.6 x 2.2-5.1 cm, ultimate pair elliptic to oblong or rarely oblanceolate, (6) 9.8-19 x (2.2) 2.8-4.2 (6.1) cm, laterals with oblique base, proximal side acute to obtuse, distal side obtuse to truncate, terminal oblanceolate to obovate, rarely broadly elliptic, (6.8) 8.3-12.7 (15) x (2.5) 3-4.2 (5) cm, base obtuse, leaflet apex abruptly and narrowly long-acuminate, acumen (1.1) 1.3-2 (3) cm long, abaxial surface with midvein obtusely prominent, secondary veins obtusely prominulous to prominent, rest of veins prominulous, midvein and secondary veins often with scattered appressed hairs to 0.1 mm long, rest of surface glabrous or with scattered thick hairs as on branchlets, adaxial surface with midvein narrowly prominulous but sunk in a groove, rest of veins prominulous, surface glabrous. Inflorescences distributed along the branchlets, pseudospicate, slender to somewhat robust, usually not reaching basal leaflet, to 0.15-0.25 times length of subtending leaf, staminate ones 4-10.5 (17) cm x 0.4-1.2 (1.7) mm, pistillate ones 1.5-4.2 cm x 0.5-1 mm, secondary axes poorly developed, 0.8-3.2 cm long, axes with sparse hairs as on branchlets; inflorescence bracts coriaceous to fleshy, ovate, apex acute to obtuse, those subtending inflorescences 0.7-1.3 mm long, those on primary axes 0.6-1.5 mm long, those on secondary axes 0.3-0.8 mm long. Flowers sessile, all 5-merous, at anthesis 2.7-3.7 (4.3) mm long; in staminate flowers calyx 0.8-1.2 x (1.8) 2.2-2.5 mm, level with apex of ovariodisk, with dense to scattered appressed hairs to 0.1 mm long, lobes triangular to deltate, sometimes somewhat saccate, 0.3-0.8 mm long, margin

long-papillate; petals white to yellow, lanceolate, fleshy to membranous, (2.2) 2.9-3.8 x 1-1.5 mm, carinate, slightly saccate at base, abaxial surface glabrous or with a few scattered appressed hairs to 0.1 mm long, margin short-papillate, at anthesis slightly reflexed; stamens in two markedly unequal series, 1.9-2.7 and (2) 2.5-3.4 mm long, filaments slender, terete to somewhat strap-shaped, 0.9-1.2 (1.8) and 1.2-1.85 (2.4) mm long, anthers dorsifixed, in dorsiventral view broadly lanceolate with lobulate base and acuminate apex (acumen sometimes retuse), in lateral profile elliptic to lanceolate, 0.5-0.6 mm long; ovariodisk convex-discoid, margin 0.35-0.4 mm high, diam 1.2-1.6 mm, at center 0.7-0.9 high, with dense flexuous hairs to 0.3 mm long; in pistillate flowers calyx (0.7) 1.1-1.5 x 2.1-2.8 mm, lobes level with or slightly exceeding top of disk, 0.4-0.7 mm long, staminodes reaching base of or part-way up style, 1.35-1.7 (2.2) and 1.7-2.3 (2.9) mm long, filaments slender, strap-shaped, 0.9-1.2 (1.8) and 1.2-1.85 (2.4) mm long, anthers dimorphic, in dorsiventral view antepetalous ones lanceolate with lobulate base, 0.3-0.55 mm long, antesepalous ones (broadly) elliptic, 0.45-0.6 mm long, in lateral profile all elliptic; disk 0.3-0.4 (0.55) x 0.2-0.35 mm, with dense flexuous hairs to 0.4 mm long; pistil 2.25-2.4 (2.85) x 0.9-1.25 mm overall, ovary sessile, ovoid, with dense ascending flexuous hairs to 0.4 mm long, gradually contracted to a long style 1-1.3 (1.6) x 0.4-0.5 mm, stigmal region 0.25-0.3 mm high, stigmas sessile, lateral, compressed-globose to almost discoid. Fruit maturing red, oblique-ovoid, gibbous, ventricose, 2.1-2.5 x 1.5-1.7 cm (to 2.7 cm diam when more than one pyrene), sessile, apex acute, surface glabrous, smooth, drying

wrinkled; pseudaril pulpy; pyrene thickly cartilaginous or bony, in dorsiventral view broadly to depressed-ovoid, base obtuse to truncate and apex rounded, in lateral profile obliquely broadly lanceolate, 1.3-1.5 x (0.6) 0.8-1.2 cm, glabrous, site of funicle below middle, funicular depression shallow, funicular scar ovate to rounded-deltate, covering 2/3-3/4 ventral face; testa papery, irregularly thickened on ventral side; cotyledons entire, convexly curved, then concavely curved (in cross-section forming two nested double-sigmoid curves; see chapter on seeds), then base (distal end of cotyledons) strongly incurved to form in profile a "6"-shaped figure.

Distribution. Widespread in Amazonia and the Guianas. Protium sagotianum is a medium-sized tree in primary terra firme forests. It often occurs on slopes and in sandy soils. In eastern Amazonia and the Guianas it flowers and fruits sporadically.

Specimens examined. Brazil. Amapá: Municip. Macapá, Perimetral Norte (BR-210), Riozinho, 131 km NW of Porto Grande, approx. 1°21'N, 53°15'W, 31 Dec 1984 (buds), Daly et al. 4015 (HAMAB, NY). Maranhão: Rio Maracaçumê, 11 Jul 1958 (fr), Frões 34471 (IAN, U); Motes Altos, Mangaba, 20 Aug 1982 (fr), Maciel et al. 837 (MG, NY); Turiaçu, km 6 of BR-106, Maracaçumê-Sta. Helena, 28 Nov 1978 (fr), Rosa & Vilar 2694 (MG, NY, US); Municip. Monção, basin of Rio Turiaçu, Ka'apor Indian Reserve, within 7 km of Urutawy, 10 Apr 1985 (fr), Balée & Gely 855 (NY). Pará: Belterra, 27 Oct 1947 (m fl), Black 47-1805 (U), 31 Oct 1947 (m fl), Black 47-1906 (IAN, U, US); region of Santarém, banks of Rio Curuá Una, Oct 1954 (buds), Frões 31368 (U); Curuatinga, Planalto de Santarém, Feb 1955 (fr), Frões 31593 (U); Tucuruí,

1 Sep 1983 (m fl), Miranda et al. 375 (NY); Belém-Brasília Highway, km 201, 15 May 1960 (m fl), Oliveira 760 (IAN), km 194, 16 May 1960 (m fl), Oliveira 769 (IAN), km 360, 29 Aug 1960 (fr), Oliveira 1078 (IAN); Rio Jarí, Monte Dourado, Varadouro, behind airfield, 26 Apr 1968 (fr), Oliveira 4326 (IAN); Colonia 3 de Outubro, between km 100 of the Bragança railway and Rio Guamã, 23 Aug 1952 (sterile), Pires et al. 4119 (U); Colonia Agricola do Guamã, Sta. Izabel, 19 Aug 1967 (sterile), Pires & Silva 11248 (IAN, NY); Belém, Utinga REserve, 24 Jan 1969 (m fl), Pires 12017A (IAN), Mocambo Reserve, 1 Feb 1969 (f fl), Pires 12047 (IAN); Municip. Paragominas, Belém-Brasília Highway, 17 km S of Ligação do Pará, near km marker 1509, approx 4°17'S, 47°32'W, 1 Mar 1980 (fr), Plowman et al. 9383 (NY); Cuiabá-Santarém Highway, km 885.5, 10 Nov 1977 (young fr), Prance et al. 25166 (NY), km 1131, 15 Nov 1977 (fr), Prance et al. 25448 (NY); São Felix do Xingú, 11 Jun 1978 (young fr), Rosário 21 (IAN, MG, NY); Municip. Almeirim, Monte Dourado, South Pacanari road, 11 Dec 1978 (m fl), Santos 514 (MG); Serra dos Carajás, 7 km SE of AMZA camp, 3-Alfa on road to Rio Itacaiunas, 5°50'S, 50°30'W, 11 Jun 1982 (f fl), Sperling et al. 6077 (NY); region of Gorotire, 31 Jul 1962 (fr), N. T. Silva 752 (IAN, US); Rio Jarí, Monte Dourado, Planalto A, 11 Sep 1968 (f fl), N. T. Silva 942 (IAN, NY), 12 Dec 1968 (m fl), N. T. Silva 1528 (IAN, NY).

French Guiana: St. Laurent, Feb 1956 (fr), BAFOG 7274 (U); Saül, La Fumée Mountain, 3°37'N, 53°12'W, 3 Oct 1982 (fr), Mori & Boom 1504 (NY), 3 Oct 1982 (m fl), Mori et al. 15045 (NY), 7 Dec 1982 (fr), Mori & Boom 15337 (NY), 25 Apr 1983 (seedling), Mori et al. 15665 (NY); Rivière Iracoubo, near Saut Génipa forest, Oldeman 2178 (NY); (without locality),

1821 (f fl and fr) Perrottet s.n. (P); Fleuve Approuague, Rivière Arataya, Saut Paraé, 4 Nov 1978 (fr), Sastre 6277 (NY, P).

Guyana: Simuni Creek, Rupununi River, Aug 1931 (buds), For. Dep. Br. Gui. Rec. No. 2139 (U).

Sectie O, Nov 1942 (sterile), BW 132 (B, GH, IAN, U), 27 Oct 1913 (fr), BW 363 (U); Forest Reserve, 30 Oct 1915 (sterile), BW 1159 (U), 12 Aug 1918 (m fl), BW 3931 (BM, IAN, U); Sectie O, 19 May 1920 (buds), BW 4671 (BR, GH); Nickerie district, Fallawatra, 28 Oct 1971 (sterile), BW 14264 (MO); area of Kabalebo Dam, 12 Nov 1976 (fr), Heyde & Lindeman 37 (U); Maratakka River, 6 km NW of camp along Snake Creek, 17 May 1965 (buds), LBB 10815 (U); Fallawatra, 6 Nov 1971 (fr), LBB 14294 (MO, U); between Moengo tapoe and Grote Zwiebelzwamp, 7 Oct 1948 (sterile), Lanjouw & Lindeman 693 (U); Rikanau near Moengo forest near Camp 8, 22 May 1954 (seedling), Lindeman 5811a (U); Raleighvallen, Coppename River, 26 Aug 1920 (m fl), Pulle 327 (BR, MO, NY, US); between Saramacca River and Boliath Mts., 8 Jun 1956 (sterile), Schulz 7698 (U); Jodensavanne, Suriname River, 5 May 1961 (sterile), Schulz 8937 (U); (without locality), (without date) (m fl), Wullschlagel 1663 (BR).

Cuatrecasas (1957) was the first to submerge P. insigne in P. sagotianum. He pointed out that the characters that Swart (1942b) used to separate the two-- number of juga, length of acumen, and solitary versus fasciculate inflorescences-- are not consistent, and may vary even on duplicates of a single collection. However, there do appear to be two basic morphotypes within the species, one characterized by oblong, coriaceous leaflets and robust inflorescence axes, the other (resembling

the type) by smaller, elliptic, chartaceous leaflets and slender inflorescence axes. However, these characters represent differences of at best varietal rank. I have not yet found other characters which correlate with these, and they do not show sharp discontinuities, therefore I have left P. sagotianum as a variable species.

Protium sagotianum is most closely related to P. robustum and P. tenuifolium. from the former it is distinguished by its more slender branchlets, smaller leaves and leaflets, larger flowers, included stamens, convex (not usually flat) disk, discoid (not globose) stigmas, oblique (not perpendicular) fruit apex, and basally incurved cotyledons. Although the discontinuities with P. tenuifolium are often not sharp, in most instances P. sagotianum has: leaflet acumen longer; pistillate inflorescence markedly shorter than staminate ones; calyx shallower; stamens and staminodes longer; pistillate flowers always diplostemonous (not sometimes isostemonous); disk in pistillate flowers shallower; and stigmas discoid (not obdeltoid).

8. *Protium pallidum* Cuatrecasas, Bol. Mus. Paraense Hist. Nat., Nov. Sér. (Bot.) 11: 8. 1961. Type. Brazil. Amapá: Serra do Navio, Rio Amapari, slopes of Curuca Ore Body down to Igarapé Sentinels, 9 Nov 1954 (m fl), Cowan 38180 (holotype: US; isotypes: F, GH, IAN, NY)

Trees, reproductive height 10-31 m, maximum reported DBH 55 cm, usually provided with (often branched) flying buttresses and prop roots, even on rather young individuals, often also with plank buttresses, buttresses high, steep and narrow; trunk cylindrical; outer bark light brown to gray, smooth, with fine, closely spaced incomplete hoops and scattered lenticels, inner bark orangish to flesh-colored, brittle, striate, when wounded exuding a clear sticky resin which dries white and powdery; branchlets relatively slender (2) 2.5-3.7 (4) mm diam, with dense appressed hairs to 0.15 mm, soon glabrescent. Leaves (1)- 2-4 (5)-jugate, (14) 19-34 (40) cm long; petiole semi-terete, often broadly and shallowly canaliculate at extreme base, longer than interjuga, (2.3) 3-7.5 (11.5) cm x 1.4-3 (3.9) mm; interjuga (1.7) 2-4 (5.1) cm; lateral petiolules (deeply) 1-canaliculate, long, (0.5) 0.7-1.6 cm long, petiolules and region of rachis between lateral leaflets often strongly thickened in older leaves, especially on fruiting specimens, terminal shallowly 2-canaliculate, (1.5) 2-3.3 cm; leaflet coriaceous, laterals (narrowly) elliptic to slightly oblanceolate, base usually subequal, acute, basal pair (6) 7.2-12.2 (13.5) x 2.4-4.5 (5) cm, ultimate pair (7.4) 8.5-13.3 (16.6) x 2.2-4.1 (5) cm, terminal broadly elliptic to obovate, (6.6) 7.7-13.5 (18) x 2.2-4.6 (6.4) cm, leaflet apex acuminate, acumen obtuse,

0.4-1 (1.3) cm, blades glabrous, adaxially dull gray above when dry, midvein and secondary veins prominulous, rest of veins inconspicuous, abaxially glossy and with a whitish cast fresh and dry, all veins prominulous. Inflorescences subterminal, apparently produced at the end of a period of growth, usually exceeding petiole, slender, lax, (2.5) 5-14 cm x 0.4-1.2 (1.5) mm, 0.2-0.5 (0.7) times length of subtending leaf, glabrous or sometimes with scattered, appressed, thick, blunt hairs to 0.05 mm long, inflorescence bracts ovate or less often lanceolate, acuminate, those subtending inflorescences rounded-deltate, fleshy, 1-1.8 mm long, fugaceous; those on primary axes (0.4) 0.5-0.8 (0.9) mm long, those on secondary axes obtuse, 0.3-0.5 (0.6) mm; pedicel long, subcylindric, in staminate flowers (1.8) 2.2-3.5 x 0.25-0.35 (0.5) mm, shorter in pistillate flowers, 1.4-3 (3.5) x 0.25-0.3 (0.5) mm, in fruit (2.5) 3-4 (4.5) x (1) 1.3-2 (2.5) mm. Flowers all 5-merous, 1.8-2.3 (2.5) mm long at anthesis, calyx deeply cupular, 1-1.7 x 1.7-2.5 (3) mm, lobes long, rounded-triangular, acute, (0.5) 0.7-1.2 mm long, greatly exceeding the disk; petals white to yellow-white to cream to green, ovate to broadly lanceolate, (2.2) 2.3-2.8 (3) x 1-1.5 (1.6) mm, apex acute, apiculum strongly inflexed, membranous, at anthesis usually strongly reflexed from 1/3 their length, abaxially glabrous, margin short-papillate; staminate flowers with stamens only slightly exceeding the pistillode, 1.15-1.3 and (1.2) 1.3-1.45 (1.55) mm long, slightly inflexed at anthesis, filaments obclavate, fleshy, subterete, (0.5) 0.6-0.7 mm and (0.5) 0.7-0.8 mm long, anthers basifixed, in dorsiventral view lanceolate (ovate after dehiscence), base lobate, apex obtuse to slightly retuse, in lateral

profile obliquely ovate, usually dimorphic, 0.5-0.75 and 0.5-0.8 mm long; disk shallow, 0.25-0.6 x (0.5) 0.65-0.75 (0.85) mm, pistillode 0.5-0.6 x (0.5) 0.65-0.75 (0.85) mm overall, deeply depressed-ovoid, provided with locules and reduced ovules, glabrous, abruptly contracted to a short, thick, markedly acutely 5-winged stylode 0.2-0.25 mm long; in pistillate flowers staminodes reaching almost to top of pistil, 0.9-1 and 1-1.1 mm long, filaments +/- strap-shaped, 0.4-0.5 and 0.5-0.6 mm long, anthers in dorsiventral view ovate, in lateral profile obliquely lanceolate, all 0.45-0.5 mm long; disk shallow, 0.2-0.3 x (0.15) 0.25-0.4 mm; pistil 1.25-1.9 x 1-1.1 mm overall, ovary ovoid, substipitate, with sparse, appressed, blunt, translucent hairs to 0.05 mm long, contracted to a short, thick, style 0.2-0.3 mm long, lengthening somewhat (to 0.6 mm) as fruit begins development, style with 5 lateral branches to 0.3 mm long, each terminated by a globose stigma, each structure laterally clavate overall, stigmatal region 0.3-0.4 mm high, style branches apparently somewhat recurved after fertilization. Fruit green when mature, usually slightly obliquely ovoid and slightly dorsiventrally compressed, otherwise essentially globose with as many lobes as developed locules, 2.1-2.8 x (1.4) 1.9-2.4 cm, sessile, apex rounded, surface glabrous, drying smooth; pseudaril thick, spongy, occurring only as a band ca 0.3 cm wide around periphery of pyrene, overlying a dense layer of matted (sub)erect fibers to 0.4 mm long; pyrene thickly cartilaginous, broader than tall, when mature 1.5-1.6 x 1.6-1.9 cm (Daly 4079, Mori 15442), in dorsiventral view depressed-ovoid, base truncate, apex sharply acuminate, in lateral view elliptic on dorsal side and oblong on ventral side, base obtuse, apex

caudate and angled toward ventral side due to deep subapical depression on ventral side, ventral face with a shallow central vertical sulca; testa with irregular thickenings, infolded with lobed and contortuplicate cotyledons.

Distribution. Although represented by an appreciable number of specimens in the herbaria, P. pallidum is known from few collection sites. Based on the available distribution data, the species occurs from central French Guiana through Amapá (though interrupted by the savannas of central Amapá) and northern Pará to western Maranhão, with disjunct populations in the region around Manaus in Amazonas.

There is one collection from western Maranhão (Rosa & Vilar 2927), but that region has been largely deforested so we cannot know how common it may have been in those "pre-Amazon forests." The species is apparently quite common in the area around Belém; most of these collections are from the various inventories carried out by what is now the Centro de Pesquisas Agropecuárias do Trópico Unido. In central Amapá it is so far known only from the type locality, the Serra do Navio, where in 1984 I was able to observe sterile individuals. P. pallidum has been encountered in two localities in French Guiana, Mont La Fumée and Mont St. Michel.

Until recently there was only one disjunct collection of Protium pallidum from the Manaus region, Cid et al. 1001, but a few individuals of the species have been found in the inventories being carried out by World Wildlife Fund-U.S. about 80 km N of the city during the past several years (i.e., Daly et al. 4079). The specimens from this region match the type collection from Amapá very closely.

With few exceptions, Protium pallidum is an understory or often canopy tree of primary terra firme forest on undulating terrain. There are two collections reported from flooded forest near Belém (Pires & N. T. Silva 10777, 10778) and one from advanced secondary forest east of Belém near Benevides (M. Silva 481). Other species of Protium occur in hilly country, but none show the strong development of flying buttresses and prop roots which characterize the species. This specialized morphology may explain the species' great competitive ability (as indicated its high density) where it occurs in eastern Amazonia.

Throughout its range, this species flowers from August to November and fruits from November to April.

Specimens examined. Brazil. Amazonas: Vicinity of Rio Uatumã, BR-174 Manaus-Caracará road km 97, km 60 of Balbina Dam road, right side, near airport, 4 Sep 1979 (buds), Cid et al. 1001 (NY); Municp. Manaus, Distrito Agropecuário da SUFRAMA, Fazenda Dimona, km 72 of BR-174, then 6 km W, Biological Dynamics of Forest Fragments Project, Reserve 2107, 5 Oct 1985 (fr), Daly et al. 4079 (INPA, MO, NY). Maranhão: Zé Doca, km 180 of BR-316, 13 km on access road, 12 Dec 1978 (young fr) Rosa & Vilar 2927 (MG, NY). Pará: Belém, Bosque Municipal, Oct 1949 (young fr), Alves s.n. (IAN); Belém, Bosque Rodrigues Alves, 9 Oct 1954 (f fl), Black 54-16838 (IAN, RB, U, US); Municp. Oriximiná, Rio Trombetas, km 23 of Cachoeira Porteira road, 27 Jun 1980 (young fr), Cid & Mota 1123 (INPA), right side of Mineração Santa Patricia, 10 July 1980, (young fr), Cid et al. 1438 (INPA), right bank, Porto Trombetas, Mineração Rio Norte, km 60 of Mineração road, behind bauxite mine, 29 Aug 1980 (fl), Cid et al. 1876

(INPA); Belém, Utinga, 25 Sep 1914 (m fl), Ducke 15490 (MG); Belém, Agua Preta, 26 Nov 1914 (m fl), Ducke 15539 (MG); matta de Jupatituba, 19 Dec 1899 (buds and m fl), M. Guedes 1819 (MG); EFB Colonia Sta. Rosa, 4 Oct 1908 (f fl), "Pessoal do Museu" 9706 (MG); Belém, Utinga, 20 Nov 1945 (buds), Pires & Black 662 (IAN); Belém, IAN, Reserva Mocambo, Mar 1953 (young fr), Pires 4471 (IAN, U), Jan 1956 (young fr), Pires & Silva 6716 (IAN, U, US), Jan 1956 (buds), Pires & Silva 6729 (IAN, U, US); forest of the Pirelli Company, Fazenda Uriboça, Aug 1958 (buds), Pires 7121 (IAN, U, US); 8 Sep 1958 (f fl), Pires 7133 (IAN, U, US), 8 Sep 1958 (m fl), Pires 7135 (IAN, US), 12 Sep 1958 (m fl), Pires 7140 (IAN, U, US); Belém, IAN, Reserva Mocambo, 23 Aug 1967 (m fl), Pires & Silva 10738 (IAN, NY), 21 Aug 1967 (m fl), Pires & N. T. Silva 10739 (IAN, NY), 23 Aug 1967 (m fl), Pires & Silva 10740 (IAN, NY), 23 Aug 1967 (m fl), Pires & Silva 10741 (NY); Belém, IAN, Reserva APEG, 23 Aug 1967 (m fl), Pires & Silva 10777 (IAN, NY); 23 Aug 1967 (m fl), Pires & Silva 10778 (IAN); Belém, IAN, Agua Preta, 25 Oct 1967 (m fl), Pires & Silva 11206 (IAN, NY); Belém, IAN, Reserva Mocambo, 29 Nov 1967 (m fl), Pires & Silva 11339 (IAN, NY), 29 Nov 1967 (m fl), Pires & N. T. Silva 11340 (IAN, NY), 29 Nov (buds), Pires & N. T. Silva 11341 (IAN, NY); Belém, IAN, Reserva Aurã, 24 Nov 1967 (f fl), Pires & N. T. Silva 11399 (IAN); Belém, IAN, Reserva Mocambo, 16 Nov 1967 (m fl), Pires & Silva 11423 (IAN), 18 Mar 1968 (fr), Pires & Silva 11440 (IAN), 25 Mar 1968 (fr), Pires & Silva 11463 (IAN); Granja Maratã, Benevides, 24 Oct 1973 (buds), Pires 13292 (IAN); vicinity of Belém, Sep-Oct 1961 (sterile), J. M. Pires 51789 (NY, US); grounds of Instituto Agronômico do Norte, Belém, 18 Aug 1964 (m fl), Prance & Silva 58760;

without locality, Dec 1965 (fr), Schubert 2229 (IAN, US); Belém, Bosque Rodrigues Alves, 21 Feb 1944 (fr), A. Silva 137 (IAN, NY, US); Benevides-Mosqueiro road, 10 Feb 1966 (young fr), M. Silva 481 (MG). French Guiana: Saül, Mont La Fumée, 3°37'N, 53°12'W, 13 Sep 1982 (sterile), Boom & Mori 1654 (NY), 16 Sep 1982 (steril), Boom & Mori 1707 (NY), 17 Sep 1982 (sterile), Boom & Mori 1734 (NY), 23 Sep 1982 (buds), Mori et al. 14973 (NY), 1 Oct 1982 (buds), Mori et al. 15009 (NY), 3 Oct 1982 (f fl), Mori et al. 15051 (NY), 7 Oct 1982 (buds), Mori et al. 15066 (NY), 4 Nov 1982 (m fl), Mori & Boom 15153 (NY), 11 Nov 1982 (m fl), Mori & Boom 15196 (NY), 30 Nov 1982 (fr), Mori & Boom 15289 (NY), 7 Dec 1982 (young fr), Mori & Boom 15339 (NY), 29 Mar 1983 (fr), S. Mori & J. Pipoly 15442 (NY), 31 Mar 1983 (fr), Mori & Pipoly 15485 (NY), 12 Apr 1983 (fr), Mori & Pipoly 15589 (NY); Haut Oyapock, Mt. St. Marcel, between Camp Poivre and Mt. St. Michel, 18 Mar 1976 (fr), Sastre 4422 (NY, P).

Local names and uses. Brazil: breu branco. French Guiana (Wayampi Indians): "waluwa?isi."

Protium pallidum is distinctive among all the species of the genus because of the usual presence (even on saplings) of branched flying buttresses and prop roots and because of the whitish cast of the underside of the leaflets, hence its name.

Protium pallidum is most closely related to the rare P. cuneatum Swart, and it has often been mistaken for that species. They share a number of characters, such as the exfoliating epidermis of the leaf petiole and rachis; petiolules 1-canaliculate; terminal petiolule long; inflorescence long; petals membranous; disk low and broad; style

stellately branched, fruit stipitate and ridged; and the same distinct form of the pyrene. P. pallidum differs by its leaflets with insertion parallel (not perpendicular) to the meridian; lateral leaflets narrowly elliptic (not ovate to obovate), all leaflets with apex less abruptly and more acutely acuminate and with reticulum much less prominent and not discolorous; petiolules longer and with strongly incrassate pulvinuli; pedicel longer and more slender; and fruits smaller.

Protium pallidum resembles P. strumosum and P. grandifolium because of its long petiolules; inflorescences long, fasciculate and lax; elliptic leaflets long-acuminate; and fruits globose. The former species can be distinguished from P. strumosum by its white 5-merous flowers; calyx deeper and markedly lobed; stamens relatively short; disk low and broad; stigmas horizontally obclavate; young fruits stipitate; mature fruits ridged when dry; and the markedly whitish cast of the abaxial leaflet surface fresh and when dry. Protium pallidum differs from P. grandifolium by its less conspicuously thickened pulvini and pulvinuli; inflorescence axes subglabrous; calyx lobes large, triangular and acute (not deltate and apiculate or acuminate); petals with the apiculum more incrassate and more strongly inflexed; and ovary the subglabrous.

Protium pallidum has occasionally been confused with P. polybotryum (Turcz.) Engl., to which it is superficially similar because of the long-petiolulate lanceolate long-acuminate leaflets, the long pedicels, and the truncate calyx base. The latter differs by the reddish cast to the leaflets when dry; branchlets and inflorescence distinctly pubescent; calyx and calyx lobes shorter; petals strongly incrassate; disk high and narrow; ovary pubescent; and ellipsoid fruits which are smooth when dry.

9. *Protium cuneatum* Swart, Rec. Trav. Bot. Néerl. 39: 191. 1942. Type.

Brazil. Amazonas: basin of Rio Solimoes, Municip. São Paulo de Olivença, near Palmares, 11 Sep-26 Oct 1936 (f fl & young fr), Krukoff 8186 (holotype: NY; isotypes, BR, F, G, MICH, MO).

Tree, reproductive height 5-20 (40) m; consistently with plank and flying buttresses; branchlets robust, (3.1) 3.4-5.4 (6) mm diam, apex with dense appressed hairs 0.1-0.4 mm long, branchlets soon glabrescent. Leaves 0-2 (3)-jugate, 14-38 cm long; petiole robust, semiterete, (2.7) 3.2-7.2 (8) cm x (1.8) 2.2-3 (3.7) mm, glabrous; interjuga approximately same length, 3.7-6.5 (7.7) cm long; petiolules inserted perpendicular to the meridian, deeply 1-canalicate, long, robust, laterals (0.5) 0.8-1.1 (1.6) cm long, pulvinuli conspicuous; interjugae (3.7) 4-6.5 (7.7) cm, terminal shorter than interjuga, (2.1) 2.5-4.2 (5.5) cm long; leaflets markedly coriaceous, laterals broadly oblong or broadly elliptic, rarely broadly oblanceolate or elliptic, basal pair (6.4) 7.9-14.7 (18) x (3.8) 4.2-6.6 (7.5) cm, ultimate pair longer and narrower, (8.2) 10-16.6 (19) x (3.4) 4-6.1 (6.7) cm, terminal obovate to broadly elliptic, (8.5) 10-17 (18.5) x (4.4) 5.1-7.8 (9.4) cm, base subequal, acute, apex abruptly and broadly short-acuminate, acumen obtuse to truncate (rarely slightly emarginate), 0-0.5 (0.7) cm long, abaxial surface with midvein acutely to obtusely prominent, higher order veins prominulous, glabrous, adaxial surface with midvein narrowly acutely prominent, secondary veins prominulous or not, higher order veins prominulous, glabrous.

Inflorescences congested near branchlet apices, short, (1.5) 2.5-7 (10) cm

x 0.6-0.9 (2.5) mm (in fruit (0.9) 1.1-2 mm diam), secondary axes somewhat robust, short, 0.5-1.5 (2) cm long (to 3.5 mm long in fruit), axes slightly succulent (drying rugose), with scattered appressed hairs to 0.1 mm long (dense near base), sometimes glabrous, inflorescence bracts (broadly) ovate, less often lanceolate, those subtending inflorescences fleshy, 1-2 mm long, others chartaceous, those on primary axes 0.5-0.8 (1.3) mm long, those on secondary axes 0.3-0.5 (0.7) mm long; pedicel subcylindric, long, (0.8) 1.7-2.2 (3) x 0.35-0.5 mm, glabrous. Flowers all 5-merous, 1.5-2 mm long; calyx shallowly cupular, (0.8) 1-1.2 x (2) 2.3-2.6 mm, glabrous or with scattered appressed hairs 0.1-0.2 mm long, calyx lobes rounded (depressed-) deltate, apex apiculate or acute, long-papillate (sometimes margin as well), occasionally acuminate; in staminate flowers calyx exceeded by disk, lobes 0.25-0.45 mm long; petals greenish-white (Irwin 48206), not very fleshy, ovate, 2.5 x 1.2-1.4 mm, apex broadly acute, apiculum conspicuous, 0.25-0.4 mm long, strongly inflexed, margin and apex long-papillate; stamens short, not greatly exceeding pistillode, 1.5-1.75 and 1.6-1.85 mm long, filaments somewhat fleshy, compressed, 0.8-1.1 and 0.9-1.2 mm long, anthers basifixed, in dorsiventral view narrowly obtuse-oblong, base lobulate (after dehiscence broadly oblong with truncate or lobulate base), apex sometimes apiculate, in lateral view obtuse-oblong to elliptic, 0.65-0.7 mm long; disk shallow and broad, 0.25-0.5 x 0.45-0.7 mm, rugose, pistillode 0.6-0.65 x 0.7-0.85 mm overall, broadly depressed-ovoid, glabrous or with a few ascending hairs to 0.25 mm long, provided with locules and reduced ovules, abruptly contracted into an obtusely 5-winged capitate apex, wings 0.15-0.2 mm

long; in pistillate flowers calyx exceeding disk, lobes (0.3) 0.4-0.5 (0.6) mm long; petals longer than in staminate flowers, 3-3.7 x 1.8-2.3 mm; staminodes reaching base of style, 1-1.3 and 1.1-1.4 mm long, filaments fleshy, subcylindric, 0.45-0.7 and 0.55-0.8 mm long, anthers in dorsiventral view broadly oblong to slightly ovate, base lobulate, apex retuse (apiculate on Daly 3777), in lateral view asymmetrically lanceolate, base truncate, apex obtuse, 0.5-0.6 mm long; disk relatively broad, 0.3-0.35 x 0.35-0.5 mm, pistil 1.25-1.5 x 1.05-1.15 mm overall, ovary very broadly ovate, negligibly substipitate, glabrous, abruptly terminated by a very short and very thick style, 0.1-0.15 (0.25) x 0.55-0.7 mm, style laterally 5-branched, branches 0.1-0.15 mm long, terminated by hemispherical stigmas, stigmatal area 0.3 mm high. In fruit pedicel 2.5-5 (5.6) x 1.5-2.2 mm, young fruit stipitate, obovoid, style branches and stigmas conspicuous, mature fruit green, slightly asymmetrical, broadly ellipsoid to sub-globose, 2.4-2.8 x 1.5-2.3 cm (to 2.9 mm wide when more than 1 pyrene), stipitate or less often substipitate, broadly short-acuminate, acumen obtuse or less often acute, style slightly excentric, style and stigmas usually persisting (style branches may break off); pseudaril occurring only as a thick band ca 0.5 cm wide around periphery of pyrene, color unknown, when removed leaving a hygroscopic layer of semi-erect fibers to 0.5 mm long; pyrene 2 x 1.7-1.8 cm, in dorsiventral view broadly elliptic to broadly ovate, base truncate to obtuse, apex obtuse and apiculate or abruptly acuminate, in lateral view essentially elliptic, sometimes ventral side obovate, ventral surface with a deep lateral subapical depression; testa with irregular

thickenings, infolded with contortuplicate cotyledons.

Distribution. French Guiana, Guyana, Venezuela (Bolívar), and in Brazil in Amapá and disjunct to western Amazonas. This poorly-collected species appears to be ecologically flexible, occurring as a small- to medium-size tree in terra firme moist forest on sandy soils (Krukoff 8186, Fanshawe (For. Dept. Br. Gui. Rec. no.) 3738, Daly et al. 3777) as well as on or near river or stream banks (Tillett & Tillett 45716, Cremers 6194, Irwin et al. 48206). The collections to date indicate that the species flowers September to October and fruits October to March.

Specimens examined. Brazil. Amapá: Municip. Oiapoque, 60 km SSE of Oiapoque on BR-156, ca. 3°18' N, 51°39' W, 1 Dec 1984 (fr), Daly et al. 3777 (HAMAB, NY); Rio Oiapoque, about 1-3 km N of Cachoeira Tres Saltos, 2°12'-13 N, 52°52'-53'W, 12 Sep 1960 (m fl), Irwin et al. 48206 (IAN, MG, NY). French Guiana: 20 km E of Saül, Saut Marie, 27 Jan 1980 (fr), Cremers 6194 (NY); Trois Sauts, upstream from Zidok town, right bank, 3 Nov 1974 (sterile), Lescure 407 (CAY); Cayenne, (without date) (m fl), Martin s.n. (K, P); Upper Approuague, on right bank at the path of Fini Saut, 28 Sep 1968 (young fr), Oldeman T-189 (CAY, NY); upper Oyapock, Crique Eulepoussing ("ipusi"), near crique Kulumuli Itu-Mt. St. Marcel, 1 km before camp Coulevre, 15 Mar 1976 (fr), Sastre 4396 (NY, P); without locality, 1840 (fr), H. F. Talbot s/n (K). GUYANA: Mahdia R., Potaro River, 107 mi Bartica-Potaro Rd., 10 Jan 1943 (fr), Fanshawe (For. Dept. Br. Gui. Rec. no.) 3738 (NY); upper Mazaruni River basin, Utschi River mouth, 20 Oct 1960 (fr), Tillett & Tillett 45716 (NY). VENEZUELA. Bolívar: 88 km S of El Dorado, El Pueblito, 30 Mar 1956 (fr), Bernardi 3045 (VEN);

88 km from El Dorado toward Sta. Elena, 29 Dec 1956 (fr), Foldats 2693 (NY, VEN).

Local names and uses. French Guiana: waluwa?isi (Wayampi), encens. Guyana: ulu. Venezuela. Bolívar: tacamajaca. No uses reported.

Protium cuneatum shares a number of characters with P. altsonii and P. demerarensis: short inflorescences; calyx not exceeding the disk; disk shallow, greatly exceeded by the pistillode; stamens not greatly exceeding the pistillode; and large, globose fruits. Protium cuneatum differs from P. altsonii by its fewer juga; leaflets larger, more broadly elliptic, and abruptly and broadly acuminate (not gradually and narrowly acuminate); stylode markedly acutely winged (not lobulate); style branched (stigmas not subsessile); fruit (sub)stipitate; and pseudaril occurring as a discrete band (not covering all of pyrene). From P. demerarensis, P. cuneatum differs by the latter's coriaceous leaflets; acumen abruptly and broadly short-acuminate (not gradually and narrowly long-acuminate); stylode markedly acutely winged; calyx exceeding disk in pistillate flowers; pistil substipitate (not sessile); and fruits smaller, green and smooth (not gray, lenticellate, and rough-textured).

10. *Protium strumosum* Daly (submitted for publication in Brittonia). Type. Brazil. Amazonas: CEPLAC, Manaus, 2 Sept 1974 (m fls), Prance et al. 22604 (holotype: INPA; isotypes: FLAS, GH, K, MICH, MO, NY, UC, US, WIS).

Small trees, reproductive height 5-15 m, branchlets with a whitish cast, robust, somewhat fleshy (wrinkled when dry), 2.5-3.5 (4.5) mm diam at 2 cm from apex, with whitish to yellow short appressed hairs to 0.15 mm long, soon glabrescent. Leaves 3-4-jugate, 25-45 (50.5) cm long; bases markedly pulvinate, fleshy (wrinkled when dry); petiole broadly and shallowly canaliculate, longer than interjuga, 4.6-12 (15) cm x (1.4) 1.6-2.6 mm, glabrous; interjuga long, (2.9) 4-5.8 (7.5) cm long; petiolules long, semiterete, narrowly 2-canaliculate, laterals 0.7-1.5 (2) mm long, terminal 3.4-4.5 (6) mm long, all with markedly swollen pulvini at both ends, interpetiolar region usually swollen also, pulvinuli with whitish cast below; leaflets elliptic to narrowly elliptic, (terminal sometimes slightly obovate), chartaceous, glabrous, basal pair (6.4) 10.6-13 x (2.5) 3-5.2 cm, ultimate pair (7) 11.9-14 (17) x (2.5) 2.8-5.2 cm, terminals smaller than ultimate pair, (7) 9.5-12.7 (15.1) x (2.6) 3-5.2 cm, base obtuse to acute, subequal to slightly oblique, leaflet apex long-acuminate, acumen 0.9-1.6 cm long, margin entire; on both surfaces primary and secondary veins prominent, higher order veins prominulous. Inflorescences subterminal, lax, long and slender, (9) 15-30 cm x 0.9-1.2 (1.4) mm, (0.5) 0.6-0.8 times as long as the subtending leaves, secondary axes (1.6) 2.8-13 cm long, axes with scattered, appressed hairs to 0.15 mm

long; inflorescence bracts lanceolate to ovate, those subtending inflorescence (when present) 0.8-1 mm long, those on primary axes (0.25) 0.35-0.6 (0.7) mm long, mostly early fugaceous, those on secondary axes narrowly to broadly triangular, 0.25-0.4 mm, apex acute to acuminate; pedicel terete, striate, long and slender, (0.7) 1.5-2.6 x 0.2-0.35 mm, longer and thickened in fruit, 3.5-5.5 (8) x 1.3-1.7 mm, often developing elliptic lenticels. Flowers all 4-merous, at anthesis 1.4-1.8 mm long (petals reflexed); calyx shallowly cupular, 0.35-0.4 (0.5) x (0.85) 1.2-1.4 (1.6) mm, exceeded by disk in both sexes, lobes discrete and separated by a sinuous sinus, negligible or very broadly depressed-deltate, 0-0.15 (0.25) mm, glabrous; petals yellow to cream, ovate, 1.75-1.85 (2.25) x 1-1.25 mm, apex broadly acute to obtuse, apiculum not strongly thickened, abaxially glabrous, adaxial surface and margin short-papillate; in staminate flowers stamens 1.15-1.25 and 1.25-1.5 mm long, filaments 0.9-1 and 1.25 mm long, anthers small, in dorsiventral view narrow-elliptic, in lateral profile laterally cuneiform, 0.2-0.25 mm long; disk broad, (0.2) 0.25-0.35 (0.4) x (0.25) 0.3-0.45 mm; pistillode only slightly exceeding disk, 0.25-0.3 x 0.35 mm overall, transverse-ellipsoid, with four vertical ridges, glabrous, provided with locules and reduced ovules, abruptly contracted into a 4-lobate stylode 0.1-0.15 mm long; in pistillate flowers staminodes level with the stigmas, subequal, 1.15 mm long, filaments 0.9 long, anthers in dorsiventral view oblong-obtuse, base lobulate, in lateral profile reniform, 0.25 mm long; disk 0.25-0.3 x 0.25-0.3 mm, weakly sulcate; pistil substipitate, 1 mm long, ovary ovoid, glabrous, contracted into a short thick style 0.1 mm

long; stigmal region 0.15 mm high, stigmas globose, oriented upward and outward. Immature fruits substipitate, globose, smooth (wrinkled when dry), disk somewhat conspicuous, mature fruits red, sessile, globose, 1.7-2.1 x 1.7-2.1 cm, disk inconspicuous, style and stigmas not persistent; pseudaril covering all of pyrene except a laterally elliptic area accounting for 1/5 of ventral surface corresponding to funicular scar; pyrene ca 2 x 2 cm (Rodrigues 7377), in dorsiventral view essentially orbicular, base truncate, in lateral view orbicular on dorsal side and ovate on ventral side, base obtuse, apex acutely acuminate and angled to ventral side due to subapical depression on ventral side, pyrene slightly obtusely ridged along both sides, ventral surface with a shallow central vertical sulca, site of funicle 5/6 distance to apex, funicular depression relatively shallow.

Distribution. Protium strumosum is apparently a disjunct between eastern and central Amazonia, with some outliers in the western part of the region. The disjunction may be explained by the presence of what has been called the "Aw belt." The term refers to a northwest-southeast swath of territory between the two regions with lower and more seasonal rainfall, where semi-deciduous forests occur. It can be seen in the climatological maps of Nimer (1977).

This type of distribution is not at all rare. Other eastern Amazonian species of Burseraceae recently found to occur near Manaus are Protium pallidum, P. altsonii, and P. guianense. Mori et al. (in press) noted that a number of plant groups have species which show disjunctions between French Guiana and central Amazonia.

These distributions tend to blur the boundaries between two floristic divisions of Amazonia which have been accepted as distinct since Ducke and Black's (1953) seminal work on Amazonian phytogeography. They might also be seen as discrediting the Manaus Pleistocene forest refuge proposed by Prance (1973) and other authors. Indeed, the loss of species from the list of Manaus endemics due to new distribution records has caused some botanists in recent years to question the validity of the Manaus refuge (i.e., Gentry, 1979). There is still a significant body of distribution data, however, which support the integrity of the floristic divisions and can be used to support the integrity of the Manaus refuge as well, or at least the integrity of Manaus as a center of endemism. New taxa are still being discovered which appear to be restricted to the Manaus region, including one new Burseraceae which is common in a limited area to the northeast of the city. It will be described in a forthcoming publication.

Protium strumosum normally flowers from August to October and fruits from August to December, but it has been collected in flower in Amazonas in March and in fruit in June, and in Pará it has been collected flowering in July.

Specimens examined: Brazil. Pará: Tapajós, Boa Vista, 24 Aug 1932 (m fl), Capucho 401 (F); Município de Oriximiná, rio Trombetas, Porto Trombetas, Mineração Rio-Norte, road of Mineração km 60, behind bauxite mine, 29 Aug 1980 (buds), Cid et al. 1876 (INPA, NY, MG); Breves, 7-30 Jul 1956 (m fl), Pires et al. 4895 (IAN); Santarém, km 70 on Palhão road, Ramal do Caetetu, 18 Sep 1969 (m fl), M. Silva & Souza 2644 (F, FLAS, GH,

K, MICH, MO, NY(2), U, US, WIS).

In Swart's (1942b) monograph of Protium, he cited Krukoff 8195 in the specimens examined for P. pedicellatum. Far from being a flowering collection of P. pedicellatum, however, Krukoff 8195 represented a new species not closely related to it, which I described as P. strumosum. They are easily separable by the latter's markedly swollen pulvini at the point of leaf insertion and at both ends of the petiolules, as well as by its soon-glabrescent branchlets initially provided with short, appressed, translucent, whitish hairs, while P. pedicellatum has a somewhat persistent, lanate, ferrugineous pubescence on its branchlets and its pulvini are only negligibly incrassate.

The type collection of P. pedicellatum, Krukoff 7226, is recognizable as belonging to section Sarcoprotium because of its leaflets which dry red and the ellipsoid fruits. In fact, P. pedicellatum is probably a taxonomic synonym of P. carnosum A. C. Smith.

P. strumosum resembles P. pallidum Cuatrec. and P. grandifolium Engl. because of its long petiolules; inflorescences long and fasciculate; leaflets long-acuminate; and fruits globose. Protium pallidum, though it shows these characters plus swollen pulvinuli and interpetiolar region, differs from P. strumosum by its white, 5-merous flowers; calyx deeper and markedly lobed; stamens relatively short; leaflets more coriaceous, with pallid abaxial surfaces indistinct tertiary veins; disk low and broad; stigmas horizontally obclavate; young fruits stipitate; mature fruits which are ridged when dry, and the markedly whitish cast of the abaxial leaflet surface when fresh or dry. Protium grandifolium differs by its

less conspicuously thickened pulvini and pulvinuli; flowers 5-merous; petals lanceolate and more involute; inflorescence axes pubescent; calyx base truncate, with acuminate to mucronulate lobes; and the ovary pubescent.

11. *Protium aracouchini* (Aublet) Marchand, *Adansonia* 8: 51. 1867-1868
(sphalm. as *Protium aracouchili*).

Icica aracouchini Aublet, *Hist. Pl. Gui. Fr.* 1: 343. 1775. Type. French

Guiana: Courourou River, without date (fr), Aublet s.n. (holotype:

BM). *Bursera aracouchili* (Aublet) Baill., *Hist. Pl.* 5: 296. 1874.

Tingulunga aracuchini (Aublet) Kuntze, *Rev. Gen. Pl.* 1: 108. 1891.

Icica heterophylla Willd., *Sp. Pl. ed. 4*, 2: 335. 1799, nom. illegit.

Elaphrium heterophyllum (Willd.) Spr. ex Dietr., *Syn. Pl.* 2: 1271. 1840.

Protium aracouchini (Aublet) Marchand var. *angustifolium* Swart, *Acta Bot.*

Néerl. 15: 45. 1966. Type. Surinam: south of Paramaribo, near

Lelydorp, 15 Aug 1953 (sterile), Lindeman 4504 (holotype: U).

Trees, reproductive height 4-12 (20) m; bark dark brown, thin, smooth; resin clear, drying white and often powdery; branchlets slender, 1-2 (2.6) mm diam, usually with scattered erect hairs to 0.05 mm long. Leaves 0-4-jugate, 10-26 cm long; petiole semi-terete, 1-5.4 cm x 0.7-1.2 mm, glabrous; interjuga 1.7-5 cm long; petiolules slender and semi-terete or shallowly 2-canaliculate, laterals 0.3-1.2 (2) cm long, terminal 1.2-4 (5.1) cm long, pulvinuli inconspicuous or more often conspicuous; leaflets chartaceous, laterals lanceolate to (broadly) elliptic or less often ovate, base subequal, acute to truncate, basal pair 5-11.2 x (1.3) 1.6-5.9 (7) cm, ultimate pair (4.6) 6-11.2 x 1.8-5 cm, terminal (broadly) elliptic to oblanceolate or obovate, base acute to obtuse, 6-15 x 2.7-6.2 cm, leaflet apex abruptly or gradually and narrowly long-acuminate, acumen

0.6-1.8 cm long, abaxial surface with midvein obtusely prominent, secondary veins prominent to prominulous, rest of veins prominulous to flat, adaxial surface with midvein prominulous but sunk in a groove, rest of veins prominulous, both surfaces glabrous. Inflorescences distributed along branchlets, long and slender, 4-11.5 (19) cm x 0.3-0.9 mm (pistillate ones usually not exceeding 6 cm length), to 0.3-0.9 times length of subtending leaf; secondary axes often well-developed, 0.5-6.5 (9) cm long, axes glabrous or rarely with scattered appressed hairs to 0.15 mm long; inflorescence bracts ovate with acute to rounded apex, glabrous or with scattered to dense appressed hairs to 0.15 mm long; those subtending inflorescences 0.4-0.8 mm long, those on primary axes 0.3-0.6 mm long, those on secondary axes 0.2-0.4 mm long; pedicel subcylindric or less often clavate, variable in length, in staminate flowers 0.6-2.7 x 0.15-0.4 mm, in pistillate flowers 0.3-1.7 (2.7) mm long, glabrous. Flowers all 4-merous, small, 1.8-2.7 mm long; calyx shallowly cupular, exceeded by the disk in both sexes, 0.3-0.7 x 1.2-1.7 mm, glabrous, lobes depressed-deltate to negligible (then discrete and separated by a flat sinus), 0-0.3 mm long; petals pale green to yellowish-green, ovate, membranous, 1.5-2.4 x 0.7-1.5 mm, margins short-papillate; staminate flowers with stamens greatly exceeding pistillode, usually the two series not level, 1-1.35 (1.6) and 1.15-1.6 (1.85) mm long; filaments slender, essentially terete, 0.8-1.1 (1.3) and 1-1.4 (1.55) mm long, usually markedly thickened and fleshy toward base; anthers basifixed, dimorphic, in dorsiventral view narrowly elliptic with acute apex before dehiscence, after dehiscence often broadly ovate with retuse apex, base lobulate,

antepetalous ones in lateral profile obliquely and short obtuse-oblong with truncate base and retuse apex, antesepalous ones laterally broadly elliptic with a central constriction (so apex retuse), 0.15-0.3 mm long (but antepetalous ones 0.05 mm longer on most flowers); disk 0.15-0.35 x 0.2-0.4 mm, glabrous; pistillode 0.3-0.45 x 0.35-0.5 mm overall, only slightly exceeding the disk, (deeply) depressed-ovoid, provided with locules and reduced ovules, glabrous or with sparse to dense appressed hairs to 0.15 mm long, abruptly contracted to a short 4-lobulate stylode 0.1-0.25 x 0.1-0.2 mm; in pistillate flowers two series of staminodes of subequal length, 0.75-1.25 mm long, usually reaching base of stigmas, filaments strap-shaped and widened at base, 0.6-0.9 and 0.55-0.85 mm long, anthers dimorphic, antepetalous ones in dorsiventral view usually obtuse-oblong with lobulate base and retuse apex, 0.2-0.35 mm long, antesepalous ones in dorsiventral view usually broadly ovate with lobulate base and retuse to obtuse apex, usually 0.05 mm shorter, 0.15-0.3 mm long, all obtuse-oblong in lateral profile; disk 0.15-0.35 x 0.15-0.4 mm; pistil 0.8-1.4 x (0.45) 0.55-0.8 mm overall, ovary (broadly) ovoid, glabrous or with scattered appressed hairs to 0.15 mm long, gradually contracted to a short, thick style 0.15-0.4 x 0.2-0.4 mm, stigmatal region 0.1-0.15 mm high, stigmas compressed-globose, oriented upward and outward. In fruit pedicel 1-2.5 x 0.5-1 (1.4) mm; maturing fruit red above and green below, obliquely narrowly ovoid, gibbous and ventricose, 1-1.6 x 0.6-1 cm (to 1.4 cm diam when more than one pyrene), sessile, apex acute or less often slightly acuminate, glabrous, surface smooth, drying wrinkled; pseudaril pulpy; pyrene cartilaginous, glabrous or with sparse erect fibers to 0.2

mm long, in dorsiventral view ovate with truncate base and slightly acuminate apex, in lateral profile essentially lanceolate to elliptic, apex sometimes slightly recurved (M. G. Silva 4247), 0.7-1 x 0.5-0.7 cm, site of funiculus 3/4 distance to apex, funicular scar essentially lunate, covering 1/5 ventral surface; testa with some irregular thickenings but not infolded with cotyledons, cotyledons entire and plano-convex.

Distribution. Widespread in Amazonia and the Guianas, extending to Eastern Brazil and to Antioquia in Colombia. Protium aracouchini is a small understory tree of primary terra firme forests. In eastern Amazonia and the Guianas it flowers from May to August and fruits from September to February.

Representative specimens examined. Brazil. Amapá: Munic. Macapá, Perimetral Norte (BR-210), 122 km NW of Porto Grande, 1°21'N, 53°15' W, 1 Jan 1985 (fr), Daly et al. 4030 (HAMAB, NY). Maranhão: Munic. Monção, basin of Rio Turiaçu, Ka'apor Indian Reserve, 4 km NW of settlement of Urutawy, 2 Feb 1985 (sterile), Balée & Ribeiro 288 (NY), 4 Feb 1985 (sterile), Balée & Ribeiro 361 (NY), 1 Jun 1985 (m fl), Balée 969 (NY), 2 Jun 1985 (f fl), Balée 1002 (NY); Colonia Betel, right bank of Rio Alto Turiaçu, approx 3°00'S, 45°55'W, 20 May 1979 (MG), Jangoux & Bahia 764 (MG). Pará: Alto Tapajós, Rio Cururú, Missão Cururú, 8 Feb 1974 (fr), W. Anderson 10642 (NY); Fazenda Santa Rosa, behind Itinga do Pará, W of Belém-Brasília Highway, approx. 4°20'S, 47°45'W, 26 Oct 1980 (fr), Daly et al. 768 (MG, NY); Belém, Mocambo Reserve, 10-17 Nov 1984 (fr), Daly et al. 3757 (IAN, NY); Anapú region, Rio Pracupi, Portel, 9 Jul 1956 (m fl), Frões 32842 (P, U, US); Belém-Brasília Highway, km 92, 28 Sep 1959 (f fl)

and young fr), M. Kuhlmann & Jimbo 311 (IAN, NY); Paragominas, Itinga do Parã, Fazenda Caborê, 30 Nov 1979 (fr), Maciel et al. 378 (MG, NY); Rio Jarí, Serra de Monte Dourado, 14 Nov 1969 (fr), Oliveira 3531 (IAN); Breves, 7-30 Jul 1956 (buds), Pires et al. 6006 (IAN); Mata da Cia. Pirelli, Fazenda Uriboça, Jul 1958 (m fl), Pires 7039 (IAN, U); Municip. Almeirim, Monte Dourado, road to Agua Azul, 11 Nov 1978 (fr), Santos 282 (MG, NY).

French Guiana: Saül, lake 1 km from Pic Matecho, 20 Jan 1980, elev. 350 m, 20 Jan 1980 (fr), de Granville 3318 (CAY, NY), Trail to La Fumée Mountain, 19 Aug 1971 (m fl), Oldeman B-4037 (CAY, NY).

Guyana: 35 mi. on Bartica-Potaro Road, 2 Mar 1948 (buds and fr), For. Dep. Br. Gui. Rec. No. 5608 (NY, U, US); by Indian Fields behind Mission, 23 Sep 1952 (m fl), For. Dep. Br. Gui. Rec. No. 7190 (NY); Marudi Mts., on top of Mazoa, 10 Nov 1982 (fr), Stoffers et al. 253 (NY).

Surinam: Sectie 0, 1 Sep 1917 (m fl), BW 3388 (NY, WIS), 5 Sep 1919 (m fl), BW 4394 (W); vicinity of Moengo, Cottica River, 26 Dec 1954 (fr), Cowan 38990 (NY); 8 km ESE of Brownsweag, 20 Jan 1965 (fr), van Donselaar 2004 (U); lower slopes of Frederik Top, 2 km SE of Julian Top, 3°36'-3°41'N, 56°30'-56°34'W, 7 Aug 1963 (fr), Irwin et al. 54576 (NY); Matakka River, Snake Creek, 4 km W of base camp, 13 May 1965 (buds), LBB 10770 (U); Fallawatra, 7 Jan 1971 (sterile), LBB 14418 (U); area of Kabalebo Dam project, 4°-5°N, 57°30'-58°W, 5 Sep 1980 (f fl), Lindeman et al. 158 (U), 9 Sep 1980 (m fl), Lindeman et al. 290 (NY, US); Jodensavanne-Mapanekreek area (Suriname R.), 20 Mar 1953 (fr), Lindeman 3560 (GH).

Protium aracouchini belongs to a group of closely-related species which includes P. elegans Engl., P. leptostachyum Cuatrec., and P. calanense Cuatrec. A taxonomic synonym for the latter species is P. divaricatum Engl. var. intermedium Swart. All of these species resemble P. aracouchini in their inflorescence structure and flower and fruit morphology.

Protium elegans (i.e., Prance et al. 12128, Boom 5170), known from only a few collections from southwestern Amazonia and the upper Rio Negro region. It differs from P. aracouchini by its canaliculate petiole; leaves and leaflets smaller; leaflet base often decurrent (petiolules appearing winged); interjuga slightly winged; leaflet acumen sparsely serrulate; petals smaller and with long-papillate margins; stamens shorter; disk (in staminate flowers) narrower; pistillode smaller; and fruits only slightly oblique and apparently not bicolored.

Protium leptostachyum, even more poorly known than P. elegans, appears to be distributed in the upper Rio Negro region, the upper Rio Orinoco in Venezuela, and Antioquia in Colombia. It is more difficult to separate from P. aracouchini, and appears to differ primarily by its shorter inflorescence (seldom exceeding the petiole); leaflets with the two surfaces discolorous, the adaxial side often glossy; petal margins long-papillate; staminodes exceeding the pistil (Schultes 14090 (type collection)); stigmas lateral and elliptic; and fruit often glossy and apparently not bicolored.

Protium aracouchini bears a strong superficial resemblance to P. plagiocarpium, but the latter is easily distinguished by its broadly and

obtusely acuminate leaflets which dry reddish; inflorescence bracts lanceolate; pedicel clavate; petals fleshy and slightly cucullate, with clawed base and conspicuous apiculum; filaments markedly fleshy; anthers with latero-introrse (not lateral) dehiscence; disk pubescent, and narrower in pistillate flowers; and fruit red only, stipitate, with lobate base and acuminate apex.

Protium aracouchini var. angustifolium, described from a sterile collectin, differs only negligibly from the type collection of the species. However, there is at least one legitimate infraspecific taxon within P. aracouchini, but it is so similar to P. calanense that it might prove to be a taxonomic synonym of the latter species. Until further material of P. calanense can be studied, P. aracouchini will be left as a single polymorphic species. Table --- provides an indication of the characters which separate the typical "variety" from that taxon which should eventually be given some rank within the species. Ironically, the typical "variety" is rather poorly represented in the herbaria. The two entities appear to be sympatric in Surinam, and in Brazil near Belém, near Manaus, and in Bahia.

Table XVII

Characters separating Protium aracouchini from its "variety"

character	typical "variety"	"var. nov." (= <i>P. calanense</i> ?)
branchlet diameter	1-1.1 mm	1.3-2 (2.6) mm
no. of interjuga	(0) 1-3 (4)	0-1 (2)
secondary axes of inflorescence	0.5-1 (3) cm long	0.5-6.5 (9) cm long
pedicel (stam.) (pist.)	0.6-1.4 x 0.25-0.4 mm 0.3-1.3 x "	(0.7) 1.3-2.7 x 0.15-0.25 mm 0.7-1.7 (2.7) x "
calyx (stam.) (pist.)	0.3-0.4 mm long "	0.3-0.4 mm long 0.5-0.7 mm long
petals	1.5-1.8 x 0.7-1 mm	1.8-2.4 x 0.8-1.5 mm
staminodes	0.8-1 mm long	(0.75) 1-1.25 mm long
anthers (stam.) (pist.)	0.15-0.2 and 0.15 mm 0.2 and 0.15 mm	0.25-0.3 and 0.2-0.3 mm long 0.25-0.35 and 0.2-0.3 mm long
style	0.15-0.25 x 0.2-0.25 mm	0.2-0.4 x 0.25-0.4 mm

12. *Protium divaricatum* Engler. Type. Brazil. Amazonas: On shaded streambank, Ega (Tefé), Oct 1831 (m fl), Poeppig 2703 (lectotype (designated by Swart, 1942b): LE; isoelectotypes: F, NY, W).

Tingulunga divaricata (Engl.) Kuntze, Rev. Gen. Pl. 1: 108. 108.

Small tree or treelet, reproductive height 3-15 m, to 20 cm diam DBH; at least occasionally with simple low to high plank buttresses; trunk angular, bark smooth, thin, with shallow fissures, lenticellate, hooped, brown to reddish-brown; resin clear, oxidizing white after five minutes (Mori et al. 15175); branchlets slender, striate, usually with elliptic raised lenticels 0.4-0.8 mm long (white when dry), (1.8) 2-3 (3.3) mm diam, with sparse to dense appressed hairs 0.05-0.2 (0.25) mm long, in fruit glabrescent but for apex. Leaves 0-3-jugate, (10) 15-36.5 cm long; petioles semiterete, seldom slightly canaliculate, slightly acutely winged, long and slender, (2.5) 4.5-9.6 (13.4) cm x 1.3-2 (2.3) mm diam, interjuga (when present) terete, striate, (2.3) 3.2-4.9 (5.5) cm long; petiolules shallowly 2-canaliculate, long and slender, laterals (0.3) 0.7-1.5 (2.2) cm long, terminal (1.1) 1.5-5.1 (6) cm long, petiolule relatively conspicuous; lateral leaflets elliptic to broadly elliptic, seldom broadly oblanceolate, basal pair (5.3) 9-13.5 (16.4) x (2.1) 4-6.1 (8.2) cm, ultimate pair (when present) (5.5) 7.6-11 (15) x (2.1) 3.3-6.1 (7.3) cm, terminal slightly obovate to broadly elliptic, large, (6.1) 9.5-16 (23) x (2.4) 3.6-7.6 (8.9) cm, leaflet base acute to obtuse, apex abruptly acuminate, varying in length, (0.3) 0.6-1.4 (1.8) mm long.

Inflorescences subterminal, solitary or rarely apparently fasciculate, long, very slender, striate, with compressed axes, (4) 10-38 (46) cm long x (0.6) 0.8-1.5 (1.75) mm (in fruit 10.5-34 cm long x 1.1-1.7 (2.3) mm), to 0.5-1.3 times length of subtending leaf, frequently but not consistently divaricately branched, secondary axes generally well developed, 1-15 cm long, axes with scattered, appressed hairs 0.05-0.2 (0.25) mm long, otherwise subglabrous; inflorescence bracts broadly ovate to broadly lanceolate, usually semi-clasping, acute to acuminate, margin papillate, bracts on panicles 0.5-0.8 (0.9) mm long, bracts on racemes large, (0.2) 0.3-0.7 (0.8) mm long, hairs as on inflorescence, sparse to scattered to glabrous; pedicel short and slightly clavate (ssp. divaricatum) to rather long and terete or slightly compressed, in flower (0.2) 0.5-3 (5.2) x 0.25-0.4 mm, hairs usually dense at base, otherwise scattered. Flowers all 4-merous, (1.7) 1.9-2.5 (2.7) mm long when dry; calyx deeply cupular, usually exceeding disk, (0.6) 0.9-1 (1.3) x (1.5) 1.8-2 (2.2) mm, base obtuse, lobes rounded-deltate, 0.3-0.5 (0.6) mm long, apex acute; petals thin to somewhat fleshy, not carinate, lanceolate to ovate, (1.65) 2-2.5 x (0.8) 1.2-1.6 mm long, base slightly or not at all narrowed, apex acute, apiculum inconspicuous, strongly inflexed, only slightly reflexed at anthesis, abaxially glabrous or rarely with scattered minute sharp erect hairs (ssp. fumarium with dense appressed hairs 0.05-0.15 mm long), margin short-papillate; stamens 4 (ssp. divaricatum) or 8, inflexed; staminate flowers with stamens greatly exceeding pistillode, 1.25-1.45 (1.55) mm long when in one series, when two series present either antesepalous stamens longer (ssp. krukoffii, stamens

1.4-1.7 and 1.6-1.8 mm long) or antepetalous stamens sometimes equal to or longer than antesealous ones (ssp. funarium), filaments slender, antesealous filaments usually with a dorsal ridge at base where the petal bases meet, anthers dorsifixed (sometimes appearing basifixed), in dorsiventral view narrowly lanceolate, acute, in lateral view asymmetrically broadly oblong to transversely ovate, anterior sporangia shorter than posterior, 0.25-0.35 mm long; disk tall, broadened at apex, 0.2-0.35 (0.5) x (0.1) 0.2-0.25 (0.5) mm; pistillode only slightly exceeding disk, (0.25) 0.35-0.6 x (0.2) 0.3-0.6 mm overall, broadly ovoid to depressed-ovoid, with reduced locules and ovules, abruptly contracted into a narrow sulcate or lobulate stylode 0.1-0.2 x 0.1 mm, pistillode with dense ascending hairs to 0.2 mm long; pistillate flowers with staminodes almost reaching stigmas, 1.1-1.15 mm long, filaments 0.8-0.85 mm long, anthers 0.3-0.35 mm long, in dorsiventral view ovate, in lateral view asymmetric, narrow-oblong; disk 0.25-0.35 x 0.25-0.35 mm; pistil 1.4-1.5 x 0.55-0.65 mm, ovary ovoid, with dense ascending hairs 0.1-0.2 mm long, gradually contracted into a long relatively thick style 0.55 x 0.35 mm, not sulcate, stigmas sessile, compressed-globose, oriented upward and outward, 0.15 mm high. In fruit pedicel becoming markedly thickened, while inflorescence axis proximal to it does not, clavate (ssp. divaricatum) or terete, (1.5) 2.5-5 (6) x 1.4-2 (2.4) mm, immature fruit stipitate, falcately semi-ellipsoid (ssp. funarium) or ovoid and broadly obliquely acuminate, the apex rounded, mature fruit reportedly green (Bamps 5436) or brown (Mori & Pipoly 15590), ovoid and broadly obliquely acuminate, acumen rounded to obtuse, (2.1) 2.5-3 (3.3) x (1.4) 1.6-2.1 (2.5) cm (to 3 cm

diam when more than 1 pyrene), stipitate (stipe (3) 4-5 (6) mm long, not much thicker than pedicel), surface glabrous, smooth, drying wrinkled, mesocarp thin, fleshy; pseudaril thin and fleshy; pyrene thin, brittle when dry, slightly coriaceous, in dorsiventral view depressed ovate to ovate to obovate (ssp. krukoffii, Arostegui 31), 1.5-2.8 x 1.3-1.6 cm; testa thicker than pyrene, smooth outside, with irregular thickenings and some intrusions into cotyledons, cotyledons entire, plano-convex.

Distribution. Widespread but infrequently collected in Amazonian Brazil-- Amazonas, Pará, Rondônia, Mato Grosso-- also in French Guiana and Bolívar in Venezuela. The maximum elevation reached is 800-900 m in Venezuela (Liesner 19459). Understory tree in terra firme forest, or often on streambanks (Cid et al. 22, Pires et al. 4943, Poeppig 2703 (type), Rosa & Santos 2070). Flowering and fruiting sporadically, but most frequently flowering August to October and fruiting September to December.

Because of its stipitate and acuminate fruits, fruiting specimens of P. divaricatum might be confused with P. krukoffii, P. plagiocarpium, P. decandrum, and P. nodulosum Swart. Protium krukoffii has bicanaliculate petiolules; usually smaller leaflets which are lanceolate and (2) 3-4-jugate; shorter inflorescences; pedicels not markedly swollen; the style and stigma notably persistent; and fruits more sharply acuminate. Protium plagiocarpium has more slender branchlets; smaller leaflets with pallid venation when dry; and smaller fruits which are trigonous, with the pedicel shorter and not markedly swollen. Protium decandrum has a usually short petiole which is canaliculate and usually acutely winged; lanceolate and gradually-acuminate leaflets, more robust inflorescence axes; pedicel

not markedly swollen; and short-stipitate fruits which are shorter and sharper-acuminate. Protium nodulosum has fruits which are larger, lenticellate, and sharply acuminate. The pedicel of this species is clavate, whereas in P. divaricatum the pedicel in fruit is markedly thicker than the inflorescence axis proximal to it. P. nodulosum also has very robust branchlets and petioles, more coriaceous leaflets, and abaxial leaflet surface with prominent veins and acutely prominent midvein.

Swart recognized three varieties of Protium divaricatum, but var. trijugum is a taxonomic synonym of P. polybotryum (Turcz.) Engl. var. polybotryum, and var. intermedium is closely related to P. aracouchini, and may be a taxonomic synonym of P. calanense Cuatrec.; var. krukoffii is accepted here as a subspecies. A further subspecies (fumarium) was described recently, so there are three subspecies accepted here and distinguished in the key below.

Key to the subspecies of Protium divaricatum

- 1 Leaves 0-1-jugate; pedicel in flower 0.2-1.1 (1.5) mm long; calyx lobes (0.3) 0.4-0.5 (0.6) mm long; petals 1.65-2 x 0.8-1.25 mm; stamens 5; pedicel in fruit markedly clavate, 1.5-2.5 x 2-2.4 mm; fruit 2.1-2.5 cm long ssp. divaricatum
- 1 Leaves 0-3-jugate; pedicel in flower 1.5-5.2 mm long; calyx lobes 0.25-0.4 mm long; petals 2.3-2.5 x 1.2-1.5 mm; stamens 10; pedicel in fruit essentially terete, (1.5) 3-6 x 1.4-2 mm long; fruit 3-3.3 cm long 2
- 2 Lateral petiolule 0.3-0.8 (1) cm long, terminal petiolule 1.1-3.5 (4.3) cm long; inflorescence bracts semi-clasping; pedicel in flower 1.5-2.2 mm long; calyx 1.1-1.3 x 2.1-2.5 mm overall, calyx and corolla abaxially with sparse to dense appressed hairs; pyrene narrowly ovate in dorsiventral view, funicular scar at apex of long acumen (Mori & Pipoly 15509) ssp. fumarium
- 2 Lateral petiolule 0.8-1.4 cm long, terminal petiolule (1.5) 3.5-4.3 (6) cm long; inflorescence bracts not semi-clasping; pedicel in flower (2) 3-5.2 mm long; calyx 0.7-0.9 x 1.6-2.1 mm overall, calyx and corolla glabrous; pyrene obovate in dorsiventral view, funicular scar 4/5 of distance to apex ssp. krukoffii

12a. *Protium divaricatum* Engl. ssp. *divaricatum*.

Leaves 0-1-jugate; lateral petiolule 0.7-1.6 cm long; terminal petiolule (1.6) 3.4-5.1 cm long; leaflets chartaceous, occasionally elliptic, terminal leaflet (9.5) 11-19 x (3.3) 4.5-8.6 (8.9) cm; inflorescence axes with scattered appressed hairs 0.05-0.15 mm long (sparse to dense at branching points, on bracts, and at base of pedicel); inflorescence bracts semi-clasping, bracts on panicles 0.5-0.9 mm long, bracts on racemes 0.3-0.8 mm long; pedicel in flower 0.2-1.1 (1.5) mm long; calyx (0.6) 0.9-1.3 x (1.5) 1.8-2 mm overall, calyx lobes (0.3) 0.4-0.5 (0.6) mm long, petals 1.65-2 x 0.8-1.25 mm; stamens 5; pedicel in fruit markedly clavate; 1.5-2.5 x 2-2.4 mm; fruit 2.1-2.5 x 1.5-2.1 cm (to 2-3 cm diam when more than 1 pyrene); pyrene ca 1.5 x 1.5 cm, broadly ovate to depressed-ovate in dorsiventral view, with truncate base and broadly short-acuminate apex, in lateral profile markedly obliquely ovate.

Distribution. Widespread in Amazonia south of the Rio Mara  n/Amazonas, with one collection known from the Rio Trombetas (Revilla et al. 7041) and one from eastern Bol  var in Venezuela (Liesner 19459). The typical subspecies flowers in August to October (January) and fruits November to February.

Specimens examined. BRAZIL. Par  : S  o Jorge; Munic  pio de Faro, 11 Nov 1950 (young fr), Black & Ledoux 50-10677 (IAN); Vila Nova, Rio Tapaj  s, just below Cachoeira Chacor  o, 12 km below Cachoeira Capoeira, 25 Dec 1951 (young fr), Pires 3629 (IAN); Munic  pio de Breves, near Igarap   Arapij  , 7-30 Jul 1956 (buds), Pires et al. 4943 (IAN); Rio Trombetas, bauxite

deposit of Alcoa Mineração, Acampamento 22, 8 Oct 1982 (m fl), Revilla et al. 7041 (NY); Município de Itaituba, km 60 Itaituba-Jacareacanga road, Parque Nacional do Tapajós, Reserva Biológica, 16 Nov 1978 (young fr), M. G. Silva & Rosário 3776 (MG, NY, US).

Protium divaricatum ssp. divaricatum is readily distinguished from the other two subspecies most notably by its isostemonous flowers, being the only taxon in Protium to show this condition. In addition to the characters used in the key, it also differs by its unifoliate or at most 1-jugate leaves; calyx lobes longer; very short pedicel which is clavate in fruit; fruit smaller; and pyrene broadly ovate or depressed-ovate in dorsiventral view (not narrowly ovate or obovate).

12b. Protium divaricatum Engler ssp. fumarium Daly (submitted for publication in Brittonia. Type. French Guiana. Saül, 3°37'N, 53°12'W, La Fumée Mountain, La Fumée Trail Nord-Est, ca 350 m elev., 17 May 1986 (m fl), S. Mori & T. Pennington 18034 (holotype, NY; isotypes: CAY, HAMAB, MG, MO, P, US).

Leaves (0) 2-3-jugate; lateral petiolule 0.3-0.8 (1) cm long, terminal petiolule (1.1) 1.5-3.5 (4.3) cm long; leaflets often coriaceous, terminal leaflet (6.1) 8.2-10.3 (13.3) x (2.4) 3.6-5.8 (6.8) cm; inflorescence bracts semi-clasping, those on primary axes 0.6-1 mm long, those on secondary axes 0.6-0.7 mm long; pedicel in flower 1.5-2.2 mm long; calyx 0.9-1.3 x 1.9-2.5 mm overall, calyx and corolla with sparse appressed hairs to 0.15 mm long (sometimes dense on petals); petals 2.3-2.5 x

1.3-1.6 mm; stamens 8, antepetalous stamens sometimes equalling or longer than antesepalous ones, 1.4-1.75 and 1.4-1.6 mm long, respectively; young fruit markedly falcately semi-ellipsoid, mature fruit 3-3.3 x 1.4-1.7 cm; pyrene ca 2 x 1.3 cm, narrowly ovate in dorsiventral view, funicular scar at apex of long acumen (Mori & Pipoly 15590).

Distribution. Known only from La Fumée Mountain, Saül, French Guiana. Based on the limited material available, this subspecies flowers approximately in May and fruits from September to April.

Specimens examined. French Guiana: Saül, 3°37'N, 53°12'W, Mont La Fumée, 9 Sep 1982 (young fr), Boom & Mori 1623 (NY), 16 Sep 1982 (sterile), Boom & Mori 1715 (NY), 17 Sep 1982 (sterile), Boom & Mori 1724 (NY), 20 Sep 1982 (young fr), Boom & Mori 1741 (NY), 20 Sep 1982 (sterile), Boom & Mori 1749 (NY), 1 Sep 1982 (young fr) Mori & Boom 14818 (NY), 3 Oct 1982 (young fr), Mori et al. 15052 (NY), 6 Nov 1982 (young fr), Mori et al. 15175 (NY), 12 Apr 1983 (fr), Mori & Pipoly 15590 (NY), Antenne Est, ca 300 m elev., 21 May 1986 (m buds), Mori & Pennington 18081 (NY).

In addition to the characters used in the key, ssp. fumarium is distinguished from the other subspecies by the greater maximum number of juga; usually shorter petiolules; leaflets usually smaller; antepetalous stamens equalling or longer than the antesepalous stamens; young fruits falcately semi-ellipsoid; mature fruits longer-acuminate; pyrene narrowly ovate in dorsiventral view; and pyrene with funicular scar at its apex.

12c. *Protium divaricatum* Engler ssp. *krukoffii* (Swart) Daly (submitted for publication in Brittonia). Type. Brazil. Amazonas: basin of Rio Jurua, near mouth of Rio Embira, (tributary of Rio Tarauaca), 7°30'S, 70°15'W, 6 Jun 1933 (m fl), Krukoff 4703 (holotype: U; isotypes: F, GH, M, MO, NY).

Protium divaricatum Engler var. *krukoffii* Swart, Rec. Trav. Bot.

Néerl. 39: 198. 1942.

Leaves 0-2-jugate; lateral petiolule 0.8-1.4 cm long, terminal petiolule (1.5) 3.5-4.3 (6) cm long; leaflets chartaceous, drying pale green, terminal leaflet 10.5-16 x 5-7.6 cm; inflorescence axes glabrous except for occasional scattered hairs at branching points, on bracts, and at base of pedicels; inflorescence bracts small, not semi-clasping, those on primary axes 0.3-0.5, those on secondary axes 0.2-0.4; pedicel in flower (2) 3-5.2 mm long; calyx 0.7-0.9 x 1.6-2.1 mm overall, calyx and corolla glabrous; petals 2.3-2.5 x 1.2-1.5 mm; stamens 10, antesealous stamens exceeding antepetalous stamens, 1.4-1.7 and 1.6-1.8 mm long, respectively; fruit ca 3 x 2.5 cm; pyrene obovate in dorsiventral view, base acute, apex obtuse, funicular scar 4/5 of distance to apex (Arostegui 31), set in a deep subapical depression.

Distribution. All six collections known to date are from a fairly limited portion of the western Amazon: the Rio Envira, on the upper reaches of the Rio Juruá basin, and upstream from Iquitos in the lower Rio Ucayali basin and near the Rio Marañon below its confluence with the

Ucayali. Only further collections will determine whether ssp. krukoffii is sympatric with ssp. divaricatum. This subspecies flowers and fruits from June to February.

Specimens examined. Peru. Loreto, Dtto. Maynas: Rfo Tahuayo, Quebrada Valentín, 13 Feb 1962 (fr), Arostegui V. 31 (NY); Quebrada Tahuayo above Tamshiyacu, 27 Aug 1972 (m fl), Croat 19787 (US); Mishana, Nanay, halfway between Iquitos and Sta. Maria de Nanay, 3°50'S, 73°30'W, 21 July 1980 (fr), Gentry et al. 28836 (NY); Nauta, 4°32'S, 73°35'W, 3 Jun 1984 (fr), Vásquez & Jaramillo 5110 (NY); Puerto Almendras (Rfo Nanay), 73°21'W, 3°48'S, 1 Feb 1985 (fr), Vásquez et al. 6217 (NY), 1 Feb 1985 (buds), R. Vásquez et al. 6219 (NY).

In addition to the characters used in the key, ssp. krukoffii can be distinguished from the other two subspecies by its subglabrous inflorescence. Although there appears to be no phenological displacement between this subspecies and ssp. divaricatum, and although they occur in the same region of Peru, the morphological differences are compelling enough to consider them to be separate subspecies.

Local names and uses. The resin is considered "medicinal" (Arostegui 31)

Although the three subspecies of Protium divaricatum are easily separated, they are very close to one another in almost all qualitative characters: the slender branchlets, petioles, and petiolules; usually broadly elliptic leaflets which are abruptly obtuse-acuminate; long and divaricately-branched inflorescence; 4-merous flowers which are very similar except for stamen number and length; pedicel which thickens in

fruit while the inflorescence axis immediately proximal to it does not; fleshy pseudaril which is thicker than the almost chartaceous pyrene; testa with irregular thickenings but not infolded with the cotyledons; and entire, plano-convex cotyledons.

Protium divaricatum is a rather rare and poorly collected species despite its broad distribution. The cotyledons are consistently entire and plano-convex, a character that blurs the distinction between Protium and Tetragastris (see section on generic limits).

The typical subspecies is notable for being consistently isostemonous-- the only taxon in Protium known to show that character (other than the isostemonous pistillate flowers of P. robustum). The significance of that character should not be exaggerated to the point that the typical subspecies is regarded as not being conspecific with the other two. It should be noted that in the genus Crepidospermum, which also belongs to the tribe Protieae, pistillate individuals of C. goudotianum may be either isostemonous or diplostemonous (Daly, 1987). In the genus Protium itself, isostemonous flowers are encountered occasionally in otherwise diplostemonous inflorescences. In the genus Canarium (tribe Canarieae), C. luzonicum A. Gray and C. caudatum King have consistently isostemonous staminate flowers, as are all flowers of C. acutifolium Merr. (Lam, 1932a).

The fact that the phenomenon occurs sporadically in the family indicates that isostemony may result from a rather simple alteration in the genome, such as a point mutation or a deletion.

13. *Protium opacum* Swart. Type. Brazil. Amazonas: Basin of Rio Juruá, near mouth of Rio Embira (tributary of Rio Tarauaca), 7°30' S, 70°48'15" W, 14 Jun 1933 (m fl), Krukoff 4816 (holotype: U; isotypes, F, G, GH, M, MICH, MO, NY, US).

Trees, reproductive height 8-30 m; branchlets moderately robust, (1.9) 3.5-4.8 (5.7) mm diam, not thickened in fruit, with dense (less often sparse) appressed hairs 0.05-0.2 (0.5) mm long; Leaves (1) 2-5-jugate, large, (17) 25.5-45.5 (58.5) cm long; petiole longer than interjuga, broadly and usually shallowly canaliculate, usually slightly acutely winged, (2.6) 5-12 (17.8) cm x (1.6) 2.3-3.6 (4.4) mm, with dense appressed hairs 0.1-0.2 (0.3) mm long, also with scattered (rarely sparse or dense) fine acute erect hairs to 0.05 (0.1) mm long, rarely also with scattered to dense long suberect hairs 0.2-0.4 (0.5) mm long; interjuga (2) 2.6-5.1 (7.6) cm long; petiolules relatively long and stout, shallowly 1- or 2-canaliculate, laterals (0.5) 0.6-1.4 (1.8) cm long, terminal shorter than interjuga, (1.5) 2-3.8 (4.7) cm long, with hairs as on petiole and rachis, pulvinuli usually conspicuous; leaflets large, usually coriaceous, laterals oblong to (broadly) elliptic, rarely narrowly elliptic, base usually oblique, proximal side acute to obtuse, distal side obtuse to truncate, sometimes base abruptly truncate (ssp. exaggeratum), basal pair (7) 9.2-18.5 (23.7) x (3.2) 3.9-6.5 (7.2) cm, ultimate pair (9) 12.6-19 (24.7) x 3.6-6.9 (9.4) cm, terminal broadly elliptic to elliptic, sometimes broadly oblanceolate, (9.2) 13.2-18.6 (26.1) x (3.8) 4.4-8 (10.1) cm, base acute to obtuse, leaflet apex abruptly or less often

gradually acuminate, acumen usually long and narrow, (0.2) 0.5-1.6 (2.3) cm long, abaxial surface with midvein and secondary veins obtusely prominent, rest of veins prominulous, midvein and sometimes secondary veins with dense (very rarely scattered or absent) flexuous hairs 0.2-0.4 (0.7) mm long, also with sparse to scattered appressed hairs to 0.2 (0.3) mm long, rest of blade with scattered short thick acute appressed hairs to 0.1 (0.2) mm long, adaxial surface with midvein narrowly obtusely prominent but partially sunk in a groove, secondary veins prominulous, rest of veins inconspicuous, midvein with scattered to sparse fine erect hairs to 0.5 (0.2) mm long (sometimes also on secondary veins), rarely with sparse suberect hairs 0.05-0.2 (0.25) mm long, rest of blade glabrous. Inflorescences congested near apex, usually long and slender, (3) 4.8-27 cm x (0.7) 1-2.7 (3.3) mm (in fruit (1.5) 2.2-2.8 (3.7) mm diam), secondary axes well-developed, 0.4-11.5 (16) cm long, axes with dense to sparse (rarely scattered) ascending to appressed hairs to 0.3 (0.4) mm long, also with scattered to sparse fine erect hairs to 0.1 mm long, inflorescence bracts usually large, semi-clasping, coriaceous to chartaceous, (broadly) ovate, those subtending inflorescences 2-2.7 mm long, those on primary axes 0.6-1.7 (2.8) mm long, those on secondary axes 0.4-1.6 (2) mm long; pedicel subcylindric, relatively stout, (0.3) 0.5-1.5 (2.2) x (0.3-0.5 (0.6) mm; in pistillate flowers usually slightly longer than staminate flowers, with hairs as on axes but usually lacking fine erect hairs. Flowers 4- or 5-merous, 2-2.5 (3.2) mm long when dry; calyx deeply cupular in both sexes, (1) 1.4-1.9 (2.4) x (2) 2.3-2.9 (3.2) mm overall, with dense or less often sparse appressed to ascending hairs

0.1-0.25 (0.3) mm long, lobes exceeding disk in both sexes, coriaceous to fleshy, (rounded) deltate to broadly so, (0.2) 0.5-1.3 (1.6) mm long, usually slightly acuminate, apex often with a fleshy apiculum (ssp. rabelianum); petals greenish to pale yellow or yellowish-white, ovate and fleshy to less often lanceolate and membranous (ssp. exaggeratum), (2.2) 2.6-3 (3.8) x 1.2-1.7 (2) mm, free or irregularly fused to as much as 1/2 their length, usually imbricate along some of the middle portion of their length but not at base or apex, slightly carinate, apex acute, apiculum usually conspicuous, abaxially with dense (rarely sparse in ssp. opacum) appressed hairs 0.1-0.25 (0.3) mm long, adaxially short-papillate, often also with scattered to sparse or rarely dense erect to ascending hairs 0.1-0.2 mm long distributed along five vertical lines (sspp. rabelianum and exaggeratum), margin long-papillate; in staminate flowers stamens relatively long, (1.35) 1.6-1.95 (2.25) and (1.45) 1.7-2.05 (2.35) mm long, greatly exceeding the pistillode, filaments usually fleshy, terete to less often compressed, (0.9) 1.05-1.4 (1.6) and (0.95) 1.15-1.5 (1.7) mm long, anthers in dorsiventral view narrowly obtuse-oblong to narrowly lanceolate (rarely lanceolate), base lobulate, apex obtuse to slightly retuse, in lateral profile (broadly) obtusely oblong, the anterior sporangia shorter than the posterior, 0.45-0.7 mm long; disk moderately deep and broad, 0.25-0.4 (0.5) x (0.15) 0.3-0.5 (0.6) mm; pistillode only slightly exceeding disk, 0.6-0.8 x 0.55-0.8 (0.9) mm overall, deeply depressed-ovoid, provided with reduced locules and ovules, with dense ascending hairs 0.1-0.3 (0.4) mm long, abruptly contracted into a rounded or 4- or 5-lobulate or laterally acutely 4- or 5-winged stylode 0.25-0.45

mm long; in pistillate flowers staminodes 1.4-1.6 (2) and 1.5-1.7 (2.1) mm long, level with the base of the stigmas or rarely slightly exceeding pistil, filaments fleshy or less often (ssp. exaggeratum) slender and strap-shaped, 0.8-1.1 (1.25) and 0.9-1.2 (1.3) mm long, slightly broadened at the base, anthers in dorsiventral view lanceolate, base lobulate, apex obtuse, in lateral profile obtuse-oblong, 0.5-0.8 mm long; disk relatively deep and narrow, 0.35-0.6 x 0.2-0.45 mm; pistil (1.3) 1.55-1.75 (2) x 0.9-1.35 (1.6) mm overall, ovary ovoid, sessile, gradually contracted into a thick style 0.25-0.4 (0.6) mm long, ovary and style with dense appressed hairs to 0.3 mm long, stigmatal region 0.25-0.4 mm high stigmas sessile, compressed-globose, lateral or oriented upward and outward. In fruit pedicel clavate (ssp. rabelianum) or subcylindric, 2-3.5 (4) x 1.7-3.5 (5) mm, style sometimes elongating in young fruit (ssp. exaggeratum), mature fruit light gray to almost white (ssp. rabelianum) or dark brown, globose to slightly obliquely ovoid and obtusely short-acuminate (some ssp. rabelianum), or ovoid and sharply acuminate (ssp. exaggeratum), variable in size, 2-5 x 1.9-4.2 (to 3.7 cm diam when more than 1 pyrene), substipitate (ssp. exaggeratum) or sessile, glabrous or with few scattered appressed hairs to 0.2 mm long, sometimes drying wrinkled (ssp. opacum), sparsely to densely (ssp. rabelianum) lenticellate, calyx usually persisting, +/- erect and forming a small cupule or less often (ssp. exaggeratum) patent, mesocarp thick and lignified or less often (ssp. opacum) relatively thin and fleshy; pyrene entirely covered by pseudaril, variable in shape and size, 1.4-3.5 x 1.5-2.7 cm, in dorsiventral view ovate to orbicular, base obtuse to truncate, apex acute to abruptly

short-acuminate to sharply acuminate, in lateral profile on dorsal side (broadly) semi-ovate to semi-orbicular, base obtuse to acute, apex acute to slightly acuminate, on ventral side essentially semi-elliptic to semi-obovate, base truncate to obtuse, site of funicle 5/6 distance to apex, funicular depression deep; testa with irregular thickenings, infolded with lobed, contortuplicate cotyledons.

Distribution. Common in French Guiana and Amapá, sporadically but widely distributed in the rest of the Guianas and Amazonia.

Protium opacum is very closely related to P. klugii Macbr., with which it shares many characters, including the long, laxly branched inflorescence; inflorescence bract large; pubescence types and distribution; deeply cupular calyx; and petals carinate and slightly imbricate. In P. klugii the level of the calyx relative to the pistillode and anthers in staminate flowers and to the stigmas in pistillate flowers is the same as that of P. opacum ssp. rabelianum. In staminate flowers, the deep narrow disk and pistillode with a distinct stylode in P. klugii are similar to those in P. opacum ssp. exaggeratum. The relatively small, essentially globose fruit of P. klugii with thin, fleshy mesocarp and which dries wrinkled is comparable to that of P. opacum ssp. opacum.

Protium opacum differs from P. klugii by the former's leaflets with long erect hairs on the abaxial midvein; fruit glabrous or subglabrous; petiole canaliculate (not semi-terete); petiolules shallowly canaliculate and not winged; pulvinuli more conspicuous; leaflets more coriaceous and drying brown (not green); pistillode hairs shorter; and pseudaril completely covering the pyrene.

Protium opacum has been confused with P. araguense Cuatrec., a species known only from Aragua and the Distrito Federal in Venezuela. A taxonomic synonym of P. araguense is P. decandrum (Aublet) Marchand var.

breviacuminatum Swart. This rare species (i.e., L. O. Williams 10128) shows a number of similarities with P. opacum, such as a long open inflorescence, large lenticellate fruits, deeply cupular calyx and long calyx lobes which in the pistillate flowers reach the anthers of the staminodes (as in P. opacum ssp. rabelianum), long-papillate petal margins, and long staminodes with long anthers (as in P. opacum ssp. exaggeratum). Although P. araguense is very poorly collected and good flowering material has yet to be collected, the material available is sufficient to conclude that it can be distinguished from P. opacum because of the former's more slender branchlets; petiolules longer; lateral leaflets elliptic to often oblanceolate, terminal leaflet the obovate or oblanceolate, leaflet acumen very short; leaflets without long erect hairs on the abaxial midvein (instead, glabrous or abaxially with scattered appressed hairs to 0.05 mm long along midvein); leaflet apices broadly and abruptly short-acuminate, inflorescence shorter; calyx even deeper (2.3-2.5 mm long overall on young fruits of L. Williams 10128) and with chartaceous lobes; absence of the short fine erect hairs which occur on many organs of P. opacum; calyx and petals abaxially with less dense and shorter appressed hairs. The fruits of P. araguense are large, asymmetrically ovoid, substipitate, and sparsely lenticillate as in P. opacum ssp. exaggeratum, but the mesocarp is thin and fleshy and the fruits dry wrinkled while the latter has a lignified mesocarp and dries

smooth.

Three subspecies of P. opacum are recognized here, and they are distinguished in the following key, which is supplemented by Table XVIII.

Key to the subspecies of Protium opacum

- 1 Maximum number of interjuga 3; petals without long adaxial hairs;
fruit 2-2.3 x 1.9-2.3 cm, fruit with mesocarp thin and fleshy, drying
wrinkled ssp. opacum
- 1 Maximum number of interjuga 4-5; petals with long adaxial hairs; fruit
2.4-3.2 (5) x 2.1-3.1 (4.2) cm, mesocarp woody, fruit drying
smooth
- 2 Leaflet acumen (0.2) 0.5-1.2 (1.5) cm long; in m flowers calyx far
exceeding pistillode and level with base of anthers, in f flowers
level with base of stigmas; petals fleshy, (2.3) 2.6-2.7 (3) mm
long (rehydrated); staminodes 1.4-1.6 and 1.5-1.7 mm long; pedicel
in fruit clavate; fruit gray to whitish, globose or obtusely
short-acuminate, sessile, densely lenticellate
ssp. rabelianum
- 2 Leaflet acumen 1.3-2.3 cm long; in m flowers calyx level with
pistillode apex (f flowers unknown); petals membranous, 3.5-3.8 mm
long; staminodes 1.9-2 and 2-2.1 mm long; pedicel in fruit
subcylindric; fruit brown, asymmetrically ovoid and sharply
acuminate, substipitate, sparsely lenticellate ssp. exaggeratum

Table XVIII

Characters Separating the subspecies of Protium opacum

character	ssp. opacum	ssp. rabelianum	ssp. exaggeratum
petiole length (cm)	(3.1) 5-9.5 (10.8)	(2.6) 5-11 (12.5)	(7.5) 10.6-17.8
maximum no. juga	3	4	5
1st let. acumen length (cm)	(0.6) 0.9-1.6 (2)	(0.2) 0.5-1.2 (1.5)	(0.7) 1.3-2.3
primary infl. bracts (mm)	0.6-1.5 (1.7)	(0.7) 1.2-2.5 (2.8)	0.7-1.5
pedicel (fl.) length (mm)	(0.5) 0.8-1.5 (2)	0.3-0.9	1.2-2
calyx (mm) total length	(1) 1.4-1.6 (2.1)	(1.5) 1.6-2.4	1.4-1.7
calyx (mm) lobe length	(0.2) 0.5-0.9 (1.3)	(0.9) 1.3-1.6	0.5-0.85
petal length (mm)	(2.2) 2.5-2.7 (3.1)	(2.3) 2.6-2.7 (3)	3.5-3.8
petal fusion occurs?	yes	yes	none seen
adaxial hairs on petals?	no	yes	yes
staminode length (mm)	1.4-1.6/ 1.5-1.7	1.4-1.6/ 1.5-1.7	1.9-2/ 2-2.1
pedicel shape in fruit	subcylindric	clavate	subcylindric
fruit size (cm)	2-2.3 x 1.9-2.3	(2.4) 2.7-3 (3.2) x (2.1) 2.4-3.1	2.9-5 x 2.2-4.2
mesocarp	thin, fleshy	thick, woody	thick, woody
pyrene size (cm)	1.4-1.8 x 1.5-1.8	(1.9) 2-2.3 (2.6) x (1.6) 1.9-2.2	2.4-3.5 x 1.8-2.7

13a. *Protium opacum* Swart ssp. *opacum*.

Tree 6-30 m. Leaves (1) 2-3-jugate, (17) 25.5-34 (37) cm long; petiole (3.1) 5-9.5 (10.8) cm long; interjuga (2.1) 2.6-4.2 (4.8) cm long; terminal petiolule (1.5) 2-2.6 cm long; leaflet acumen (0.6) 0.9-1.6 (2) long. Inflorescence bracts: those on primary axes 0.6-1.5 (1.7) mm long, those on secondary axes 0.4-1.3 (2) mm long; on staminate flowers pedicel (0.5) 0.8-1.5 (2) mm long, on pistillate flowers (0.8) 1.2-1.4 (2.2) mm long; flower (dry) (2) 2.2-2.5 (2.7) mm long; calyx slightly exceeding the disk in both sexes, +/- level with pistillode apex in staminate flowers, (1) 1.4-1.6 (2.1) mm long overall, calyx lobes (0.2) 0.5-0.9 (1.3) mm long; petals (rehydrated) (2.2) 2.5-2.7 (3.1) x (1.2) 1.4-1.7 (2) mm, adaxial surface without long hairs; staminate flowers with broad disk 0.25-0.4 (0.45) x (0.2) 0.3-0.45 (0.6) mm; apical portion of pistillode 4- or 5-lobulate, 0.25-0.3 (0.4) mm high; in pistillate flowers staminodes 1.4-1.6 and 1.5-1.7 mm long, filaments fleshy, 0.9-1.1 and 1-1.2 mm long, anthers 0.5 mm long; pistil 1.3-1.7 x 0.95-1.1 mm, style 0.25-0.3 mm long. In fruit pedicel subcylindric; fruit brown, globose, usually slightly rounded-acuminate, 2-2.3 x 1.9-2.3 cm, sparsely lenticellate, sessile, mesocarp thin and fleshy, drying wrinkled; pyrene in dorsiventral view depressed-ovate, base obtuse, apex abruptly short-acuminate, in lateral profile dorsal side slightly semi-obovate, base acute, apex acuminate, ventral side essentially semi-orbicular below funicular depression.

Distribution. Rare but rather widespread in most of Amazonia: northern Bolívar in Venezuela, Loreto in Peru, and in Brazil in Roraima, Amazonas

(near Manaus and in Rio Juruá basin), Rondônia, and Pará south of the Rio Amazonas (Tucuruí, Santarém). Most specimens of ssp. opacum are from terra firme forest, but it has been collected in forest on white sand (Prance et al. 9708), forest bordering savanna (Steyermark 60782), old secondary forest (Rodrigues (INPA no.) 2083), and várzea (Lleras et al. P17504). The typical subspecies flowers March to August (November) and fruits November to March (July).

Specimens examined. Brazil. Pará: plateau of Santarém, Igarapé da Lama, 18 Jun 1954 (m fl), Frões 30872 (IAN); region of Igarapé Pitoró, 25 Sep 1958 (fr), Frões 34706 (IAN); Tucuruí, campina on right side of Rio Tocantins, BR 263, km 16, 30 Jan 1980 (fr), Lisboa et al. 1305 (MG, NY).

Protium opacum ssp. opacum is readily distinguished from the other subspecies by the characters in the key and the table which follows the key.

13b. Protium opacum ssp. rabelianum Daly (submitted for publication in Brittonia). Type. Brazil. Amapá: Agua Azul, road to Amapá, km 134, 24 Jul 1962 (m fl), Pires & Cavalcante 52257 (holotype: MG; isotypes F, G, GH, IAN, MO, NY).

Trees, reproductive height (5) 8-20 (30) m; trunk cylindrical; buttresses (consistently reported) simple or branched, plank or flying, up to at least 80 cm high; bark brown to whitish, smooth, with incomplete hoop marks; resin clear when fresh. Leaves (1) 2-4-jugate, (22) 30-40 (52.7) cm long; petiole (2.6) 5-11 (12.5) cm long, interjuga (2) 3-5.1

(7.6) cm long; terminal petiolule (1.5) 2.7-3.8 (4.7) cm long; leaflet acumen (0.2) 0.5-1.2 (1.5) cm long. Inflorescence bracts: those on primary axes (0.7) 1.2-2.5 (2.8) mm long, those on secondary axes 0.4-2.6 (3) mm long; in staminate flowers pedicel 0.3-0.9 mm long, in pistillate flowers 0.5-1.2 mm long. Flowers: in staminate flowers calyx far exceeding pistillode and level with base of anthers, in pistillate flowers level with base of stigmas, (1.5) 1.8-2.4 mm long overall, lobes (0.9) 1.1-1.6 mm long, with thickened apiculum; petals (2.3) 2.6-2.7 (3) x 1.3-1.7 (1.9) mm, adaxial surface with scattered erect to ascending hairs 0.1-0.2 mm long (rarely lacking) distributed along five vertical lines; in staminate flowers disk broad, (0.3) 0.4-0.5 x (0.25) 0.35-0.55 mm; stylode (0.25) 0.3-0.4 mm high, laterally acutely 5-winged; in pistillate flowers staminodes 1.4-1.6 and 1.5-1.7 mm long, filaments 0.8-0.9 (1) and 0.9-1 (1.1) mm long, anthers (0.5) 0.6-0.7 mm long; pistil (1.55) 1.6-1.75 (2) x (0.9) 1-1.35 (1.6), style 0.25-0.4 (0.6) mm long; pedicel in fruit clavate and robust, (2) 2.3-3.5 (4) x (1.8) 2.2-3.5 (5) mm, calyx in fruit usually persistent, remaining cupular; fruit gray to whitish, densely lenticellate, globose to slightly asymmetrically obtusely short-acuminate, sessile, (2.4) 2.7-3 (3.2) x (2.1) 2.4-3.1 cm; mesocarp thick and lignified, fruit not drying wrinkled; pyrene in dorsiventral view essentially ovate to depressed-ovate, base obtuse to truncate, apex gradually to abruptly sharp-acuminate, in lateral profile the dorsal side hemi-ovate, the base obtuse and apex acute, the ventral side essentially semi-orbicular to -elliptic below depression at funicle, 1.9-2.3 (2.6) x (1.6) 1.9-2.2 cm.

Distribution. French Guiana; Guyana; Venezuela in NW Amazonas and Bolívar; and Brazil in Amapá and northern Pará. Within its range, Protium opacum ssp. rabelianum is a common understory or canopy tree, occurring with equal frequency in forests on terra firme or along riverbanks. The subspecies flowers May to October and fruits July to March (May).

Specimens examined. Brazil. Amapá: Rio Amapari, Serra do Navio, 8 Nov 1954 (fr), Cowan 38166 (F, NY, US); Município. Oiapoque, 109 km SSE of Oiapoque on BR-156, edge of Reserva Indígena Uaçá, ca 3°00'N, 51°30'W, 3 Dec 1984 (fr), Daly et al. 3810 (HAMAB, NY), 5 Dec 1984 (fr), Daly et al. 3824 (HAMAB, NY), 60 km SSE of Oiapoque on BR-156, ca 3°18'N, 51°39'W, 1 Dec 1984 (fr), Daly et al. 3778 (HAMAB, NY); Município. Macapá, Perimetral Norte (BR-210), ca km 156 NW of Porto Grande, ca 1°30'N, 53°30'W, 30 Dec 1984 (fr), Daly et al. 4009 (HAMAB, NY); banks of Rio Oiapoque, 4 Jun 1904 (m fl), Ducke 4751 (MG, NY); Rio Oiapoque, immediately of Colônia Agrícola de Oiapoque, 14 Aug 1960 (m fl), Egler et al. 47505 (NY), Rio Oiapoque, Boa Esperança, opposite mouth of Riviêre Camopi, 3°12'N, 52°19'W, 19 Aug 1960 (fr), Egler 47674 (NY); Rio Oiapoque, below Cachoeira do Caxiry, 2 Jan 1950 (fr), Frões 25797 (IAN); Oiapoque, road to airport, 13 May 1950 (young fr), Frões 26602 (IAN); Rio Oiapoque, margin of river opposite Pedra Alice, 3°40'N, 52°01'W, 18 Aug 1960 (fr), Irwin et al. 47662 (NY), first cachoeira on Rio Iaue, 0.5 km E of confluence with Rio Oiapoque, 2°53'N, 52°22'W, 21 Aug 1960 (fr), Irwin & L. Westra 47691 (NY); road between Oiapoque and Clevelândia, 22 Jul 1960 (m fl), Maguire et al. 47107 (NY); Rio Oiapoque, ca 0.5 km W of Cachoeira Utussansain, 2°18'N, 52°55'W, 8 Sep 1960 (fr), Irwin et al. 48090 (F, NY, US); (without locality), 1956

(fr), Miranda Bastos (RB herb. no. 96232) (NY, RB); Municíp. Oiapoque, BR-156, at bridge over Rio Caciporê on road between Calçoene and Oiapoque, 134 SSE of Oiapoque, ca 2°53'N, 51°27'W, 9 Dec 1984 (fr), Mori & Souza 17316 (HAMAB, NY); Municíp. Macapã, vicinity of Serra do Navio, 8 km NNW of village of Serra do Navio on road to Agua Branca, ca 1°03'N, 52°04'W, 3 Jan 1985 (fr), Mori & J. Cardoso 17649 (HAMAB, NY); Rio Araguari, 27 Aug 1961 (m fl), Pires et al. 50527 (F, G, NY), ca. 2°13'n, 51°58'W, 3 Sep 1961 (f fl & young fr), Pires et al. 50682 (MG), coastal region, along road to Amapã, ca km 108, Rio Pedreira, 19 Jul 1962 (fr), Pires & Cavalcante 52209 (F, GH, IAN, MG, NY); Serra do Navio, 7 Nov 1980 (fr), Rabelo & R. Nonato 315 (HAMAB, NY); Municíp. Oiapoque, BR-156, 84 km SSE of Oiapoque, ca 3°05'N, 51°31'W, 5 Dec 1984 (fr), Rabelo & Cardoso 2893 (HAMAB, NY); Municíp. Calçoene, BR-156, 96 km NW of Calçoene, ca 2°48'N, 51°23'W, 7 Dec 1984 (fr), Rabelo & Cardoso 2913 (HAMAB, NY), between Calçoene and Oiapoque, 110 km NW of Calçoene, ca 2°52'N, 51°27'W, 9 Dec 1984 (fr), Rabelo & R. Cardoso 2942 (HAMAB, NY); Municíp. Macapã, vicinity of Serra do Navio on road to Agua Branca, ca 1°03'N, 52°04'W, 4 Jan 1985 (young fr), Rabelo et al. 3186 (HAMAB, NY); Municíp. Macapã, road from Cupixi to Rio Vila Nova, 18 km SSW of Cupixi, ca 0°32'N, 51°52'W, 5 Jan 1985 (fr), Rabelo et al. 3202 (HAMAB, NY); Serra do Navio, 1961 (fr), Rodrigues 2870 (INPA); between Porto Platon and Serra do Navio, 15 Dec 1976 (sterile), N. Rosa 1210 (MG); Munguba, 2 km from Perimetral Norte (BR-210), 23 Mar 1977 (fr), N. Rosa & Santos 1819 (MG, MO, NY); Porto Platon, Colonia do Matapi, 13 Sep 1976 (sterile), M. Silva 2806 (MG, NY); Sta. Patrícia, left bank of Rio Jarí, 12 Mar 1970 (fr), N. T. Silva 2965

(IAN), 13 Mar 1970 (fr), N. T. Silva 2972 (IAN); Rio Trombetas, Planalto Saracá, bauxite mine, 27 May 1978 (fr), N. T. Silva & Santos 4645 (MG, NY). French Guiana: (without locality), (without date) (fr), Aublet s.n. (W acquisition no. 119165) (W); region of Roura, 27 Nov 1956 (sterile), P. Bena 15-N (CAY); Saül, Mont La Fumée, 3°37'N, 53°12'W, 17 Sep 1982 (sterile), Boom & Mori 1725 (NY); 25 Sep 1982 (young fr), Boom & Mori 1828 (NY); 7 Oct 1982 (young fr), Boom & S. Mori 1875 (NY); 13 Oct 1982 (young fr), Boom & Mori 2033 (NY); 15 Oct 1982 (sterile), Boom & Mori 2112 (NY); 15 Oct 1982 (sterile), Boom & Mori 2120 (NY); 20 Oct 1982 (sterile), Boom & Mori 2186 (NY); 20 Oct 1982 (sterile), Boom & Mori 2197 (NY); 21 Oct 1982 (sterile), Boom & Mori 2253 (NY); 21 Oct 1982 (sterile), Boom & Mori 2282 (NY); 24 Oct 1982 (sterile), Boom & Mori 2350 (NY); 26 Oct 1982 (sterile), Boom & Mori 2397 (NY); on the Tampol, Saut Koumakou Soula, 25 Mar 1977 (fr), Cremers 4510 (NY); Upper Riv. Mana, above Saut Ananes, 15 Aug 1981 (fr), Cremers 7549 (NY); Saül, Tacé Montagne Galbao, km 2.8, 21 Sep 1974 (m fl), de Granville B-5157 (NY), 7 Jul 1978 (m fl), Granville B-5473 (CAY); Sinnamary, Ste. Elie road, ECEREX, 30 May 1983 (seedling), de Granville 5588 (CAY); Rio Oiapoque, Pedra Alice, 3°40'N, 52°01'W, 16 Aug 1960 (m fl), Irwin et al. 47552 (GH, VEN, NY), 16 Aug 1960 (fr), Irwin et al. 47553 (F, NY, US); Saül, 3°37'N, 53°12'W, La Fumée Mountain, La Fumée West Trail ca 200 m elev, 8 May 1986 (m fl), Mori & Pennington 17935 (NY), La Fumée Mountain, 11 May 1986 (m fl), Mori & Pennington 17975 (NY), La Fumée Trail Nord-Est, 17 May 1986 (m fl), Mori & Pennington 18045 (NY); Upper Approuague, Rivière Emérillon, 27 Sep 1968 (m fl), Oldeman T-180 (CAY); Fleuve Oyapock, Crique Armontabo, at Saut Bace, 3 Jul 1969 (buds),

Oldeman T-277 (CAY, NY); Upper Oyapock, Trois Sauts, 21 May 1970 (fr),
Oldeman T-783 (CAY, NY), above Trois Sauts, 5 Sep 1973 (frt), Oldeman
T-965 (CAY, NY); Rivière Comté, Crique Galibi on Crique Rupert, ca 5 km
upstream, 22 Jul 1967 (young fr), Oldeman B-1116 (CAY, NY); Fleuve
Oyapock, on Crique Armontabo ca 9 km upstream from Saut Canori, 3 Mar 1968
(frt), Oldeman B-1494 (CAY); Fleuve Approuague, ca 500 m upstream from
Saut Corvata, 31 Jul 1968 (buds), Oldeman 1724-A (CAY); Trois Sauts,
Rivière Camopi, below Montagne Alikene, 29 Jul 1982 (f fl), Oldeman 2092
(NY); forest bordering Rivière Camopi (affluent of Oyapock) at Roche José,
7 Dec 1967 (fr), Oldeman 2588 (CAY, NY); lower Crique Courouaïe (affluent
of lower Approuague), ca 4,800 m upstream from the Deux Fourches (dé
Fouca), 10 Jan 1970 (fr), Oldeman 2702 (CAY, NY); Grand Circuit Montagne
Pelée, on Montagne Peau-Blanche, at km 3,100, 18 Aug 1971 (m fl), Oldeman
B-4029 (CAY, NY); Cayenne, (without date) (fr), Poiteau s.n. (F, GH, P,
US); Piste de St. Elie, 4 May 1982 (sterile), Sabatier 200 (CAY); Rivière
Camopi (affluent of Oyapock), east slope of Montagne Yanioué, 8 Feb 1968
(frt), P. Sastre 102 (CAY); (without locality), (without date) (fr), H. F.
Talbot s.n. (K); Rio Oiapoque, near Cachoeira Camaraua, ca 3 km S of mouth
of Riv. Camopi, 3°10'N, 52°19'W, 29 Sep 1960 (young fr), L. Westra 48522
(F, NY). Guyana: Upper Mazaruni River Basin, Mt. Ayanganna, 800-900 m, 1
Aug 1960 (fr), Tillett et al. 44948 (NY), Kako River, E arm of Karowtipu,
950 m, 1 Oct 1960 (f fl), Tillett & Tillett 45585 (NY), just below base of
Great Falls, 26 Oct 1960 (fr), Tillett & Tillett 45817 (NY). Venezuela.
Amazonas: Depto. Atabapo, slope of Marahuaca, 1-2 km N of Sima Camp, 8-9
Mar 1985 (frt), Liesner 18466 (NY). Bolívar: Sta. Elena, near marker no.

10, 3 Sep 1979 (m fl), N. A. Rosa & Nascimento 3240 (MG, NY); ca km 119 S of El Dorado, 12 Jan 1964 (m fl), Steyermark et al. 93008 (VEN).

Local names and uses. Brazil. Amapá: breu branco, maraximbe (Cowan 38166). French Guiana: encens, encens grand-bois, waluwa?-i (Wayampi, de Granville B-5157), arbre miroir (Lescure 328), auwau (Palikur; Lescure 796). Resin used in French Guiana (Palikur) to caulk canoes.

Protium opacum ssp. rabelianum is distinguished from both other subspecies by the characters in the key and in the table which follows it

13c. Protium opacum ssp. exaggeratum Daly (submitted for publication in Brittonia. Type. Venezuela. Amazonas: Depto. Río Negro, Lower Cano Barfa ca 5-10 km above Point of Tambores of Camisioa de Limita and Camp of Comisión de Limite at Boca Secha going to Brazil, ca 0°56' N, 66°17' W, 31 Mar 1984 (m fl), Liesner 17063 (holotype: NY; isotypes, INPA, MO (not seen), U).

Trees, reproductive height 8-30 m. Leaves (2) 3-5-jugate, 45.5-51.5 cm long; petiole (7.5) 10.6-17.8 cm long; terminal petiolule 1.8-2.4 cm long; leaflet base usually abruptly truncate to slightly lobulate, acumen (0.7) 1.3-2.3 cm long. Inflorescences: bracts on primary axes 0.7-1.5 mm long, those on secondary 0.4-1.6 mm long; pedicel in flower 1.2-2 mm long; Flowers (dry) 2.5-3.2 mm long; calyx 1.4-1.7 mm long overall, lobes 0.5-0.85 mm long; petals membranous, 3.5-3.8 mm long (rehydrated), partial fusion of petals not observed, adaxial hairs on petals dense along five vertical lines, erect to ascending, 0.05-0.2 mm long; in staminate flowers

calyx level with apex of pistillode, 1.3-1.5 mm long overall, lobes 0.5-0.85 mm long; disk narrow, 0.4-0.45 x 0.15-0.2 mm; pistillode 0.8 x 0.6-0.65 mm overall, with distinct stylode 0.25-0.3 mm long; pistillate flowers with staminodes 1.9-2 and 2-2.1 mm long, filaments 1.15-1.25 and 1.2-1.3 mm long, anthers dimorphic, 0.75 and 0.8 mm long. In fruit terete; style in young fruit elongating to as long as 0.6 mm, fruit brown, sparsely lenticellate, large, asymmetrically ovoid and sharply acuminate, 2.9-5 x 2.2-4.2 cm, mesocarp lignified, not drying wrinkled; pyrene, in dorsiventral view broadly ovate, base obtuse, apex acute, in lateral profile on dorsal side hemi-ovate, base obtuse and apex acute, on ventral side obtuse-oblong below deep lateral depression at funicle, 2.4-3.5 x 1.8-2.7 cm.

Distribution. Known only from southern Amazonas in Venezuela. All the collections known to date are from a rather limited area near Cerro Neblina, but three of them (Bernardi 951, Gentry & Stein 46644 and Liesner & Stannard 16932) are from cloud forests at about 1000-1250 m elevation while the rest are from alluvial or swamp forests at under 150 m elevation. The upland material consists of very poor collections with fruits; their fruits tend to be more broadly and shorter-acuminate than in the lowland collections, but in all other recognizable aspects of their morphology they agree with the circumscription of the subspecies.

Specimens examined. Venezuela. Amazonas: in montane forests of Aprada Tepui, Aug 1953 (fr), Bernardi 951 (VEN); Dpto. Río Negro, upper Río Baria, ca 0°55'N, 66°15'W, 2-3 Jul 1984 (fr), Davidse & Miller 26914 (NY), Río Mawarinuma, near Neblina Base Camp, 0°20'N, 66°10'W, 20 Jul 1984 (fr),

Davidse 27515 (NY), Cerro Neblina, between base camp and "Puerto Chimo," along río Mawarinuma, 0°50'N, 66°08'W, 26 Apr 1984 (fr), Gentry & Stein 46953 (NY), Campamento 5, N base of Pico Cardona, 0°49'N, 66°00'W, 14 Apr 1984 (fr), Gentry & Stein 46644 (NY), below Cerro Neblina base camp, margin of río Mawarinuma, 4 May 1984 (fr), Gentry & Stein 47155 (NY), 0 to 3 km W of base camp, along river, 24 Feb 1984 (frt), Liesner 16237 (NY), Camp 5, valley north base of Pico Cardona, 0°49'N, 66°00'W, 21-24 Mar 1984 (fr), Liesner & Stannard 16932 (NY), 1.5 km E of Cero de la Neblina Base Camp (on Río Mawarinuma), 0-3 km S of main river, 0°50'N, 66°10'W, 2-3 Dec 1984 (m fl), Liesner 17405 (NY), 2-6 km E of base camp, along río Mawarinuma, between base camp and "Puerto Chimo" camp, 0°50'N, 66°08'W, 26 Apr 1984 (young frt), W. Thomas 3199 (NY), vicinity of base camp, along río Mawarinuma, 0°50'N, 66°09'W, 4 May 1984 (fr), W. Thomas 3356 (NY).

Protium opacum ssp. exaggeratum can be distinguished from both other subspecies by the characters listed in the key and in the table which follows it.

14. *Protium morii* Daly, (submitted for publication in Brittonia. Type.

Brazil. Amapá: near Cachoeira Utussansain, 2°08'N, 52°55'W, 9 Sep 1960 (buds and m fl), H. S. Irwin et al. 48119 (holotype, MG; isotypes, F, NY, US, W).

Tree, reproductive height (8) 20-46 m, DBH to 60-70 cm (Irwin et al. 48119), with thin tall plank buttresses; bark light gray to brown, whitish or reddish-gray, finely lenticellate, smooth, with incomplete hoop marks; resin clear and sticky when fresh. Branchlets robust, 3.8-6 mm diam, with sparse to scattered hairs to 0.1 mm long, conspicuously lenticellate. Leaves 3-5-jugate, (20.2) 26.5-40.5 (50) cm long; petiole broadly and shallowly canaliculate, rarely semi-terete, slightly acutely winged, relatively long and robust, longer than interjuga, (4.2) 5.4-11 (13) cm x (2.2) 2.5-3.7 (6) mm, with scattered to sparse appressed hairs to 0.1 mm long, rarely glabrous; interjuga (1.8) 2.2-4.5 (5.2) cm long; petiolules shallowly 1-canalicate, long and slender, 0.5-1.2 (1.7) cm long, terminal petiolule shorter than interjuga, 0.5-1.1 (1.5) cm long; leaflets coriaceous, dull, laterals acute-oblong to elliptic or narrow-elliptic, basal pair (7.2) 9-14.5 (17.5) x (2.3) 3.6-5.3 (5.6) cm, ultimate pair larger, (10) 11-19 (21) x (3.2) 3.5-5.2 (7) cm, base oblique, proximal side acute, distal side obtuse, terminal elliptic to oblanceolate, (9.3) 10-17.2 (21) x (2.8) 4-5.5 (7.5) cm, base acute to obtuse, leaflet apex abruptly acuminate, acumen usually long and narrow, 0.5-1.1 (1.8) cm long, abaxial surface with midvein acutely prominent, secondary veins obtusely prominent, remainder of reticulum prominulous or not, midvein and

secondary veins with scattered appressed hairs to 0.1 mm long, sometimes over all of surface, otherwise glabrous, adaxial surface with midvein narrowly obtusely prominent or prominulous, rest of veins inconspicuous, surface glabrous. Inflorescences subterminal, initiating a new flush of growth, relatively short and robust, (3.5) 5-9.5 (15) cm x (1.1) 1.2-2.2 (2.4) mm (in fruit 2.2-3.5 (4.5) mm diam), secondary axes short and robust, 0.4-5 (5.8) cm long (to 8 cm long in fruit), tertiary branches congested, usually reduced to a simple cymule, axes with scattered to sparse appressed hairs 0.05-0.1 mm long; inflorescence bracts ovate, acute, those on primary axes 0.3-0.8 (1.2) mm long, those on secondary axes 0.2-0.6 (0.8) mm long; pedicel relatively short, subcylindric to slightly clavate, with sparse to scattered appressed hairs 0.05-0.1 mm long, in staminate flowers 0.5-1.2 x 0.35-0.5 mm, in pistillate flowers longer and stouter, 0.9-1.5 x 0.4-0.6 mm. Flowers all 4-merous, (2) 2.5-3.2 (4) mm long; calyx shallowly cupular, exceeded by disk in both sexes, (0.6) 0.9-1.2 x (2) 2.2-2.5 mm, with hairs as on pedicel, lobes short, rounded depressed-deltate, 0.2-0.4 mm long, apex obtuse or acute; petals pale green to yellowish-green, ovate, somewhat fleshy, 3-3.3 (4.1) x 1.6-2 (2.2) mm, apex acute, apiculum conspicuously thickened, 0.25-0.4 mm long, strongly inflexed, at anthesis petals slightly inflexed to slightly reflexed, abaxial surface with sparse to scattered appressed hairs to 0.1 mm, adaxial surface short-papillate, also with scattered appressed to ascending hairs 0.1-0.25 mm long, distributed along three discrete vertical lines, apex and margin short-papillate (sometimes long-papillate); in staminate flowers stamens not greatly exceeding

pistillode, 1.7-1.95 and 1.85-2.05 mm long, filaments slender, slightly compressed, 1.05-1.3 and 1.2-1.4 mm long, anthers orange, in dorsiventral view narrowly obtuse-oblong (after dehiscence broadly obtuse-oblong), base lobulate, in lateral view obtuse-oblong, 0.6-0.7 mm long; disk relatively deep and broad, 0.35-0.5 x 0.3-0.5 mm; pistillode relatively large, greatly exceeding disk, 0.6-0.8 x 0.6-0.7 mm overall, ovoid to depressed-ovoid, provided with locules and reduced ovules, with dense appressed hairs 0.1-0.2 mm long, gradually contracted to a thick stylode 0.1-0.25 mm long, flared and 4-lobulate distally, each lobule with a vertical sulca, lobules erect or divergent; in pistillate flowers staminodes long, almost reaching stigmas, 1.65-1.85 and 1.75-2.05 mm, filaments somewhat fleshy, slightly compressed, 0.9-1.1 and 1-1.25 mm long, antesealous filaments broadened at base, anthers large, in dorsiventral view broadly obtuse-oblong, slightly broadened and lobulate at base, in lateral view acute-oblong, 0.7-0.85 mm long; disk relatively deep and broad, 0.4-0.5 (0.6) x (0.3) 0.35-0.5; pistil 1.6-2.1 x 1.1-1.25 (1.4) overall, ovary ovoid, not substipitate, with dense appressed hairs 0.05-0.15 mm long, often scattered on style as well, ovary gradually contracted into a thick 4-sulcate style 0.25-0.4 x 0.4-0.5 mm long, stigmatal region 0.3-0.35 mm high, stigmas large, lateral, sessile, slightly compressed-globose. In fruit pedicel terete, 1.5-2.8 (3) x (1.8) 2-2.6 (2.8) mm, fruit substipitate, in lateral view asymmetrically ovate, gibbous, sharply acute, large, 2.2-2.9 x (1.6) 1.8-2 cm (to 2.5 mm wide when more than 1 pyrene), glabrous, not drying rugose, larger maturing fruits becoming gray, lenticellate and rough-textured; pyrene thickly

cartilaginous, in dorsiventral view orbicular, base truncate, apex abruptly broad-acuminate, apex acute, in lateral view asymmetric, on dorsal side broadly obovoid, base and apex obtuse, on ventral side elliptic, base acute, apex with a lateral subapical depression, ca 2 x 1.7 cm (Daly et al. 4069), fully mature fruit and seed unknown.

Distribution. This species appears to be restricted to eastern Surinam, southern French Guiana, and Amapá on the Guiana Shield, with one disjunct collection on the Brazilian Shield near Santarém. It is interesting to note that it is near Santarém that the Brazilian and Guiana Shields are closest to one another. All collections have been from terra firme forest in hilly terrain. The species flowers from September to November and fruits from October to May.

Specimens examined. BRAZIL. Amapá: Municip. Macapá, Serra do Navio, 6 km NNW on Serra do Navio-Agua Branca road, ca. 1°03' N, 52°04' W, 3 Jan 1985 (fr), Daly et al. 4049 (HAMAB, NY), 8 km NNW on Serra do Navio-Agua Branca road, 3 Jan 1985 (fr), Mori & Cardoso 16646 (HAMAB, NY); Municip. Macapá, road from Cupixi to Vila Nova, 8 km SSW of Cupixi, ca. 0°32' N, 51°52' W, 6 Jan 1985 (fr), Rabelo et al. 3221 (HAMAB, NY); Oiapoque River, Pékouétan, 2 hours upstream from confluence of Yaroupi R., 9 Mar 1976 (fr), Sastre 4360 (P). Pará: Santarém, km 35 of road to Palhão, side road to Igarapé do Palhão, 18 Aug 1969 (fr), M. Silva & Souza 2303 (MG, NY). FRENCH GUIANA: Saül, Mont la Fumée, 3°37' N, 53°12' W, 19 Oct 1982 (buds), Boom & Mori 2144 (NY), 20 Oct 1982 (buds), Boom & Mori 2198 (NY), 21 Oct 1982 (buds), Boom & Mori 2264 (NY); Trois Sauts, downstream from Pakusili, 15 Oct 1975 (m fl), Grenand 1151 (CAY); near Cachoeira Tres Saltos, 2°12'

N, 52°53' W, 10 Sep 1960 (buds and f fl), Irwin et al. 48142 (GH, NY, US, VEN); Yaroupi River, 0.5 km from confluence with Oiapoque R., 2°48' N, 52°28-31' W, 25 Sep 1969 (f fl & young fr), H. S. Irwin et al. 48474 (B, F, GH, NY, US, VEN); Trois Sauts, 3 Nov 19974 (fr), Lescure 449 (CAY); Saül, Mont La Fumée, 3°37' N, 53°12' W, 8 Dec 1982 (fr), Mori & Boom 15348 (NY); 1 km upstream of Ilets Yacarescin, Oyapock, 10 Dec 1965 (young fr), Oldeman 1728 (CAY (3)); Haut Oyapock, about 2 km upstream from confluence of Yaroupi, 5 May 1970 (fr), Oldeman T-651 (CAY); Route de Belizon, 3 km from Saül, 16 Oct 1982 (fr), Prance & Boeke 28121 (NY (2)).

Local names and uses. Like all Burseraceae, in Amazonian Brazil this species is called "breu." In French Guiana, the generic Creole name for all Burseraceae is "encens." In the Wayampi Indian language two names are applied to this taxon: "yaya?i" and "waluwa?i." The latter name has been applied to several other species of Protium.

Protium morii is known from relatively few collections, and further collections with mature fruits are necessary to confirm the color of the mature fruit, distribution of the pseudaril on the pyrene, and the morphology of the testa and seed. Still, there is ample material to distinguish this species from its closest relatives, P. giganteum Engl. and P. carolense Daly. These species all show large usually oblong lateral leaflets; the same type and distribution of pubescence on all parts; short robust inflorescences with poorly developed secondary axes and congested reduced tertiary axes; 4-merous flowers; relatively shallow calyx, broad disk; large pistillode; long slender staminodes; large pistil with short appressed hairs; and the style usually elongating somewhat in young

fruits. Protium morii differs most conspicuously by its much larger fruits-- in lateral profile asymmetrically ovate, gibbous, and sharply acute-- with the petals persisting often to maturity. It also differs by the more robust branchlets; petiole not deeply canaliculate; terminal petiolule shorter; inflorescence bracts not semi-clasping; calyx lobes smaller; calyx exceeded by the disk in pistillate flowers; petal margin short-papillate; and presence of long appressed to ascending hairs on the adaxial surface of the petals.

It is interesting to note that Protium morii and P. giganteum do not appear to occur sympatrically, based on the rather intensive collecting carried out in recent years near Saül in south-central French Guiana.

Because of the shape of the fruits the species also resembles Protium decandrum (Aublet) Marchand, but it differs by its more robust branchlets, leaves 3-5 (not 0-2)-jugate; lateral leaflets usually oblong (instead of elliptic); petiole longer and lacking dense fine erect short hairs; flowers 4-merous, with larger more membranous petals; pistillode larger and with a longer stylode; style longer; and maturing fruit larger, gray, somewhat asperous, and lenticellate.

15. *Protium grandifolium* Engler in Mart. Fl. bras. 12(2): 269. 1874. Type. Venezuela. Amazonas: Río Casiquari, Jan 1854 (f fl), Spruce 3304 (lectotype (designated by Swart, 1942b)): P; isoelectotypes: BM, BR, G, K, LE, NY, W).

Tingulunga grandifolia (Engl.) Kuntze, Rev. Gen. Pl. I: 108. 1891.

Protium llewelyni Macbr., Candollea 5: 378. 1934. Type. Peru. Loreto: near Iquitos, Oct. 1929 (f fl), L. O. Williams 3704 (holotype: F; isotype: US).

Trees, reproductive height 8-15 m, branchlets robust, 2.2-3.5 (4.5) cm diam, with dense to sparse appressed hairs to 0.15-0.2 mm long, often also with dense to sparse fine erect hairs to 0.05 mm long. Leaves (2) 3-5-jugate, 16.8-39 cm long longer than interjuga; petiole semi-terete to slightly canaliculate, sometimes slightly acutely winged, 2.7-9 cm x 1.3-3 (4) mm, interjuga 1.5-4.1 cm long, rachis pubescence as on branchlets but sparse to scattered; petiolules 1-canaliculate, long, with relatively conspicuous pulvinulus, laterals (0.3) 0.5-1.4 (2) cm long, terminal 0.8-2.5 (3.1) cm long; leaflets coriaceous, laterals elliptic or rarely lanceolate, base subequal to oblique, acute, or proximal side acute and distal side obtuse to truncate, basal pair (5.20 6.8-14 x (2.1) 3-4.9 cm, ultimate pair (7.1) 8.2-13.8 (17) x (2.1) 3-4.4 cm; terminal elliptic or rarely lanceolate or oblanceolate, base acute, (6) 8.5-14.7 x (2.2) 3.2-5.7 cm; leaflet apex usually gradually and broadly short-acuminate, acumen 0.3-1.1 cm long; abaxial surface with midvein obtusely prominent,

rest of veins obtusely prominulous, midvein with scattered fine erect hairs to 0.05 mm long, rest of surface with scattered blunt appressed hairs to 0.15 mm long; adaxial surface with midvein obtusely prominulous, rest of veins inconspicuous, midvein and sometimes secondary veins with scattered to sparse fine erect hairs to 0.05 mm long. Inflorescences congested near apex, fasciculate, long and slender to robust, 3-18.4 cm x 0.5-2 (2.5) mm, 0.4-0.5 times length of subtending leaves, secondary axes poorly developed, 0.5-3.5 cm long, axes with scattered appressed hairs to 0.15 mm long, also with sparse fine erect hairs to 0.05 mm long, bract subtending inflorescence ovate, 0.8-1.3 mm long, those of primary axes 0.5-1.1 mm long, those on secondary axes 0.3-0.6 mm long; pedicel subcylindric or sometimes clavate, 1.1-3 x 0.25-0.45 mm, hairs as elsewhere on inflorescence. Flowers usually 5-merous, some 4-merous, 2.5-3 mm long; staminate flowers with calyx exceeded by the disk, 0.5-0.8 (1.1) x 1.8-2.4 mm, with scattered to sparse appressed hairs to 0.15 mm long, lobes (rounded-) depressed-deltate or reduced to an apiculum, usually discrete and separated by a flat sinus, 0.05-0.3 mm long; petals pale green to greenish-white, lanceolate, fleshy, 2-2.7 (3) x 0.9-1.4 mm, apiculum usually conspicuous, hairs as on calyx, margin short- or long-papillate, reflexed at anthesis; stamens greatly exceeding pistillode, 1.45-1.55 and 1.55-1.65 mm long, filaments often strap-shaped, broadened at base, 0.9-1 and 1-1.1 mm long, anthers basifixed, in dorsiventral view (narrowly) elliptic, base lobulate, apex acute, in lateral profile obliquely elliptic, 0.55 mm long; disk 0.25-0.4 x 0.2-0.4 mm; pistillode 0.5-0.65 x 0.5-0.6 mm overall, basal portion

depressed-ovoid, provided with locules and reduced ovules, abruptly constricted to an acutely (4) 5-winged stylode 0.25-0.35 x 0.25-0.3 mm; in pistillate flowers calyx level with or slightly exceeding disk, 0.7-1.1 x 2-2.6 mm, lobes (0) 0.1-0.3 (0.4) mm long; staminodes usually reaching base of stigmas, 1.2-1.4 (1.5) and 1.3-1.5 (1.6) mm long, filaments strap-shaped, 0.7-0.85 and 0.8-0.95 mm long, anthers lanceolate to ovate in dorsiventral view, base lobulate, apex truncate to slightly retuse, in lateral profile obliquely obtuse-oblong, 0.4-0.65 mm long; disk 0.2-0.4 x 0.2-0.35 mm; pistil 1.3-1.65 x 0.85-1 (1.25) mm overall, ovary broadly ovoid, with dense appressed (sometimes ascending) hairs to 0.2 mm long, gradually contracted to a thick style 0.3-0.4 x (0.35) 0.45-0.65 mm, stigmas compressed-globose, oriented slightly upward and outward, stigmatal region 0.2-0.35 mm high. In fruit inflorescence diameter 2-3.7 mm, pedicel 1.5-3.2 x 1.7-3.7 mm; fruit possibly reaching 4 x 3.4 cm (Steiermark 125821) mature fruits not known, when immature sessile, globose, drying wrinkled, surface smooth but slightly lenticellate, usually with sparse to scattered appressed hairs to 0.1 mm long.

Distribution. Rarely collected but widespread in Amazonia, apparently more common in the central and western parts of the region. Brazil: Acre, Amazonas, Mato Grosso, Pará. Venezuela: Amazonas near Cerro Duida and Cerro de Neblina. Peru: Loreto and Pasco. Ecuador: Pichincha. Protium grandifolium appears to be a small understory tree in primary terra firme forest (Silva & Rosário 3842 is from mature secondary forest). Based on the scant fertile material at hand, this species flowers in September to November (March) and fruits from September to January (June).

The identity of P. grandifolium has been confused by the paucity of material, the publication of an unusual disjunct collection as a distinct species, and the inclusion (by annotation) of many collections of a more abundant undescribed species, especially by the present author.

Swart (1942b) recognized P. llewelynii, separating it from P. grandifolium in his key by the leaflet shape, number of secondary nerves, and pedicel length. However, the collections are essentially identical in all other respects, especially in their flower morphology, and several collections are intermediate between the two in the characters used by Swart.

Protium grandifolium is similar to P. giganteum in its overall vegetative appearance, deeply cupular calyx, densely pubescent ovary, and globose fruits. It differs from the latter species by its dull (not glossy) leaflets with more arcuate secondary veins and more prominent abaxial veins; shorter terminal petiolule; shorter inflorescence bracts; discrete calyx lobes, shorter style; and pubescent fruit.

Until more collections of P. grandifolium became available recently, it was confused with an undescribed but abundant and widespread species exemplified by Clark 7183. This new species is the most common Burseraceae-- indeed, perhaps the most common tree-- on the World Wildlife Fund-U.S. reserves near Manaus, Brazil. It differs from P. grandifolium by these and other characters: leaflet apex usually abruptly and narrowly long-acuminate; pedicel longer and more slender; calyx shallower and narrower; flowers smaller; petals ovate (not lanceolate); stamens and staminodes shorter; stylode lobulate (not winged); style shorter;

secondary inflorescence axes longer; and fruit which dries smooth due to a more lignified mesocarp. The new taxon appears to be represented in eastern Amazonia by a single collection in rather poor condition, Frões 31272. This collection is from the Planalto do Santarém, where many disjuncts with central and western Amazonia occur.

Specimens examined: Brazil. Pará: Região Igarapé Pitoró, 25 Sep 1958 (young fr), Frões 34706 (US). Parque Nacional do Tapajós, km 70 of Itaituba-Jacareacanga road, side road to Patuã, 19 Nov 1978 (young fr), M. G. Silva & Rosário 3842 (F, MG, NY, US).

16. *Protium decandrum* (Aublet) Marchand, *Adansonia* 8: 51. 1867-1868. Type.
French Guiana: (without locality), (without date) (f fl), Aublet s.n.
(holotype: BM).

Icica decandra Aublet, *Hist. Pl. Guian. Fr.* 1: 346, t. 135. 1775. Amyris
decandra (Aublet) Willd., *Linn. Sp. Pl.* (ed. 4) 2: 336. 1799.

Elaphrium decandrum (Aublet) Spr. ex Dietr., *Syn Pl.* 2: 1272. 1840.

Bursera decandra (Aublet) Baill., *Hist. Pl.* 5: 296. 1874.

Icica enneandra Aublet, *Hist. Pl. Guian. Fr.* 1: 345, t. 134. 1775. Type.

French Guiana: (without locality), (without date) (m fl), Aublet s/n
(holotype: BM). Amyris enneandra (Aublet) Willd., *Linn. Sp. Pl.* (ed. 4)
2: 335. 1799. Elaphrium enneandrum Spr. ex Dietr., *Syn. Pl.* 2: 1271.
1840. Tingulunga enneandra (Aublet) Kuntze, *Rev. Gen. Pl.* 1: 107.
1891.

Protium schomburgkianum Engl., *Mart. Fl. bras.* 12(2): 276. 1874. Type.

Guyana: banks of Sururu River, Sep 1843 (m fl), Rich. Schomburgk 1468
(holotype: GH (other syntype (B) destroyed)).

Protium orinocense Rusby, *Descr. New Sp. S. Am. Pl.*: 35. 1920. Type.

Venezuela, lower Orinoco, Eleanor Creek, May 1897 (m fl), Rusby &
Squires 133 (lectotype (here designated): NY; isolectotypes: M, MO).

Trees, reproductive height (8) 15-25 (41) m; resin clear when fresh;
trunk fluted, with narrow plank buttresses and often simple or branched
flying buttresses; bark gray to 'blackish' (Oldeman B-1454), thin, smooth;
branchlets slender to somewhat robust, (1.9) 2.2-3 (4) mm diam in flower,

branchlets with sparse to scattered appressed hairs 0.05-0.2 mm long, also with and sparse erect hairs to 0.05 mm long. Leaves (0) 1-2-jugate, (11.5) 15-24 (29) cm long; petiole usually shorter than interjuga, semi-terete, broad, (1.5) 1.7-6 (8.5) cm x 1.2-2.3 (2.7) mm, sometimes broadly and shallowly canaliculate, then slightly acutely winged, upper surface of petiole with sparse erect hairs and dense to sparse appressed hairs, remainder with scattered appressed and sparse to scattered erect hairs, sometimes subglabrous; interjuga (when present) (1.8) 2.3-4.2 (6) cm long; petiolules long, 1-canaliculate, slender to somewhat robust, laterals (0.3) 0.6-1.5 (2.1) cm long, terminal (1) 2-4 cm long, pulvinuli relatively conspicuous; leaflets chartaceous to coriaceous, laterals elliptic to slightly oblanceolate, basal pair (5.5) 8.5-13 (19) x (2) 3.2-5.4 (6.9) cm, ultimate pair (6.7) 11-12.5 (15.1) x (2) 3.1-4.8 (5.8) cm, base subequal, acute to obtuse, terminal leaflet (7.1) 9.5-16.2 (18.5) x (2.7) 3.7-6.8 (9.3) cm, base acute, leaflet apex abruptly broadly acuminate, acumen (0.2) 0.3-1.2 (1.4) cm long, abaxial surface with midvein and sometimes secondary veins acutely prominent, rest of veins prominulous, surface with scattered appressed hairs to 0.1 mm long, adaxial surface with midvein narrowly obtusely prominulous, rest of veins inconspicuous, midvein with scattered erect hairs to 0.05 mm long.

Inflorescences congested near branchlet apices, (2.2) 4-12.5 (17.5) cm x (0.5) 0.8-2 (2.8) mm, 0.25-0.5 times length of subtending leaf, secondary axes well-developed, 0.4-2.5 (7) cm long, axes with sparse to scattered erect hairs to 0.05 mm long and sparse to scattered appressed hairs 0.1-0.2 (0.25) mm long; pedicel slightly clavate, 0.5-1.5 (1.8) x 0.3-0.55

mm, with scattered appressed hairs 0.1-0.25 mm long. Flowers 5-merous (rarely some flowers 4-merous), variable in size, (1.5) 1.8-2.5 (3) mm long; calyx (0.8) 1.1-1.5 (1.7) x (1.7) 2.2-2.7 (2.9) mm overall, with scattered appressed hairs 0.1-0.15 mm long, lobes rounded-deltate, apex acute or acuminate; in staminate flowers calyx lobes (0.3) 0.4-0.6 (0.7) mm long; petals pale green to greenish yellow to white, (broadly) ovate, (1.3) 2.3-3.3 (3.8) x (1) 1.2-1.6 (2.1) mm, apex acute, apiculum inconspicuous, 0.2-0.25 (0.3) mm long, abaxially with sparse to scattered appressed hairs 0.05-0.2 mm long, rarely hairs dense or surface glabrous, margin short-papillate (rarely long-papillate, i.e. Daly et al. 239), only weakly reflexed at anthesis; stamens (1.55) 1.7-2.05 (2.2) and (1.65) 1.8-2.15 (2.3) mm long, filaments slender, strap-shaped, not very fleshy, (1.05) 1.2-1.3 (1.5) and (1.15) 1.3-1.4 (1.6) mm long, anthers basifixed, in dorsiventral view narrowly obtuse-oblong (ovate after dehiscence), base lobulate, in lateral view obtuse-oblong to elliptic, base obtuse, (0.5) 0.55-0.7 (0.8) mm long; disk relatively shallow and broad, (0.25) 0.35-0.5 (0.65) x (0.25) 0.5-0.55 (0.65) mm; pistillode only slightly exceeding disk, 0.5-0.65 (0.75) x (0.6) 0.7-0.85 mm overall, (deeply) depressed-ovoid, with dense ascending to appressed hairs 0.1-0.25 (0.3) mm long, provided with rudimentary locules and ovules, abruptly contracted into a thick stylode 0.2-0.3 (0.4) x 0.35-0.4 mm; pistillate flowers with calyx lobes variable in length, 0.25-0.75 (0.85) mm long; staminodes +/- level with stigmas, (1.1) 1.4-1.7 and (1.2) 1.5-1.8 (1.85) mm long, filaments fleshy, slightly compressed, (0.6) 0.7-1 (1.15) and (0.7) 0.8-1.1 (1.25) mm long, anthers in dorsiventral view ovate to

obtuse-oblong, base lobulate, in lateral view asymmetrically
obtuse-oblong, anterior sporangia shorter than posterior, (0.5) 0.55-0.7
(0.8) mm long; disk relatively shallow and narrow, 0.25-0.4 (0.6) x (0.25)
0.3-0.45 mm; pistil (1.3) 1.55-1.8 x (0.8) 1.05-1.25 (1.3) mm overall,
ovary ovoid (rarely orbicular), sessile, with dense appressed hairs to
0.25 mm long (sparse near style), gradually contracted into a clavate or
sometimes subcylindric style 0.15-0.35 x 0.4-0.55 mm, stigmatal region
0.25-0.35 mm high, stigmas sessile, depressed-globose to almost discoid,
oriented upward and outward. In fruit pedicel (2) 2.2-3.5 (5) x (1.2)
1.5-1.8 (2) mm, subcylindric, immature fruit obliquely ovoid, somewhat
gibbous, mature fruit red, substipitate, broadly obliquely ovoid with the
apex abruptly and sharply acute (Guyana, Venezuela, some specimens from
Pará and Maranhão in Brazil) or subglobose with a broad short acumen
(French Guiana, central and western Amazonia, some specimens from Pará and
Maranhão), 1.5-2.1 (3.1) x 1.6-2.1 cm (x 2.8 cm wide when more than 1
pyrene), glabrous, drying smooth; pyrene completely covered by spongy
pseudaril; pyrene in dorsiventral view depressed-ovate to almost orbicular
or rarely broadly obtuse-oblong (Oliveira 704, Prance et al. 1962), base
truncate, apex abruptly acuminate or apiculate, in lateral view
essentially orbicular, ventral side with a deep subapical depression at
site of funicle, ventral surface also slightly vertically 2-keeled, (1.2)
1.6-1.8 x 1.4 (1.9) cm, with dense layer of suberect fibers to 0.4 mm long
except on funicular scar, funicular scar laterally (broadly) elliptic,
covering 1/4-1/3 (1/2) of ventral face, testa with irregular thickenings,
infolded with lobed and contortuplicate cotyledons.

Distribution. Widespread in Amazonia and the Guianas, with the exception of Surinam. Protium decandrum is a medium-sized to very large tree, often occurring as a canopy tree. It is a primary forest species, but otherwise it appears to be flexible ecologically, since it is known from sandy soils and clay soils, terra firme and várzea, level terrain and regions characterized by hilly terrain, moist forest with high rainfall (Belém) and liana forest on the drier periphery of Amazonia in Maranhão. The species has often been collected near riverbanks. In Pará, Amapá, and French Guiana, P. decandrum usually flowers from September to December and fruits from November to March. In Guyana the phenology is shifted back, flowering January to May and fruiting May to October. This may be explained by the more bimodal pattern of precipitation in most of Guyana (see rainfall charts in Schwerdtfeger, 1976). This phenological shift in Guyana is encountered in other plant groups (S. Mori, pers. comm.).

Specimens examined. Brazil. Amapá: Cupixi, margin of road to Amapá, 16 Oct 1976 (buds), Ribeiro 1524 (MG, NY). Maranhão: Municíp. de Monção, basin of Rio Turiaçu, Ka'apor Indian Reserve, 4 km NY of settlement of Urutawy, 1 Feb 1985 (sterile), Balée & Ribeiro 213 (NY); km 133 of BR-316, S of Fazenda Guarany, ca 2°46'S, 45°43'W, 21 Sep 1980 (young fr), Daly et al. 147 (INPA, NY); km 162 of BR-316, S of Fazenda Primavera, Araguañã, ca 3°00'S, 45°40'W, 24 Sep 1980 (f fl and young fr), Daly et al. 239 (MG, NY); Upper Rio Turiaçu, Nova Esperança, 2°55'S, 45°45'W, 5 Dec 1978 (fr), Jangoux & Bahia 236 (NY); Turiaçu, km 6 of BR-106, Maracaçumê-Sta. Helena road, Fazenda Maracaçumê Agro Industrial Grupo Mesbla, 30 Nov 1978 (fr), N. Rosa & Vilar 2752 (MG, NY); Turiaçu, Astonas, 6 Dec 1978 (buds), N.

Rosa & Vilar 2857 (MG). Pará: Ruropolis Presidente Medici, 4°00'S, 55°04'W, 9 Feb 1976 (fr), Bamps 5339 (BR, NY); Rio Capim, Caratateua, 28 Mar 1948 (m fl), Black 48-2356 (IAN); Fazenda Santa Rosa, entrance behind town of Itinga do Pará, W of Belém-Brasília highway, ca 4°20'S, 47°45'W, 26 Oct 1980 (m fl), Daly et al. 762 (NY); Municíp. Acará, Fazenda Borba Gato, near Rio Acará, 30 km W of Tomé Açú-Paragominas road, ca 2°40'S, 48°35'W, 5 Nov 1980 (f fl), Daly et al. 819 (INPA, NY); Belém, EMBRAPA, Mocambo Reserve, ca 1°23'S, 48°27'W, 10-17 Nov 1984 (buds & young fr), Daly et al. 3758 (IAN, NY), 10-17 Nov 1984 (fr & buds), Daly et al. 3760 (IAN, NY), 10-17 Nov 1984 (buds), Daly et al. 3760 (IAN, NY); 8 Jan 1985 (immat fr), Daly et al. 4058 (IAN, NY); Belém, Utinga, 2 Jun 1914 (m fl), Ducke 15333 (MG); Rio Tapajós, Cachoeira do Mangabal, near Igarapé Botica, 5 Sep 1916 (m fl), Ducke 16457 (MG); Belém, Agua Preta, Aurá, 9 May 1918 (m fl), Ducke 17025 (MG); Belém-Brasília highway km 95, 8 Sep 1959 (young fr), M. Kuhlmann & Jimbo 210 (IAN, MG, WIS); Municíp. Paragominas, Itinga do Pará, Fazenda Caboré, 4 Dec 1979 (fr), Maciel et al. 424 (MG, NY); Belém-Brasília highway km 62.5, 22 Nov 1959 (fr), Oliveira 137 (IAN), 11 Dec 1959 (buds), Oliveira 268 (IAN); km 177, 8 May 1960 (fr), Oliveira 704 (IAN); Belém, IPEAN, Reserva Mocambo, 22 Sep 1963 (fr), Oliveira 2614 (IAN); Belém, várzea of IAN, 19 Oct 1953 (f fl & young fr), Pires 4541 (IAN); Belém, IAN, Reserva Mocambo, Jan 1956 (buds and fr), Pires & N. T. Silva 6735 (IAN), 6 May 1966 (buds), Pires & N. T. Silva 10216 (IAN), 19 Jan 1967 (frit), Pires & N. T. Silva 10615 (NY), 5 Sep 1967 (fr), Pires & N. T. Silva 10887 (IAN); Belém, IPEAN, Reserva Aurá, 24 Aug 1967, Pires & N. T. Silva 11353 (NY); Belém-Mosqueiro road (SUDAM), 8 Aug 1968 (f fl and

young fr), Pires & N. T. Silva 11914 (NY); Belém, Reserva Aurã, 22 Jan 1969 (f fl), Pires 12002 (NY), 22 Jan 1969 (f fl), Pires 12003 (NY); Belém, Reserva Utinga, 24 Jan 1969 f fl), Pires 12020 (IAN); Municfp. Paragominas, Belém-Brasília highway (BR 010), 17 km S of Ligação do Pará, near km marker 1509, ca 4°17'S, 47°32'W, 1 Mar 1980 (fr), Plowman et al. 9418 (NY); 6 km N of Ligação do Pará, near km marker 1532, ca 4°05'S, 47°32'W, 3 Mar 1980 (fr), Plowman 9506 (NY); BR 22, Capanema, km 64, vicinity of Piritorô, 4 Nov 1965 (fr), Prance & Pennington 1962 (NY); Bragança-Viseu road, 4 km W of Curapiti and Rio Piria, 10 Nov 1965 (f fl), Prance 2060; BR 22, km 64, 25 Aug 1964 (fr), Prance & N. T. Silva 58880 (NY); Tucuruí, PA-149, 5 Oct 1983 (m fl), Revilla et al. 8552 (INPA, NY), 5 Oct 1983 (buds), Revilla et al. 8573 (INPA, NY); Belém-Brasília highway, Paragominas, Rio Urain, 16 Jan 1966 (fr), M. Silva 400 (MG); Tomé Açú, Acará, banks of Rio Ipiranga, 29 Oct 1979 (f fl), M. G. Silva & Pinheiro 5117 (MG, NY); Belém, road to Barra, 20 Aug 1902 (buds), Siqueira Rodrigues (MG No.) 2853. French Guiana: Route de Mana, 15 Dec 1955 (fr), BAFOG 7094 (NY, P, U), 9 Jan 1956 (fr), BAFOG 7143 (NY, P), 19 Mar 1956 (fr), BAFOG 7389 (NY, P); Saül, Mont La Fumée, 3°48'N, 53°12'W, 24 Sep 1982 (buds) Boom & Mori 1820 (NY); Saül, 23 Dec 1976 (fr), Mori & de Granville 8825 (NY); Saül, Mont La Fumée, 3°48'N, 53°12'W, 7 Oct 1982 (m fl), Mori & Boom 15061 (NY), 13 Nov 1982 (f fl), Mori & Boom 15206 (NY), 2 Apr 1983 (fr), Mori & Pipoly 15488 (NY), 25 Nov 1982 (young fr), Mori & Boom 15625 (NY), 5 Nov 1982 (m fl), Mori & Boom 15712 (NY); Oyapock River, on Crique Armontabo ca 1 km upstream of confluence with river, 2 Mar 1968 (fr), Oldeman B-1454 (CAY, NY); Cayenne, (without date) (f fl), D. Richard

s/n (G). Guyana: NW Distr., Barima, Aruka River Head, 3 Jul 1908 (m fl), C. W. Anderson 34 (NY); Siba Creek, 31 Mar 1941 (f fl), For. Dep. Br. Gui. Rec. No. 3402 (NY); Matthews Ridge, New Camp Clearing, 5 Feb 1955 (m buds), Cowan 39381 (GH, NY, US); Pomeroon District, Pomeroon River, 14-20 Jan 1923 (m fl), de la Cruz 3032 (GH, NY, US); Bartica, Nov 1888 (buds), Jerman 4732 (NY, U); vicinity of Matthew's Ridge, 5 km S of ridge on road to Papaya, 28 Aug 1976 (immat frt), Mori et al. 8232 (NY); Roraima, 1842-1843 (buds), Schomburgk 292 (G); Upper Mazaruni River basin, Mt. Ayanganna, NE side along base, 1 Aug 1960 (fr), Tillett et al. 44953 (NY); Upper Mazaruni River basin, Kamarang River, Camp No. 3, Kako River, S bank, 23 Sep 1960 (fr), Tillett & Tillett 45497 (MO, NY), Kamarang River, 15 Oct 1960 (fr), Tillett & Tillett 45687 (MO, NY); Cuyuni River, Kauri Creek, 17 May 1933 (f fl), Tutin 113 (BM, RB, U, US).

Local names and uses. Brazil: breu branco (Amazonas and Pará), arakandei'y (Ka'apor of Maranhão). French Guiana: moni, tingui moni, grand moni (Paramaka). Guyana: kurokai (Arawak), bartara haiowa, purokai, common korokai.

Swart (1942b) tried to separate P. decandrum from P. schomburgkianum on the basis of pubescence, but I found no differences in pubescence between the two type specimens. Engler (1874) distinguished them by the number of juga, but this character is very unreliable in the Burseraceae, and later (Engler, 1883) he placed P. schomburgkianum in synonymy with P. decandrum.

There is a problem in P. decandrum regarding the number of flowers parts, because although the type collection of P. medianum has 4-merous

flowers, on every other collection of P. decandrum a few 4-merous flowers may occur as an aberration on a given inflorescence, and indeed one character which can be used to separate it from P. giganteum is the 4-merous flowers of the latter species.

Protium decandrum resembles and is most closely related to P. giganteum, but the former can be distinguished by: petiole with erect hairs; 5-merous flowers; petals fleshier, margin usually short-papillate; pistillode only slightly exceeding disk; style shorter and often clavate; pistil hairs shorter; stigmas oriented upward and outward (not lateral); fruit larger and more oblique.

17. *Protium giganteum* Engler in Mart. Fl. Bras 12(2): 277. 1874. Type.
Brazil. Pará: Santarém, Dec 1828 (f fl), L. Riedel 1561 (lectotype
(here designated), NY; isoelectotype, LE).

Tingulunga gigantea (Engl.) Kuntze, Rev. Gen. Pl. 1: 108. 1891.

Tree, reproductive height 8-18 (26.5) m, no buttresses reported; apex with dense appressed hairs 0.05-0.25 (0.3) mm long, branchlets relatively slender, (2.2) 2.9-4 (4.2) mm diam, usually soon subglabrescent. Leaves (0) 1-4-jugate, large, (11) 17.5-35.5 (40) cm long; petiole usually deeply canaliculate and slightly acutely winged at base, terete distally, longer than interjuga, (2.5) 3.1-7.8 (10.5) cm x 1.5-3 (3.8) mm, with scattered short, thick, appressed hairs to 0.15 mm long, less often glabrous; interjuga terete to slightly angular, (1.5) 2.5-4.8 (5.5) cm long; petiolules broadly 1-canalicate, long, laterals (0.4) 0.6-1.4 cm long, terminal slightly longer than interjuga, (1.2) 1.5-3.5 (4) cm long; leaflets coriaceous to markedly so (var. crassifolium), laterals broadly oblong, less often elliptic, narrowly oblong or narrowly elliptic, base somewhat oblique to subequal, large, basal pair sometimes ovate (var. crassifolium) (6.8) 8.8-14.6 (17) x (2.1) 3-6.5 (7) cm, ultimate pair larger, (7.2) 10-17.5 (18.5) x (2.4) 3.5-6.6 (7.6) cm, terminal leaflet (broadly) elliptic to slightly obovate, (7.2) 10.7-16 (19.8) x (3.4) 4.4-6.2 (8.6) cm, leaflet base obtuse to acute, apex abruptly and broadly short-acuminate, sometimes gradually acuminate (var. crassifolium), acumen (0.2) 0.5-1.4 (1.6) cm long; leaflet margin sometimes markedly involute

(var. crassifolium), abaxial surface with midvein broadly obtusely prominent, rest of veins prominulous, midvein and occasionally on secondary veins with scattered appressed hairs 0.05-0.2 mm long, resot of surface with sparse erect blunt hairs to 0.05 mm long, adaxial surface with midvein narrowly obtusely prominulous, rest of veins prominulous, glabrous. Inflorescences subterminal, robust, usually exceeding petiole, (2.5) 3.5-10 (15) cm x (0.8) 1.5-2.3 (3.2) mm, 0.2-0.5 (0.6) times length of subtending leaf; secondary axes usually short, robust, 0.4-5 (7.8) cm long, axes with sparse to scattered or dense, thick, appressed, hairs to 0.1 mm long; inflorescence bracts chartaceous to membranous, ovate to rounded deeply depressed-deltate, usually semi-clasping, apex acuminate to acute, papillate, those on primary axes 0.5-1.2 mm long, those on secondary axes (0.25) 0.3-1 mm long; pedicel short, stout, slightly compressed-clavate, in staminate flowers 0.5-1.2 x (0.3) 0.4-0.55 mm; in pistillate flowers usually longer, (0.7) 0.9-1.2 (2) x (0.3) 0.4-0.6 mm; Flowers all 4-merous, (1.7) 2.5-2.8 (3.3) mm long; in staminate flowers calyx deeply cupular, usually exceeded by disk, (0.4) 0.5-0.9 (1.1) x (1.3) 1.5-1.9 (2.3) mm overall, sometimes attenuate and so not easily distinguished from pedicel, with dense to sparse or rarely scattered thick appressed hairs to 0.1 mm long, lobes often patent or relexed at anthesis, rounded-deltate, apiculate to acuminate, (0.25-0.5 (0.7) mm long; petals green or yellow or greenish-white or white or reddish-white (Pires & Silva 10246), membranous, broadly lanceolate to lanceolate, rarely narrow-oblong, (2.1) 2.4-2.7 (3.3) x 0.9-1.3 (1.7) mm, apex acute, apiculum negligible to +/- fleshy, to 0.2 (0.25) mm long, at anthesis

petals usually strongly reflexed at 1/2 their length, abaxially with sparse to dense hairs as on calyx, margin and apex short-papillate; stamens greatly exceeding pistillode, inflexed, 1.2-1.65 (1.75) mm and (1.35) 1.5-1.8 (1.85) mm long, filaments slender, subterete except broadened and compressed at base, (0.7) 0.85-1.2 (1.25) mm and (0.85) 1-1.35 mm long, not papillate, anthers basifixed, erect, in dorsiventral view acutely narrow-oblong to slightly lanceolate, base lobulate, abaxially deeply concave, in lateral view obliquely obtuse-oblong, the anterior sporangia shorter, large, (0.35) 0.45-0.6 mm long; disk low and broad, undulate and sinuate, 0.15-0.3 (0.35) x (0.15) 0.2-0.35 (0.5) mm; pistillode depressed-ovoid, (0.5) 0.6-0.65 (0.75) mm long overall, with dense appressed to ascending hairs 0.05-0.15 (0.2) mm long, provided with reduced locules and ovules, abruptly contracted to a stylode 0.25-0.3 mm long with an acutely 4-winged capitate apex; in pistillate flowers calyx more deeply cupular, usually exceeding disk, (0.7) 1.1-1.3 (1.5) x (1.3) 1.7-2 (2.3) mm, calyx lobes 0.3-0.6 (0.7) mm long; staminodes usually reaching base of stigmas, (1.1) 1.25-1.35 (1.45) and (1.2) 1.3-1.55 mm long, filaments compressed, narrow, (0.55) 0.75-0.8 (0.9) and (0.65) 0.85-1 mm long, anthers broadly lanceolate in dorsiventral view, base lobulate, apex retuse, abaxially slightly concave or flat, in lateral view asymmetrically narrowly obtuse-oblong, 0.45-0.55 mm long; disk low and narrow, 0.2-0.3 (0.4) x 0.15-0.25 (0.3) mm; pistil (1.2) 1.25-1.5 x (0.6) 0.65-0.85 (0.9) mm overall, broadly ovoid, sessile, with dense appressed hairs 0.05-0.2 mm long, often occurring on part of the style, style long and thick, (0.35) 0.4-0.55 (0.6) x 0.3-0.35 mm, stigmatal region 9.2-0.3

mm high, stigmas slightly compressed-globose. In fruit pedicel terete or slightly clavate, 1.5-2.5 x (1.2) 1.3-1.7 mm; young fruit soon glabrescent, mature fruit globose to slightly ovoid, (1.3) 1.5-1.8 x 1.1-1.5 cm (to 1.7-2 cm diam when more than 1 pyrene) (Pires & Silva 6642 with one fruit 2.1 x 1.4 cm), substipitate, either abruptly and acutely short-acuminate, the style persisting and slightly excentric or slightly obtusely acuminate, the style not persisting (var. crassifolium), color unknown; pseudaril spongy, not covering most of ventral side of pyrene, overlying a layer of matted fibers to 0.4 mm long; pyrene thickly cartilaginous, 1-1.3 x 1-1.3 cm (Pires & Silva 6642 with one pyrene 3 x 1.4 cm), in dorsiventral view depressed-ovoid base truncate to slightly obtuse, apex abruptly sharp-acuminate, in lateral view asymmetrically broadly ovoid, dorsal side more deeply convex, base truncate to obtuse, apex sharp-acuminate to abruptly so, apex with two deep depressions on ventral side so apex trigonous, ventral side often with broad vertical central sulca of varying depth, site of funicle 3/4-4/5 distance to apex; testa with irregular thickenings, infolded with contortuplicate cotyledons.

Protium giganteum is very closely related to P. decandrum (see discussion under that species) and to P. carolense Daly, a species restricted to the upper Rio Negro region. Protium carolense differs from P. giganteum by former's well-developed secondary inflorescence axes, with fine erect hairs on the inflorescence; pedicel longer and more slender; pedicel and calyx subglabrous; petals with scattered long ascending hairs, the margin long-papillate; and young fruits globose (not ellipsoid).

Two varieties of P. giganteum are recognized here and distinguished in the key below. Although there is a geographic component to their differences, the morphological characters which separate them are rather weak.

Key to the varieties of Protium giganteum

- 1 Leaflets oblong, margin not involute, apex abruptly acuminate, style (0.4) 0.5-0.55 (0.6) mm long, fruit apex usually abruptly sharp-acuminate with persistent style

var. giganteum

- 1 Leaflets broadly lanceolate (basal pair often ovate), margin involute, apex gradually acuminate, style 0.35-0.4 long, fruit depressed-ovoid to globose

var. crassifolium

17a. Protium giganteum Engler var. giganteum

Protium duckei Huber, Bol. Mus. Paraense Hist. Nat. 5: 432. 1908. Type.

Brazil. Pará: Rio Mapuera (affluent of Rio Trombetas), 2 Dec 1907 (m buds), Ducke 9016 (holotype: RB).

Protium cupreatum Cuatrecasas, Bol. Mus. Paraense Hist. Nat., Nov. Sér.

(Botânica) 11: 1. 1961. Type. Brazil. Pará: region of Anapû, Rio Tapacû, Portel, 10 May 1956 (fr), Frões 32784 (holotype: US; isotype: U).

Protium pernervatum Cuatrecasas, Bol. Mus. Paraense Hist. Nat., Nov. Sér.

(Botânica) 11: 5. 1961. Type. Brazil. Pará: forest of Pirelli Company, Fazenda Uriboça, Jul 1958 (m buds), Pires 6963 (holotype: US; isotype: U).

Leaves (0) 1-3-jugate; basal portion of petiole deeply canaliculate; leaflets oblong, apex abruptly acuminate, not usually glossy adaxially, margin not involute. Pistillate flowers with staminodes (1.1) 1.25-1.35 and (1.2) 1.35-1.5 mm long; disk 0.2-0.25 (0.3) x 0.15-0.2 (0.3) mm; pistil (1.2) 1.25-1.45 mm high, style (0.4) 0.5-0.55 (0.6) mm long, often elongating slightly in young fruit, stigmas 0.25-0.3 mm high. Fruit apex usually abruptly sharp-acuminate with persistent style.

Distribution. Guyana, and Brazil in Amazonas, Maranhão, and Pará exclusive of Marajó Island. This variety flows from August to December (February) and fruits from September to March.

Specimens examined. BRAZIL. Pará: Tapajós region, Boa Vista, 12 Dec 1932 (f buds), Capucho 375 (F, IAN); Santarém, Rio Curuá Una, above Cachoeira do Palhão, 8 Dec 1966 (galled fl), Cavalcante & Silva 1625 (MG); ca. 25 km S of Tucuruí, of old BR-422, ca. 3°58' S, 49°38' W, 30 Oct 1981 (f fl & young fr), Daly et al. 1091 (MG, NY); Serra dos Carajás, "Azul," near camp at Serra Norte (22 km NW, then 10-15 km SW), ca. 5°59' S, 50° 28' W, 8-12 Dec 1981 (fr), Daly et al. 1885 (MG, NY); Belém, 5 Oct 1962 (f fl), Duarte 7049 (NY); Rio Xingu, margin of Rio Tucuruí, 24 Aug 1919 (f fl), Ducke 11403 (RB); Belém, Água Preta, 26 Nov 1914 (f fl), Ducke (MG no.) 15535 (MG); Rio Tapajós, morros do Quataquara, 13 Aug 1923 (buds),

Ducke 18398 (RB); Rio Curuá Una, flanks of Planalto do Santarém, 30 Oct 1954 (buds), Frões 31276 (US); grounds of Instituto Agronômico do Norte, 5 Aug 1947 (young fr), R. Lima 23 (IAN); Tucuruí, left side of Rio Tocantins, km 20 of BR-422, left fork, 5 Nov 1980 (fr), Lisboa et al. 1414 (MG, NY); Tomé Açu, right side of road to Fazenda Cafezal, 29 Dec 1977 (young fr), Nascimento 341 (MG, NY); Belém-Brasília highway, 6 Dec 1959 (f fl, fr), Oliveira 239 (IAN); Rio Jarí, Monte Dourado, 2 Dec 1967 (buds), Oliveira 3808 (IAN), 23 Jan 1968 (fr), Oliveira 3964 (IAN, NY); Belém, 5 Oct 1945 (young fr) Pires & Black 359 (GH, IAN); Breves, site of forest inventory, Oct-Nov 1957 (fr), Pires & Silva 6642 (IAN, US); forest of Companhia Pirelli, Fazenda Uriboça, Aug 1958 (fr), Pires 7080 (U, US); Belém, IPEAN, Mocambo, 10 Oct 1966 (m fl), Pires & Silva 10246 (IAN, NY), 20 Oct 1966 (fr), Pires & Silva 10296 (IAN, NY), 19 Aug 1967 (m fl), Pires & Silva 10736 (NY), 16 Oct 1967 (m fl), Pires & Silva 11121 (IAN, NY); Belém-Mosqueiro road (SUDAM), 27 Oct 1967 (m fl), Pires & Silva 11238 (IAN, NY); Belém, IPEAN, Reserva Aurã, 5 Dec 1967 (f fl), Pires & Silva 11386 (IAN); Belém, IPEAN, Reserva Mocambo, 13 Mar 1968 (fr), Pires & Silva 11435 (IAN), without date (fr), Pires & Silva 12024 (IAN, NY); Belém, Mocambo Reserve, (without date) (fr), Pires 12025 (IAN); Municip. Paragominas, Belém-Brasília highway (BR 010) 17 km S of Ligação do Pará, near km marker 1509, approx. 4°17'S, 47°32'W, 1 Mar 1980 (fr), Plowman et al. 9418 (NY); vicinity of Cachoeira, km 96 of BR-22, 27 Oct 1965 (buds), Prance & Pennington 1714 (NY); Santarém, without date (buds), Riedel s.n. (NY); Municip. Almeirim, Monte Dourado, road to Agua Azul, 11 Nov 1978 (galled fl), Santos 280 (MG, NY); Rio Jarí, Monte Dourado and Munguba, 5

Feb 1968 (m fl), N. T. Silva 1509 (IAN, NY); Jari region, road between Tinguelim and Braço, 20 Oct 1969 (buds), N. T. Silva 2838 (IAN); Jari region, road between São Miguel and Braço, 22 Jan 1970 (young fr), N. T. Silva 2904 (IAN); Jari region, Tinguelim km 21, 30 Sep 1970 (m fl), N. T. Silva 3344 (IAN); Belém, Museu Goeldi near Pisciculture building, 27 Aug 1963 (m fl), Viana (MG no.) 30589 (MG). Guyana: Basin of Essequibo River, near mouth of Onoro Creek, approx. 35°N, 15-24 Dec 1937 (m buds), A. C. Smith 2728 (F, GH, MO, NY).

Local names and uses. Brazil. Pará, Amazonas: breu preto, breu manga, breu vermelho, breu branco. Maranhão: kandeia'ka'y, kande-i-y tuwy (Ka'apor). Used for caulking canoes, firewood, and wood for sidings (Pará, Capucho 375), also fruit eaten and resin burned for illumination (Maranhão, Balée & Ribeiro 1055, 1061).

17b. *Protium giganteum* Engler var. *crassifolium* (Engler) Daly (submitted for publication in Brittonia).

Protium crassifolium Engler in Mart. Fl. bras. 12(2): 270. 1874. Type.

French Guiana: banks of Kourou River, without date (young fr), Richard s.n. (lectotype (designated by Swart, 1942b): P; isolectotype: C).

Leaves 1-4-jugate; basal portion of petiole shallowly canaliculate; leaflets broadly lanceolate (basal pair often ovate), apex gradually acuminate, usually glossy adaxially, margin usually involute. Pistillate flowers with staminodes 1.45 and 1.55 mm long, also with disk 0.35-0.4 x

0.2-0.25 mm; pistil 1.5 mm long, style 0.35-0.4 long, stigmas 0.2 mm high.
Fruit depressed-ovoid to globose, very slightly acuminate.

Distribution. French Guiana, Suriname, and in Brazil on Marajó Island. This variety flows from September to November and fruits from August to April.

Specimens examined. Brazil. Pará: Marajó Island, S. Sebastião da Boa Vista, 19 Sep 1971 (m fl), Pena 261 (IAN). French Guiana: Cayenne, 25 Nov 1955 (m fl), Bena (BAFOG no.) 1026 (CAY, U); Cayenne, Tour de l'île au Gallion km 22,500, left side, 150 m from road, 17 Apr 1956 (fr), Bena (BAFOG no.) 1165 (CAY, U); without locality, without date (fr) Lemée A.11 (P); without locality, without date (fr), LePrieur 322 (G, P); road to Ste. Elie, experimental clear-cut, 20 Oct 1977 (sterile), Lescure 767 (CAY); Cayenne, without date (f fl), E. Martin s.n. (P); new road to Brazil (Route de l'Est), near bridge on the Compté River, 45 km S of Cayenne, 30 Dec 1976 (NY), Mori 8851 (NY); Cayenne, without date (m fl), Poiret s.n. (P); banks of Aracouany River, Oct 1854 (fr), Sagot 8 (P); Karouany, Aug 1856 (fr and m buds), Sagot 970 (BM, K, P, U). Surinam: Via secta Moengo tapoe ad Grote Zwiebelzwamp, near km 10.5, 7 Oct 1949 (buds), Lanjouw & Lindeman 694 (NY), near km 14.5, 13 Oct 1949 (buds), Lanjouw & Lindeman 812 (NY).

Local names and uses. French Guiana: encens blanc, encens gris. Wood used in French Guiana for constructing boats, frames, joinery, and cabinet-making.

The most striking characters which distinguish var. crassifolium from the typical variety are the involute margin of the very coriaceous broadly

lanceolate leaflets, shorter style, and more globose fruits without a sharp acumen. In all other qualitative and quantitative characters not noted above, including the shape of the pyrene, the two varieties are alike.

Because of its relative consistency, the involute leaflet margin of var. crassifolium does not appear to be an artifact of drying. Associated with this character is the occurrence of an undulation between each pair of secondary nerves, something noted about the fresh material of one collection (Lescure 767).

Although there is a geographic component to the differences between these two taxa, they are given varietal rank here because the characters separating them are not absolutely constant, because there are apparent intermediates, and because the identity of several specimens of each in their respective territories is uncertain. Some collections of var. giganteum (Ribeiro 1277, Oliveira 3964) have weakly acuminate fruits, although vegetatively they are typical. A few collections of var. crassifolium (Martin s.n., Poiret s.n., Sagot 8) have leaflet margins apparently not involute, in one case (Martin s.n.) possibly because the leaves are immature; one collection (Bena 1026) has three sheets, and the leaflets on only two of them have involute margins.

The Jari region of Pará is intermediate geographically between the distributions of the two varieties, and the collections from there (N. I. Silva 1509, 2904)-- both with staminate flowers-- tend to be intermediate morphologically as well, at least in vegetative characters. Staminate flowers of the two varieties are difficult to distinguish, so in this

region specimens with pistillate flowers or fruits are needed to resolve their identity. It is worth noting that the Jarí region appears to be an interface between the two varieties of Protium polybotryum (Turcz.) Engl., which are otherwise almost completely separated geographically.

Well within the apparent range of var. crassifolium, two collections from Cayenne (Martin s.n., Poiret s.n.) have the leaves of the typical variety but the former has staminate flowers and the latter has badly damaged pistillate flowers, so their identity cannot be definite. .

The typical variety is reasonably well represented in the herbaria, but var. crassifolium is under-collected and most of the material is in poor condition. Indeed, one unfortunate character which distinguishes dried material of the species as a whole is its extreme susceptibility to herbarium pests.

In this species, the occurrence of sterile flowers in the genus Protium can be documented for the first time. On W. A. Rodrigues (INPA no.) 2028, a pistillate plant, there are a number of flowers without any functional reproductive organs (see chapter on flowers).

Another intriguing aspect of sexual expression in Protium is indicated by Sagot 970, which may show a sequential transition of gender (see chapter on flowers). The several duplicates of this collection consist of fruits as well as new staminate inflorescences. Unfortunately, the fruits are not attached to the flowering branchlets, so the evidence is inconclusive.

Table XIX

Table of characters separating the varieties of Protium giganteum

character	var. giganteum	var. crassifolium
no. of juga	(0) 1-3	1-4
calyx (f fls)	(0.7) 1.1-1.3 x 1.7-1.8 (2) mm	(1) 1.2-1.3 (1.5) x (2) 2.2-2.3 mm
calyx lobes (f fls)	0.3-0.5 (0.6) mm	0.5-0.7 mm
staminodes	(1.1) 1.25-1.35 and (1.2) 1.35-1.5 mm	1.45 and 1.55
disk (f fls)	0.2-0.25 (0.3) x 0.15-0.2 (0.3) mm	0.35-0.4 x 0.2-0.25 mm
pistil	(1.2) 1.25-1.45 mm	1.5 mm
style	(0.4) 0.5-0.55 (0.6) mm	0.35-0.4 mm

18. *Protium paniculatum* Engler in Mart. Fl. bras. 12(2): 270. 1874. Type. Brazil. Amazonas: Rio Uaupés near Panurê, Dec 1852 (f fl and fr), Spruce 2770 (lectotype (designated by Swart, 1942b): P; isoelectotypes: BR, OXF, W). *Icica paniculata* (Engl.) VillaFranca. Bull. Thér. Méd. et Chir. 1880: 4. 1880. *Tingulunga paniculata* (Engl.) Kuntze, Rev. Gen. Pl. 1: 108. 1891.

Tree, reproductive size (5) 8-20 (27) m x 12-26 cm diam; often with low buttresses; trunk often angular; bark rough, flaky, with shallow vertical fissures; resin clear, sticky, drying as a white crystalline mass; branchlets robust or less often slender, (2.1) 2.5-5 mm diam, to 6 mm diam in fruit, soon subglabrous or less often with persistent scattered hairs to 0.2 mm long. Leaves (1) 2-3 (5)-jugate, usually long, (14) 23-38 (49) cm long; petiole semi-terete to very slightly canaliculate and slightly acutely winged, longer than interjuga, (2.6) 5-9.3 (14.5) cm x (1.3) 2-3 (3.8) mm, with scattered appressed hairs to 0.5 mm long, often with exfoliating epidermis (black when dry); interjuga (2.1) 3-5.5 (7.9) cm long; petiolules often short and robust but of variable length, usually broadly and shallowly 1-canaliculate, 0.4-1.1 (1.8) mm long, pulvinuli usually negligible, making apex of petiolule broader but not deeper; leaflets coriaceous, laterals elliptic to broadly elliptic to broadly lanceolate (rarely oblanceolate), basal pair smaller than others, (7.7) 9.5-15.3 (19.5) x (2.6) 4.2-5.9 (8) cm, ultimate pair (9.4) 12.2-17.4 (26) x (3) 3.9-6.5 (10.5) cm, terminal broadly elliptic or often obovate,

usually larger than laterals, (9) 11.5-17 (22) x (3) 4.6-6.5 (10) cm, leaflet base subequal, acute to obtuse, apex usually abruptly acuminate, sometimes gradually acuminate, acumen of variable length, (0.5) 0.8-1.6 (2.3) cm long, abaxial surface with midvein broadly obtusely prominulous, rest of veins discolorous and prominulous, blade glossy or (var. riedelianum) dull and strongly discolorous, with scattered appressed hairs to 0.1 mm long, adaxial surface with midvein narrowly prominulous but depressed in a groove, rest of veins discolorous and prominulous, blade glossy, glabrous or midvein with scattered fine erect hairs to 0.05 mm long. Inflorescences subterminal, profusely branched, usually long and robust (6) 17-33 (45.7) cm x (1.2) 1.8-3.5 (4) mm, to (0.4) 0.7-1.3 times length of subtending leaf, secondary axes usually well-developed, compressed, 1.4-11.5 (20.5) cm long, axes reddish (J. M. Pires 350); inflorescence bracts ovate, chartaceous, usually semi-clasping, those on primary axes often short, 0.5-1.1 mm long, rarely to 1.8 mm long on pistillate plants, bracts on secondary axes 0.3-0.8 (1) mm long, to 1.8 mm long on pistillate plants, axes with sparse to scattered, thick, acute appressed hairs 0.05-0.2 mm long, also with fine erect hairs to 0.5 mm long; pedicel compressed-obclavate, (0.4) 0.6-1.5 (2) x (0.25) 0.3-0.45 (0.6) mm, with sparse hairs of both types. Flowers 4- or 5-merous, (sometimes on same inflorescence, i.e., Prance et al. 16019, Frões 25599), (2) 2.5-3 mm long; calyx deeply cupular, (0.7) 1-1.3 (1.9) x (1.6) 1.9-2.2 (2.4) mm, with scattered to sparse (rarely dense) hairs of both types, lobes (depressed-) deltate, rarely reduced to apicula separated by flat sinuses, (0.1) 0.2-0.45 (0.7) mm long, margin often with dense ascending

hairs to 0.1 mm long; petals green or greenish-yellow, ovate (broadly lanceolate when 5-merous), (1.85) 2-2.4 (3) x (0.7) 1-1.2 (1.45) mm, somewhat saccate at base, apex acute, sometimes acuminate, apiculum usually inconspicuous, at anthesis petals suberect or usually reflexed from upper 1/3 their length, abaxially with pubescence as on calyx but denser, often concentrated near margin, adaxially short-papillate, also with sparse to dense or rarely scattered, erect to ascending, translucent hairs to 0.25 mm long, often restricted to distal 2/3 of surface, usually concentrated along 5 discrete vertical lines, margin short-papillate; in staminate flowers calyx usually exceeded by disk; stamens greatly exceeding pistillode, (1) 1.25-1.8 (1.95) and (1.1) 1.3-1.9 (2.15) mm long, filaments subcylindric, (0.55) 0.75-1.4 and (0.6) 0.85-1.5 (1.65) mm long, inflexed, anthers erect, dorsifixed but sometimes appearing basifixed, in dorsiventral view narrow-lanceolate to lanceolate base lobulate, apex acute or rarely mucronulate, in lateral profile lanceolate to oblong, apex acute, 0.4-0.55 (0.6) mm long; disk of variable height and width; 0.2-0.5 (0.6) x (0.1) 0.2-0.3 (0.5) mm; pistillode only slightly exceeding disk, 0.55-0.7 (0.95) x (0.35) 0.45-0.55 (0.6) mm overall, depressed-ovoid to obovoid or globose, with dense, ascending to appressed hairs (0.05) 0.15-0.3 (0.5) mm long, provided with reduced locules and ovules, contracted to a long, thick, 4- or 5-lobulate stylode 0.2-0.35 (0.4) x 0.2-0.25 mm; in pistillate flowers calyx usually exceeding disk, staminodes usually slightly exceeding pistil, 1.3-1.75 and 1.4-1.85 mm long, filaments erect, strongly compressed and abruptly broadened basally, 0.8-1.25 and 0.9-1.35 mm long, anthers in dorsiventral view broadly

lanceolate, base lobulate, apex obtuse to retuse, in lateral profile narrow-lanceolate, 0.4-0.6 mm long, disk (0.15) 0.25-0.4 (0.5) x (0.1) 0.15-0.3 mm; pistil (0.95) 1.25-1.45 (1.65) x 0.7-0.9 mm overall, ovary broadly ovoid, sessile, occasionally acuminate, with dense, ascending to appressed hairs 0.05-0.25 (0.3) mm long gradually or sometimes abruptly contracted into a slightly clavate style of variable length, (0.1) 0.25-0.5 (0.6) x (0.2) 0.35-0.4 mm, stigmatal region 0.25-0.4 mm high, stigmas sessile, lateral or oriented very slightly upward and outward, compressed-globose to almost discoid. In fruit pedicel becoming clavate, young fruit sessile or rarely slightly stipitate, subglobose to ovoid to slightly obovoid, slightly acuminate, quickly glabrescent or pubescence persistent (var. riedelianum), mature fruit green, globose to rotund, (1.3) 1.4-2.1 (2.2) x 1.2-1.6 (1.7) cm (to 1.8 cm diam when more than one pyrenes), broadly substipitate, apex slightly excentric, rounded, color or inside of valves and inner wall of mesocarp unknown; pseudaril white, not covering most of ventral face, overlying a dense layer of matted fibers to 0.4 mm long; pyrene (1.2) 1.3-1.6 x (0.8) 0.9-1.3 cm, thinly cartilaginous, brittle, in dorsiventral view obovoid to rotund, base and apex obtuse, ventral side more deeply convex, ventrally deeply concave on both sides near apex such that apex is trigonous, sometimes with a ventral vertical ridge from median to base, site of funicle 4/5 distance to apex, funicular depression shallow; cotyledons fleshy, plane-convex, slightly uncinately curved (A. Loureiro (INPA no.) 37802); A. Ducke 10523).

Two varieties of P. paniculatum are recognized in this treatment. Although there is a geographic component to their differences, they are

sympatric in several localities and the morphological characters separating them are rather weak. They are distinguished in the following key:

Key to the varieties of Protium paniculatum

1. Abaxial surface of leaflets not strongly discolorous, both surfaces glossy; young fruits soon glabrescent var. paniculatum
1. Abaxial surface of leaflets strongly discolorous, dull; fruits with dense appressed hairs 0.05-0.2 mm long var. riedelianum

18a. Protium paniculatum Engler var. paniculatum

Protium paniculatum Engler var. pentamerum Swart, Rec. Trav. Bot. Néerl.

39: 198. 1942. Type. Peru. Loreto: Maynas, Mishuyacu, near Iquitos, Oct-Nov 1929 (m fl), G. Klug 348 (holotype: F; isotype: NY).

Lateral petiolules often narrow and narrowly canaliculate, (0.4) 0.5-1.6 (2.1) cm long; leaflets glossy on both surfaces, not strongly discolorous when dry. Flowers 4- or 5-merous; staminodes in pistillate flowers 1-1.3 mm long, disk in staminate flowers 0.25-0.35 (0.4) x (0.1) 0.15-0.3 (0.5) mm, in pistillate flowers 0.15-0.2 (0.45) x 0.15-0.3 mm; pistillode (0.5) 0.55-0.65 (0.7) x 0.35-0.45 (0.5) mm; pistil (0.95) 1.25-1.45 x 0.7-0.9 mm. Young fruits soon glabrescent.

Distribution. Infrequent in the understory of terra firme forests on

sandy soils in the Rio Negro basin. This variety flowers in October and fruits from December to May.

Specimens examined. Brazil. Amazonas: Basin of Rio Negro, Camanaus, 31 Oct 1971 (m fl), Prance et al. 15899 (NY (2)); basin of Rio Solimoes, Municip. São Paulo de Olivença, basin of creek Belém, 26 Oct-11 Dec 1936 (young fr), Krukoff 8864 (GH, MICH, NY); Municip. São Paulo de Olivença, near Palmares, 11 Sep-26 Oct 1936 (m fl), Krukoff 8523 (F, GH, NY, US). Peru. Loreto: Dtto. Alto Nany, Sta. Maria, Rio Nany, 7 Oct 1967 (f fl), Reyna R. 21 (F); 7 Oct 1967 (f fl), Reyna R. 22 (NY). VENEZUELA. T. F. Amazonas: 0.5 to 3 km N of San Carlos de Río Negro, 5 May 1979 (fr), Liesner 7218 (MO, NY).

Local names and uses. In Peru, the common name in Spanish for this and most other Burseraceae is "copal." The label for one collection (Reyna 22) notes the indigenous name "shininga arana" for the tree and the Spanish name "sacha sapote" for the fruit. The pericarp-- reported as being yellow in the same collection-- is edible. The resin is used for caulking canoes (Reyna 21), and the wood is used for cooking and for making charcoal (Reyna 22).

18b. *Protium paniculatum* Engler var. *riedelianum* (Engler) Daly (submitted for publication in Brittonia)

Protium riedelianum Engler in Mart. Fl. bras. 12(2): 279. 1874. Type.

Brazil, Rio Negro, Sep 1828 (m fl), L. Riedel 1402 (lectotype (here designated): LE; isoelectotypes: M, NY). Tingulunga riedeliana (Engl.) Kuntze, Rev. Gen. Pl. 1: 108. 1891.

Protium nitidum Engler in Mart. Fl. bras. 12(2): 271. 1874. Type.

Brazil. Amazonas. Rio Uaupés near Panurê, Oct 1852-Jan 1853 (m fl),

Spruce 2662 (lectotype (here designated): OXF; isoelectotypes: BR, W).

Tingulunga nitida (Engl.) Kuntze, Rev. Gen. Pl. 1: 108. 1891.

Lateral petiolules short, broad, and broadly canaliculate, (0.3) 0.4-0.9 (1.2) cm long; abaxial surface of leaflets matte and strongly discolorous. Flowers 4-merous; staminodes in pistillate flowers (1.3) 1.35-1.6 mm long; disk in staminate flowers (0.3) 0.4-0.5 (0.6) x 0.15-0.3 (0.4) mm, in pistillate flowers (0.3) 0.35-0.4 x (0.1) 0.2-0.25 (0.3) mm. Fruit with dense appressed to ascending hairs 0.5-0.15 mm long.

Distribution. Widespread if infrequent in the understory of terra firme forests on various soils in Pará, frequent near Manaus, occasional in the Rio Madeira basin, and rare in the upper Rio Negro basin. One collection is known from várzea forest (Prance et al. 1475). This variety flowers from September to November and fruits from November to March.

Specimens examined. Brazil. Pará: Altamira-Itaituba road, km 115, elev 270 m, 19 Jan 1976 (fr), Bamps 5187 (BR, NY); Município Acará, Fazenda Borba Gato, near Rio Acará, 30 km W of Tomé Açu, approx. 2°48'S, 48°35' W, 5 Nov 1980 (bud and fr), Daly et al. 827 (MG, NY, INPA); Faro, forest near the city, 23 Jan 1910 (fr), Ducke 10523 (MG); Município Paragominas, Belém-Brasília highway (BR010) 6 km N of Ligação do Pará, near km marker 1532, approx. 4°05' S, 47°32' W, 3 Mar 1980 (fr), Plowman et al. 9519 (NY); line SW of Ilha de Breu, km 7-8.5, 2°33'-2°50' S, 50°38'-50°50' W, 27 Sep 1965 (m and f fl), Prance et al. 1475 (NY); Tucuruí, area of

deforestation, PA-263, side road "massa falida" km 15, 7 Nov 1983 (buds), Ramos 1039 (NY); Parque Nacional do Tapajós, km 70 of Itaituba-Jacareacanga road, side road to Patuá, 19 Nov 1978 (fr), M. G. Silva 3831 (HAMAB, K, MG, NY, US); road between Planalto A and Tinguelim, km 13, 22 Sep, 1969 (buds), N. T. Silva 2787 (NY), km 21, 18 Mar 1970 (fr), N. T. Silva 2990 (IAN).

In his treatment of the Burseraceae for Flora brasiliensis, Engler (1874) described Protium paniculatum and P. nitidum, both based on pistillate-flowering material. He perceived the similarities between them, separating them in his key only by leaflet shape: oblong-elliptic and ovate-elliptic, respectively. In the same treatment he also described Protium riedelianum, based on staminate-flowering material. Because of Engler's misunderstanding of sexual dimorphism in the flowers of Protium (see chapter on flowers), one finds P. riedelianum far from the the other two species in the key.

Swart considered all three to be taxonomic synonyms, noting that based on the limited material available to him "the differences between each two of these...are ever linked by the intermediate character of the third one." (Swart, 1942, p. 347). Swart, however, based this judgment on rather variable characters: inflorescence length, petiole shape, leaflet size, shape of the terminal leaflets, and the number of secondary nerves.

In the present treatment P. riedelianum is considered a variety of P. paniculatum, while P. nitidum is considered a taxonomic synonym of P. riedelianum. Protium nitidum was not chosen as the source for the varietal name because the type material is poor and because the epithet would be

misleading considering the characters which differ from the typical variety.

All individuals of the species appear to be quite uniform in all but two qualitative characters, indicated in the key above, which consistently separate vars. paniculatum and riedelianum. From the material available it appears that quantitatively there are differences but no sharp discontinuities. The type locality for both P. paniculatum and P. nitidum is Panuré near the Rio Uaupês, and they are not far apart in Spruce's number series, so the two varieties recognized here may occur sympatrically. In the approximately 100 hectares of forest inventoried by the World Wildlife Fund-U.S. near Manaus, var. riedelianum is unquestionably sympatric with a population of P. paniculatum which may constitute an undescribed variety (i.e., Daly et al. 4051). Both entities are frequent in the inventories, and there are no morphological intermediates among the material sampled to date, which includes some fertile material of both.

This third entity corresponds well with several collections from Amazonas in Venezuela and elsewhere in the Rio Negro basin. Although it has the glabrous fruits and non-discolorous leaflets of the typical variety, it has consistently shorter leaves, longer and more slender petiolules, more asymmetrical leaflet bases, more narrowly elliptic leaflets-- often slightly falcate-- which are dull on both surfaces, and more gradually acuminate leaflet apices. Further fertile collections are needed to determine if this entity diverges in other characters.

Protium paniculatum appears to be rather plastic in a number of

characters. While in most species of the genus changes in number of flower parts are found rarely if at all, 4-merous and 5-merous individuals occur in the species and some collections may have a number of 4- or 5-merous flowers on one inflorescence (i.e., Fröes 25599, Prance et al. 16016). Notwithstanding Swart's brief diagnosis of P. paniculatum var. pentamerum, no other morphological characters can be correlated with heteromorphic flowers.

Flower size may also vary considerably in this species. This is reflected in the wide range of measurements for the length of the calyx, petals, and especially stamens.

Some collections of the species appear to have an acuminate ovary and short style. This may be due to swelling of the distal part of the ovary immediately after fertilization, something which occurs in P. pallidum.

Protium paniculatum var. riedelianum also shows the first confirmed occurrence of a monoecious plant in the genus, Prance et al. 1475, with typical staminate and pistillate flowers on the same inflorescence (see chapter on flowers).

19. *Protium krukoffii* Swart, Rec. Trav. Bot Néerl. 39: 193. 1942. Type. Brazil. Amazonas: Municip. São Paulo de Olivença, near Palmares, 11 Sep-26 Oct 1936 (f fl), Krukoff 8180 (holotype: NY; isotypes: BR, F, MICH, MO).

Protium piresii Swart, Acta Bot. Neerl. 15: 53. 1966. Type. Brazil. Pará: Belém, Aurã, 27 Nov 1950 (m fl), Pires 2693 (holotype: IAN).

Trees, rarely with shrub habit (fide Archer 8143), reproductive size 4-20 m x 8-35 cm DBH; branchlets slender, 2-2.6 (3.7) mm diam, with erect hairs to 0.05 mm long, also with appressed hairs to 0.2 mm long (both sparse to scattered). Leaves (1) 2-4-jugate, (11.5) 14.5-28 (32) cm long (to 37 cm long on sterile branchlets (fide part of Sastre 117)); petiole semi-terete to terete, shorter than interjuga, slender, (1.6) 2.5-5.4 (6.3) cm x (0.8) 1.3-1.9 (2.1) mm, with scattered hairs as on branchlets; interjuga terete, (1.9) 2.5-4.4 (5) mm long; petiolules 2-canaliculate, long and very slender, (0.3) 0.5-1.1 (1.4) cm long, with sparse erect hairs, pulvinuli not conspicuous, terminal shorter than interjuga, (0.9) 1.5-3 (4.2) cm long; leaflets chartaceous, laterals ovate to (broadly elliptic), basal pair 6-10.5 (12.2) x (1.8) 2.6-4.7 (5.8) cm, ultimate pair (6.3) 7.5-11.5 (13) x (2) 2.6-4.1 (4.9) cm, base usually strongly oblique, acute on proximal side, truncate to obtuse on distal side, terminal elliptic, (5.5) 7.8-11 (13) x (2.2) 3.2-5 (6) cm, base acute to obtuse, leaflet apex gradually long-acuminate, acumen 0.6-1.7 (2.5) cm long, abaxial surface with midvein narrowly obtusely prominulous,

secondary veins prominulous, rest of veins inconspicuous, midvein with scattered appressed hairs, adaxial surface with midvein narrowly obtusely prominulous, rest of veins, midvein and secondary veins with scattered erect hairs. Inflorescences distributed along branchlet, sometimes exceeding petiole, 2-9.5 (11.5) cm x (0.3) 0.4-1.1 (1.5) mm (x 0.8-1.5 (2) mm in fruit), to (0.25) 0.3-0.4 (0.45) times length of subtending leaf, secondary axes relatively well-developed, 0.4-3 (4.2) cm long, with sparse to dense erect hairs and scattered appressed hairs, occasionally subglabrous (sparse erect hairs only on type of Protium piresii); inflorescence bracts small, lanceolate to ovate, acute, those on primary axes 0.3-0.6 (0.7) mm long, those on secondary axes 0.3-0.5 (0.6) mm long; pedicel subcylindric, slender, usually with scattered hairs of both types (subglabrous on type of P. kruckhoffii, hairs sparse to dense on type of P. piresii), in staminate flowers (0.6) 1-2 x 0.25-0.4 mm, in pistillate flowers usually shorter, 0.6-1.5 (2.8) x 0.3-0.4 mm. Flowers all 4-merous, (1.7) 2-2.8 (3.5) mm long; calyx shallowly cupular, exceeded by the disk in staminate flowers and level with the disk in pistillate flowers, 0.4-0.7 (1) x (1.3) 1.4-1.8 (2.2) mm, base usually truncate but occasionally funnel-form, with scattered hairs as on pedicel, lobes deeply depressed-deltate or usually negligible and reduced to an apiculum, 0-0.3 mm long; petals green, white, cream, or yellowish-green, broadly ovate, (2.1) 2.5-2.7 (3) x (1.05) 1.25-1.5 mm, weakly adnate to antepetalous filament, with a central cleft at base corresponding to position of filament, apex acute, often slightly acuminate, apiculum conspicuous, 0.25-0.35 mm long, abaxially glabrous, margin and apiculum long-papillate,

at anthesis petals reflexed from upper 1/3 their length; in staminate flowers stamens greatly exceeding pistillode, 1.35-1.75 and 1.45-1.85 mm long, filaments subcylindric, 0.75-1.05 and 0.85-1.1 mm long, not papillate, antesepalous filaments markedly broadened at base, antepetalous filaments less so, anthers basifixed, in dorsiventral view narrowly lanceolate, lobulate, apex acute, in lateral view narrowly obtuse-oblong, long, 0.6-0.75 mm long; disk shallow and broad, 0.15-0.25 x 0.25-0.4 mm, pistillode 0.45-0.65 (0.8) x 0.35-0.4 mm overall, greatly exceeding disk, ellipsoid to ovoid, glabrous, glossy, gradually contracted to a thick, terete (rarely sulcate) stylode 0.25-0.3 mm long, apex rounded; in pistillate flowers staminodes reaching base of stigmas, 1.15-1.35 and 1.2-1.4 mm, filaments slender, compressed, 0.45-0.7 and 0.55-0.8 mm, slightly broadened at base, anthers of the two series dimorphic, in dorsiventral view the antesepalous ones broadly lanceolate, apex obtuse, antepetalous ones obtuse-oblong, both lobulate at base, apex obtuse, in lateral view both asymmetrically obtuse-oblong, both 0.5-0.7 mm long; disk shallow, 0.15-0.25 (0.3) x 0.15-0.35 mm; pistil (1.2) 1.3-1.5 (1.6) x 0.7-0.9 (1) mm overall, ovary ovoid, sessile or negligibly substipitate, glabrous or rarely with a few ascending hairs 0.2-0.5 mm long (Pires 10609), gradually contracted to a short thick style, (0.25) 0.4-0.55 x 0.3-0.4 (0.5) mm, stigmatal area 0.25-0.3 mm high, stigmas sessile, lateral or oriented slightly upward and outward, depressed-globose to almost discoid. Fruit maturing green (fide Rosa & Cordeiro 1731); (broadly) obliquely ovoid, substipitate, 2-2.8 x 1.2-1.7 cm (to 2.5 cm wide when more than 1 pyrene), apex gradually and acutely long-acuminate;

pseudaril spongy, white, covering all but the upper 1/3 of ventral surface, overlying a dense layer of matted (sub)erect fibers to 0.4 (0.5) mm long; pyrene thinly cartilaginous, 1.4-1.6 x 1.1-1.2 cm, in dorsiventral view depressed-ovate, base truncate, apex abruptly acutely acuminate, in lateral view asymmetric, narrowly semi-ovate on dorsal side and broadly semi-ovate on ventral side, ventral face with a shallow vertical central sulca, also with two deep subapical depressions forming a trigonous apex, site funicle 5/6 distance to apex, funicular depression shallow, funicular scar essentially triangular, covering 1/3 of ventral face; testa with some irregular thickenings but not infolded with cotyledons (Rabelo 2043, Sastre 117), cotyledons with external folding but not contortuplicate (Rabelo 2043, Oliveira 4407).

Distribution. Although Protium krukoffii was originally described from western Amazonas in Brazil, it is apparently far more common in eastern Amazonia. This species occurs usually as a small riverside tree, less frequently in várzea forest, and rarely in terra firme. In eastern Amazonia P. krukoffii flowers in October to January, less often in July, and fruits March to June, less often in December and January.

Specimens examined. BRAZIL. Amapá: margin of Rio Castanhal, between São João and the first "deserto," 21 Nov 1967 (f fl and young fr), E. Oliveira 3653 (IAN); Rio Matapi between the road and mouth of Rio Macapá, 4 Mar 1983 (fr), Rabelo et al. 1860 (HAMAB, NY); Rio Vila Nova, 7 Apr 1983 (fr), Rabelo et al. 2043 (HAMAB, NY); Mazagão, Vila Sossego, Igarapé Maracá-Mirim, 11 May 1983 (fr), Rabelo et al. 2111 (HAMAB); Macapá, middle Rio Pedreira, 24 Apr 1984 (fr), Rabelo et al. 2583 (HAMAB). Pará: Belém,

south forest of IAN, 30 Nov 1942 (f fl & young fr), Archer 7905 (F, IAN, MO, NY, US(2)), 13 Dec 1942 (fr), Archer 7970 (F, IAN, NY, US(2)), 11 Jan 1943 (young fr), Archer 8143 (US); várzea of Rio Tajapurú, Ilha São Sebastião and Nazarê, 21 Jul 1948 (f fl), Black 48-3018 (IAN); Rio Jari, Monte Dourado, road to Igarapé Pacanari, 8 Nov 1978 (m fl), Cavalcante 3317 (MG); E.F.B. Santa Isabel, Caraparú, 24 Oct 1957 (m fl), Egler 614 (MG); Belém, igapô of Rio Guamã, 19 Nov 1914 (m fl), Ducke 15530 (MG); Gurupã, margin of creeks on margin of Rio Amazonas, 16 May 1916 (fr), Ducke 16175 (MG); Tomé Açu, right margin of road to Fazenda Curmã, 30 Dec (m fl), Nascimento 359 (NY); region of Rio Jari, Lugarejo Bandeira, Serra do Encrenca, Igarapé do Inferno, 24 Apr 1963 (fr), Oliveira 2501 (IAN); region of Rio Jari, Rio Caracurú, Igarapé do Centrinho, 1 May 1963 (fr) Oliveira 2516 (IAN); margin of Rio Guamã, 20 Aug 1964 (young fr), Oliveira 3130 (IAN, NY); Rio Jari, between S. Melitão and Monte Dourado, 7 Jun 1968 (fr) Oliveira 4407 (IAN, NY); Muanã, Rio Patauateua, 4 Mar 1970 (fr), Oliveira 5149 (IAN); Belém, Reserva Aurã, 2 Jan 1950 (f fl), Pires 1839, 27 Nov 1950 (m fl), Pires 2693 (IAN), 28 Jul 1967 (f fl), Pires & Silva 10609 (IAN, NY), 15 Sep 1967 (f fl, young fr), Pires & Silva 11214 (IAN, NY), 14 Nov 1967 (m fl), Pires & Silva 11230 (NY), (no date) (m fl), Pires & Silva 11312 (IAN), 21 Mar 1968 (young fr), Pires & Silva 11506 (IAN), 28 Mar 1968 (fr), Pires & Silva 11524 (IAN); Belém, Anandieua, margin of Rio Aurã, tributary of Rio Guamã, 6 Jun 1977 (fr), N. A. Rosa & Cordeiro 1731 (MG, NY); Rio Aurã, margin of Rio Guamã, 12 Mar 1968 (fr), Sastre 117 (CAY, IAN, NY, P); Belé, on lands of IAN, 13 Jan 1944 (f fl and young fr), A. Silva 23 (IAN, K, US(2)); Parque Nacional do Tapajós, km 60 of

Itaituba-Jacareacanga road, 28 Nov 1978 (m fl), M. G. Silva & C. Rosário
3988 (HAMAB, MG, NY); Belém, EMBRAPA, APEG reserve, Aurá, 8 Feb 1977 (fr),
Vilhena 118 (MG, NY).

Local names and uses. Brazil: breu, breu branco. In Pará, the wood has
been used for lumber, the resin for waterproofing boats (Archer 7970).

The fruit of P. krukoffii resembles that of P. divaricatum, but the
former can be distinguished by its smaller and more narrowly elliptic
leaflets with gradually acuminate apex; greater number of juga;
inflorescence shorter; flowers larger; stamens only slightly exceeding the
pistillode, with much longer anthers; disk shallower; pistillode glabrous
and greatly exceeding the disk, with stylode longer; pistil glabrous or
with only scattered hairs; pyrene thinly cartilaginous (not papery), with
fiber layer. Vegetatively, P. krukoffii resembles P. guianense, but the
former can be distinguished by the longer inflorescence; flower larger;
stamens and anthers longer; disk shallower, greatly exceeded by
pistillode; pistillode glabrous, with longer stylode; pistil glabrous or
with only scattered hairs; and fruit much larger and long-acuminate (not
acute) apex.

20. *Protium crenatum* Sandwith, Kew Bull. Misc. Info. 7(40): 327. 1933.

Type. Guyana. N side of Kanuku Mts., E of Takutu River, Sep 1931 (m fl), T. A. W. Davis (For. Dept. Br. Gui. Rec. No.) 2195 (holotype: K).

Trees, reproductive size 5-40 m x 10-65 cm diam; buttresses often or usually present, reaching at least 0.65 m high (de Bruijn 1669); trunk cylindrical, bark thin, rough, lenticellate, grayish-brown; resin colorless, sticky, drying white; two kinds of hairs present, one erect, very slender and acute, to 0.05 mm long, also appressed (rarely ascending or erect), stouter, to 0.2 (0.3) mm long; branchlets slender, 2.3-2.5 mm diam (in fruit 2.5-4 mm diam), with sparse to scattered appressed hairs; leaves (1) 3-4 (6)-jugate, (12) 15-28 (31) cm long (to 40 cm long when sterile); petiole terete to semiterete (dorsally compressed), (2.2) 3-7.5 (8.6 sterile) cm x 1.2-2.1 (2.8 sterile) mm, with scattered to sparse erect hairs, usually also with sparse to scattered appressed hairs; interjuga (1.6) 2.1-4 (5) (5.4 sterile) cm long; petiolules 1-canaliculate, short, laterals (0.2) 0.3-0.5 (0.7) cm long, terminal 1.1-2.2 (2.9) cm long; leaflets chartaceous or sometimes coriaceous, glossy above, basal pair broadly lanceolate to ovate, (4.8) 5.6-10.8 (11.5) (20 sterile) x (1.9) 2.4-3.6 (3.8) (7.8 sterile) cm, ultimate pair (broadly) elliptic, (6.3) 7-11.4 x (1.9) 2.2-3.6 (3.9) cm, terminal elliptic to slightly lanceolate or oblanceolate, (6) 7.2-12 (18 sterile) x (2.1) 2.3-4.1 (4.4) (16.5 sterile) cm, base subequal, truncate to obtuse, apex shortly and broadly acuminate, acumen (0.3) 0.5-1.2 (2.5 sterile) cm long, leaflets obtusely serrulate (rarely some leaflets entire), teeth

0.1-0.3 mm long, irregularly spaced, never closer than 1.5 cm apart, usually ca 3.5 cm apart; abaxial surface with midvein acutely prominent, rest of veins prominulous, surface with scattered scattered ascending to appressed hairs, sometimes confined to midvein, adaxial leaflet surface with midvein obtusely prominent, rest of veins prominulous, midvein and secondary veins with scattered to sparse erect hairs. Inflorescences subterminal, sometimes exceeding petiole, slender, (1) 3.5-17 cm x (0.4) 0.7-0.8 (1) mm diam (x (0.9) 1-1.5 (2) mm diam in fruit), to 0.25 (0.45) times length of subtending leaf, secondary axes sometimes well-developed, 0.4-5 cm long, axes with sparse to scattered appressed hairs to 0.1 (0.2) mm long, also with sparse to dense or sometimes scattered erect hairs, inflorescence bracts lanceolate to triangular to deltate, acute or acuminate, those subtending inflorescences deltate, somewhat fleshy, (0.9) 1-1.5 mm long, those on primary axes 0.3-0.5 mm long, those on secondary axes 0.15-0.3 mm long; pedicel subcylindric, short, in flower (0.2) 0.35-0.5 (0.8) x 0.3-0.5 mm (in fruit (1.2) 1.3-2.1 x 1.2-1.5 (1.7) mm). Flowers all 4-merous, small, (1.1) 1.4-1.7 mm long; calyx shallowly cupular, 0.5-0.8 x (0.9) 1.1-1.4 mm, reaching nearly to top of disk, pedicel and calyx with sparse to dense erect hairs 0.05-0.1 mm long, calyx lobes depressed-deltate with apices acute to apiculate, 0.1-0.25 (0.3) mm long, or often reduced to apicula separated by flat sinuses; petals yellow, ovate, membranous, (1.9) 2-2.3 x 1.1-1.5 mm, narrowed to 0.7 mm wide at base, apex acute, reflexed from 1/2-2/3-way up at anthesis, apiculum 0.25-0.3 mm long, long-papillate, abaxially with sparse to dense hairs 0.05-0.1 mm long, denser toward apex, margin short-papillate;

in staminate flowers stamens 1.3-1.5 and 1.4-1.6 mm long, greatly exceeding pistillode, filaments compressed-columnar, somewhat fleshy, (0.85) 0.9-1 and (0.95) 1-1.1 mm long, anthers dorsifixed, in dorsiventral view narrowly lanceolate, base lobulate, apex acute, abaxially deeply concave, in lateral view asymmetric (anterior sporangium shorter than posterior), obtuse-oblong 0.4-0.5 mm long; disk low, broad, fleshy, only slightly undulate, 0.1-0.3 x 0.25-0.5 mm; pistillode only slightly exceeding disk, 0.5-0.55 x 0.25-0.3 mm overall, ovoid to subglobose, with dense ascending hairs to 0.1 mm long, provided with reduced locules and ovules, abruptly contracted to a long, thick, 4-sulcate stylode 0.3 mm long; in pistillate flowers staminodes 0.9-1.25 and 1-1.35 mm long, reaching base of stigmas, filaments 0.55-0.85 and 0.65-0.95 mm long, anthers in dorsiventral view lanceolate, base lobulate, apex slightly retuse, in lateral view asymmetric, narrowly obtuse-oblong, 0.35-0.45 mm long; disk low and broad, 0.2-0.3 x 0.3-0.35 mm; pistil 1.25-1.35 x 0.75-0.8 mm long overall, ovary ovoid, sessile, with sparse to scattered appressed hairs 0.05-0.1 mm long, abruptly contracted to a long style 0.4-0.6 x 0.35 mm diam, stigmatal region 0.25-0.3 mm high, stigmas sessile, compressed-globose, oriented upward and outward. Fruit maturing red, broadly and slightly obliquely obtuse-oblong, soon glabrescent, 1.5-2 x 1.3-1.8 cm (to 2 cm wide when more than 1 pyrene), sessile (young fruits slightly stipitate), surface glabrous, smooth, drying wrinkled, mesocarp thinly-coriaceous; pseudaril copious; pyrene bony, glabrous, 1.2-1.3 x 0.8-0.9 cm, laterally compressed, both sides concave, in dorsiventral view narrowly obtuse-oblong to oblanceolate, in lateral view obliquely obovate,

apex truncate, on ventral side with subapical funicular depression which continues around to both sides such that apex is obtusely uncinat toward ventral side, site of funicle 4/5 distance to apex, funicular scar essentially lunate, covering 1/5 of ventral face; testa with irregular thickenings, infolded with contortuplicate cotyledons.

Distribution. Sporadic in southern Venezuela, Guyana, and central Pará. In Guyana, Protium crenatum is known only from the type locality. It has been collected a number of times in the Venezuelan states of Bolívar, (Territory) Delta Amacuro, Apure, and especially Barinas. There is one collection from Meta in Colombia (Idrobo & Schultes 1322). It is known from only two localities south of the Rio Amazonas-- Boa Vista on the Rio Tapajós (Capucho 434) and the lower Rio Xingu (Prance et al. 26424 and other collections listed below). Interestingly, in the latter locality P. crenatum was one of the more common species in an inventory of 3 hectares of terra firme forest (Campbell et al., 1986). These localities are areas of either relatively low rainfall or of edaphically dry conditions due to sandy soils.

Protium crenatum is an understory or frequently canopy tree in high forest on undulating terrain, apparently on the periphery of the Amazon Valley in eastern Amazonia. Available collections indicate that it flowers and fruits sporadically throughout the year.

Specimens examined. Brazil. Pará: Tapajós region, Boa Vista, 12 Sep 1932 (young fr), P. Capucho 434 (F); Serra Buritirama, Sep 1970 (m fl), Pires & Belém 12651 (NY); Basin of Rio Xingu, Gleba Bacajã, lote 88, just below mouth of Rio Bacajã, approx. 50°47'50"W, 3°22'20"S, Nov-Dec 1980 (f

fl and young fr), Prance et al. 26424, 27444 (NY), (sterile), Prance et al. 227314, 27712 (NY). Colombia. Meta: savannas of San Juan de Arama, left margin of río Güejar, vicinity of airstrip "Los Micos," 26 Jan 1951 (f fl), Idrobo & Schultes 1322 (GH, US). Venezuela. Barinas: distrito Pedraza, Reserva Forestal de Caparo, 7°30'N, 70°45'W, 31 Jan 1969 (m fl), Bautista 2168 (VEN). Bolívar: Reserva Forestal "El Caura," SE of forest camp El Limón, Jun 1970 (fr), Blanco 859 (MO); along road between km 11 and km 18.5 south of El Dorado, 23 Jul 1960 (fr), Steyermark 86596 (NY, VEN). Apure: Reserva Forestal San Camilo, 7 km E of La Ceiba, 16 km E of El Jordán (viejo), 6 Apr 1968 (fr), Steyermark et al. 101909 (NY, VEN). Delta Amacuro: E of río Grande, ENE of El Palmar, near limits of Estado Bolívar, 17 Jan 1965 (sterile), Marcano Berti 593 (MO, NY).

Local names and uses. Used for firewood (Pará: Capucho 434). Venezuela (Barinas): merey, triaco, anime blanco, marámo; (Bolívar) sipuede.

Because of its serrulate leaflets and glabrous fruits, P. crenatum has been confused with Crepidospermum goudotianum (Tul.) Tr. & Pl. but the latter is distinguished by the teeth acute, longer, and more densely and regularly spaced on its pubescent leaflets; the snail-shaped glands on most surfaces; and the U-shaped embryo. Protium subserratum (Engl.) Engl. has serrulate leaflets as well, but the leaflets of this lactiferous species have teeth which are longer, acute, and more widely spaced; also, the short inflorescence and branchlets are robust with persistent pubescence, the flowers are larger with the petals villous adaxially, and the fruits are oblique-ovoid with a sharply acute apex.

21. *Protium guianense* (Aublet) Marchand, *Adansonia* 8: 52. 1867-1868.

Shrub or tree, reproductive height 2-13 (20) m; often with simple plank buttresses to 55 cm high; branchlets slender, 1-1.8 (2.2) mm diam, with sparse to dense flexuous hairs 0.1-0.6 (0.8) mm long, often also with sparse fine erect hairs to 0.1 mm long. Leaves 0-4-jugate, (7) 8-16.5 (24.5) cm long; petiole semi-terete, shorter than interjuga, 1-3.7 (6.5) cm x 0.6-1.6 (1.8) mm, with scattered to dense hairs as on branchlets; interjuga (1.5) 2-3.3 (5.3) cm long; petiolules variable in length, usually slender, shallowly 2-canaliculate, pulvinuli inconspicuous or rarely absent, laterals 0.2-1 cm long, terminal usually shorter than interjuga, 0.9-3.3 cm long; leaflets chartaceous to slightly coriaceous, lateral leaflets ovate to broadly lanceolate or elliptic, less often lanceolate, basal pair 3.7-10.4 x (1.3) 1.7-4.1 (5) cm, ultimate pair (4.8) 5.7-9 (12) x 2-4 (4.4) cm, base oblique with proximal side acute to obtuse and distal side truncate to obtuse, terminal leaflets (broadly) ovate to elliptic or oblanceolate, rarely lanceolate, (4) 5.6-12 (13.2) x 1.8-5.2 (6.5) cm, base acute, leaflet apex gradually broad-acuminate, acumen 0.3-1.3 (1.8) cm long, abaxial surface with midvein obtusely prominent, rest of venation prominulous or less often prominent, midvein and usually secondary veins with scattered fine erect hairs to 0.1 mm long, sometimes also with sparse long flexuous hairs, rest of surface glabrous, otherwise (ssp. pilosissimum) all of abaxial surface with sparse to scattered, fine erect hairs to 0.5 (0.75) mm long, sparse to dense on midvein and secondary veins; adaxial surface with midvein narrowly

prominulous but partially sunk in a groove, secondary veins inconspicuous or less often prominulous, rest of venation inconspicuous, midvein and usually secondary veins with scattered to sparse fine erect hairs to 0.1 mm long, rest of surface glabrous, otherwise (ssp. pilosissimum) midvein and secondary veins with sparse to dense (less often scattered) erect hairs to 0.5 (0.7) mm long, these also scattered on remainder of adaxial surface. Inflorescence arranged along branchlets, fasciculate, short and slender, 0.4-3 cm x 0.3-1 mm, secondary axes poorly developed, 0.4-1.2 cm long, axes with sparse to scattered fine erect hairs to 0.1 mm long, also with scattered ascending to appressed hairs to 0.2 mm long, otherwise (ssp. pilosissimum) axes with sparse to scattered, stiff, erect to ascending hairs to 0.3 (0.5) mm long, sometimes also with scattered to sparse fine erect hairs to 0.1 mm long; inflorescence bracts coriaceous to chartaceous, ovate to lanceolate, not semi-clasping, those subtending inflorescences 0.5-1.1 mm long, those on primary axes 0.2-0.6 (0.8) mm long, those on secondary axes 0.2-0.5 mm long; pedicel terete, slender, 0.7-2.2 x 0.25-0.35 (0.45) mm, with hairs as on axes. Flowers all 4-merous, at anthesis usually urceolate in overall shape, 2-3 mm long; calyx shallowly cupular, 0.3-0.8 (1) x 1.7-2.5 (2.8) mm overall, exceeded by the disk in both sexes (occasionally level with disk in pistillate flowers), lobes short, rounded depressed-deltate, usually contiguous but often discrete and separated by a flat sinus, 0-0.3 mm long, acuminate, apex and sometimes margin short-papillate, calyx rarely glabrous or with scattered erect hairs to 0.1 mm long, often also with scattered appressed hairs to 0.1 mm long, otherwise (ssp. pilosissimum) with sparse to

scattered erect hairs to 0.3 (0.5) mm long (often some of the hairs ascending), occasionally calyx lobes with dense erect hairs 0.05-0.25 mm long; petals cream to pale green to yellow, membranous to fleshy (ssp. pilosissimum), ovate, 2-2.5 (3) x 1.2-1.7 (2) mm, fleshy, apiculum not markedly thickened, abaxially glabrous or with scattered erect to appressed (then erect near apex) hairs to 0.1 mm long (to 0.2-0.5 mm long in ssp. pilosissimum), adaxial surface short-papillate, margin short-papillate; in staminate flowers stamens 1.3-1.9 (2.05) and 1.4-2 (2.15) mm long, greatly exceeding the pistillode, filaments markedly fleshy, terete, 0.75-1.35 and 0.85-1.45 mm long, anthers basifixed, in dorsiventral view obtusely oblong to slightly lanceolate, in lateral profile obtuse-oblong, (0.35) 0.5-0.7 mm long; disk relatively deep and broad, 0.2-0.4 (0.6) x 0.25-0.5 (0.6) mm; pistillode 0.4-0.6 (0.85) x 0.35-0.7 mm overall, only slightly exceeding disk, depressed-ovoid to slightly compressed-globose, provided with locules and reduced ovules, with dense ascending hairs to 0.15 (0.5) mm long, gradually contracted into a short, thick, 4-lobulate stylode 0.2-0.3 mm long; pistillate flowers with staminodes 1.1-1.6 (1.7) and 1.2-1.7 (1.8) mm long, reaching part-way up the style, filaments dorsiventrally compressed, 0.5-1.1 (1.2) and 0.6-1.2 (1.3) mm long, anthers basifixed, in dorsiventral view ovate with lobulate base and truncate to slightly retuse apex, in lateral profile slightly asymmetrically acute-oblong 0.4-0.65 mm long; disk relatively deep and broad, 0.15-0.4 (0.5) x 0.25-0.5 (0.6) mm; pistil 1.2-1.8 x 0.7-0.9 mm overall, ovary (broadly) ovoid, sessile, with dense ascending to appressed hairs to 0.25 mm long (to 0.4 mm long in ssp.

pilosissimum), gradually contracted into a thick style 0.25-0.55 x 0.25-0.4 mm, stigmas sessile, compressed-globose to almost discoid, lateral or oriented slightly upward and outward. In fruit pedicel (1.3) 1.5-2.6 x 0.4-0.8 mm, terete; fruit red when mature, markedly obliquely ellipsoid to ovoid, gibbous, 1.2-1.6 x 0.5-1.2 mm (to 1.8 mm diam when more than 1 pyrene), sessile, base truncate, apex narrowly acute to slightly acuminate, surface glabrous or with scattered ascending to erect hairs to 0.2 mm long (in ssp. pilosissimum hairs scattered to sparse, to 0.3 (0.5) mm long, sometimes also with scattered fine erect hairs to 0.05 mm long), smooth, drying wrinkled, mesocarp relatively thin, fleshy, pseudaril spongy, covering all of pyrene; pyrene cartilaginous, in dorsiventral view essentially broadly lanceolate to broadly ovate, base obtuse, apex acute to abruptly apiculate, in lateral profile essentially oblong to obliquely lanceolate, base obtuse, apex acute, erect or slightly reflexed to dorsal side, 0.9-1.4 x 0.4-0.8 cm, site of funicle 4/5 distance to apex, funicular scar rounded (depressed-) deltate, margin sinuate, covering 1/4-1/5 of ventral surface, remainder of pyrene with dense layer of erect to appressed fibers 0.2-0.5 mm long; testa with some irregular thickenings but not infolded with cotyledons, cotyledons entire and plano-convex.

Distribution. Widespread in Amazonia and the Guianas, and extending onto the Brazilian Planalto (ssp. pilosissimum). Protium guianense is a small tree of variable morphology which occurs in a range of forest types.

Swart (1942b) was not able to examine the type of the species, but it has since surfaced at BM. Although only buds remain on the type specimen,

it is easily matched with the type of P. hostmannii-- over which the species has priority-- by the short semi-terete petiole; adaxial midvein narrowly prominulous but sunk in a groove and provided with sparse fine erect hairs to 0.1 mm long; secondary veins few, arcuate, adaxially flat.

Protium guianense is related to and most closely resembles P. heptaphyllum. The former species is distinguished by: leaflets pubescent; adaxial midvein narrowly prominulous but sunk in a groove (not obtusely prominent); petal margin short-papillate (not long-papillate); pistillode only slightly (not greatly) exceeding disk, stylode shorter; pistil sessile and densely pubescent (not substipitate and glabrous); and style shorter.

Two subspecies of P. guianense are recognized here. Although most individuals of the two taxa have markedly different appearances, in almost all quantitative and qualitative characters they are extremely close. Indeed, they are separated by only rather weak characters, and morphological intermediates have been found. These may be hybrids, since they occur in regions of apparent sympatry. However, the suite of characters which separate them and the compelling differences in their distributions are considered here sufficient to maintain them as separate subspecies.

Key to the subspecies of Protium guianense

1. Leaflets, inflorescences, and calyx with short hairs (to 0.1 mm long),
on leaflets restricted to midvein and secondary veins; petals
membranous; style 0.35-0.55 mm long; fruit 0.9-1.2 cm diam; pyrene
1.1-1.4 cm long ssp. guianense
1. Leaflets, inflorescences, and calyx with long hairs (to 0.3 (0.5) mm
long), usually sparse abaxially on leaflet blade, scattered adaxially;
petals fleshy; style 0.25-0.3 mm long; fruit 0.5-0.8 cm diam; pyrene
0.9-1 cm long ssp. pilosissimum

21a. Protium guianense (Aublet) Marchand ssp. guianense

Icica guianensis Aublet, Hist. Pl. Gui. Fr. 1: 340, 131. 1775. Type.

French Guiana: without locality, without date (buds), Aublet s.n.

(holotype: BM). Icica viridiflora Lam., Enc. Méth. Bot. 3: 225. 1789,

nom. nov. ill. Amyris guyanensis (Aublet) Willd., Sp. Pl. ed. 4: 335.

1799. Elaphrium gujanense (Aublet) Spr. ex Dietr., Syn Pl. 2: 1271.

1840. Tingulonga guianensis (Aublet) Kuntze, Rev. Gen. Pl. 1: 107.

1891.

Protium hostmannii (Miq.) Engl. in Mart. Fl. bras. 12(2): 266. 1874 (as P.

hostmannii). Icica hostmannii Miq., Stirp. Sur. Sel.: 66. 1850. Type.

Surinam: without locality, without date (m fl), Hostmann & Kappler

1247 (lectotype (designated by Swart, 1942b): U; isoelectotypes: BM, C,

G, GOET, K, NY, P, S, W). Tingulonga hostmannii (Miq.) Kuntze, Rev.

Gen. Pl. 1: 108. 1891.

Protium heptaphyllum (Aublet) Marchand var. puberulum Engl. in Mart. Fl. bras. 12(2): 263. 1874. Type. Surinam: (without locality), (without date), (f fl), Hostmann & Kappler 1292 (lectotype (designated by Swart, 1942b): P; isolectotypes: G, K, NY, U, W).

Lateral petiolules 0.5-1 cm long; on leaflet abaxial surface midvein and usually secondary veins with scattered fine erect hairs to 0.1 mm long, sometimes also with sparse long flexuous hairs, rest of surface glabrous; adaxially midvein and secondary veins with scattered to sparse fine erect hairs to 0.1 mm long, rest of surface glabrous; inflorescence axes with sparse to scattered fine erect hairs to 0.1 mm long, also with scattered ascending to appressed hairs to 0.2 mm long; calyx 1.7-2.1 (2.5) mm diam, rarely glabrous or with scattered erect hairs to 0.1 mm long, often also with scattered appressed hairs to 0.1 mm long; petals abaxially glabrous or with scattered erect to appressed (then erect near apex) hairs to 0.1 mm long; in pistillate flowers filaments 0.5-0.9 and 0.6-1 mm long; disk 0.15-0.3 x 0.25-0.35 mm; hairs on ovary to 0.25 mm long; style 0.35-0.55 mm long; fruit glabrous or with scattered ascending to erect hairs to 0.2 mm long.

Distribution. Widespread in Amazonia and the Guianas, extending onto the Brazilian Shield in Pará. The typical subspecies is a small understory tree of primary terra firme forests. In eastern Amazonia and the Guianas it flowers in October to February, but it can be found fruiting at various times of year.

Representative specimens examined. Brazil. Anapá: between Porto Platon and Serra do Navio, Oct-Dec 1976 (sterile), Rosa 1394 (MG); (without locality), 2 Apr 82 (fr), Rosa et al. 4130 (INPA, NY), 5 Apr 1982 (fr), Rosa & Santos 4138 (INPA, NY). Maranhão: Fazenda Bacaba, 5 km S of MA-119, from entrance 3 km NW of Lago do Junco, 5 Oct 1980 (buds), Daly et al. 507 (MG, NY). Pará: Parque Indígena do Tumucumaque; Rio Paru de Oeste, Missão Tiriyo, 2°20'N, 55°45'W, 12 Feb 1970 (f fl), Cavalcante 2370 (MG, NY); Fazenda Sta. Rosa, entrance behind town of Itinga do Pará, W of Belém-Brasília Highway, approx 4°20'S, 47°45'W, 26 Oct 1980 (buds), Daly et al. 776 (MG, NY); 70 km from Tucuruí, 65 km SSW on old BR-422, then 5 km NW on new logging road, 18-20 Nov 1981 (m fl), Daly et al. 1425 (MG, NY); Rio Curuatinga, flank of Planalto do Santarém, 14 Feb 1955 (sterile), Frões 31600 (US); Municip. Porto de Móz, Rio Xingu, across from Souzel, 17 Nov 1955 (galled fl), Frões 32305 (U, US); Rio Gurupi, 20 Mar 1958 (fr), Frões 34242 (U, US); Santa Izabel, Feb 1905 (fr), J. Huber 6994 (NY); Tucuruí, left margin of Rio Tocantins, km 20 of BR-422, 5 Nov 1980 (fr), Lisboa et al. 1420 (MG); Tomé Açu, right side of road to Fazenda Curiman, 30 Dec 1977 (m fl), Nascimento 359 (MG); Municip. Almeirim, Monte Dourado, Beiradão, 6 Dec 1978 (f fl), Santos 484 (NY).

French Guiana: Saül, La Fumée Mountain, 3°37'N, 53°12'W, 15 Sep (sterile), Boom & Mori 1679 (NY); hillside forest, left bank of the Oyapock, 2 km above Camopi, Saut Coumaloua, 8 Apr 1970 (fr), de Granville 296 (CAY); Saül, ORSTOM trail Belvedere Nord, 19 Dec 1976 (buds), de Granville 2735-A (CAY); (without locality), 1863 (young fr), Mélinon s.n.

(P); Rivière Tampok, saut Koumakou, 22 Mar 1977 (fr), Moretti 624 (CAY); banks of the Yaroupi (affluent of the Oyapock), above Saut Couéki, 27 Apr 1970 (fr), Oldeman 483 (CAY, NY); Rivière Tonégrande, right bank, 13 Jan 1967 (young fr), Oldeman B-879 (CAY, P); Oyapock River, on creek Armontabo ca 17 km above its confluence, 2 Mar 1968 (fr), Oldeman B-1472 (CAY); Mariaflor, Oyapock, 2 Dec 1965 (buds), Oldeman 1845 (CAY).

Guyana: (without locality), 15 Feb 1910 (sterile), C. W. Anderson s.n. (NY); upper Rupuni R., near Dadanawa, 2°45'N, 24-29 Jul 1922 (fr), de la Cruz 1731 (F, GH, NY); Mazaruni Station, 20 Dec 1942 (fr), Fanshawe 964 (NY); near Oko Creed, Cuyuni R., Nov 1932 (f fl), For. Dept. Br. Gui. 2336 (U); vicinity of Kartabo, junction of Mazaruni and Cuyuni rivers, 13 Jul 1924 (fr), Graham 244 (NY, US); Kaietur Plateau, along Potrao River above Kaiatuk, 10 May 1944 (fr), Maguire & Fanshaw 23353 (F, GH, NY, US); southern Pakraima Mts., Kopinang Falls and Savanna, 31 Aug 1961 (fr), Maguire et al. 46306a (NY).

Surinam: Zanderij I, Sep 1944 (sterile), BW 132a (U), 16 Mar 1915 (fr), BW 438 (BM); Wilhelmina Mts., 9 Jun 1926 (sterile), BW 7072 (US); 8 km ESE of Brownswey, 6 Apr (sterile), van Donselaar 2326 (U); Jodensavanne-Mapanekreek area, 7 Mar 1963 (fr), Elburg LBB 9425 (NY); (without locality), (without date) (m fl), Hostmann & Kappler 1292 (G); Fallawatra, 15 Dec 1971 (sterile), Jimenez-Saa (LBB) 14413 (U); Rijdsdijkweg, 25 km S of Paramaribo, 21 Aug 1953 (sterile), Lindeman 4553 (U); upper Coppename River, near Volzberg, 23 Sep 1956 (sterile), Schulz 7841 (U).

21b. *Protium guianense* (Aublet) Marchand ssp. *pilosissimum* (Engl.) Daly
(submitted for publication in Brittonia). Type. Brazil. Goiás:
Cavalcante, 1828-1830 (f fl), Burchell 7890 (lectotype: P;
isolectotypes, B, GH, K). (see Smith & Smith, 1967, for source of data
for locality and date).

Protium pilosissimum Engler in DC. Mon. Phan. 4: 80. 1883.

Lateral petiolules 0.2-0.6 (0.8) mm long; all of abaxial leaflet surface with sparse to scattered fine erect hairs to 0.5 (0.75) mm long, sparse to dense on midvein and secondary veins, adaxially midvein and secondary veins with sparse to dense (less often scattered) erect hairs to 0.5 (0.7) mm long, these also scattered on remainder of adaxial surface; inflorescence axes with sparse to scattered, stiff, erect to ascending hairs to 0.3 (0.5) mm long, sometimes also with scattered to sparse fine erect hairs to 0.1 mm long; calyx 2-2.5 (2.8) mm diam, with sparse to scattered erect hairs to 0.3 (0.5) mm long (often some of the hairs ascending); petals abaxially with hairs to 0.2-0.5 mm long; in pistillate flowers, filaments 0.7-1.1 and 0.8-1.3 mm long; disk 0.25-0.4 (0.5) x 0.3-0.5 (0.6) mm; hairs on ovary to 0.4 mm long; style 0.25-0.3 mm long; hairs on fruits scattered to sparse, to 0.3 (0.5) mm long, sometimes also with scattered fine erect hairs to 0.05 mm long.

Distribution. Except for its perplexing occurrence near Manaus, ssp. pilosissimum is found almost exclusively near the edges of the Brazilian and Guiana shields which flank the Amazon Valley. For the most part it

occurs as an understory shrub or tree in the gallery forests or semi-deciduous forests in the foothills of the low mountain ranges which form an irregular ring around southern Amazonia. In eastern Amazonia, ssp. pilosissimum occurs in the Maranhão transition zone, the Serra dos Carajás, and the hilly country near Itaituba. In addition, a number of populations occur on both sides of the Rio Amazonas in the region around Santarém, Oriximinã, and Alenquer. There, the Brazilian and Guiana shields are closest together. Also, in this region the precipitation and forest physiognomy are often comparable to those in the transition regions of southern Amazonia.

Elsewhere, ssp. pilosissimum is found in the regions of the Serra Dourada in Goiás, the Serra dos Pacaás Novos in Rondônia, and the Serra Formosa (near Sinop), Serra do Roncador, and Chapada dos Guimarães in Mato Grosso. There is an anomalous collection from Loreto in Peru, with glabrous fruits (Croat 17598), for which no habitat is indicated.

Two collections are known from Amazonian Bolivia. Rusby 2523 and W. Anderson 11821 were both collected in the region between Riberalta and Guayaramerin. Although the former gave no habitat data, the latter collection was made in "old second-growth forest on sandy soil, with scattered huge trees." The natural source of seed for this population may have been the edaphic savannas which occur near Guayaramerin.

There is one disjunct collection from the Rio Jarí basin in northeastern Pará (north of the Rio Amazonas), but the Jarí region has close floristic affinities with the area around Santarém.

This subspecies has been reported from terra firme forest, secondary

forest (Ducke 4902), riverbank forest (Schatz et al. 787), and forest with stone outcrops (Maciel et al. 779). Flowering collections are too few to see a phenological pattern, but the species fruits from December to August.

Specimens examined. Brazil. Maranhão: Municf. Barra do Corda, Cachoeirinha, 57 km SSW of Barra do Corda, along Rio Corda, ca 5°53'S, 45°22'W, 2 Mar 1983 (fr), Schatz et al. 787 (NY). Pará: Santarém-Rurópolis road, km 103, ca 3°15'S, 55°00'W, 27 Jan 1976 (fr), Bamps 5257 (BR, NY); Itaituba-Humaitã road, km 210, ca 5°10'S, 57°00'W, 12 Feb 1976 (fr), Bamps 5355 (BR); Municf. Oriximinã, Rio Mapuera, left side, 28 Jun 1980 (fr), Cid & J. Ramos 1161 (INPA, NY); Serra dos Carajás, 20-25 km NW of Serra Norte mining camp, ca 5°55'S, 50°26'W, 6 Dec 1981 (fr), Daly et al. 1760 (MG, NY); Alenquer, 26 Dec 1903 (buds), Ducke 4902 (MG); Marabã, Serra dos Carajás, Serra Norte, road N-1, 29 km from camp, 7 Aug 1982 (fr and buds), Maciel et al. 779 (MG, NY); Jari, Munguba road, 12 Feb 1969 (fr), N. T. Silva 1726 (IAN, NY); Serra dos Carajás, Estrada N-13, km 7, 25 Aug 1972 (fr), N. T. Silva & Ribeiro 3599 (NY).

Possibly because of its fragmented distribution, ssp. pilosissimum is variable in the size and shape of its leaflets and in the density and length of the pubescence.

The distributions of the two subspecies of P. guianense overlap in Brazil near Manaus (Amazonas) and near Barra do Corda (Maranhão). In the latter region ssp. pilosissimum and ssp. guianense are clearly sympatric (Schatz et al. 787 and 792, respectively). Several collections which are intermediate between the two taxa have been encountered near Santarém and

in the Jarí region. Most of these have leaflets with scattered erect hairs to 0.2 mm long on the abaxial blade, and the petiole and rachis with dense, long, flexuous hairs, combined with either the fruit pubescence of ssp. guianense (N. T. Silva 1726; Ducke 4902) or the inflorescence pubescence of ssp. pilosissimum (N. T. Silva 1534). One collection (Lobo et al. 136) has the glabrous leaflet blades of ssp. guianense but the dense, long hairs on the inflorescence and calyx characteristic of ssp. pilosissimum. It is possible that the two subspecies hybridize in their zones of overlap.

22. *Protium spruceanum* (Benth) Engler, Mart. Fl. bras. 12(2): 276. 1874.

Type. Brazil. Amazonas: Rio Negro, Barra (Manaus), Feb 1851 (frt),

Spruce 1319 (lectotype (designated by Swart, 1942b): K; isoelectotype:

P). Icica spruceana Benth., Hook. J. Bot. 4: 16. 1852. Tingulunga

spruceana (Benth.) Kuntze, Rev. Gen. Pl. 1: 108. 1891.

Protium almecega Marchand, Vid. Medd. Kjbhn. 1873: 56. 1873. Type. Brazil.

Minas Gerais: Lagoa Santa, 19 Jul 1864 (f fl), Warming s.n. (holotype:

C). Tingulunga almacega (Marchand) Kuntze, Rev. Gen. Pl. 1: 108. 1891.

Trees, reproductive height 10-25 m; buttresses low, plank or flying, simple or branched; trunk sometimes slightly fluted; bark smooth or sometimes warty, brittle, thin; resin clear and rather watery when fresh, usually drying to a white powder; branchlets (1.7) 2.1-3.2 (3.8) mm diam, with dense (sometimes sparse) appressed hairs to 0.15 mm long, also usually with sparse erect hairs to 0.05 (0.1) mm long. Leaves 1-4 (5)-jugate, (9.5) 13.5-26 (33) cm long; petiole shallowly and broadly canaliculate, less often semi-terete, usually slightly acutely winged, longer than interjuga, (2.2) 3-7.1 (7.9) cm x (1.1) 1.4-2.4 (2.8) mm diam, with dense to sparse (rarely scattered) fine erect hairs to 0.3 (0.5) mm long, also with dense to sparse appressed hairs to 0.25 mm long; interjuga (1.3) 1.8-3.3 (4) cm long; petiolules usually long and slender, usually shallowly 2-canalicate (rarely terete), laterals 0.3-1 (1.4) cm long, terminal shorter than interjuga, (0.8) 1.2-2.6 (3.2) cm long, pulvinuli inconspicuous; leaflets chartaceous to coriaceous, lateral leaflets oblong

to elliptic or lanceolate, base oblique, proximal side obtuse and distal side acute, basal pair (5.8) 6.8-11.8 (14.5) x (2) 2.5-4.5 (5.2) cm, ultimate pair (6) 8-11.6 (15.3) x (2) 2.5-3.9 (5.1) cm, terminal leaflet elliptic to oblanceolate, base acute, (6.5) 8.3-12 (14) x (1.8) 2.8-4.6 (5.2) cm, leaflet apex gradually and narrowly long-acuminate (in central and southern Brazil broader and shorter), acumen (0.2) 0.6-1.5 (2.2) cm long, abaxial surface with midvein prominent, rest of veins prominulous, secondary veins discolorous, midvein and sometimes secondary veins with sparse to dense, long flexuous hairs 0.2-0.5 (0.75) mm long, (rarely sparse on blade (Heringer 5932; Prance 51901; Spruce 2692)), very rarely long hairs scattered or absent, rest of blade usually with scattered thick appressed hairs 0.05-0.15 (0.2) mm long, adaxial surface with midvein narrowly prominent but partially sunk in a groove, rest of veins inconspicuous, secondary veins discolorous, midvein and usually secondary veins with sparse fine erect hairs 0.05-0.2 (0.3) mm long (sometimes absent on older leaflets), rest of blade glabrous.

Inflorescences distributed along branchlets, short and slender, 0.8-3.5 (4.5) cm x (0.4) 0.6-1.5 (1.8) mm (in fruit (2) 2.5-4.6 cm x (0.6) 0.9-1.5 mm), profusely branching, secondary axes 0.4-1.5 (2.4) cm long (to 3.2 cm long in fruit), axes with sparse to scattered erect hairs to 0.5 (0.1) mm long, also with scattered sparse appressed hairs to 0.2 (0.3) mm long, axes also normally with deposits of white, powdery, dried resin; bracts subtending inflorescences broadly lanceolate to ovate, 0.7-1.5 mm long; inflorescence bracts (narrowly) lanceolate, chartaceous, those on primary axes 0.4-1 (1.5) mm long, those on secondary axes 0.3-0.7 (1.1) mm long;

pedicel terete, long and slender, (0.5) 1.2-2.6 (3.2) x 0.25-0.4 (0.5) mm, with hairs as on inflorescence (appressed hairs rarely dense). Flowers all 5-merous, 1.5-2.2 (2.5) mm long when dry; calyx shallowly cupular, (0.5) 0.6-1 (1.2) x 1.8-2.5 mm overall, usually approximately level with the disk in both sexes, with scattered appressed hairs to 0.2 mm long, or subglabrous, lobes depressed-deltate, variable in length, (0.15) 0.3-0.55 (0.7) mm long, rarely long-acuminate (Amapá collections); petals pale yellow to green, lanceolate, of variable length, 2.5-3.7 (4) x (1) 1.2-1.5 (2) mm, fleshy, apiculus conspicuous and strongly inflexed, abaxial surface glabrous or with a few scattered appressed hairs to 0.1 mm long, margin long-papillate, at anthesis usually strongly reflexed ca the upper 2/3 their length; in staminate flowers stamens greatly exceeding the pistillode, 1.45-1.9 (2.05) and 1.55-2 (2.15) mm long, filaments fleshy, essentially terete, slightly broadened at base, (0.75) 0.9-1.2 (1.5) and (0.85) 1-1.3 (1.6) mm long, slightly inflexed, anthers in dorsiventral view lanceolate (ovate after dehiscence) with lobulate base and acute apex, in lateral profile obtuse-oblong, (0.55) 0.6-0.75 (0.85) mm long; disk usually shallow and broad, 0.2-0.4 x 0.3-0.6 (0.7) mm; pistillode 0.6-0.8 (0.9) x (0.45) 0.55-0.75 (0.85) mm overall, greatly exceeding disk, globose to depressed-ovoid, glabrous or with less often with scattered long ascending hairs to 0.35 mm long, provided with locules and reduced ovules, contracted to a long thick stylode 0.25-0.35 (0.4) mm long, stylode either acutely 5-winged (Amazonia) or 5-lobulate (most of specimens from central or southern Brazil); in pistillate flowers staminodes 0.9-1.3 (1.5) and 1-1.4 (1.6) mm long, reaching base of style

or as high as base of stigmas, filaments slender and compressed, (0.35) 0.45-0.75 (0.9) and (0.45) 0.55-0.85 (1) mm long; anthers in dorsiventral view broadly lanceolate to obtuse-oblong with lobulate base and truncate to slightly retuse apex, in lateral profile obliquely oblong (anterior sporangia shorter than posterior), 0.5-0.7 mm long; disk shallow and usually narrow, 0.2-0.35 x (0.2) 0.25-0.45 mm; pistil 1.25-1.7 (1.85) x (0.55) 0.8-1.25 mm overall, ovary depressed-ovoid, sessile, glabrous, gradually contracted into a short thick style (0.15) 0.25-0.3 (0.35) x 0.5-0.6 (0.7) mm, stigmatal region 0.25-0.35 mm high, stigmas globose to slightly compressed-globose, sessile, oriented slightly upward and outward or rarely lateral. In fruit pedicel subcylindric, 2.3-3.5 (4.5) x (0.5) 0.8-1 (1.2) mm; fruit maturing red (a few collections from central Brazil report yellow fruits), substipitate, essentially ellipsoid, slightly oblique and gibbous, (1.3) 1.7-2 (2.3) x (0.8) 0.9-1.2 (1.3) cm, apex slightly incurved, style and stigmas usually persisting, surface glabrous, smooth, drying wrinkled, mesocarp relatively thin, fleshy; pseudaril completely covering pyrene; pyrene thickly cartilaginous to bony, 0.8-1.5 x 0.5-0.9 cm, in dorsiventral view (broadly) ovate or less often broadly lanceolate, base truncate to less often obtuse, apex acute, less often obtuse or slightly acuminate, in lateral profile essentially lanceolate with truncate base and acute apex, site of funicle ca 2/3 distance to the apex, funicular depression shallow, funicular scar broadly oblobate, covering 1/5 to 1/4 ventral surface, testa with irregular thickenings but not infolded with cotyledons, cotyledons entire and plano-convex.

Distribution. Widespread in Amazonia, central Brazil, and inland

tropical southern Brazil. In Amazonia the species occurs as an understory or canopy tree in primary forest on terra firme, usually on sandy or sandy-clay soils. In the drier climate of central and inland southern Brazil it is usually found as a small tree in gallery forests. In Amazonia it flowers from September to February and fruits from November to May.

Specimens examined. Brazil. Amapá: Acampamento Carnot and Cunani, 10 Oct 1979 (m fl), Austin et al. 7369 (NY); Municfp. Macapá, Rio Falsino, ca 10 km upstream of confluence with Rio Araguari, west bank, ca 0°50'S, 51°45'W, 16 Dec 1984 (fr), Daly et al. 3902 (NY); (without locality), 1956 (fr), Miranda Bastos 2267 (NY); Municfp. Macapá, 156 km NW of Porto Grande on Perimetral Norte (BR-210), ca 1°30'N, 53°30'W, 30 Dec 1984 (fr), Mori & Cardoso 17572 (NY); Porto Platon, Colonia do Matapi, 13 Sep 1976 (galled fr), M. Silva 2803 (MG, MO); BR-156, Carnot, 10 Oct 1979 (m fl), Rabelo 124 (HAMAB). Maranhão: Municfp. de Monção, basin of Rio Turiaçu, Ka'apor Indian Reserve, within 7 km of settlement of Urutawy, 18 Feb. 1985 (fr), Balêe & Ribeiro 843 (NY). Pará: Belém, EMBRAPA, Mocambo Reserve, ca 1°23'S, 48°27'W, 10-17 Nov 1984 (fr), Daly et al. 3754 (IAN, NY), 10-17 Nov 1984 (fr), Daly et al. 3763 (IAN, NY), 10-17 Nov 1984 (fr), Daly et al. 3766 (IAN, NY), 10-17 Nov 1984 (fr and buds), Daly et al. 3770 (IAN, NY), 8 Jan 1985 (fr), Daly et al. 4060 (IAN, NY); NE of Rio Cuminã-Mirim, 16 Dec 1906 (buds), Ducke 7981 (MG); Belém, Catiê, 1 Jan 1923 (fl), Ducke 18399 (RB); Municfp. Porto de Móz, Rio Xingu, across from Souza, 18 Oct 1955 (fr), Frões 32362 (IAN, RB, US), across from Porto do Móz, 29 Nov 1955 (fr), Frões 32423 (IAN); Belém, Mocambo Reserve, 9 Feb 1981 (fr), O. P. Monteiro 59 (INPA, NY); Mosqueiro, Furo das Marinhas, Belém-Mosqueiro

road, 13 May 1971 (fr), Oliveira 5483 (IAN, NY); Ilha do Mosqueiro, 11 Mar 1971 (sterile), Oliveira 5533 (IAN); Belém, IPEAN, Mocambo Reserve, 27 Sep 1966 (m fl), Pires & Silva 10294 (IAN), 27 Sep 1966 (fl), Pires & N. T. Silva 10303 (IAN), 17 Jul 1966 (fr), Pires & Silva 10925 (IAN); 6 Feb 1968 (f fl), Pires & Silva 11424 (IAN), Aurã Reserve, 2 Feb 1968 (buds), Pires & Silva 11489 (IAN), 19 Feb 1968 (young fr), Pires & Silva 11528 (IAN), Serraria, 8 May 1968 (fr), Pires & Silva 11660 (IAN), Mocambo Reserve, 7 May 1968 (fr), Pires & Silva 11699 (IAN); vicinity of Belém, Sep-Oct 1961 (m fl), Pires 51908 (K, NY, US, UBR); BR-163, km 884, northern foothills of Serra do Cachimbo, 11 Nov 1977 (fr), Prance et al. 2547 (NY); Trans-Amazon Highway (BR-230), 10 km W of Rurópolis Presidente Medici towards Itaituba, 29 Nov 1977 (young fr), Prance et al. 25870 (NY); Itaituba, km 63 of Itaituba-Jacareacanga road, Parque Nacional do Tapajós (IBDF), 12 Nov 1978 (fr), M. G. Silva & C. Rosário 3667 (MG, NY, US), Parque Nacional do Tapajós, right bank of river, 24 Dec 1978 (m fl), M. G. Silva & Rosário 3918 (INPA, K, MG, NY, US); Mocambo Reserve, 23 Oct 1972 (fr), N. T. Silva s.n. (IAN); Rio Trombetas, flank of Planalto Saracá, 27 May 1978 (galled frs), N. T. Silva & M. R. Santos 4654 (MG, NY).

Local names and uses. Brazil. Maranhão: kande'i'y tuwyr (Ka'apor), used for firewood and burnable resin. Pará: breu.

In this treatment Protium spruceanum and P. almecega are considered to be taxonomic synonyms. Engler (1874) placed the two species far from each other in his key to the genus for Brazil because the types are of different gender (see section above on flowers). Swart (1942) acknowledged their similarity but asserted that P. spruceanum lacks the long hairs on

the abaxial midvein which characterize P. almecega. However, examination of the types and of hundreds of specimens confirms that those hairs are present on virtually all individuals of P. spruceanum.

Collections of Protium spruceanum from central and southern Brazil-- invariably identified as P. almecega-- tend to have leaflets which are more elliptic to ovate and more coriaceous, with a broader and shorter acumen (Ironically, the lectotype of P. spruceanum, Spruce 1319, has leaflets of a similar morphology, but most of the Amazonian collections outside of the Rio Negro region have more chartaceous leaflets). The fruits tend to be smaller, and some have been described as being yellow, although these may have been immature. On Irwin 11923, a collection from the Serra Dourada of Goiás, in central Brazil, the fruits were observed as being yellow on the underside and red on the insolated side, the only report of this kind for the species. The only species of Protium which consistently has such bicolored fruits is the only distantly related P. aracouchini (Aublet) Marchand. In all other respects the Amazonian collections and those of central Brazil cannot be consistently distinguished.

In central and southern Brazil, Protium spruceanum usually occurs as a small tree in gallery forests, indicating that the species probably originated in Amazônia and later radiated southward. Because it is a widespread and relatively versatile species, it is rather variable in some aspects of its morphology, notably in the distribution and density of pubescence but also in the size of the leaflets, flowers, and fruits. Collections from Peruvian Amazonia have larger fruits than elsewhere.

Protium spruceanum strongly resembles and is very closely related to P. llanorum Cuatrec., a poorly known species from gallery forests of the savanna regions of Guarico, Monagas, and Apure in Venezuela. The two taxa are very similar in most aspects of their leaf and flower morphology. P. llanorum can be distinguished by the latter's glabrous abaxial midvein of the leaflets; far greater number of secondary veins; tertiary veins inconspicuous; pedicel much shorter; petal surface abaxially with sparse to scattered appressed hairs 0.1-0.2 (0.25) mm long; stigmas papillate; and fruits sessile (not substipitate), smaller, and with a shorter and broader acumen.

23. Protium heptaphyllum (Aublet) Marchand, Vidensk. Meddel. Dansk Naturhist. Foren. Kjobenhavn 1873: 54. 1873.

Shrubs or trees, reproductive height 1-18 m; resin clear, watery; branchlets slender, 1.4-3 (3.5) mm diam, with scattered fine erect hairs to 0.1 mm long, rarely (type of P. octandrum) also with scattered appressed hairs to 0.2 mm long. Leaves (0) 1-3-jugate, 6-30 cm long; petiole semi-terete, short and slender, (0.8) 1.3-5.5 (6.7) cm x 0.7-1.8 (2.2) mm, with hairs as on branchlets, also with scattered appressed hairs to 0.1 mm long; interjuga (1) 1.6-4 cm long; petiolules shallowly 2-canaliculate, variable in length, laterals 0.2-1.2 cm long, terminal 0.4-2.2 (4) cm long, pulvinuli inconspicuous; leaflets chartaceous or less often slightly coriaceous, laterals (narrowly) elliptic or lanceolate, less often oblanceolate, base usually oblique, proximal side acute, distal side obtuse to truncate (cordate in ssp. cordatum), basal pair 3.4-11 (12.6) x 1.2-3.8 (5) cm, ultimate pair (3.2) 4.2-11 (13.4) x 1.2-4.4 cm, terminal elliptic to oblanceolate, base acute to obtuse, (3.5) 4.3-11 (15) x 1.4-5.2 (5.8) cm, apex gradually and broadly short-acuminate, acumen 0.2-1.2 (1.6) cm long, abaxial surface with all veins narrowly prominulous, adaxial surface with midvein obtusely prominent to prominulous (flat in ssp. cordatum), rest of veins prominulous, both surfaces glabrous. Inflorescences distributed along branchlets, usually densely branched, short and slender, 0.5-3 (4) cm x 0.3-0.9 (1.5) mm, secondary axes poorly developed, 0.5-1.1 (1.5) cm long, axes with dense to sparse (rarely scattered) fine erect hairs to 0.1 (0.15) mm long, rarely

only with scattered appressed hairs to 0.15 mm long; inflorescence bracts chartaceous, lanceolate, rarely semi-clasping (type of P. angustifolium), apex acuminate, with sparse appressed hairs to 0.1 mm long; pedicel terete, variable in length, (0.5) 0.7-2.3 x 0.0.25-0.4 (0.5) mm, with hairs as on axes. Flowers all 4-merous, relatively large, variable in size, 2.6-3.8 (4.2) mm long; calyx in both sexes +/- level with top of disk; in staminate flowers calyx 0.4-0.7 (1) x 1.8-2.3 (2.5) mm, glabrous or with sparse to dense fine erect hairs to 0.1 mm long, less often only with scattered ascending to appressed hairs to 0.1 (0.2) mm long, lobes contiguous or discrete and separated by a flat sinus, rounded depressed-deltate or reduced to a papillate apiculum, 0-0.3 (0.4) mm long; petals pale green to greenish-white, lanceolate (ovate in ssp. cordatum), membranous, variable in size, (2.5) 2.8-4.2 x 1-2 (2.4) mm, apiculum inconspicuous, abaxially glabrous or with scattered appressed hairs to 0.1 (0.2) mm long, margin long-papillate; stamens not greatly exceeding pistillode, 1.4-2.35 and 1.5-2.4 mm long, filaments markedly fleshy, terete, 0.6-1.45 and 0.7-1.5 mm long, anthers basifixed, in dorsiventral view lanceolate to narrowly obtuse-oblong (often broadly lanceolate after dehiscence), base lobulate and apex rounded, in lateral profile lanceolate to elliptic, large, (0.55) 0.75-1 mm long; disk usually broad, 0.25-0.4 x 0.25-0.65 mm; pistillode greatly exceeding disk (slightly so on type of var. unifoliolatum), (0.5) 0.7-1.05 x (0.3) 0.4-0.65 mm overall, ovoid, provided with locules and reduced ovules, glabrous or less often with scattered ascending hairs to 0.15 mm long, gradually contracted to a stylode (0.15) 0.25-0.4 (0.6) x 0.2-0.4 mm, distinctly 4-lobulate at apex;

in pistillate flowers calyx 0.4-0.9 x 1.7-2.5 mm, lobes 0-0.2 mm long; staminodes usually reaching base of stigmas, 1-1.55 (1.8) and 1.15-1.6 (2) mm long, filaments +/- terete, (0.35) 0.5-0.85 (1) and (0.45) 0.6-1 (1.2) mm long, anthers in dorsiventral view broadly lanceolate, base lobulate and apex rounded, in lateral profile obliquely elliptic to acute-oblong, (0.5) 0.65-0.8 mm long; disk shallow and narrow, 0.15-0.4 x 0.2-0.4 (0.5) mm; pistil (1.5) 1.85-2.25 x 0.75-1 (1.15) mm overall, ovary substipitate, depressed-ovoid, glabrous, usually abruptly contracted to a long style (0.55) 0.8-1.1 x 0.25-0.4 (0.5) mm, stigmatal area 0.25-0.4 mm high, stigmas sessile, lateral, compressed-globose. In fruit inflorescence to 2.2-2.8 (4.3) cm x 0.7-1.2 (1.9) mm, pedicel 1.5-2.7 x 0.5-1 (1.3) mm; fruit maturing red, oblique-ovoid, gibbous, ventricose, (1.2) 1.4-2.3 x 0.8-1.2 cm (to 1.4 cm diam when more than one pyrene), sessile, apex acute, surface glabrous, smooth, drying wrinkled; pyrene thickly cartilaginous, in dorsiventral view elliptic to lanceolate to ovate (broadly so in ssp. cordatum), base truncate, apex rounded to less often acute, in lateral profile essentially broadly elliptic to ovate, less often lanceolate, 0.7-1.1 (1.5) x 0.5-0.7 cm, site of funicle 1/2-2/3 distance to apex, funicular depression shallow, funicular scar rounded-deltate to +/- broadly elliptic, covering 1/3 ventral face, rest of surface with a dense layer of flexuous fibers to 0.4 mm long, or glabrous (?); testa papery, without irregular thickenings; cotyledons entire, plano-convex.

Distribution. Widespread in northern South America, extending onto the Brazilian Planalto and into eastern Brazil. Protium heptaphyllum is an

extremely variable, weedy small tree which can be found in a variety of forest types, including secondary forest. It appears to flower and fruit sporadically.

Protium heptaphyllum is related to and most closely resembles P. guianense. The former species is distinguished by: leaflets glabrous; terminal leaflet elliptic (not usually obovate); adaxial midvein glabrous and obtusely prominent (not narrowly prominulous and sunk in a groove); petal margin long-papillate; pistillode greatly exceeding disk; stylode longer; pistil substipitate and glabrous; and style shorter.

Even in eastern Amazonia and the Guianas, P. heptaphyllum presents a great deal of variation. However, examination of the type material and representatives of the varieties which have been reported from Amazonia and the Guianas failed to yield any discontinuities deserving of taxonomic rank. The species is rather consistent in its flower structure, although the absolute (not relative) size of organs varies. The characters which have been used to define varieties-- number of juga, leaflet size and shape, inflorescence length-- show continuous variation. Of the taxa listed in synonymy above, perhaps P. angustifolium will prove to be deserving of taxonomic rank because of its long, lanceolate, semi-clasping inflorescence bracts and long inflorescences. It is intriguing that the label notes for the type of P. hostmannii var. brasiliense indicate that the "aril" was red, but there are no characters observable on the specimen which show it to be anything other than P. heptaphyllum. Further material is needed from poorly-collected Marajó Island, the type locality for that taxon.

Most of the variation within P. heptaphyllum, as well as most of its closest relatives, occur outside of Amazonia. The varieties described in the species from central and eastern Brazil need to be examined more closely, in addition to the species which resemble it in those regions: P. ovatum Engl., P. kleinii Cuatrec., P. widgrenii Engl., and P. dawsonii Cuatrec.

In this treatment, P. heptaphyllum is recognized as having two subspecies. The two diverge both morphologically and ecologically, and are distinguished in the key below.

Key to the subspecies of Protium heptaphyllum

1. Lateral leaflet base acute to obtuse or truncate; tertiary veins prominent; petals lanceolate, 2.8-4.2 mm long; anthers 0.75-1 mm long, antherodes 0.65-0.8 mm long; disk in pistillate flowers 0.15-0.35 x 0.2-0.4 mm; pistil (1.65) 1.85-2.25 mm long, style (0.6) 0.8-1.1 mm long; fruit 1.4-2.3 cm long ssp. heptaphyllum
1. Lateral leaflet base cordate, rarely truncate; tertiary veins flat; petals ovate, 2.5 mm long; anthers 0.55-0.6 mm long, antherodes 0.5 mm long; disk in pistillate flowers 0.4 x 0.45-0.5 mm; pistil 1.5 mm long, style 0.55 mm long; fruit 1.2 cm long ssp. cordatum

23a. *Protium heptaphyllum* (Aublet) Marchand ssp. *heptaphyllum*

Protium heptaphyllum (Aublet) Marchand, Vidensk. Meddel. Dansk Naturhist.

Foren. Kjobenhavn 1873: 54. 1873. Type. French Guiana: (without

locality), Sep (without year) (buds), Aublet s.n. (holotype: BM).

Icica heptaphylla Aublet, Hist. Pl. Gui. Fr. 1: 337. 1775. *Elaphrium*

heptaphyllum (Aublet) Spr. ex Dietr., Syn. Pl. 2: 1272. 1840.

Tingulonga heptaphylla Kuntze, Rev. Gen. Pl. 1: 107. 1891.

Protium heptaphyllum (Aublet) Marchand var. *multiflorum* (Engl.) Swart. A

monograph of the genus *Protium* and some allied genera (Burseraceae):

297. 1942. Type. Brazil. Pará: near Santarém, Jul 1850 (m fl), Spruce

994 (lectotype (designated by Swart, 1942b): P; isoelectotypes: K, LE).

Protium multiflorum Engl. in Mart. Fl. bras. 12(2): 273. 1874.

Tingulonga multiflora (Engl.) Kuntze, Rev. Pl. 1: 108. 1891.

Protium heptaphyllum (Aublet) Marchand var. *floribundum* Swart, Rec. Trav.

Bot Néerl. 39: 191. 1942. Type. Brazil. Mato Grosso: near Cuiabá, Jun

1833 (sterile fl and f fl), Manso 127 in Herb. Martius 1277 (lectotype

(designated by Swart, 1942b): BR; isoelectotypes: BM, G, K, L, LE, M,

NY, S).

Protium heptaphyllum (Aublet) Marchand var. *surinamense* (Miq.) Swart, A

monograph of the genus *Protium* and some allied genera (Burseraceae):

298. 1942. Type. Surinam: (without locality), (without date) (m fl),

Hostmann & Kappler 1242 (lectotype (designated by Swart, 1942b): U;

isoelectotypes: C, L, P, S, W). *Icica surinamensis* Miq., Stirp. Sur.

Sel.: 65. 1853.

Protium heptaphyllum (Aublet) Marchand var. unifoliolatum Swart, Rec.

Trav. Bot. Néerl. 39: 191. 1942. Type. Surinam: (without locality),

Sep (without year) (m fl), Kappler 2112 (holotype: P; isotype: GOET).

Protium angustifolium Swart, Rec. Trav. Bot. Néerl. 39: 190. 1942. Type.

Colombia. Bolívar: San Martín de Loba, Apr-May 1916 (m fl), Curran 15

(holotype: US; isotypes: F, GH).

Protium octandrum Swart, Rec. Trav. Bot. Néerl. 39: 198. 1942. Type.

Surinam: Saramacca River, Watramiri, Sep 1919 (m fl), BW 4404

(holotype: U; isotypes: BM, BR, NY, US).

Protium hostmannii (Miq.) Engl. var. brasiliensis Swart, Acta Bot. Néerl.

15: 52. 1966. Type. Brazil. Pará: Soure, Ilha do Marajó, 17 Nov 1948

(frt), Black 48-3613 (holotype: IAN).

Leaflets drying green or brown, gradually acuminate, tertiary veins prominent; calyx in staminate flowers 0.4-0.7 mm long, level with the disk; petals only with scattered appressed hairs to 0.1 (0.2) mm long; pyrene in dorsiventral view elliptic to lanceolate, rarely ovate.

Representative specimens examined. Brazil. Maranhão: Ilha de São Luiz, reservatório Sacaven, 15 Jan 1951 (m fl), Frões 26813 (IAN); Alto Rio Turiaçu, Nova Esperança, 2°55'S, 45°45'W, 4 Dec 1978 (m fl), Jangoux & Bahia 219 (MG, NY); Montes Altas, Mongaba, 20 Aug 1982 (m fl), Maciel et al. 836 (NY); Road from Carolina to Estreita, 2-15 km from Estreita, 9 Aug 1964 (m fl), Prance & Silva 58626 (NY). Pará: Almeirim, 18 Dec 1902 (m fl), Ducke 3067 (MG); Santa Cruz dos Martírios, 14 Jun 1953 (m fl), Frões 30088 (IAN); Monte Alegre, Colônia Japonêsa, Assaizal, 24 Sep 1953 (m fl),

Frões 30341 (IAN); near Santarém, 17 Aug 1927 (m fl), Ginzberger & Zerny s.n. (W); Ilha de Mosqueiro, 3-9 Nov 1929 (fr), Killip & Smith 30457 (NY); Belém, Mocambo Reserve, 24 Sep 1963 (fr), Oliveira 2650 (IAN); Rio Jarf, Monte Dourado, 24 Nov 1967 (m fl), Oliveira 3893 (IAN); Municp. Ponta de Pedras, Pindobal, near Fazenda São Marçal, 27 Nov 1969 (m fl), Pena 164 (IAN); BR-22, Capanema to Maranhão, km 10, banks of Rio Piria, 28 Oct 1965 (m fl), Prance & Pennington 1766 (NY); near Santarém, Nov 1849 (m fl), Spruce 477 (K, M), Jul 1850 (m fl), Spruce 608b (C, GH, NY, P).

French Guiana: Cayenne, 24 Sep 1913 (f fl), Bénoist 6 (P); Paricabo, 21 Oct 1954 (f fl), Black & Klein 54-17069 (CAY, IAN); Montjoly, 5 km E of Cayenne, 4°55'N, 52°17'W, 19 Feb 1978 (fr), Leeuwenberg 11840 (NY); (without locality), 1864 (f fl), Mélinon s.n. (GH); Maroni, 1876 (m fl), Mélinon 315 (P); (without locality), 1820 (m fl), Perrottet (P); Cabassou, 7 Feb 1979 (fr), Prévost 425 (NY); Maroni, at village of Tapouis, 1857 (f fl), Sagot 757 (BM, P).

Guyana: NW District, Waini River, 2 Feb 1922 (f fl), de la Cruz 1249 (GH, NY); vicinity of Bartica, on the Essequibo River, 6°25'N, 3-12 Sep (m fl), de la Cruz 1950 (GH, NY, US); Kaieteur Falls, Potaro River, 23 Oct-3 Nov 1923 (f fl), de la Cruz 4386, (NY), (buds and young fr), de la Cruz 4487 (NY); Pomeroon District, Moruka River, Jul 1927 (f fl), de la Cruz 4558 (GH, NY); Mazaruni Station, 9 Nov 1942 (f fl), For. Dep. Br. Gui. 3660 (NY); Upper Demerara River, Sep 1889 (m fl), Jenman 4774 (NY); (without locality), 1868 (m fl), R. Schomburgk 33 (P).

23b. *Protium heptaphyllum* (Aublet) Marchand ssp. *cordatum* (Huber) Daly,
(submitted for publication in Brittonia). Type. Brazil. Pará: Faro
Campo do Tigre, 21 Aug 1907 (m fl), Ducke 20522 (MG no. 8463)
(lectotype (designated by Swart, 1942b): B (destroyed); isoelectotypes:
MG, NY, RB).

Protium cordatum Huber, Bol. Mus. Paraense Hist. Nat. 5: 433. 1908.

Leaflets drying reddish, usually abruptly and broadly short-acuminate,
tertiary veins flat; calyx in staminate flowers 0.7-1 mm long, exceeding
the disk; petals with scattered appressed hairs to 0.1 mm long, also with
sparse fine erect hairs to 0.05 mm long; pistillode 0.6-0.7 mm long;
pyrene in dorsiventral view broadly ovate.

Distribution. This subspecies is restricted to the campinas-- or low
forest on very sandy soils-- in Pará near Tukurui, Santarém, and the upper
Rio Tocantins. It flowers from August to February and fruits from October
to January.

Specimens examined. Brazil. Pará: Alto Tapajós, Rio Cururú, region of
Missão Velha, a Mundurukú village, 7°45'S, 57°20'W, 13 Feb 1974 (m fl), W.
Anderson 10915 (IAN); 18 km E of Tukurui and Rio Tocantins, near BR-263,
3°30'S, 49°32'W, 28 Oct 1981 (fr), Daly et al. 980 (MG, NY); 25 km S of
Tukurui, just off old BR-422 at junction with old railroad bed, 3°58'S,
49°38'W, 30 Oct 1981 (fr), Daly et al. 1080 (MG, NY); campos E of Faro, 20
Jan 1910 (sterile), Ducke 10497 (MG); Lago de Faro, above Tauacuera, 12
Feb 1910 (m fl), Ducke 10678 (MG); Rio Tapajós, Bella Vista, 6 Dec 1915

(fr), Ducke 15850 (MG); Tukurui, right bank of Rio Tocantins, BR-263, km 16, 31 Jan 1980 (fr), Lisboa et al. 1326 (NY); Tukurui, PA-149, 2 Sep 1983 (f fl and young fr), Miranda et al. 395 (INPA, NY), 2 Sep 1983 (buds), Miranda et al. 408 (INPA, NY); Tukurui, campina de Santa Rosa, 13 Sep 1983 (fr), J. Ramos 626 (INPA, NY), right bank, PA-149, km 35, 20 Sep 1983 (f fl), J. Ramos 883 (NY), campina de Santa Rosa, 18 Nov 1983 (young fr), J. Ramos 1147 (INPA, NY), 4 Oct 1983 (fr), Revilla 8502 (INPA, NY), Tukurui-Goianêsia road, right bank of Rio Tocantins, 19 Aug 1980 (m fl), W. Rodrigues 10239 (MG, MO), BR-263, km 16, 8 Nov 1980 (fr), M. G. Silva 5806 (MG, NY).

This subspecies is closely related to P. almecega Marchand var. ulei Swart, a taxon restricted to forests on very sandy soils in the Rio Negro region. The latter belongs in P. heptaphyllum, probably as an additional subspecies. Further material of ssp. cordatum is needed before their differences can be well defined and the transfer made.

24. *Protium pilosum* (Cuatrecasas) Daly, (submitted for publication in Brittonia). Type. Brazil. Pará: forest of Cia. Pirelli, Fazenda Uriboça, Aug 1958 (m fl), Pires 7119 (holotype: US).

Tetragastris pilosa Cuatrec., Bol. Mus. Paraense Hist. Nat., Nov. Sér.

(Bot.) 11: 8. 1961.

Protium belemense Swart, Acta Bot. Néerl. 18: 466. 1969. Type. Brazil.

Pará: Belém, Bosque Municipal, (without date) (m fl), IAN Registro No. 210 (holotype: IAN). Protium paraense Swart, nom. illegit., Acta Bot. Néerl. 15: 52. 1966.

Small trees or shrubs, reproductive height 1-12 m; branchlets slender, 1.2-1.9 mm diam in flower, (1.6) 1.8-2.6 mm diam in fruit, with dense to sparse erect to ascending hairs to 0.05 mm long, also with sparse to scattered erect to appressed hairs to 0.6 mm long. Leaves 0-5-jugate, 7-24 cm long; petiole semi-terete (rarely slightly canaliculate), sometimes slightly acutely winged, short and slender, usually shorter than interjuga, (0.8) 1-2.9 (4) cm x (0.8) 1-1.5 (1.7) mm, with hairs as on branchlets; interjuga (1) 1.2-2.8 (3.5) cm long, petiolules short, shallowly 2-canaliculate, lateral petiolules 0.05-0.3 cm long, terminal usually shorter than interjuga, 0.7-2 (2.2) cm long, pulvinuli inconspicuous or absent; leaflets chartaceous, laterals narrow-elliptic to elliptic, basal pair (3.5) 4-8.5 (9.6) x 1.2-2.7 (4) cm, ultimate pair 5.5-9 (10.6) x 1.3-2.4 (3.4) cm, base subequal to somewhat oblique, proximal side acute to cuneate, distal side acute to obtuse, terminal

(narrowly) elliptic to oblanceolate, (4.3) 5-9 (10.5) x 1.5-3.1 (4) cm, base acute, leaflet apex gradually and narrowly long-acuminate, usually sparsely serrulate, margin often slightly revolute, abaxial surface with midvein and secondary veins prominulous, rest of venation prominulous or inconspicuous, midvein with scattered appressed hairs 0.1-0.2 mm long, rest of surface also with (sub)marginal ascending hairs 0.1-0.3 mm long, adaxial surface with midvein narrowly prominent to prominulous, secondary veins prominent to inconspicuous, rest of veins inconspicuous, surface glabrous. Inflorescences distributed along branchlets, short and slender, 0.4-1.1 cm x 0.3-0.7 mm at base (in fruit 2-3 cm x 0.8-1.5 mm), secondary axes poorly developed, 0.3-0.8 cm long, axes with dense appressed thick acute hairs to 0.1 mm long; inflorescence bracts broadly ovate, semi-clasping, apex acute to obtuse, those subtending inflorescences (0.3) 0.6-1.2 mm long, those on primary axes 0.4-1 mm long, those on secondary axes 0.3-0.7 mm long; pedicel compressed-clavate, much shorter than flowers, (0) 0.2-0.8 (0.9) x (0.2) 0.3-0.5 mm, with sparse to scattered hairs as on inflorescence. Flowers all 4-merous, 2-2.5 mm long when dry; calyx deeply cupular, 1-1.6 (1.8) x (1.5) 1.7-2.2 mm overall, glabrous or with a few scattered hairs as on pedicel, lobes rounded-deltate, 0.5-0.9 mm long, apex acute; petals white to greenish to cream to yellow, (broadly) ovate, 2-2.7 x (1) 1.2-1.5 (2) mm, fused (3/10) 2/5-3/5 their length, apiculum inconspicuous, weakly inflexed, abaxially glabrous, margin short-papillate, at anthesis petals straight or slightly inflexed or reflexed; in staminate flowers calyx greatly exceeding disk, also exceeding pistillode; stamens greatly exceeding pistillode, (1.35)

1.5-1.85 and (1.45) 1.6-1.95 mm long, filaments terete, fleshy, 1.1-1.5 and 1.1-1.6 mm long, anthers basifixed, in dorsiventral view (broadly) ovate with lobulate base and obtuse apex, in lateral profile broadly obtuse-oblong to slightly ovate, small, 0.3-0.4 mm long; disk relatively deep and broad, (0.25) 0.3-0.45 x 0.3-0.4 mm; pistillode only slightly exceeding disk, 0.4-0.5 x 0.4-0.5 mm overall, compressed-globose to depressed-ovoid, glabrous, with locules and reduced ovules, abruptly contracted into a short, thick, striate stylode 0.2-0.3 x 0.25-3 mm; in pistillate flowers calyx greatly exceeding the disk; staminodes 1.1-1.5 and 1.5-1.6 mm long, approximately level with top of pistil, filaments slender, slightly compressed, 0.7-1.1 and 1.1 mm long, anthers in dorsiventral view ovate with lobulate base and truncate apex, in lateral profile asymmetrically obtuse-oblong, slightly incurved, 0.4-0.5 mm long; disk 0.3-0.45 x 0.3-0.45 mm; pistil 1.25-1.35 (1.75) x 0.85-1 (1.25) mm overall, ovary broadly ovoid, glabrous, gradually contracted into a thick style (0.3) 0.5 x 0.35-0.45 mm, stigmatal region 0.15-0.2 mm high, stigmas sessile, globose, oriented slightly upward and outward. In fruit pedicel 1.2-1.8 x 1-1.4 mm; fruit green (Oldeman T-670) to greenish-white or almost white (Mori & Pipoly 15434) at maturity usually substipitate, markedly obliquely ovoid and markedly trigonous, 1.5-2.2 x 1.1-1.5 cm (to 1.8 cm diam when more than 1 pyrene), base truncate above stipe, apex acuminate or narrowly acute, apex usually slightly recurved, calyx usually persisting in fruit, surface glabrous, smooth, drying wrinkled, mesocarp relatively thin and fleshy; pseudaril fleshy, covering all of pyrene; pyrene thickly cartilaginous, 1.6-1.8 x 1.3-1.5 cm, in dorsiventral view

(broadly) ovoid to essentially deltate, base truncate, apex acute to slightly acuminate, in lateral profile essentially lanceolate, base obtuse to truncate, apex acute to broadly acuminate and slightly recurved, with a dense layer of erect to appressed fibers 0.1-0.4 mm long except on funicular scar, site of funicle $3/4$ to $4/5$ distance to apex, funicular depression shallow, funicular scar essentially rounded-deltate, covering $1/5$ - $1/7$ of ventral face; testa thin, with some irregular thickenings but not infolded with cotyledons, cotyledons entire and plano-convex, distally slightly incurved.

Distribution. Protium pilosum is relatively common, but within a restricted range in northeastern and north-central (north of the Rio Amazonas) Pará, Amapá, and French Guiana. In this region it often occurs as a common understory shrub or tree on terra firme, in primary or less often secondary forest. The species flowers from July to January and fruits from (October) January to May.

Specimens examined. Brazil. Amapá: 1956 (m fl), Miranda Bastos 88 (NY); Municf. Macapá, 156 km NW of Porto Grande on Perimetral Norte (BR-210), ca $1^{\circ}30'N$, $53^{\circ}30'W$, 29 Dec 1984 (f fl and young fr), Mori et al. 17544 (NY); Cupixi, 16 Oct 1976 (buds), B. G. Ribeiro 1529 (NY); Porto Grande, region of Colonia Agrícola do Matapi, 12 Nov 1976 (buds), N. A. Rosa 1037 (MG, NY). Pará: Belém, 1828-1830 (m fl), Burchell 9847-2 (GH); Belém, Agua Preta-Aurá, 26 Nov 1914 (buds), Ducke 15537 (NY); (without locality), (without date) (buds), Egler 692 (MG); Municf. Vizeu, Rio Piriá, 1 May 1968 (fr), Frões 34260 (IAN, US); (without locality), (without date), Glaziou 9710 (C); Belém, Sacramento, 22 Oct 1897 (young

fr), M. Guedes 1251 (MG); Estrada da Barra, third bridge, 28 Sep 1898 (buds), M. Guedes 1598 (MG, NY); Aribuquinha, 6 Aug 1899 (sterile), M. Guedes 1659 (MG); Belém, Bosque Municipal, 12 Jul 1901 (buds), J. Huber 2111 (MG); Peixe Boi, 20 Nov 1906 (m fl), J. Huber 7824 (MG, NY); 20 km S of Belém, 2 Aug 1964 (m fl), Irwin 5016 (NY, US); Tapanã, near Belém, 29 Oct 1929 (fr), Killip & Smith 30372 (NY, US); Municfp. Benevides, Belém-Mosqueiro road, 28 Jul 1964 (buds), Oliveira 3120 (IAN, NY); Belém, IAN, Reserva Mocambo, Jan 1956 (m fl), Pires & Silva 6715 (US), 22 Aug 1967 (m fl), Pires & Silva 10742 (US), 21 Sep 1967 (m fl), Pires & Silva 10943 (IAN), Agua Preta, 30 Oct 1967 (fl), Pires & Silva 11198 (IAN); Ilha do Mosqueiro, 15 Dec 1967 (m fl), Pires & Silva 11421 (IAN); Belém, IAN, Reserva Mocambo, 26 Mar 1968 (fr), Pires & Silva 11457 (IAN); BR-22, Capanema to Maranhão, km 96, vicinity of Cachoeira, 29 Oct 1965 (buds), Prance 1812 (NY, W), km 64, vicinity of Piritoro, 3 Nov 1965 (buds), Prance & Pennington 1921 (NY); Belém, grounds of Instituto Agronômico do Norte, 17 Aug 1964 (m fl), Prance & Silva 58747 (NY); Belém, EMBRAPA, 7 Apr 1977 (fr), N. A. Rosa 1755 (MG), Reserva Mocambo, 7 Mar 1968 (fr), Sastre 56 (IAN, NY, P), Guamã research area, Dec 1965 (young fr), Schubert 2241 (NY); Cuiabã-Santarém highway, km 1180, 17 Nov 1977 (galled fls), A. S. Silva 229 (NY); Belém, 8 km NE of IAN, near Catu, 15 Sep 1942 (m fl), M. B. Silva 69 (NY, US); Benevides-Mosqueiro road, 10 Feb 1966 (young fr), M. G. Silva 483 (MG); Murutucú, Sep 1902 (fl), Siqueira Rodrigues 2995 (MG); Ourém, S. José, 11 Dec 1903 (m fl), Siqueira Rodrigues 4063 (MG); Benevides-Mosqueiro road, 14 Aug 1965 (buds), M. S. Vieira 2 (MG); Municf. Sta. Izabel, ca km 35 of Belém-Brasflia Highway, Fazenda Boa Esperança, 5

Sep 1979 (buds), Zarucchi et al. 2521 (K). French Guiana: Saül, Mont Galbao, Sommet Nord, 14 Dec 1976 (m fl), Cremers 3981 (CAY), Layon du Grand "Circuit Boeuf Mort," 13 Dec 1971 (fr), de Granville 885 (CAY), 8 km W, Source de la Mana at the foot of Mont Galbao, 8 Mar 1975 (fr), Granville 2356 (CAY); sur le circuit du Plateau "La Douane," km 0.6, 17 Jan 1972 (fr), de Granville B-4251 (CAY), Tracé Montagne Galbao, 27 Sep 1974 (buds), de Granville B-5171 (CAY, NY); Saül, 17 Dec 1976 (f fl), Mori & de Granville 8790 (NY), 22 Dec 1976 (fr), Mori 8822 (NY); Mont La Fumée, 3°37'N, 53°12'W, 16 Sep 1982 (m fl), Mori et al. 14936 (NY), 13 Oct 1982 (f fl), Mori et al. 15078 (NY), La Fumée, near junction of Antenne Nord, 28 Mar 1983 (fr), Mori & Pipoly 15434 (NY), Airport road on outskirts of Saül, 25 Mar 1983 (fr), Mori et al. 15369 (NY); Rivière Camopi (tributary of R. Oyapock) on upper slope of Montagne Yanioué, 8 Feb 1968 (fr), Oldeman & Sastre 85 (CAY); Cacao, ca 60 km S of Cayenne, 7 Apr 1966 (fr), Oldeman B-470 (CAY); forest on left bank of Oyapock River, above Saut Kouamantapéré, 9 May 1970 (fr), Oldeman T-670 (CAY); Upper Oyapock, Saut Couyari, 9 May 1978 (fr), Oldeman B-3168 (CAY); Saül, Tracé Crique Eau Noire, km 2500, 9 Mar 1972 (fr), Oldeman B-4354 (CAY).

Local names and uses. Brazil. Pará: breu branco. French Guiana: encens. No uses reported.

Protium pilosum most closely resembles P. guianense (Aublet) Marchand because of the inconspicuous pulvinuli on the petiolules, the small chartaceous leaflets with a relatively long acumen, the reduced inflorescence, and the pilose flowers with partly fused petals. Protium pilosum differs by its shorter petiolules; leaflets usually narrowly

elliptic (not usually lanceolate), with subequal, acute (not markedly asymmetrical and obtuse to truncate) base; leaflet acumen usually sparsely serrulate; smaller number of straight (not arcuate) secondary veins; inflorescence shorter; calyx more deeply cupular (not subtruncate) and with larger lobes; and petals erect and consistently partially fused.

Protium pilosum is distinguished from the other species in its group-- P. trifoliolatum and P. unifoliolatum-- by the former's greater number of juga; leaflets usually narrowly elliptic, petiolules short, calyx deeply cupular, anthers small; petals which are consistently fused $2/5$ - $3/5$ their length; and the fruit markedly trigonous and pale green to greenish-white at maturity.

Protium pilosum is the most difficult of the four species in its group to separate from Tetragastris. Like Tetragastris and unlike the rest of its group, P. pilosum has a deeply cupular calyx and petals which are consistently and uniformly fused to more than $1/2$ their length and which are (sub)erect at anthesis. While the lateral petiolules in Tetragastris always lack pulvinuli, in P. pilosum pulvinuli may be absent or present, even on different leaves of a single branchlet. The species in question also differs from Tetragastris because it has a regularly divided calyx tube, a distinct pistillode in pistillate flowers, stamens with long terete filaments and small sagittate anthers, and a distinct disk (not fused with pistillode to form an "ovariodisk") which is usually broader than deep.

25. Protium trifoliolatum Engler in Mart. Fl. bras. 12(2): 266. 1874.

Type. Brazil. Amazonas: Rio Uaupês, near Panurê, Oct 1852-Jan 1853 (frt), Spruce 2845 (lectotype (designated by Swart, 1942b): P; isoelectotypes: BR, C, G, GH, LE, NY, OXF, W).

Tingulunga trifoliolata O. Kuntze, Rev. Gen. Pl. 1: 108. 1891.

Tetragastris trifoliolatum (Engl.) Cuatrecasas, Bol Mus. Paraense Hist. Nat., Nov. Sér. (Bot.) 11: 10. 1961.

Protium martianum Engl. in Mart. Fl. bras. 12(2): 266. 1874. Type. Brazil. Amazonas: Rio Japurã, Dec (no year) (frt), Martius s.n. (holotype: M).

Tingulunga martiana OK., Rev. Gen. Pl. 1: 108. 1891.

Protium titubans Macbride, Candollea 5: 379. 1934. Type. Peru. Loreto, near Iquitos, July 1929 (m fl), L. O. Williams 1521 (holotype: F).

Protium pauciflorum Swart, Rec. Trav. Bot. Néerl. 39: 196. 1942. Type. Brazil. Amazonas: basin of Rio Solimoes, São Paulo de Olivença, near Palmares, Sep-Oct 1936 (f fl), Krukoff 8182 (holotype: NY; isotypes: BR, F, G, MO).

Protium joannis Cuatrec., Bol Mus. Paraense Hist. Nat., Nov. Sér. (Bot.) 11: 2. Type. Brazil. Pará: forest of Cia. Pirelli, Fazenda Uriboça, Aug 1958 (f fl), Pires 7114 (holotype: US; isotypes, MG, NY, RB).

Small tree or shrub, reproductive height 1.5-15 m; branchlets slender to somewhat robust, (1) 1.2-1.9 (2.5) mm diam, (to 3 mm diam in fruit) with sparse fine erect hairs to 0.05 mm long, also with sparse to scattered appressed hairs 0.1-0.2 mm long, often also with scattered to

sparse erect to appressed hairs 0.3-1 (1.3) mm long. Leaves 0-2 (3)-jugate, (8) 9.5-25 (31) cm long; petiole usually shorter than interjuga, semi-terete, (0.4) 0.8-2.8 (3.5) cm x (0.8) 1-1.7 (2) mm, with dense to sparse fine erect hairs to 0.05 mm long, also with scattered erect hairs 0.3-1 (1.3); interjuga (when present) 0.9-4.1 (5.7) cm long; petiolules shallowly 2-canaliculate, short and usually robust, laterals 0.2-1 (1.5) cm long, terminal longer than interjuga, (0.5) 1.3-3.5 (5.2) cm long, pulvinuli conspicuous; leaflets coriaceous to somewhat chartaceous, laterals (broadly) lanceolate to elliptic, basal pair (4.3) 5.8-11.1 (13.5) x (1.6) 2-5.2 (5.9) cm, ultimate pair (when more than one jugum) (6.2) 7.8-13.3 (14.8) x (1.8) 2.5-4.8 (6) cm, base subequal to slightly oblique, obtuse to acute, terminal (broadly) elliptic, (6.5) 7.8-14 (16.5) x (2.4) 2.9-6.1 (7.8) cm, base acute, leaflet apex usually gradually and broadly acuminate, acumen 0.4-1.4 cm long, abaxial leaflet surface with midvein and secondary veins obtusely prominent, rest of veins prominent to prominulous, midvein with sparse fine erect hairs to 0.05 (0.1) mm long, also with scattered erect hairs 0.3-1 (1.3) mm long, the latter sometimes present on the secondary and tertiary veins, adaxial surface with midvein narrowly prominent to prominulous but partly sunk in a groove, secondary veins prominulous to impressed, rest of veins inconspicuous or less often prominulous, midvein and secondary veins with dense fine erect hairs to 0.05 (0.1) mm long, midvein also with scattered long erect hairs 0.3-1 (1.3) mm long, leaflet margin usually with scattered ascending hairs 0.3-1 (1.3) mm long. Inflorescences distributed along branchlets, short, 0.4-1.8 (2) cm x 0.4-1 mm, secondary axes poorly

developed, to 0.7 cm long, axes compressed, inflorescence with sparse (rarely dense) erect hairs 0.3-1 (1.3) mm long; inflorescence bracts (broadly) lanceolate, semi-clasping, chartaceous, those subtending inflorescences 0.4-0.9 mm long, those on primary axes 0.4-0.8 (1) mm long, those on secondary axes 0.3-0.6 (0.8) mm long; pedicel subcylindric to slightly clavate, long, (0.5) 0.8-2.2 (2.6) x (0.25) 0.3-0.5 mm, glabrous or rarely with scattered stiff erect hairs 0.3-0.1 (1.3) mm long (Cid et al. 3286 in Brazilian Amazonas; Maguire 32736 in Venezuelan Amazonas). Flowers all 4-merous, small; staminate flowers (1.8) 2-2.8 mm long when dry; calyx shallowly cupular, 0.5-0.8 (1) x 1.8-2.2 (2.5) mm overall, usually glabrous, lobes rounded depressed-deltate, 0.2-0.5 mm long, apex usually apiculate and papillate; petals ovate, fleshy, 2.3-3.1 (3.3) x 1.2-1.8 (2) mm, free or more often irregularly fused to 3/5 their length, glabrous abaxially, margin short-papillate, apiculum usually conspicuous and strongly inflexed; stamens greatly exceeding pistillode, (1.6) 2-2.2 (2.4) and (1.7) 2.1-2.3 (2.5) mm long, filaments markedly fleshy, terete, (1.1) 1.5-1.6 (1.8) and (1.2) 1.6-1.7 (1.8) mm long, anthers in dorsiventral view elliptic or less often obtuse-oblong or slightly ovate with lobulate base and obtuse to truncate apex, in lateral profile asymmetrically obtuse-oblong, 0.5-0.65 mm long; disk relatively deep and broad without (often shallow within), (0.35) 0.45-0.65 x 0.4-0.65 mm, provided with locules and reduced ovules, globose to slightly depressed-ovoid, abruptly contracted to a short thick 4-lobulate stylode 0.15-0.25 (0.3) x 0.35-0.4 mm; pistillate flowers with calyx (0.5) 0.7-1 (1.2) x 1.7-2.2 (2.4) mm overall, lobes 0.2-0.5 (0.7) mm long; staminodes

long, usually level with base of the stigmas, (1) 1.2-1.7 (1.85) and (1.1) 1.3-1.8 (1.95) mm long, filaments (0.5) 0.6-1.1 (1.25) and (0.6) 0.7-1.2 (1.35) mm long, anthers in dorsiventral view broadly lanceolate to lanceolate, with lobulate base and truncate to slightly retuse apex, in lateral profile narrowly oblong to slightly lanceolate, 0.5-0.6 mm long; disk relatively broad and deep, 0.3-0.5 (0.6) x 0.2-0.45 mm, usually very shallow within; pistil 1.1-1.4 (1.6) x 0.7-1 (1.1) mm overall, ovary (broadly) ovoid, sessile, glabrous, gradually contracted into a short thick style (0.15) 0.25-0.3 (0.4) x (0.3) 0.35-0.5 mm, stigmas sessile, compressed-globose, oriented slightly upward and outward; pedicel in fruit (1.1) 1.6-2.1 (2.5) x 0.7-1.2 mm. Fruit maturing red, obliquely ovoid and gibbous, (1.4) 1.6-2 x 0.9-1.3 cm (to 2.1 cm diam when more than 1 pyrene), substipitate, apex obtuse, drying wrinkled, mesocarp relatively thin and fleshy; pseudaril spongy, covering all of pyrene; pyrene cartilaginous, in dorsiventral view (broadly) lanceolate to ovate, with truncate base and broadly short-acute apex, in lateral profile essentially (broadly) elliptic, 1.1-1.5 x 0.6-0.8 (1) cm, with dense layer of erect to appressed fibers to 0.4 mm long except on funicular scar, site of funicle 3/5-3/4 distance to apex, funicular depression shallow, funicular scar rounded-deltate or triangular, with sinuate margin, covering 1/5-1/4 of ventral surface; testa with few irregular thickenings, not infolded with cotyledons; cotyledons entire, plano-convex, distal portion of the posterior one often uncinately incurved.

Distribution. Widespread in Amazonia, the Guianas, and southern Venezuela. Protium trifoliolatum is a shrub, or small to medium-size tree, of terra firme forests.

Representative specimens examined. Brazil. Amapá: Oiapoque, road to airport, 13 Oct 1950 (f buds), Frões 26019 (IAN); Municip. Macapá, banks of Rio Dois Irmãos, 12 km from Cupixi, near Perimetral Norte highway, 20 Apr 1977 (fr), Rosa & Santos 1774 (MG, NY). Maranhão: Municip. Monção, basin of Rio Turiaçu, Ka'apor Indian Reserve, 4 km NW of Urutawy, 15 Apr 1985 (frt), Balée 22 (NY), 2 km N of Urutawy, 8 Apr 1985 (fr), Balée & Ribeiro 116 (NY), 4 km NW of Urutawy, 8 Apr 1985 (fr), Balée & Ribeiro 206 (NY), 5 Feb 1985 (f fl), Balée & Ribeiro 413 (NY); S of Fazenda Primavera, Araganã, km 162 of BR-316, 24 Sep 1980 (buds), Daly et al. 234 (MG, NY); Alto Rio Turiaçu, Nova Esperança, 2°55'S, 45°45'W, 1 Dec 1978 (buds), Jangoux & Bahia 122 (MG, NY), 16 May 1979 (fr), Jangoux & Bahia 678 (MG); Turiaçu, km 6 of BR-106 (Maracaçumê-Sta. Helena), 29 Nov 1978 (buds), Rosa & Vilar 2717 (NY, US); Tocantins-Belém road, km 345, 13 Nov 1963 (m fl), N. T. Silva 57790 (NY). Pará: Belém south forest of IAN, 16 Nov 1942 (buds), Archer 7827 (US), 25 Nov 1942 (buds), Archer 7884 (F, MO, US); Fazenda Borba Gato, near Rio Acará, 30 km W of Tmoê Açu-Paragominas road, leaving rd. 30 km S of Tomê-Açu, 2°40'S, 48°35'W, 5 Nov 1980 (buds), Daly et al. 842 (MG, NY); Rio Mojú, 16 Apr 1957 (fr), Frões 33921 (US); Belém, Marca da Léguas, 16 Sep 1898 (buds), M. Guedes MG 1589 (MG, NY); Acará, Rio Acará, 27 Dec 1948 (m fl), Pires 1477 (IAN); Municip. Paragominas, Belém-Brasília Highway (BR-010) 17 km S of Ligação do Pará, near km marker 1509, 4°17'S, 47°32'W, 1 Mar 1980 (fr), Plowman et al. 9431 (NY), 2 Mar 1980 (fr), Plowman et al. 9466 (MICH, MO, NY); Rio Jarí, Monte Dourado, 7 Oct 1968 (f fl), N. T. Silva 1127 (NY); Peixe-Boi, mata, 23 Jul 1907 (young fr), Siqueira Rodrigues s.n. (MG).

French Guiana: Route de Cayenne, km 11, 24 Feb 1954 (sterile), BAFOG 152M (CAY); Route de Mana, 12 Jan 1956 (fr), BAFOG 7160 (NY, P), 14 Jan 1956 (fr), BAFOG 7169 (NY), 16 Jan 1956 (fr), BAFOG 7174 (NY); Saül, Mont La Fumée, 3°37'N, 53°12'W, 19 Oct 1982 (f fl), Boom & Mori 451 (NY); Saut Ouaimicouaré, Yaroupi River (tributary of Oyapock), 11 Apr 1970 (fr), de Granville 326 (CAY); right bank of the Yaroupi, 29 Apr 1970 (fr), de Granville 501 (CAY); Trois Sauts, 6 Jun 1975 (sterile), Grenand 1007 (CAY); La Mana, 1823-1824 (buds), Leschenault s.n. (P); Saül, Mont La Fumée, 3°37'N, 53°12'W, 3 Oct 1982 (buds), Mori et al. 15050 (NY); Cacao, approx. 60 km S of Cayenne, Tracé Pauvert, 29 Mar 1966 (fr), Oldeman B-426 (CAY).

Guyana: Marudi Mts., Mazoa Hill near Norman Mines camp, 224815'N, 59°10'W, 12 Nov 1982 (buds), Stoffers et al. 304 (NY).

Surinam: Zanderij I, Apr 1939 (fr), BW 6043 (NY); Sipaliwini savanna area on Brazilian frontier, 3-5 km NW of Meyers farm, Feb 1970 (fr), Lindeman 1974 (U), Feb 1970 (fr), Oldenburger et al. 1251 (U).

At first, Protium pauciflorum and P. joannis may appear to be anomalous within P. trifoliolatum, P. pauciflorum because of its large 2-3-jugate leaves with long petiolules, and P. joannis because of its subglabrescent petiole and interjuga. Their flowers and fruits are not unusual at all for P. trifoliolatum. In this treatment they are considered morphological extremes of a single very plastic species which shows a broad continuum of variation for a number of characters, as the measurements in the description indicate.

Protium trifoliolatum is distinguished from P. guianense by the

former's glabrous pedicel, calyx, abaxial petal surface, pistillode, and pistil; inflorescence shorter; calyx deeper; petals usually partially fused; and longer staminodes which are level with the stigmas.

From P. pilosum (Cuatrec.) Daly, P. trifoliolatum is distinguished by the latter's petiolules with pulvinulus conspicuous (not inconspicuous or absent); leaflet acumen not sparsely serrulate; calyx much shallower; anthers larger in both sexes; petals irregularly fused; and fruit smaller.

Protium trifoliolatum is distinguished from P. unifoliolatum Engl. by the former's leaves usually 1-2-jugate; inflorescences longer, with semi-clasping bracts; flowers smaller; calyx not exceeding disk in staminate flowers; stamens, anthers, and antherodes shorter; stylode shorter; pistillode only slightly exceeding disk; and style shorter.

26. Protium unifoliolatum Spruce ex Engler in Mart. Fl. bras. 12(2): 262. 1874. Type. Brazil. Amazonas: Ega (Tefê), Dec (no year) (f fl), Martius Obs. 2918 (lectotype (designated by Swart, 1942b): M; isolectotypes: BR, LE, W).

Icica pubescens Benth, J. Bot. (Hooker) 4: 16. 1852. Type. Barra (Manaus), Dec 1850 (f fl and immat frt), Spruce 1142 (lectotype (designated by Swart, 1942b): K; isolectotype: GH; isolectotypes (under Spruce 1122): BM, C, F, G, LE, M, NY, W). Protium pubescens (Benth.) Engl. in Mart. Fl. bras. 12(2): 265. 1874. (Nom. illegit.). Tingulona simplicifolia Kuntze, Rev. Gen. Pl. I: 107. 1891. Protium benthami Swart, A monograph of the genus Protium and allied genera (Burseraceae): 324. 1942.

Protium unifoliolatum var. suberratum Engl. in Mart. Fl. bras. 12(2): 262. 1874. Type. Brazil. Amazonas: along Rio Negro, between Barcelos and São Gabriel, Dec 1851 (m fl), Spruce 1960 (lectotype (here designated): NY; isolectotypes: C, G, GH, MG).

Protium unifoliolatum var. macrophyllum Huber, Bol. Mus. Paraense Hist. Nat. 5: 432. 1908. Type. Brazil. Pará: Alenquer, 26 Dec 1903 (f fl), Ducke 4898 (holotype: MG).

Protium unifoliolatum var. puberulum Hoehne, Comm. Lin. Tel. Estr. Matto Grosso ao Amazonas, Bot. VI, Anexo 5: 31. 1915.) Type. Brazil. Mato Grosso: Rio Arinos, Dec 1914, J. G. Kuhlmann 507-511 (holotype not seen; location unknown)

Protium unifoliolatum var. inconforme Swart, Acta Bot. Neerl. 1: 249.

1952. Type. Venezuela. Amazonas: Sierra Parima, headwaters of Rfo Siapa, 11-23 Mar 1946 (m fl), F. Cardona 1327 (holotype: US).

Trees, reproductive height 2-10 m; branchlets 1.1-2.5 mm diam, with sparse to dense flexuous hairs to 0.35 (0.5) mm long, sometimes (collections from Venezuela, Peru) also with scattered fine erect hairs to 0.05 mm long, rarely subglabrous. Leaves often opposite on branchlets, unifoliolate, rarely trifoliolate and in only two observations 2-jugate, variable in size even on a single branchlet, (4.5) 6.5-25.5 (33.5) cm long; petiole semi-terete, variable in length, 0.2-3 (4.3) cm x (0.5) 0.7-1.5 (2) mm, subglabrous or with dense to sparse fine erect hairs to 0.1 mm long, otherwise (SW Amazonia and Rio Negro) with dense flexuous hairs to 0.4 (0.5) mm long; petiolules shallowly 2-canaliculate, laterals (when present) 0.2-1.2 cm long, terminal (usually synonymous with petiole) 0.2-3.3 (4.3); leaflets chartaceous or rarely coriaceous, (broadly) elliptic to (broadly) lanceolate, laterals (when present) (5.5) 7-13.8 x (1) 2.4-3.9 (6.9) cm, terminal (4.2) 5.5-20 (30.2) x (1.4) 1.9-6.6 (9.2) cm, base acute or sometimes attenuate, apex usually gradually long-acuminate, acumen 0.4-1.9 cm long, abaxial surface with midvein broadly prominent, secondary veins prominent to prominulous, rest of veins prominulous, surface glabrous or with scattered to sparse erect hairs to 0.15 mm long and scattered fine erect hairs to 0.05 mm long, occasionally with dense flexuous hairs to 0.5 mm long, adaxial surface with midvein broadly prominent to prominulous, secondary veins prominent, rest of veins

prominulous to inconspicuous, midvein and sometimes secondary veins with dense to sparse erect hairs to 0.1 (0.35) mm long and sparse to scattered fine erect hairs to 0.1 mm long, less often subglabrous, margin entire or often sparsely serrulate. Inflorescences distributed along branchlets, dense, short and slender, 0.5-1 cm x 0.4-0.9 mm, secondary axes poorly developed, to 0.5 cm long, axes glabrous or with sparse to scattered appressed hairs to 0.15 mm long; inflorescence bracts fleshy (to chartaceous on secondary axes), lanceolate, acute, those subtending inflorescences 0.7-1.7 (2) mm long, those on primary axes 0.3-0.5 (0.8) mm long, those on secondary axes 0.3-0.6 mm long; pedicel subcylindric, slender, on staminate inflorescences (0.4) 0.8-2.5 (3) x 0.25-0.45 mm, on pistillate inflorescences 0.7-1.8 (2.6) x 0.25-0.35 mm, shorter than flowers, glabrous or rarely with scattered appressed hairs to 0.1 mm long. Flowers all 4-merous, relatively large, usually urceolate at anthesis, (2.5) 3.1-4.5 mm long; calyx variable but usually deeply cupular, exceeding the disk in both sexes, 0.6-1.2 (1.4) x (1.6) 2-2.5 mm, glabrous, lobes (depressed-) deltate, apex acuminate; petals white to cream to yellow, membranous, (broadly) lanceolate or rarely ovate, (3) 3.5-4.3 (5) x 1.1-1.9 mm, adaxially glabrous, margin short-papillate, slightly reflexed at anthesis, usually (but not always) fused basally to 0.2-0.4 (0.6) times their length; in staminate flowers stamens greatly exceeding pistillode, (1.55) 1.8-2.55 (2.95) and (1.65) 1.9-2.65 (3.05) mm long, filaments fleshy and terete, (0.55) 1-1.65 (2.05) and (0.65) 1.1-1.75 (2.15) mm long, anthers basifixed, in dorsiventral view narrowly lanceolate (often obtuse-oblong after dehiscence), base lobulate, apex

acute, in lateral profile obliquely lanceolate to elliptic with obtuse apex, large, (0.6) 0.8-1.1 mm long; disk varying in size but usually broad, 0.2-0.5 x 0.25-0.5 (0.6) mm; pistillode glabrous, greatly exceeding disk, (0.55) 0.65-1 (1.25) x 0.4-0.75 mm overall, (broadly) ovoid, provided with locules and reduced ovules, gradually contracted to a long, rounded or 4-lobulate stylode (0.2) 0.4-0.65 x 0.2-0.45 mm; pistillate flowers with calyx usually +/- level with base of anthers; staminodes reaching base of style or part-way up style, rarely to base of stigmas, 1.4-1.75 and 1.4-1.85 mm long, filaments fleshy and +/- terete, broadened at base, 0.5-1.1 and 0.5-1.2 mm long, anthers in dorsiventral view lanceolate (rarely ovate) with lobulate base and rounded apex, in lateral profile narrowly elliptic to slightly lanceolate, 0.6-0.8 (0.9) mm long; disk variable in size but usually broad, 0.2-0.4 (0.5) x 0.25-0.4 (0.5) mm; pistil (1.5) 1.75-2.3 x 0.9-1.2 (1.4) mm overall, ovary (depressed-) ovoid, glabrous, gradually contracted to a style of variable length, 0.6-1.2 x 0.3-0.5 mm, stigmatal region 0.25-0.3 mm high, stigmas sessile, compressed-globose, oriented upward and outward. In fruit inflorescence to 1.7 cm long, 1-1.5 mm diam, pedicel 1.6-2.6 x 0.6-0.8 mm, maturing fruit red, oblique-ovoid, gibbous, ventricose, 1-1.8 x 0.8-1 cm (to 1-1.8 cm diam when more than one pyrene), sessile, apex acute, surface glabrous, smooth, drying wrinkled; pseudaril pulpy; pyrene thinly cartilaginous, in dorsiventral view elliptic to lanceolate to (broadly) ovate, base obtuse to truncate, apex rounded, in lateral profile obliquely lanceolate, 0.9-1.4 x 0.5-0.8 cm, with dense appressed fibers to 0.3 mm long except on funicular scar, site of funicle 2/3-3/4 distance to apex, funicular

depression shallow, funicular scar essentially rounded-deltate, covering 1/5-1/4 ventral face; testa papery, with some irregular thickenings but not infolded with cotyledons; cotyledons entire, plano-convex.

Distribution. Widespread in Amazonia and the Guianas, extending via gallery forests into the Brazilian Planalto. Protium unifoliolatum is a small tree which occurs primarily in gallery forests and forests which are flooded for relatively short periods. It is also found with some frequency in secondary forests. In eastern Amazonia and the Guianas it flowers in November to January and fruits from January to June.

Representative specimens examined. Brazil. Pará: Rio Cuparí, Inatuba, 28 Dec 1947 (m fl), Black 47-2083 (U); Rio Tocantins, near Igarapé Cajazeirinha, 30 km N of Itupiranga, 4°01'S, 49°21'W, 28 Nov 1981 (f fl), Daly et al. 1607 (MG, NY); Faro, Castanhal de Boa Vista, 31 Jan 1910 (fr), Ducke 10572 (MG); Rio Tapajós, paranã de Bela Vista, 14 Jan 1918 (m fl), Ducke MG 16919 (NY); Reserva Florestal de Gorotire, surroundings of Gorotire village at Rio Fresco, 7°47'S, 51°07'W, 14 Jan 1983 (fr), Gottsberger & Posey 13-14183 (NY); Tucuruí, margem esquerda do Rio Tocantins, BR-422, km 45, old railway, 1 Feb 1980 (fr), Lisboa et al. 1373 (NY); Municip. Oriximiná, Rio Cachorro, near shelter of Ponto da Serra, 12 km NW of Cachoeira Porteira, 22 Jun 1980 (fr), Martinelli 7062 (INPA, NY); Serra do Cachimbo, 16 Dec 1956 (fr), Pires 6346 (IAN, NY); Municip. Conceição do Araguaia, 20km W of Redenção near Córrego and Troncamento Santa Teresa, 8°03'S, 50°10'W, 9 Feb 1980 (fr), Plowman et al. 8537 (NY); Municip. Jacundá, source of Igarapé Pitinga, Rio Tocantins, 12 Dec 1980 (m fl), J. Ramos et al. 790 (NY); Itaituba, km 63 of road to Jacareacanga,

Parque Nacional do Tapajós, 12 Nov 1978 (young fr), M. G. Silva & Rosário
3668 (MG, NY); Sete Varas airstrip on Rio Curua, 10 Aug 1981 (fr),
Strudwick et al. 4496 (NY).

The rather variable nature of this species is evidenced by the names of the varieties which have been described within it: vars. subserratum, macrophyllum, puberulum, inconforme. The fact is that P. unifoliolatum does not even conform to its name, hence the publication of var. inconforme and of Icica pubescens (= P. benthami). The discontinuities indicated by all these extraneous taxa can be found within a population, among duplicates of a collection, or often on a single herbarium specimen. Only the type collection of var. macrophyllum is at all odd, and not because of leaf size, but rather because it is mostly glabrous.

Protium unifoliolatum most closely resembles P. trifoliolatum, but it can be distinguished by the former's petiole and rachis with short flexuous hairs (not with scattered to sparse, stiff, erect hairs 0.3-1 (1.3) mm long); inflorescence bracts not semi-clasping; flowers larger; calyx exceeding disk in staminate flowers; petals lanceolate (not usually ovate); stamens, anthers and antherodes longer; stylode longer, pistillode greatly exceeding disk; and style longer.

27. *Protium demerarens* Swart, Acta Bot. Néerl. 15: 46. 1966. Type.

Guyana: Mahdia Creek, Potaro River, Bartica-Potaro Rd, 27 Jun 1942 (f fl), Fanshawe (For. Dept. Br. Gui. Record No.) 3479 (holotype, K; isotypes, NY, U).

Tree, reproductive size (7) 10-30 m x 8-40 cm DBH; resin clear when fresh (reported as red on Oldeman 1918); often with low buttresses; bark gray to black, scaly; wood white, fibrous; branchlets slender, 2.5-3.5 mm diam, with sparse to scattered appressed hairs 0.1-0.25 mm long. Leaves (1) 2-4 (5)-jugate, moderately long, (14) 21.5-30 (36) cm long; petiole semi-terete, at base negligibly canaliculate and acutely winged, slender and relatively short, (2.5) 3.4-4.8 (7.4) cm x 1.3-2.3 mm, with scattered appressed hairs (sometimes absent distally) 0.1-0.25 mm long, also with scattered erect (often sparse, rarely dense on adaxial surface of petiole) to 0.05 mm long, epidermis often exfoliating; petiolules shallowly and narrowly 2-canalicate or almost terete and striate, long and slender, laterals (0.6) 0.7-1.2 (1.8) mm long, terminal (2.2) 2.7-4 (5) mm long, pulvinuli inconspicuous; leaflets thinly chartaceous in flower, becoming slightly coriaceous in fruit, (broadly) elliptic, laterals with base subequal or usually asymmetric, proximal side acute, distal side obtuse, basal pair (6.4) 8.6-12.2 (13) x (2.6) 3-4.3 (5.6) cm, ultimate pair (7.8) 9-12.5 (14) x (2.5) 3.1-4.1 (5.4) cm, terminal (7) 9.6-1.25 (1.3) x 3.4-4.6 (5.7) cm, base obtuse, leaflet apex abruptly narrowly broad-acuminate, acumen (0.8) 0.9-1.8 (2) cm long, mature leaflets glossy on both sides, abaxial surface with midvein and secondary vein obtusely

prominent, rest of veins prominulous, glabrous but for scattered appressed hairs 0.1-0.2 mm long along midvein, sometimes on all of surface, adaxial surface with midvein and secondary veins narrowly obtusely prominulous, remainder of reticulum prominulous, surface glabrous; inflorescences fasciculate. Inflorescences short and slender, (1) 2.2-6 (7) cm x 0.5-1.3 mm diam (in fruit (1.7) 2.2-2.9 (4) mm diam), secondary axes poorly developed, 0.5-0.8 cm long, (in fruit 1.5-3.5 (4) cm long), axes with sparse to scattered appressed hairs 0.1-0.25 mm long (dense at base and on bracts), sometimes also with scattered to sparse erect hairs to 0.05 mm long; inflorescence bracts ovate, those subtending inflorescences fleshy, 0.8-1.5 mm long, apex obtuse, those on primary axes chartaceous, 0.4-0.7 mm long, apex acute, those on secondary axes 0.2-0.6 mm long; pedicel subcylindric, long and robust, with scattered appressed hairs 0.05-0.2 mm long (dense to sparse at base), in staminate flowers (1.2) 2.2-2.9 x 0.65-0.7 mm, in pistillate flowers shorter, (1) 1.5-2 x 0.65-0.7 mm; Flowers 5-merous (rarely 4-merous), 3-4 (4.8) mm long; in staminate flowers calyx approximately level with disk, 1.2-1.3 x 2.4-2.5 mm, with hairs as on pedicel, lobes 0.25 mm long, apex papillate, occasionally also with several appressed hairs 0.05-0.15 mm long; petals pale yellow to cream, lanceolate, long, 3.6-3.8 x 1.4-1.7 mm, fleshy, apiculum inconspicuous or up to 0.35 mm long and weakly inflexed, glabrous abaxially, adaxially with obtusely prominent midvein and secondary veins, margin abruptly involute and short-papillate, at anthesis petals strongly reflexed 3/4 their length; stamens 1.7 and 1.85 mm long, filaments slightly compressed, glabrous, slightly exceeding pistillode, 0.9 and 1.05

mm long, anthers basifixed, in dorsiventral view very narrowly elliptic, base lobulate, apex obtuse (after dehiscence elliptic with base obtuse), in lateral view narrowly obtuse-oblong, long, 0.8 mm long; disk shallow and broad, 0.2-0.3 x 0.45-0.55 mm, rugose; pistillode 0.6 x 0.8-0.85 mm overall, depressed-ovoid, with scattered to sparse ascending hairs to 0.25 mm long, provided with reduced locules and ovules, abruptly contracted to an acutely 5-winged apex 0.2-0.25 (0.4) mm high; pistillate flowers with calyx 0.9-1.3 x (2) 2.2-2.5 mm, lobes (0) 0.15-0.25 mm; staminodes reaching base of stigmas, 1.65-1.7 and 1.75-1.8 mm long, filaments slightly compressed, not greatly exceeding disk, 0.9-0.95 and 1.-1.05 mm long, anthers in dorsiventral view broadly lanceolate, base truncate, apex acute or apiculate, in lateral view narrowly acute-oblong, base obtuse, long, 0.75-0.8 mm long; disk deep and broad, 0.4-0.5 x 0.4-0.5 mm; pistil 1.6-1.9 x 1.2-1.25 mm overall, ovary broadly ovoid, sessile, glabrous, gradually contracted to a short thick style 0.15-0.25 (0.35) x 0.55-0.65 mm, stigmatal region 0.3-0.35 (0.4) mm high, stigmas sessile, compressed-globose, oriented upward and outward. Fruits mostly solitary in the leaf axils of outer branches, pedicel (3) 3.5-4 (5) x (2) 2.4-3 (4) mm, young fruits ellipsoid to slightly obovoid, soon lenticillate, mature fruits fruit orbicular to broadly ellipsoid, large, (2.8) 3-3.2 (3.5) x (1.8) 2.1-2.3 (2.7) cm (to 3.5 cm wide when more than 1 pyrene), broadly substipitate, occasionally negligibly bluntly short-acuminate, styles and stigmas usually persistent, brown to tan or cream and densely covered with white to light brown lenticels, epidermis exfoliating so fruit with rough texture, when dry lenticels usually filled with resinous deposits; pyrene

2.1-2.5 x 1.7-2 cm, in dorsiventral view orbicular to very broadly obtuse-oblong, base obtuse, apex abruptly short-apiculate, in lateral view essentially orbicular, base obtuse, apex broadly acute, ventral side with two deep laterally elliptic depressions at apex so that apex trigonous, site of funicle subapical, funicular depression deep, small and laterally elliptic to semi-elliptic, funicular scar corresponding to the depression, covering 1/10 ventral face, surface with dense suberect fibers to 0.25 mm long except on funicular scar; testa with irregular thickenings, infolded with contortuplicate cotyledons.

Distribution. Rare in French Guiana, Guyana, and in Brazil in Amapá and in Pará in the Rio Trombetas basin near Amapá. The scant ecological data available do not indicate any restricted edaphic tolerances or preferences for this species, except that it occurs in regions characterized by moist forest on hilly terrain. It has been reported from lateritic soils in Guyana and French Guiana, clay soils in Pará and Amapá, and sandy soils in Guyana. It appears to flower and fruit sporadically.

Specimens examined. French Guiana: Orapu, km 6 Fourgassié road, 15 Oct 1966 (f fl), Oldeman B-667 (CAY (3), NY). GUYANA: Mahdia River, Potaro River, km 64 Bartica-Potaro road, 16 Jan 1943 (young fr), For. Dept. Br. Gui. Rec. no. 1031 (NY, U); 21 Jan 1943 (young fr), For. Dept. Br. Gui. Rec. no. 3796 (NY, U); Puruni, 10 Mar 1953 (fr), For. Dept. Br. Gui. Rec. no. 7706 (NY, U); near Mabura Hill sawmill, along logging road (under construction, 5°19' N, 58°38' W, 30 Oct 1982 (young fr), Stoffers et al. 133 (NY). BRAZIL. Pará: Municip. Oriximiná, Rio Trombetas, km 23 of road to Cachoeira Porteira, left side, 27 Jun 1980 (fr), Cid & Mota 1123 (MG,

NY); Rio Trombetas, right side of Mineração Santa Patricia, access road 22, 10 Jul 1983 (fr), Cid et al. 1438 (MG, NY (2). Amapá: Municip. Oiapoque, 35 km SSE of Oiapoque on BR 156, ca. 3°18' N, 51°39' W, 2 Dec 1984 (young fr), Daly et al. 3781 (HAMAB, NY); 121 km SSE of Oiapoque on BR 156, near edge of Reserva Indígena Uaçã, ca. 3°00' N, 51°30' W, 6 Dec 1984 (fr), Daly & Souza 3835 (HAMAB, NY); Municip. Calçoene, BR 156, road between Calçoene and Oiapoque, 114 SSE of Oiapoque, ca. 3°00' N, 51°30' W, 6 Dec 1984 (fr), Rabelo & Cardoso 2902 (HAMAB, NY); BR 156 in vicinity of government road camp "Carnot," 53-72 km WNW of Calçoene, ca. 2°33'-2°38' N, 51°16' W, 11 Dec 1984 (young fr), Rabelo et al. 2968 (HAMAB, NY).

Local names and uses. Guyana: "purokai" (Arawak) (Fanshawe, For. Dep. Br. Gui. Record no. 3479); "hiawa" (For. Dept. Br. Gui. Rec. no. 7706). French Guiana: "encens" (Oldeman B-667).

Vegetatively, P. demerarensis closely resembles P. laxiflorum Engl., a species from western and southwestern Amazonia. The latter differs by its longer inflorescence; pistillate flowers with shallow disk exceeded by the calyx; ovary substipitate (not sessile); style longer; stigmas discoid (not compressed-globose); and fruit acuminate (not globose). Protium demerarensis also shares a number of characters with P. cuneatum and P. altsonii: short inflorescences; calyx not exceeding the disk; disk shallow, greatly exceeded by the pistillode; stamens not greatly exceeding the pistillode; and large, globose fruit. It is distinguished from them in the discussions of the two latter species.

28. *Protium altsonii* Sandwith, Bull. Misc. Inform. 1928(9): 369. 1928. (as *P. altsoni*). Type. Guyana: Ireng District, near Paramacutoi Savanna, May 1926 (m fl), Altson 529 (holotype, K; isotype, NY).

Protium puberulenta Steyermark, Field Mus. Nat. Hist., Bot. Ser. 28(2):

266. 1952. Type. Venezuela. Bolívar: along mesa escarpment between Santa Teresita de Kanavayên and wooded gully about 8 km NW of Kavanayên, 23 Nov 1944 (m fl), Steyermark 60640 (holotype: F; isotypes: NY, VEN).

Protium paraense Cuatrecasas (non Swart), Bol. Mus. Paraense Hist. Nat.,

- Nov. Sér. (Bot.) 11: 14. 1961. Type. Brazil. Pará: forest of Cia. Pirelli, Fazenda Uriboça, Jul 1958 (m fl), Pires 6960 (holotype: US).

Trees, reproductive height (4.5) 15-20 (30) m, diameter 13-36 cm; resin clear, readily inflammable (Pires & Black 153); low buttresses present; bark thin, brittle, with raised lenticels, slash orange to red; branchlets usually slender, (1.9) 2.2-3.4 (4.2) mm diam, more robust in fruit, (2.6) 2.8-3.5 (4.5) mm, conspicuously lenticellate; branchlets with sparse, appressed, ferrugineous hairs to 0.2 mm long, also with sparse erect hairs to 0.05 mm long, hairs dense on apex; leaves (15.5) 18.5-32.5 (41.5) cm long, (3) 4-7 (9)-jugate; petiole slender, very slightly broadly canaliculate, slightly acutely winged, longer than interjuga, (2.8) 4-7.2 (9.3) cm x 1.5-2.6 (2.8) mm, with hairs as on branchlets or occasionally only with erect hair type; interjuga (1.5) 2-3.2 (4.1) cm long; petiolules short and slender, narrowly 2-canaliculate, laterals (0.4) 0.5-1 (1.1) cm

long, terminal short, (1) 1.5-2.2 (2.8) cm long, pulvinuli inconspicuous; leaflets usually slightly coriaceous and glossy, deep green above, laterals oblong to narrowly so or less often narrow-elliptic (Venezuela and Guyana), basal pair sometimes broadly oblong or ovate, 6-9 (10.5) x 2.2-3.6 cm, ultimate pair (6.3) 7.2-10.2 (12.5) x (1.6) 2.1-3.3 (3.8) cm, base usually oblique, proximal side acute, distal side obtuse to truncate, terminal oblanceolate to oboate, (5.8) 6.7-9 (10.9) x (1.8) 2.7-3.6 (4.3) cm, base acute, leaflet apex abruptly acuminate or less often gradually so (Venezuela and Guyana), acumen narrow, (0.6) 0.8-1.5 (1.9) cm long, often sparsely serrulate, abaxial surface with midvein narrowly prominulous but sunk in a groove, rest of veins prominulous, blade with scattered appressed hairs 0.05-0.15 (0.2) mm long, adaxial surface with midvein narrowly obtusely prominent, secondary veins prominulous, rest of veins inconspicuous, blade glabrous. Inflorescences short and slender, (1) 1.5-5 (6) cm x (0.5) 0.8-1.5 (1.8) mm (x (1.4) 1.8-2.5 (2.8) mm in fruit), secondary axes poorly developed, 0.5-1.3 (2) cm long (to 3.5 cm long in fruit), axes with sparse to scattered hairs as on branchlets, or rarely dense (Venezuela, Guyana); inflorescence bracts ovate to lanceolate, coriaceous, semi-clasping, those subtending inflorescences (broadly) ovate, 0.8-1.3 (2) mm long, those on primary axes (0.3) 0.5-0.9 (1.3) mm long, those on secondary axes 0.3-0.5 (0.7) mm long; pedicel robust, subcylindric, 0.7-1.5 (1.8) x 0.35-0.5 (0.55) mm, with appressed hairs 0.05-0.15 mm long, dense at base becoming scattered (sometimes sparse) distally. Flowers 5-merous (rarely some flowers 4-merous), at anthesis (1.8) 2-2.5 mm long; calyx strongly dimorphic, in staminate flowers calyx

shallowly cupular but often exceeding disk, 0.5-0.8 (1) x (1.7) 1.9-2.1 (2.4) mm, glabrous, lobes (broadly) depressed-deltate, sometimes rounded, often negligible or reduced to an apiculum, 0-0.25 (0.3) mm long, often with sparse appressed hairs 0.1-0.2 mm long, lobe apex apiculate to acute, short-papillate and with sparse appressed thick hairs 0.05 mm long; petals pale green to cream to white, (broadly) lanceolate, (2.3) 2.5-3 x 1.2-1.5 mm, fleshy, apiculum inconspicuous, 0.25-0.35 mm long, strongly inflexed, abaxially glabrous, adaxially with prominent midvein, long-papillate, margin and apex conspicuously long-papillate, at anthesis petals weakly to strongly reflexed from the upper 1/3 their length; stamens light yellow, long, (1.15) 1.25-1.4 and 1.35-1.5 mm long, filaments subterete, slightly exceeding pistillode, (0.45) 0.65-0.75 and 0.7-0.9 mm long, slightly to strongly broadened at base, anthers basifixed, in dorsiventral view narrowly obtusely oblong or lanceolate (obtuse-oblong after dehiscence), base lobulate (broadly obtuse after dehiscence), in lateral view acute-oblong, base truncate (0.5) 0.6-0.7 mm long; disk shallow, 0.15-0.25 x (0.25) 0.3-0.35 (0.5) mm, not strongly undulate, markedly rugose; pistillode 0.5-0.6 (0.7) x (0.4) 0.5-0.6 mm overall, depressed-ovoid, with dense to sparse appressed hairs 0.1-0.15 mm long (glabrous in central and western Amazonia), provided with reduced locules and ovules, abruptly contracted into a 5-lobed clavate stylode (0.2) 0.25 mm long, each lobe vertically sulcate at apex; in pistillate flowers calyx more deeply cupular, 0.9-1.3 x 1.9-2.1 (2.6) mm, lobes (0.05) 0.2-0.25 (0.4) mm long; staminodes 1-1.25 (1.4) and 1.1-1.35 (1.5) mm long, filaments narrowly triangular in dorsiventral view, subterete, fleshy, 0.5-0.65 (0.8) and

0.6-0.75 (0.9) mm long, anthers in dorsiventral view broadly obtuse-oblong, base lobulate, apex obtuse to truncate, sometimes mucronate, in lateral view obliquely obtuse-oblong, 0.5-0.6 mm long; disk relatively shallow and broad, 0.2-0.3 x (0.35) 0.4-0.5 mm; pistil light yellow, (1.1) 1.45-1.75 (1.85) x (0.7) 0.85-1 (1.2) mm overall, ovary ovoid, sessile, gradually contracted to a thick, broadly clavate style (0.2) 0.25-0.4 (0.5) x (0.3) 0.5-0.6 (0.7) mm, stigmatal region 0.25-0.3 mm high, stigmas subsessile, depressed-globose, oriented downward and slightly outward, slightly 2-lobed. In fruit pedicel robust, subcylindric, (2) 2.3-5 (5.5) x (1.2) 1.8-2.5 (3.2) mm, fruit maturing red, broadly obtuse-oblong to sub-globose, substipitate, (1.8) 2.3-2.5 (2.8) x 1.8-2.3 cm (to 3-3.5 cm diam when more than 1 pyrene), apex rounded, surface glabrous, glossy, usually drying smooth, younger fruits often apiculate due to persistent style; pseudaril spongy, covering all of pyrene; pyrene thickly cartilaginous, 1.7-2.5 x 1.4-2 cm, in dorsiventral view orbicular, base obtuse, apex acutely short-acuminate, in lateral view asymmetric, on ventral side oblong with acuminate apex, on dorsal side broadly ovate, ventral surface with a shallow central vertical sulca, apex trigonous, surface with dense (sub)erect fibers 0.2-0.5 mm long except on funicular scar, site of funicle 4/5 distance to apex, funicular depression shallow, funicular scar reverse rounded-lunate shaped, covering 1/5 of ventral surface; testa with irregular thickenings, infolded with contortuplicate cotyledons.

Distribution. Widespread in the Guianas and Amazonia, but (judging by the material available) frequent only in Pará. Known from Guyana,

Suriname, Brazil (Amapá, Pará, northwestern Maranhão, northern Mato Grosso, Amazonas near Manaus, Roraima), Venezuela (T. F. Amazonas, Bolívar), and Peru (San Martín, Loreto, Amazonas). The material from Peru is sparse and of poor quality, so further material is needed to confirm this extension of the range.

Protium altsoni is a medium-sized to large tree, often among the canopy species and occasionally an emergent (Daly et al. 3771). While it is frequent in the moist forests near Belém, it is often found in localities which are climatically or edaphically somewhat drier. It occurs near forest-savanna interfaces (Altsoni 529), in areas with sandy soils (Clark 7099, Mello 1880) or rocky soils (Prance et al. 24801), in regions toward the periphery of Amazonia (Jangoux & Bahia 665, Silva & Pinheiro 4319, Plowman et al. 9490), and mountainous areas with semi-deciduous forest (Lindeman 7001; Steyermark 60640), reaching 1220 m elevation.

This species shows a very broad phenological pattern, flowering June to November and fruiting January to May (fruiting in November near the Serra do Cachimbo, Prance et al. 24801).

Specimens examined: BRAZIL. Amazonas: Manaus, km 17 of BR 17, 12 Sep 1955, (m fl) F. Mello 1880 (MG). Amapá: between Porto Platon and Serra do Navio, 10 Oct-15 Dec 1976 (sterile), N. A. Rosa 1299 (MG). Maranhão: basin of Rio Turaçu, Municip. Monção, Ka'apor Indian Reserve, 4 km NW of settlement of Urutawy, 22 Sep 1985 (fr), Balée & Ribeiro 99 (NY); Nova Esperança, Rio Alto Turiaçu, 2°55' S, 45°45' W, 16 May 1979 (fr), Jangoux & Bahia 665 (MG, NY). Mato Grosso: Aripuanã, km 245 of BR 174, Proeto Fuina, 18 Jan 1979 (fr), M. G. Silva & Pinheiro 4319 (MG, NY). Pará:

Belém, EMBRAPA, Mocambo Reserve, 1°23'S, 48°27'W, 10-17 Nov 1984 (f fl & fr), Daly et al. 3771 (IAN, NY); Belém, Bosque Rodrigues Alves, 11 Mar 1977 (fr), D'arc 11 (MG, RB); Belém, Utinga, 10 Nov 1923 (fl), Ducke 18400 (RB); Municfp. Belterra, 16 Nov 1976 (galled fl), Fausto (INPA herb. no.) 64201 (INPA); Utinga, 14 May 1901 (buds), J. Huber 2028 (MG, NY); Belém, IPEAN, Mocambo Reserve, 22 Sep 1963 (buds), Oliveira 2609 (IAN); Belém, Bosque Municipal, 18 Aug 1945 (m fl), Pires & Black 153 (GH); Belém, Mocambo Reserve, Jan 1956 (fr), Pires & Silva 6722 (IAN, U, US); forest of Cia. Pirelli, Fazenda Uriboça, Jan 1958 (buds), Pires 6815 (IAN, U, US); Jul 1958 (buds), Pires 6889 (U, US); Jul 1958 (buds), Pires 6937 (U); Jul 1958 (buds), Pires 6997 (US); Jul 1958 (f fl), Pires 7030 (IAN, U); Jul 1958 (buds), Pires 7034 (U); Jul 1958 (buds), Pires 7039 (US); Jul 1958 (buds), Pires 7060 (U); Aug 1958 (buds), Pires 7116 (U, US); Belém, Mocambo Reserve, 15 Aug 1967 (m fl), Pires & Silva (IAN, NY); 19 Aug 1967 (galled fl), Pires & Silva 10735 (NY); 12 Sep 1967 (buds), Pires & Silva 10952 (NY); 18 Oct 1967 (m fl), Pires & Silva 11115 (IAN); Belém, Reserva APEG, 1967 (fr), Pires & Silva 11180 (IAN, NY); Belém, IPEAN, Agua Preta, 25 Oct 1967 (m fl), Pires & Silva 11207 (NY); Belém, IPEAN, sawmill, 8 May 1968 (fr) Pires & Silva 11659 (IAN); Benavides, Granja Maratã, 30 Nov 1973 (m fl), Pires & Silva 13647 (IAN); Municfp. Paragominas, Belém-Brasília Highway (BR-010), 6 km N of Ligação do Pará, near km marker 1532, ca. 4°05' S, 47°32' W, 3 Mar 1980 (fr), Plowman et al. 9490 (MG, NY); Cachoeira de Curuã, north slope of Serra do Cachimbo, 4 Nov 1997 (fr), Prance et al. 24801 (MG, NY); Belém, 9 km NE of IAN, near Providencia, 27 Sep 1942 (f fl), M. B. Silva 106 (IAN, K, NY, US). French Guiana: Oyapock

River, right bank of Crique Armontabo, 800 m from mouth, 3 Jul 1969 (f fl and young fr), Oldeman B-2422 (CAY, NY). Surinam: plateau of Nassau mountains, elev 550 m, 5 Jan 1955 (sterile), Lindeman 7001 (U). VENEZUELA. Território Federal Amazonas: San Carlos de río Negro, ca. 20 km S of confluence of río Negro and Brazo Casiquiare, 4.3 km NNE on Solano road, 1°56' N, 67°03' W, 15 Mar 1979 (fr), Clark 7099 (MO, NY).

Local names and uses. Brazil. Amazonas: breu branco (Mello 1880); Amapá: breu mescla (N. A. Rosa 1299); Maranhão: kandeiape'y (Ka'apor, Balée & Ribeiro 99). The resin has been used by Indians in Pará for torches. Guyana: tsepur (Patamona dialect, Altson 529). Suriname: tiengimonnie (Lindeman 7001). Venezuela: catamajaca (Clark 7099), chipoi-yek (Steyermark 60640).

The collections of this species from Guyana and Venezuela, including the type collection of Protium altsoni, differ from the eastern Amazonian collections only by their narrow-elliptic and gradually acuminate leaflets and by the denser pubescence on the inflorescence, which continues farther up the pedicel and often onto the calyx. In his discussion P. puberulenta, Steyermark indicated that its puberulent adaxial leaflet surface and puberulous adaxial petal surface set it apart from P. altsonii, but examination of the type material of both taxa shows them to be identical in all qualitative aspects. Both have scattered appressed hairs to 0.05-0.15 (0.2) mm long on the adaxial leaflet surface, and both have papillate adaxial petal surfaces.

Protium altsonii shares a number of characters with P. cuneatum and P. demerarensis: short inflorescences; calyx not exceeding the disk; disk

shallow, greatly exceeded by the pistillode; stamens not greatly exceeding the pistillode; and large, globose fruits. Protium altsonii differs from P. cuneatum by the greater number of juga; leaflets smaller, more narrowly elliptic, and narrow-acuminate; stylode lobulate (not markedly acutely winged); substipitate stigmas (style not branched); fruit sessile; and pseudaril covering all of pyrene. From P. demerarensis, P. altsonii differs by the latter's leaflets usually glossy adaxially; shallower calyx; petals with conspicuous apiculum and long-papillate margin; stylode longer; and fruit green, glossy and smooth (not gray, lenticellate, and rough-textured).

Doubtful species

Two doubtful species are not included in this treatment. Protium melinonis is known only from the holotype at Paris, and it resembles no known species of Protium. There are no pulvinuli on the lateral petiolules, a character which is very rare in the genus. There is an axillary spine on the branchlet, and this character is unknown in mature individuals of Protium, although spines have been reported from seedlings of the Asian species, P. javanicum (see chapter on seedlings). There are few flowers on the specimen, and the specimen is rather fragile, therefore it was not possible to examine flower structure first-hand. The descriptions in the literature are ambiguous enough that the genus of this plant is impossible to determine. Finally, it is puzzling that such a distinctive plant has not been found again, considering that French Guiana is relatively well-collected.

Protium crassipetalum probably occurs in the Guianas, but this species is poorly defined as yet. The collections tentatively referred to it are listed in the discussion of P. polybotryum.

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Figure 1.

Schematic inflorescence diagrams of Protium:

- a) P. polybotryum ssp. blackii
- b) P. polybotryum ssp. polybotryum
- c) P. heptaphyllum

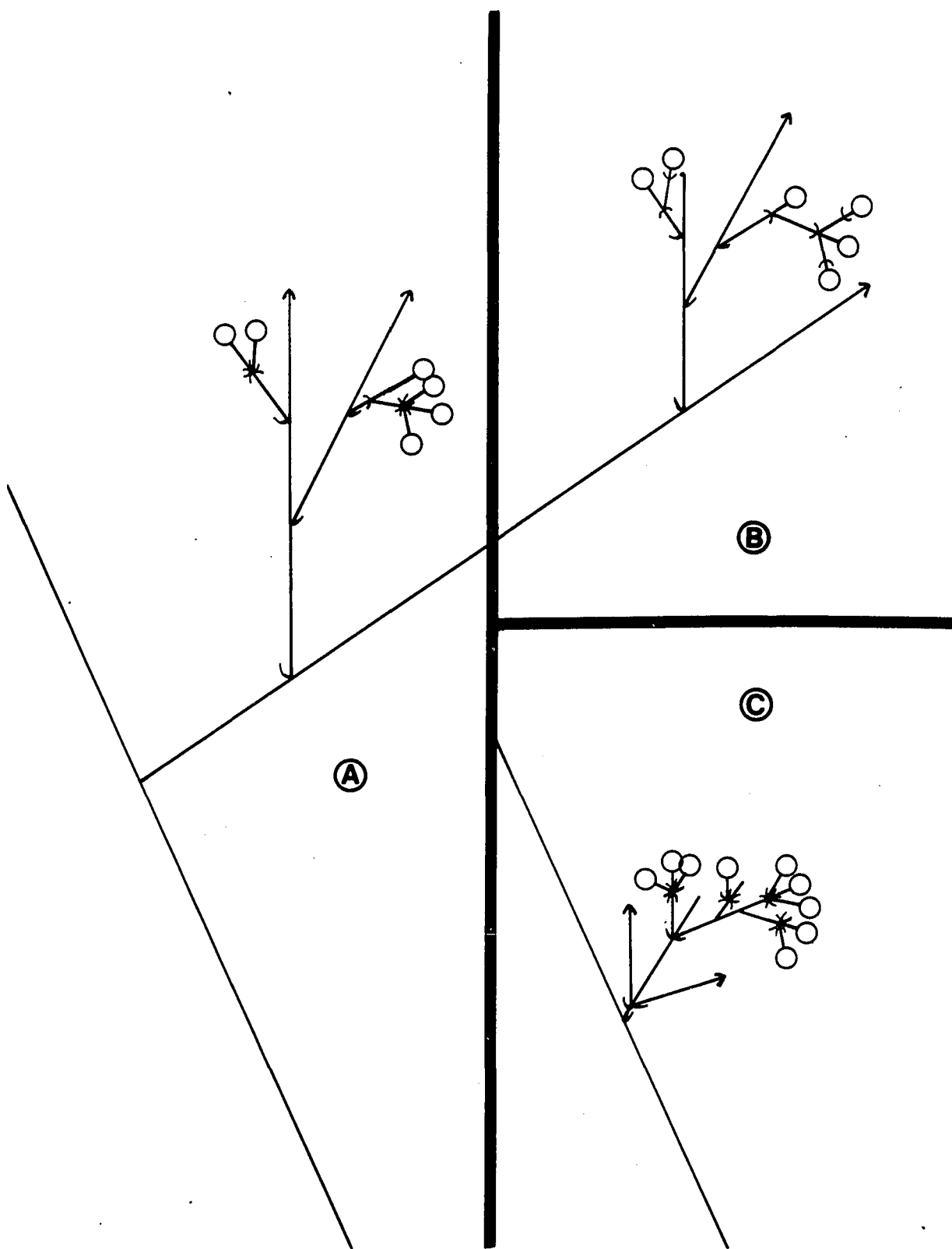


Figure 2.

Longitudinal sections of Protium and Tetragastris flowers,
showing reduction series involving the pistillode:

- a) P. altsonii
- b) P. polybotryum ssp. polybotryum
- c) P. robustum
- d) T. panamensis (Engl.) Kuntze



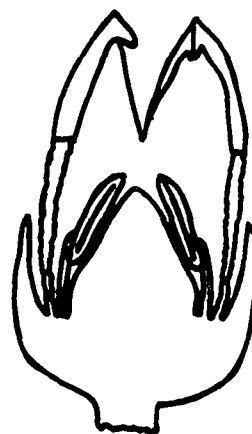
(A)



(B)



(C)



(D)

Figure 3.

SEM micrographs of Protium pollen:

- a) P. apiculatum (N. T. Silva 2966)
- b) P. robustum (M. Silva 2454)
- c) P. opacum (Maguire et al. 47107)
- d) P. polybotryum ssp. polybotryum (Daly et al. 4089)

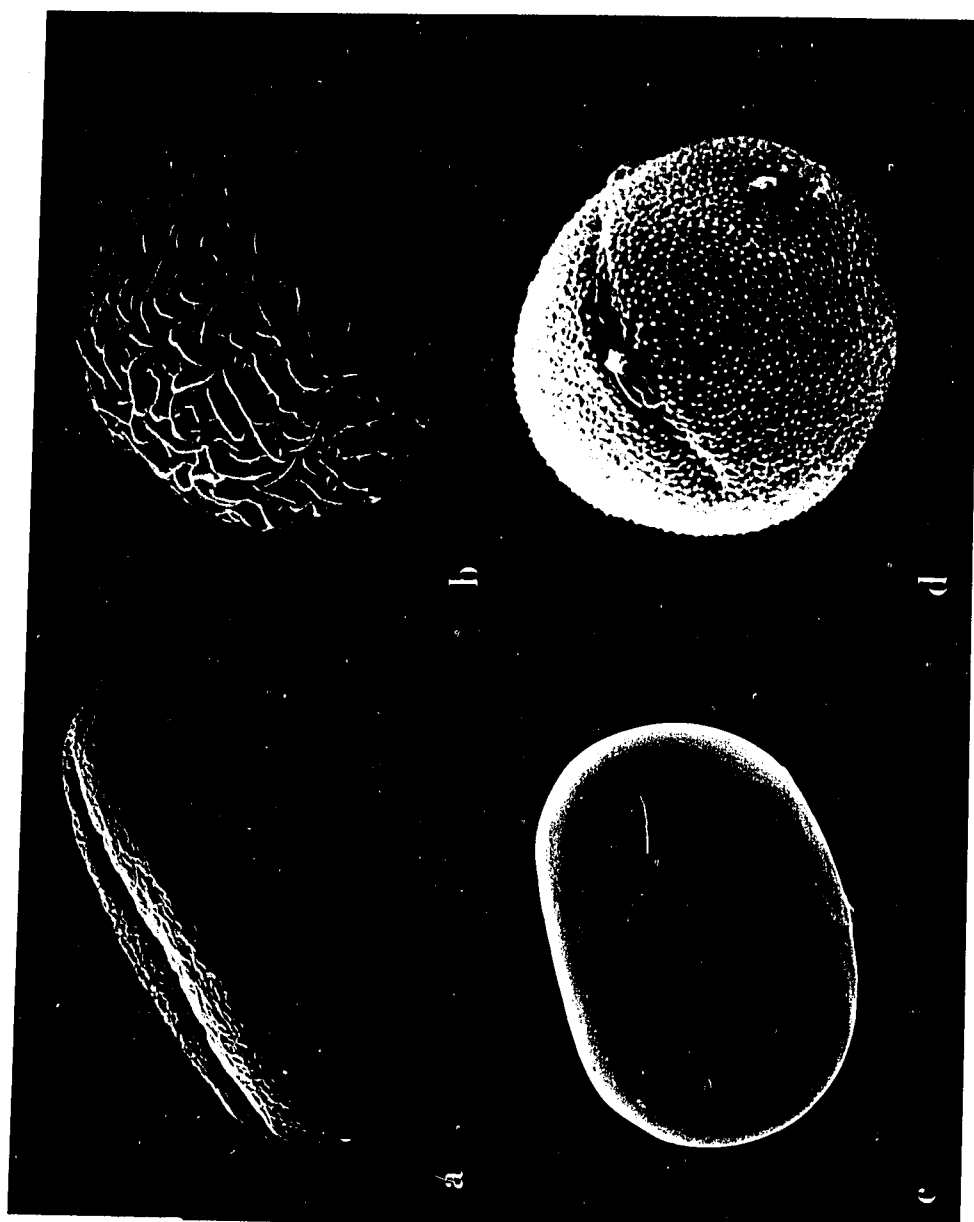


Figure 4.

SEM micrographs of Protium pollen:

- a) P. fimbriatum (Anaral et al. 141)
- b) P. macgregorii (R. D. Hoogland 5192)
- c) P. plagiocarpium (Mori & Boom 17410)
- d) P. obtusifolium (Fl. Maurit. 199)

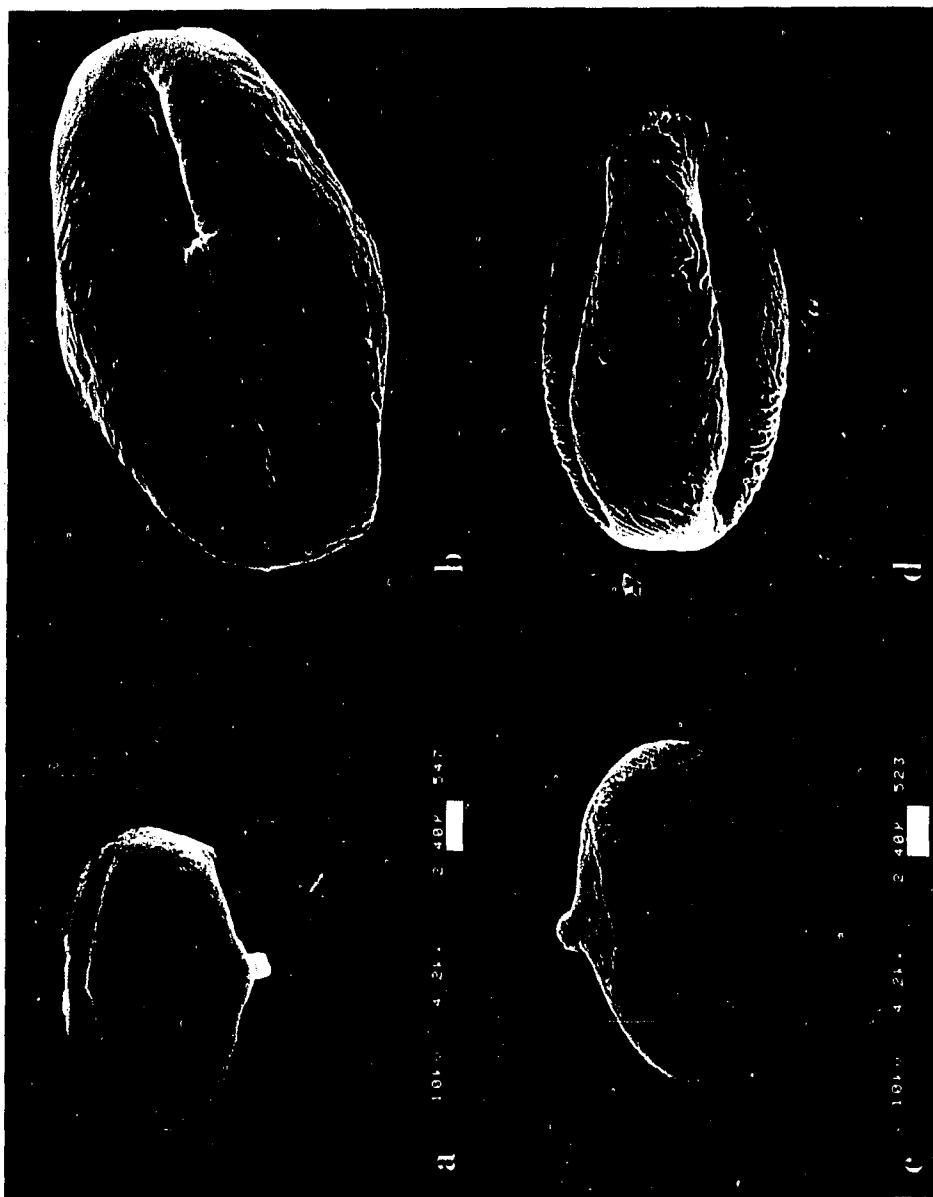


Figure 5.

SEM micrographs of Protium pollen:

- a) P. paniculatum (Prance et al. 1475)
- b) P. sagotianum (Pulle 327)
- c) P. tenuifolium (Sperling et al. 6219)
- d) P. divaricatum (Cid et al. 349)



Figure 6.

SEM micrographs of Protium pollen:

- a) P. aracouchini (Balée 469)
- b) P. strumosum (Cid et al. 1876)
- c) P. pilosum (Prance & Silva 11421)
- d) P. krukoffii (Cavalcante 3317)



Figure 7.

SEM micrographs of Protium pollen:

- a) P. spruceanum (M. Silva 3918)
- b) P. altsonii (Pires & Silva 10683)
- c) P. heptaphyllum (Prance & Silva 58602)
- d) P. unifoliolatum (J. Ramos et al. 796)

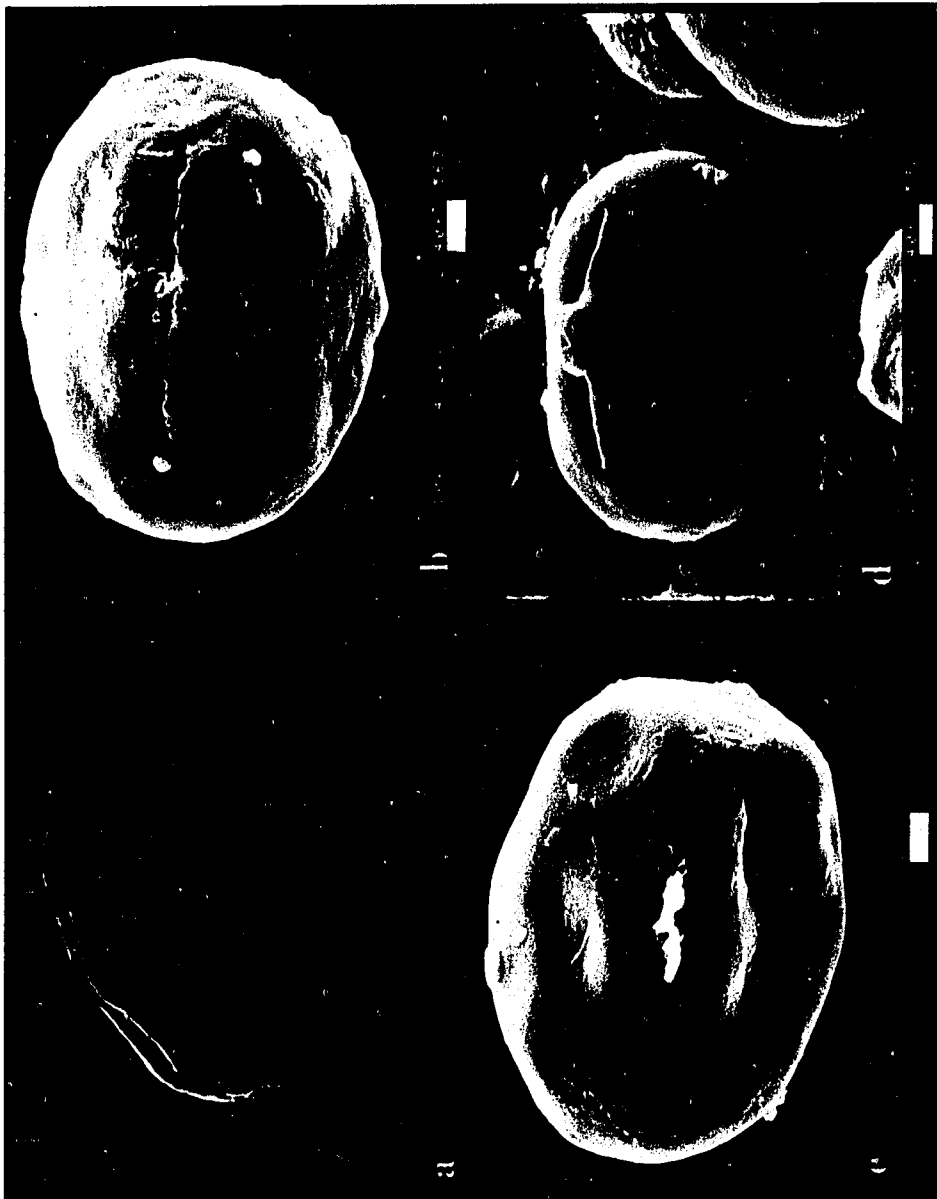


Figure 8.

SEM micrographs of Protium pollen:

- a) P. guianense (Daly et al. 1475)
- b) P. grandifolium (Cid et al. 787)
- c) P. decandrum (Mori & Boom 15061)
- d) P. morii (Irwin et al. 48119)

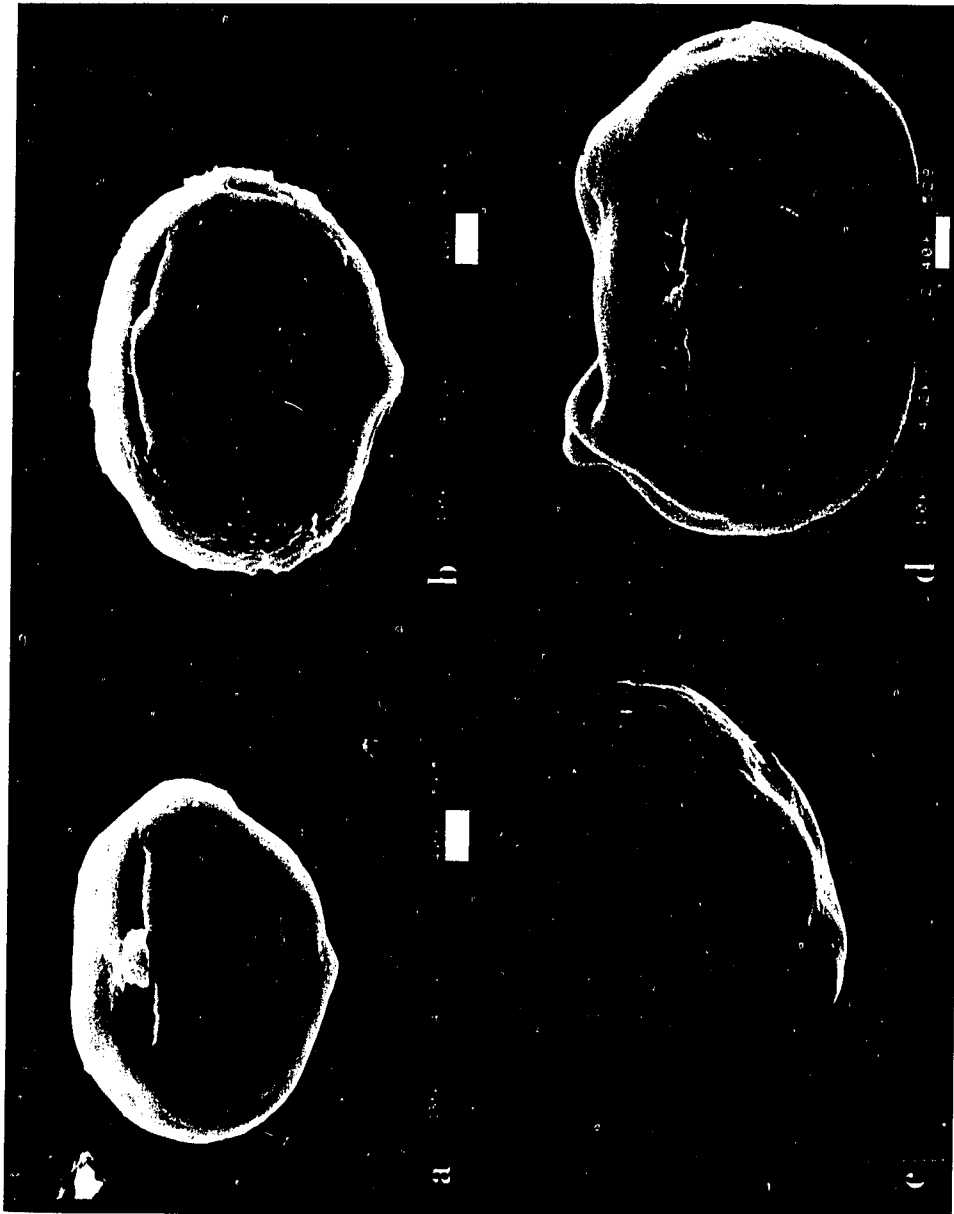


Figure 9.

SEM micrographs of pollen in the Protieae:

- a) Protium trifoliolatum (Pires 10805)
- b) "Paraprotium" (= Protium) vestitum (Cuatrecasas 14193)
- c) Tetragastris panamensis (Solomon 6400)
- d) Crepidospermum prancei (Vásquez & Jaramillo 5657)



Figure 10.

Pyrenes and dehiscence in Protium:

- a) pyrene of Protium morii (Daly et al. 4049), showing zone of weakness at apex
- b) pyrene of P. altsonii (Plowman et al. 9490), showing hygroscopic layer of fibers
- c) SEM micrograph of fiber layer on pyrene of P. giganteum (Pires & Silva 11435)
- d) dehiscing fruit of P. apiculatum (Mori & Boom 15547), showing V-shaped structure from which pyrene is suspended

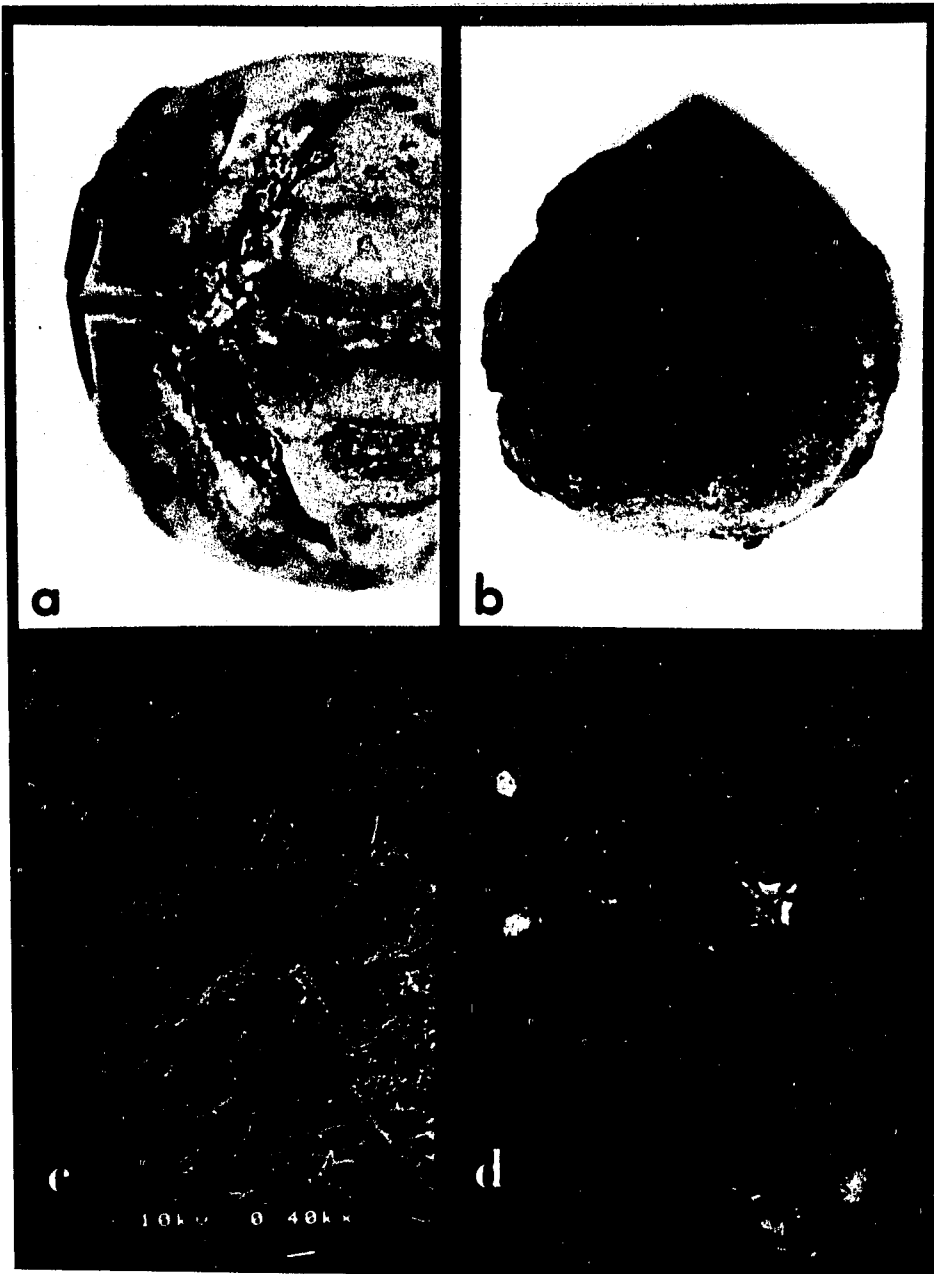


Figure 11.
Fruits of Protium

species	voucher
1. <i>P. heptaphyllum</i>	Daly et al. 3776
2. <i>P. aracouchini</i>	Daly et al. 3765
3. <i>P. spruceanum</i>	Daly et al. 3759
4. <i>P. plagiocarpium</i>	BAFOG 7263
5. <i>P. subserratum</i>	Daly et al. 3970
6. <i>P. apiculatum</i>	Mori & Pipoly 15610
7. <i>P. robustum</i>	Rabelo et al. 3044
8. <i>P. cuneatum</i>	Daly et al. 3777
9. <i>P. krukoffii</i>	Sastre 117
10. <i>P. altsonii</i>	Daly et al. 3771
11. <i>P. decandrum</i>	Daly et al. 3871
12. <i>P. polybotryum</i> ssp. <i>blackii</i>	Daly et al. 3756
13. <i>P. morii</i>	Oldeman T-651
14. <i>P. opacum</i> ssp. <i>rabelianum</i>	Daly et al. 4009
15. <i>P. demerarense</i>	Daly et al. 3835
16. <i>P. fimbriatum</i>	Huashikat 1160

fruits of Protium



1



2



3



4



5



6



7



8



9



10



11



12



13



14



15



16

2cm

Figure 12.

Pyrenes of Protium

species	voucher
1. <i>P. unifoliolatum</i>	French Guiana Forest Service 5895
2. <i>P. guianense</i> ssp. <i>pilosissimum</i>	D. Coêlho (INPA no.) 3127
3. <i>P. guianense</i> ssp. <i>guianense</i>	de Granville 483
4. <i>P. crenatum</i>	Blanco 540
5. <i>P. giganteum</i> var. <i>giganteum</i>	Pires & Silva 6642
6. <i>P. subserratum</i>	Daly et al. 3762
7. <i>P. paniculatum</i> var. <i>riedelianum</i>	Rodrigues & Coêlho 7613
8. <i>P. spruceanum</i>	Steward et al. P20309
9. <i>P. krukoffii</i>	Rosa & Cordeiro 1731
10. <i>P. plagiocarpium</i>	Mori 15468
11. <i>P. pilosum</i>	de Granville 2356
12. <i>P. robustum</i>	Mori 17470
13. <i>P. polybotryum</i> ssp. <i>polybotryum</i>	Rabelo 2178
14. <i>P. decandrum</i>	Rosa & Vilar 2752
15. <i>P. pallidum</i>	Mori & Pipoly 15442
16. <i>P. strumosum</i>	Rodrigues 7377
17. <i>P. morii</i>	Daly et al. 4049
18. <i>P. opacum</i> ssp. <i>rabelianum</i>	Cremers 4510
19. <i>P. altsonii</i>	D'Arc 11
20. <i>P. demerarensis</i>	Cid et al. 1123

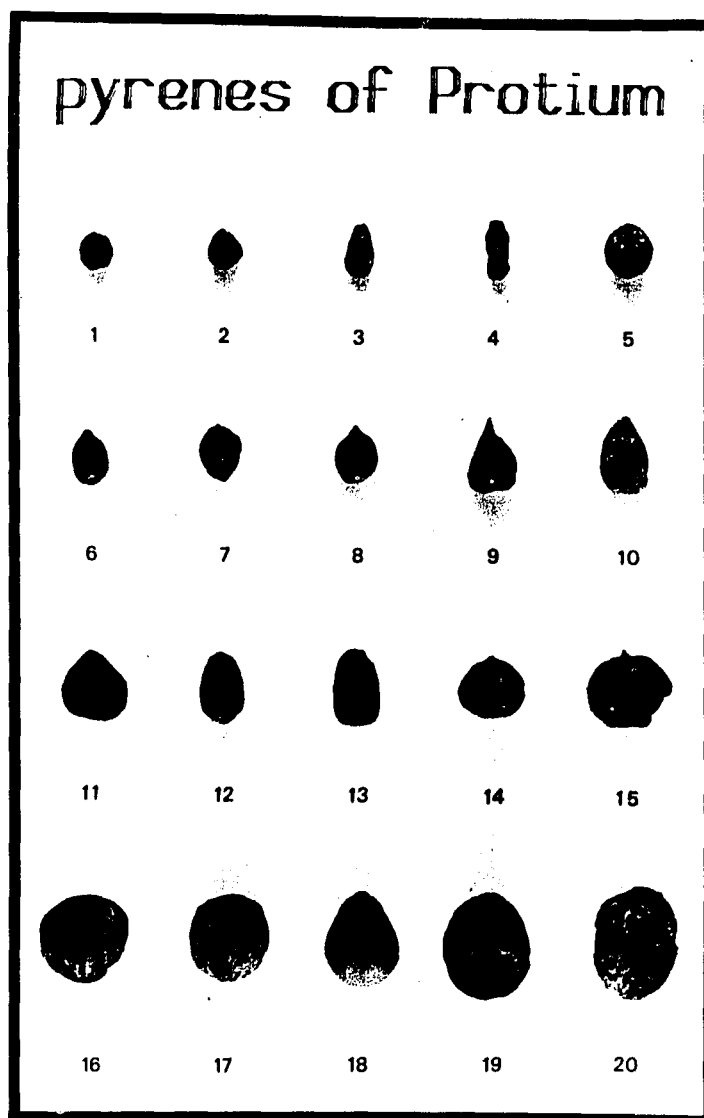


Figure 13.

Embryos of Protium

- a) longitudinal section of mature fruit of P. pallidum (Daly et al. 4079), showing contortuplicate cotyledons
- b) immature fruit of P. decandrum (Daly et al. 4274), opened to show precocious folding of cotyledons
- c) fruit of P. polybotryum (Daly et al. 3773), opened to show hymenopteran which has eaten the embryo
- d) drawing of entire embryos of P. robustum (above left and left-center) and of P. sagotianum (right-center and above right), and both in cross-section (below), showing transverse folding of cotyledons

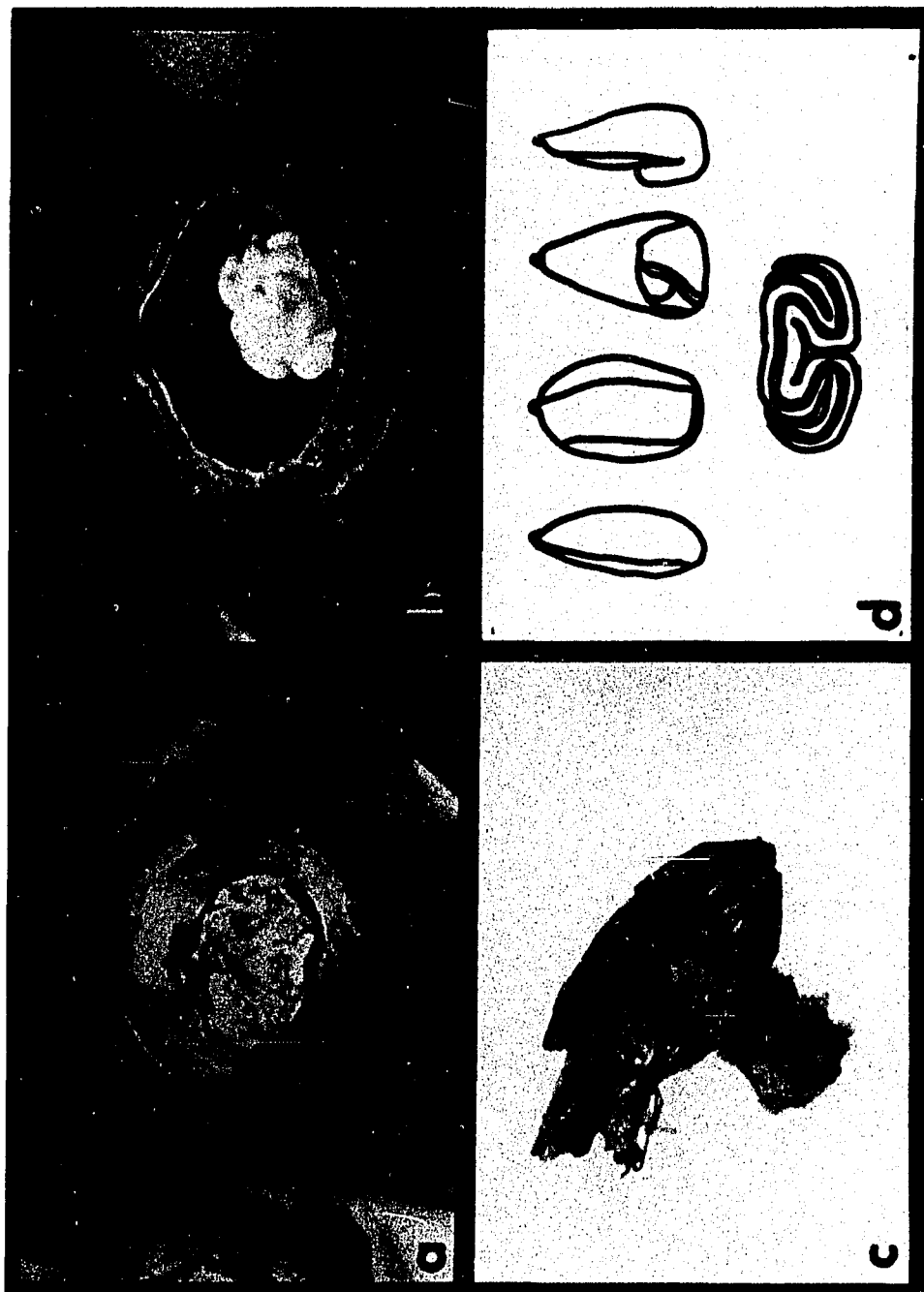


Fig. 14a

Locations of quantitative forest inventories carried out in
Amazonia and the Guianas.

(numbers correspond to localities on map)

Bolivia	Beni:	Alto Ivõn (17)	Boom, 1987.
Brazil	Acre:	Santa Luzia (23)	Campbell, in prep.
		Serra da Moa,	
		Rio Azul (22)	Campbell, in prep.
	Amapã:	Camaipí (12)	Mori et al., in prep.
		Falsino (12)	Daly et al. (in prep.)
		Serra do Navio (11)	Miranda Bastos, 1960; Rodrigues, 1963.
	Amazonas:	Benjamin	
		Constant (26)	Soares, 1970.
		Manaus (7)	Rodrigues, ined.; Fittkau & Klinge, 1973; Keel & Prance, 1979; Lovejoy et al., 1983; Prance et al., 1976; Rodrigues, 1967; Takeuchi, 1961a, 1961b.
		Reserva Ducke (7)	Soares, 1957; Lechthaler, 1956; Soares, 1957; Rodrigues & Valle, 1964.
		Rio Apuau	Rodrigues, 1961b.
		São Gabriel (4)	Takeuchi, 1962c.
		Taracuã (3), Ilha das Flores (4)	Rodrigues, 1961a; Pires & J. S. Rodrigues, 1961.
		Uaupés (4)	Takeuchi, 1962a; Rodrigues, 1961a.
	Maranhão:	Monção (16)	Miranda Flor, 1967.
	Parã:	Altamira (9)	Dantas & Müller, 1979.
		Belém (14)	Black et al., 1950; Cain et al., 1956; Pires & Prance, 1977; Pires et al., 1953; Pires & Koury, 1958; Hatheway, 1971.
		Breves (13)	Pires, 1966.
		Capitão Poço (15)	Dantas et al., 1980.
		Gleba Bacajã	Campbell et al., 1987.
		Tapajós National Forest (8)	Carvalho, 1980; Carvalho, 1981; Carvalho, 1983; Silva & Lopes, 1982.
	Roraima	Maracã (6)	Campbell, in prep.
Colombia	Amazonas:	Leticia (26)	Takeuchi, 1973.
Ecuador	Napo:	Añangu (2)	Balslev et al., 1987.
		Shinguipino (1)	Grubb et al., 1962.
French Guiana:		Saül (30)	Mori et al. (in press)
Guyana:		Moraballi	
		Creek (27)	Davis & Richards, 1934

Figure 14a (contd.)

Peru	Loreto:	Bosque von	
		Humboldt (21)	Gentry (ined.)
		Cabeza de Mono (20)	"
		Cocha Cashu (19)	Gentry (ined.)
		Mishana (24)	"
		Yanamono (25)	Gentry (ined.)
	Madre de		
	Dios	Tambopata (18)	Hartshorn (ined.)
Surinam:		(northern) (29)	Shulz, 1966
		(western) (28)	Maas, 1971
Venezuela/Amazonas:		San Carlos (5)	Uhl & Murphy, 1981; Saldarriaga (in prep.); Putz, 1983; Uhl, 1982.

Figure 14b

Importance of Burseraceae in forest inventories
conducted in Amazonia and the Guianas

Numbers in circles refer to relative density of most common species of Burseraceae; those in squares refer to relative density of the family as a whole.

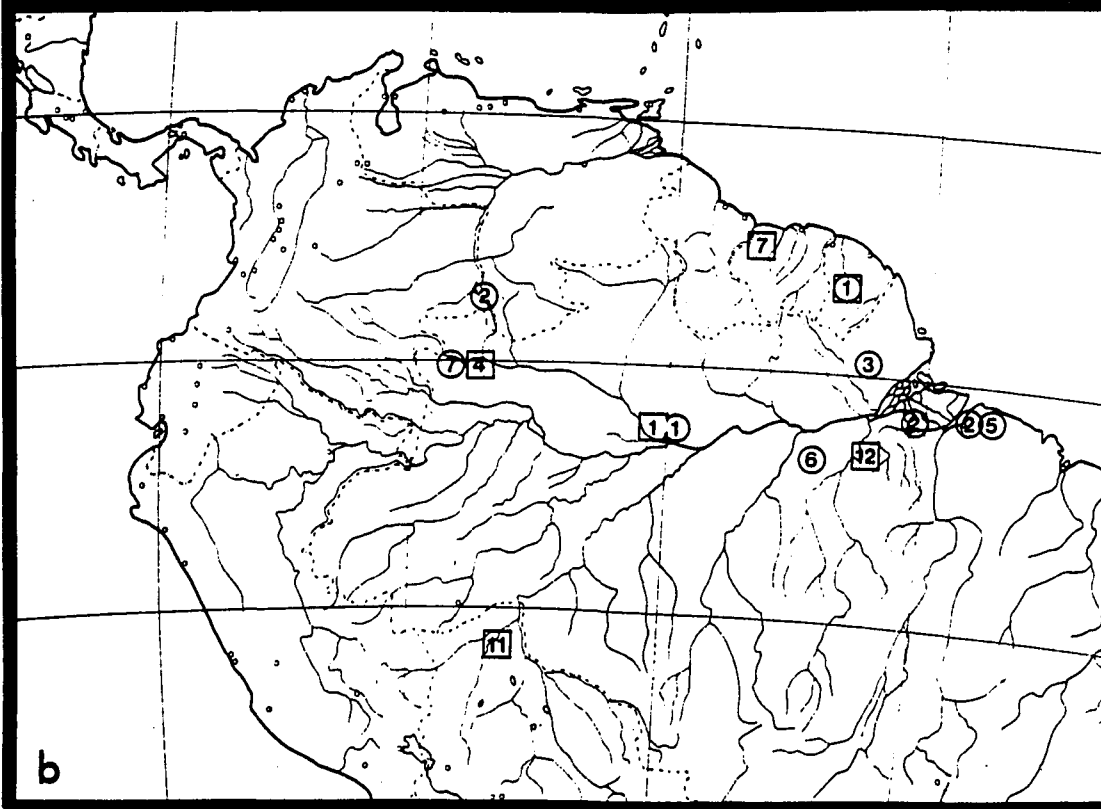
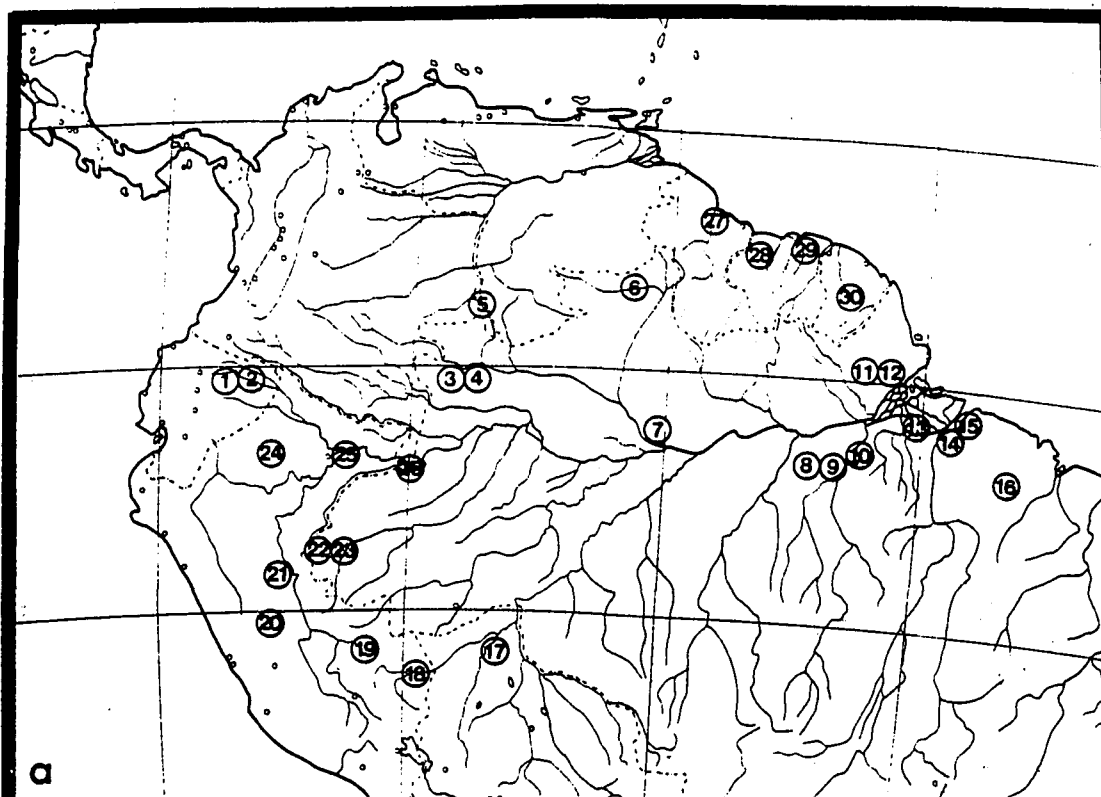


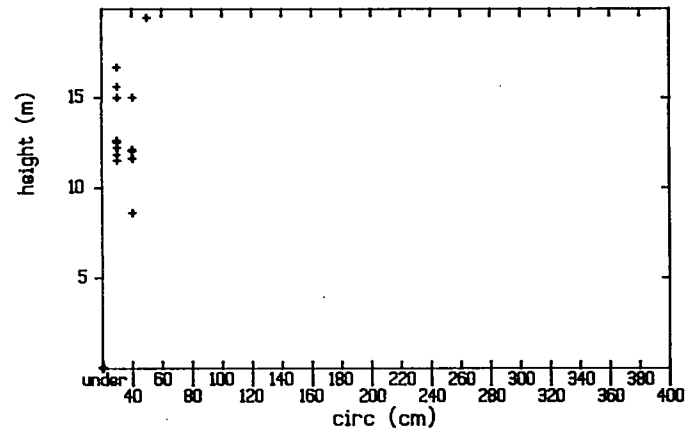
Figure 15.

Height-diameter scattergrams for four species of Burseraceae
on the Mocambo Reserve, Belém
(N.B.: P. niloi = P. subserratum)

Height vs. Circumference Scattergrams—Mocombo

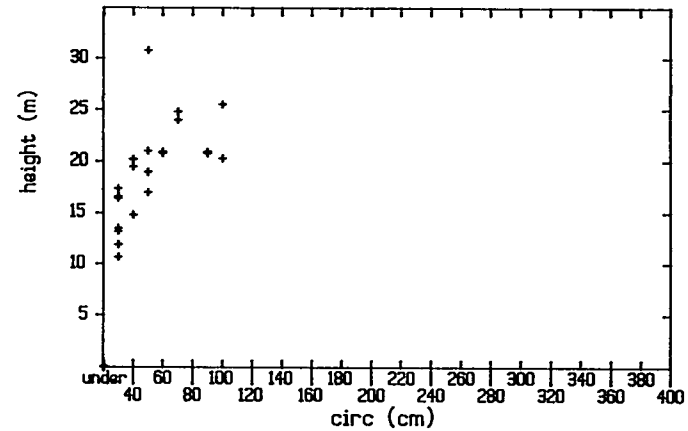
a

P. aracouchini



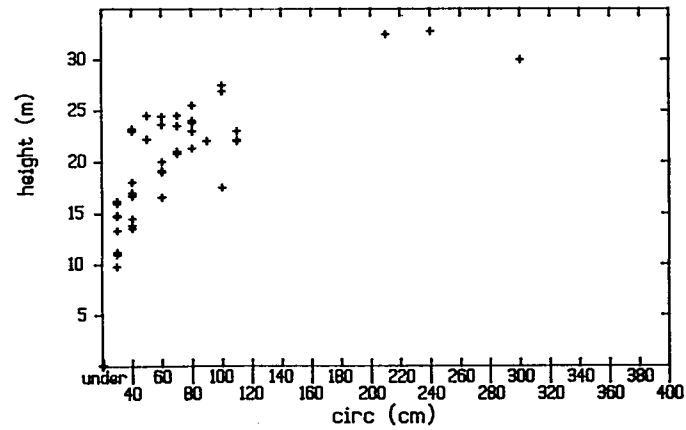
b

P. niloi



c

P. decondrum



d

Trottinnickia

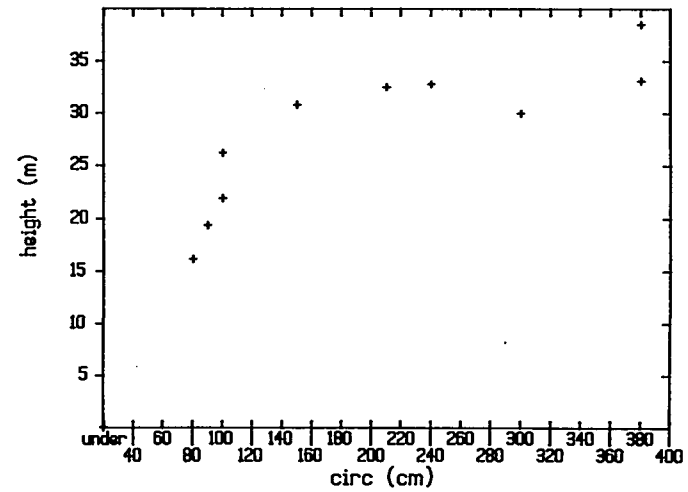


Figure 16.

Ecological preferences of three species of Protium at Mocambo
(area circumscribed is terra firme, surrounded by várzea)

- a) P. trifoliolatum
- b) P. giganteum
- c) P. decandrum

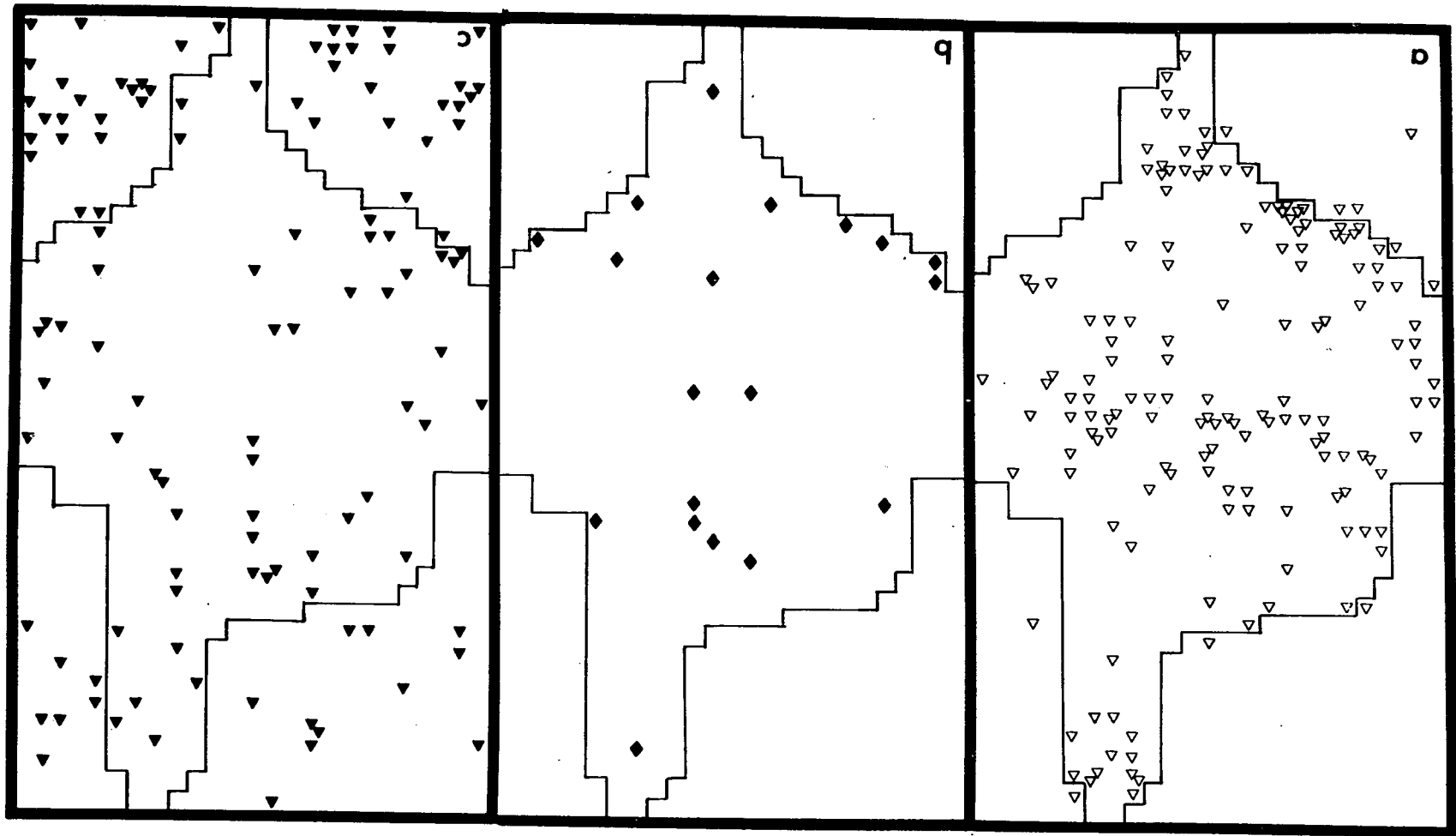


Figure 17.

Phenology of Protium at Mocambo

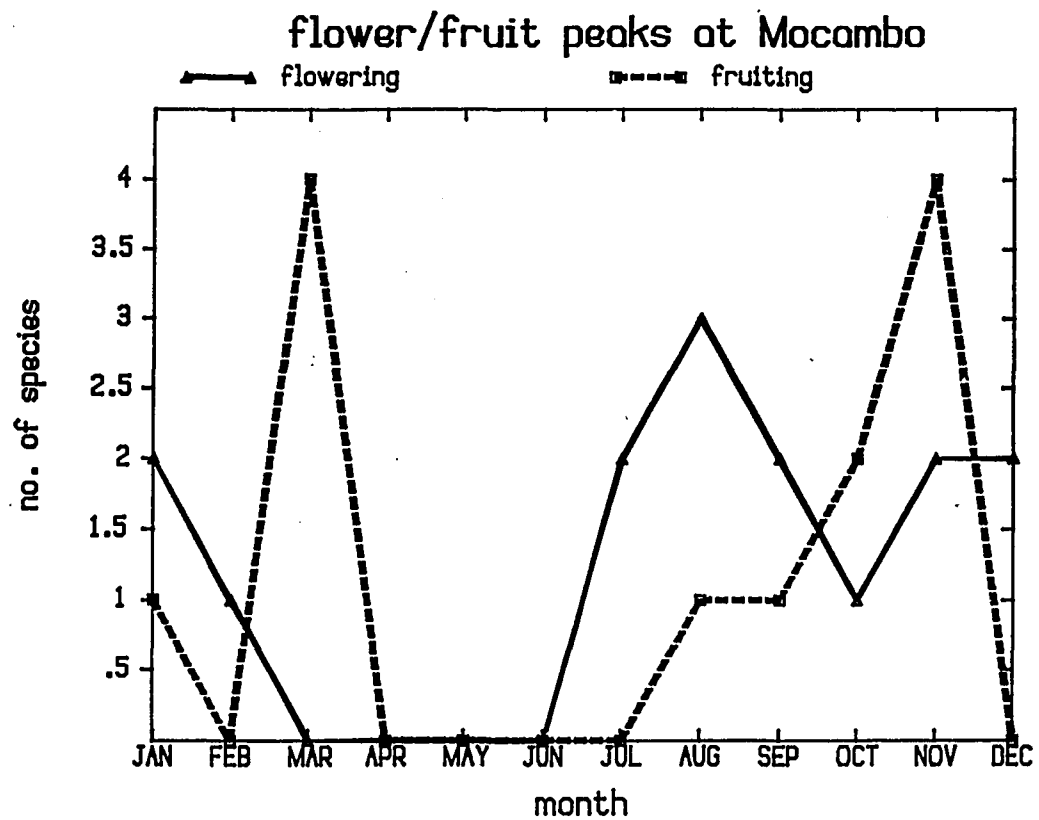


Figure 18.

Distribution patterns of Protium:

- a) ● = P. cuneatum; (N.B.: type collection of P. cuneatum is disjunct
in western Amazonia)
▲ = P. pallidum
- b) P. pilosum
- c) P. demerarensis
- d) P. plagiocarpium

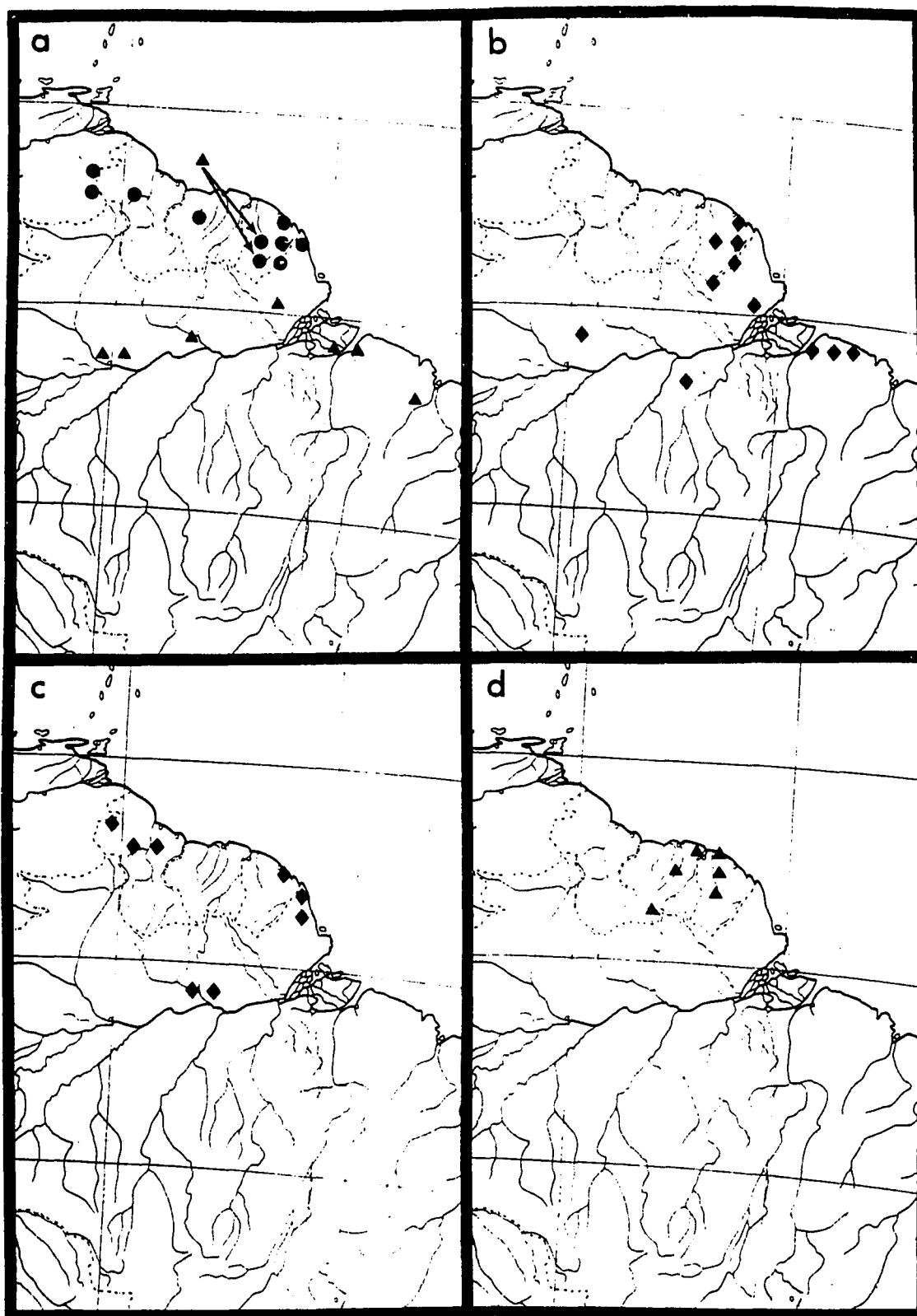


Figure 19.

Distribution patterns of Protium

- a)  = P. pittierii;
  = P. klugii
  = P. araguense
- b)  = P. opacum ssp. opacum
  = ssp. rabelianum
  = ssp. exaggeratum

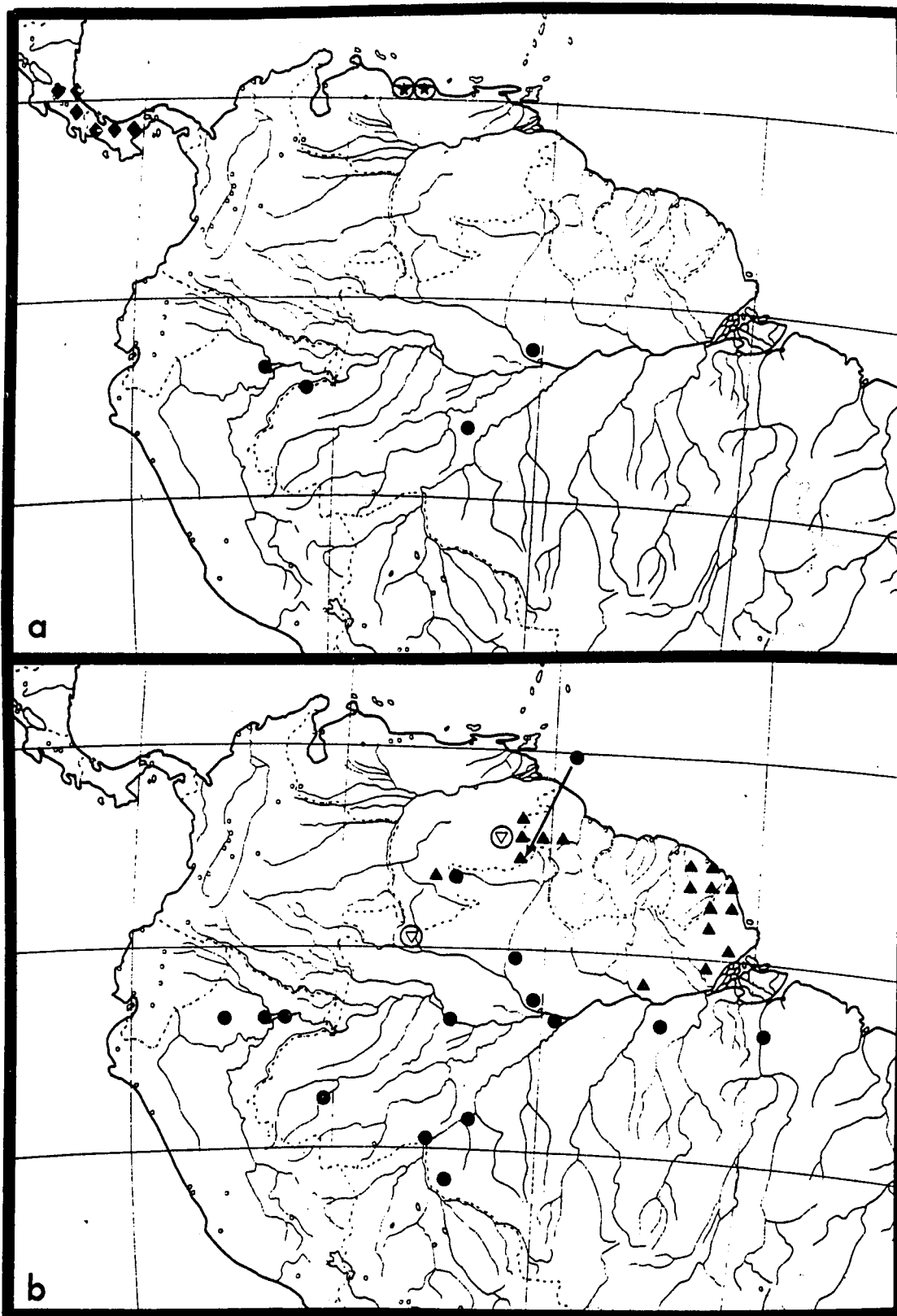


Figure 20.

Distribution patterns of Protium

- a)  = P. paniculatum var. paniculatum
 = var. riedelianum
- b)  = P. altsonii var. altsonii
 = var. nov.?

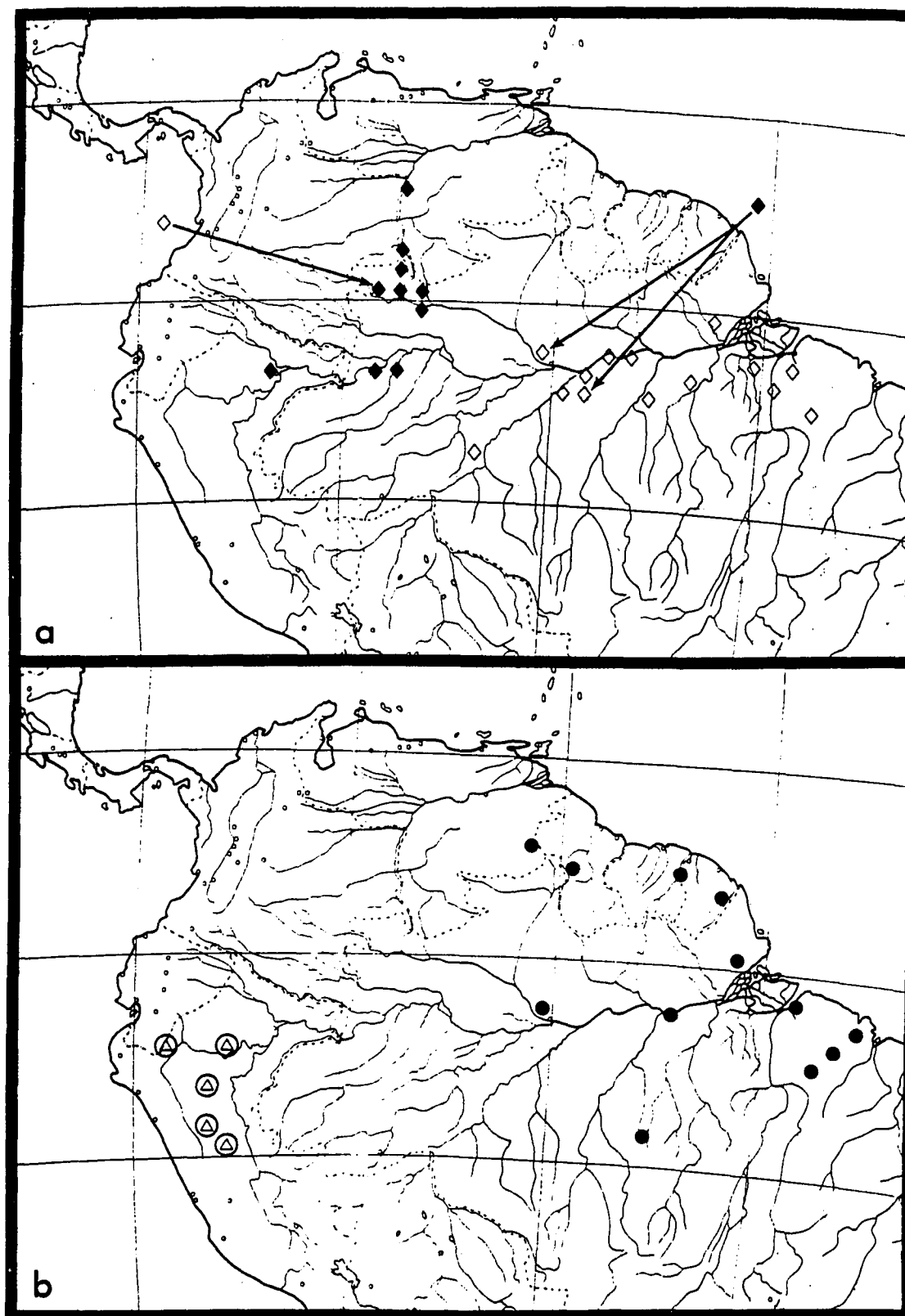


Figure 21.

Distribution patterns of Protium

- a) ★ = P. giganteum var. giganteum
 ▲ = P. giganteum var. crassifolium
 ● = P. morii
 ◆ = P. carolense
- b) ● = P. guianense ssp. guianense
 ▲ = ssp. pilosissimum

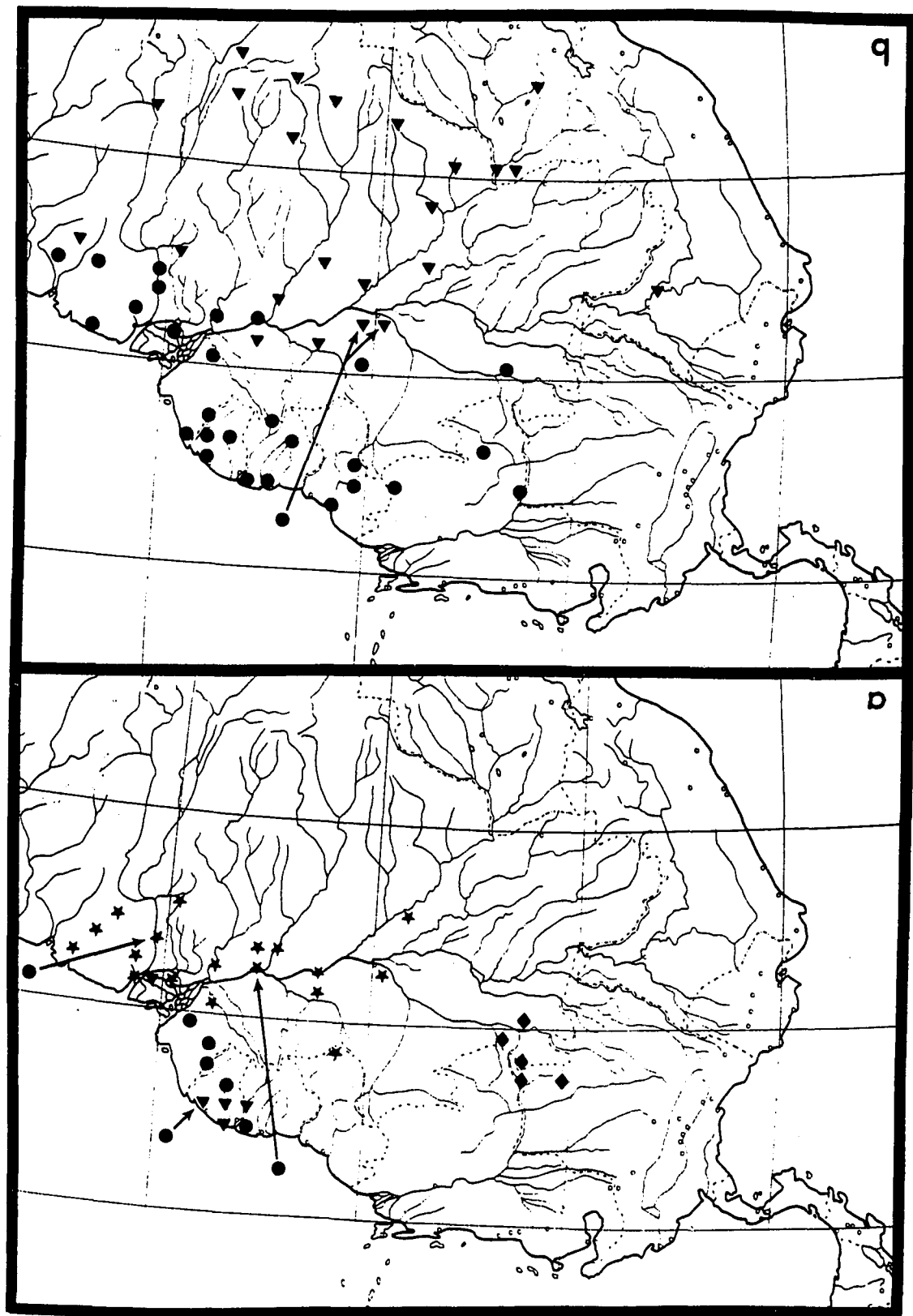


Figure 22.

Distribution patterns of Protium

- a) ▲ = P. divaricatum ssp. divaricatum
 ● = ssp. krukoffii
 ★ = ssp. fumarium
- b) P. crenatum

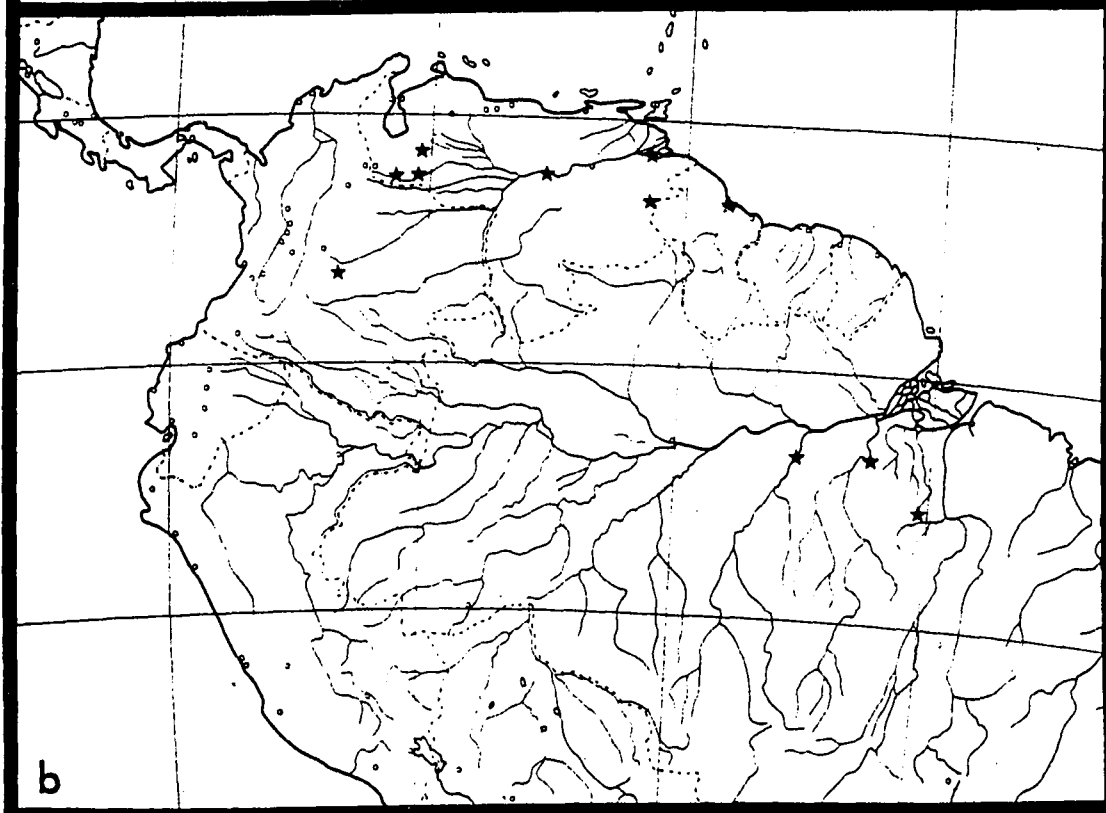
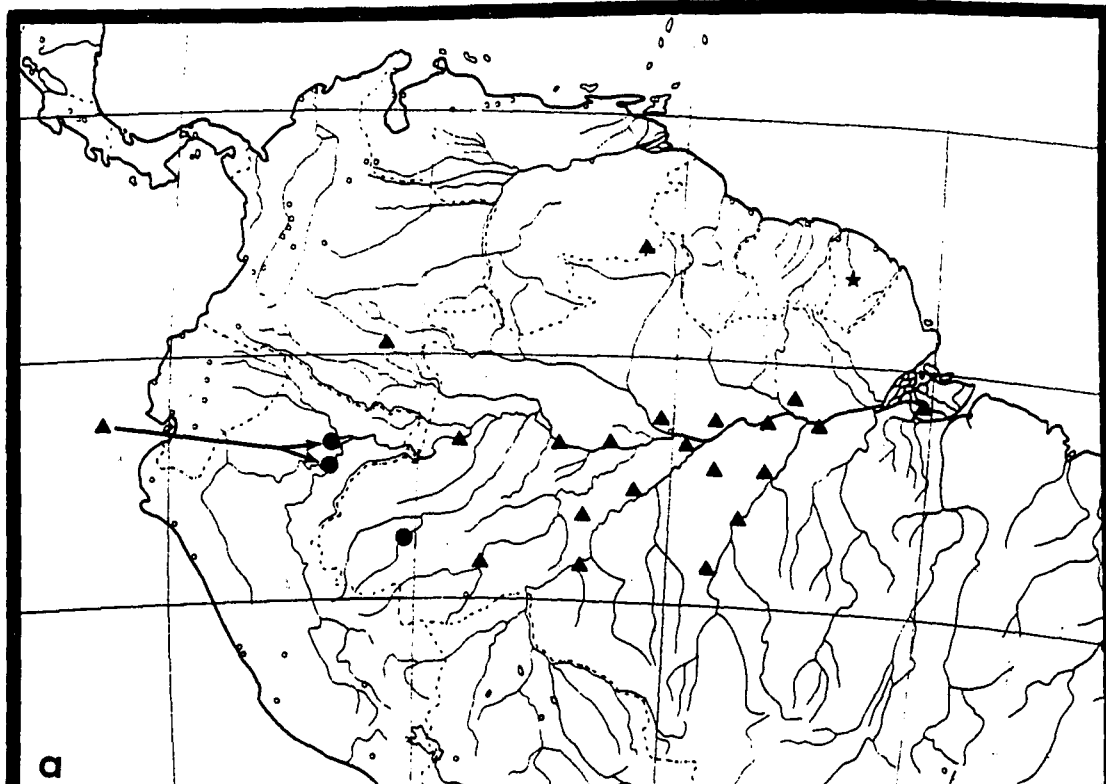


Figure 23.

Distribution patterns of Protium

- a) ★ = P. polybotryum ssp. polybotryum
☆ = ssp. blackii
- b) ◆ = P. carnosum
● = P. crassipetalum

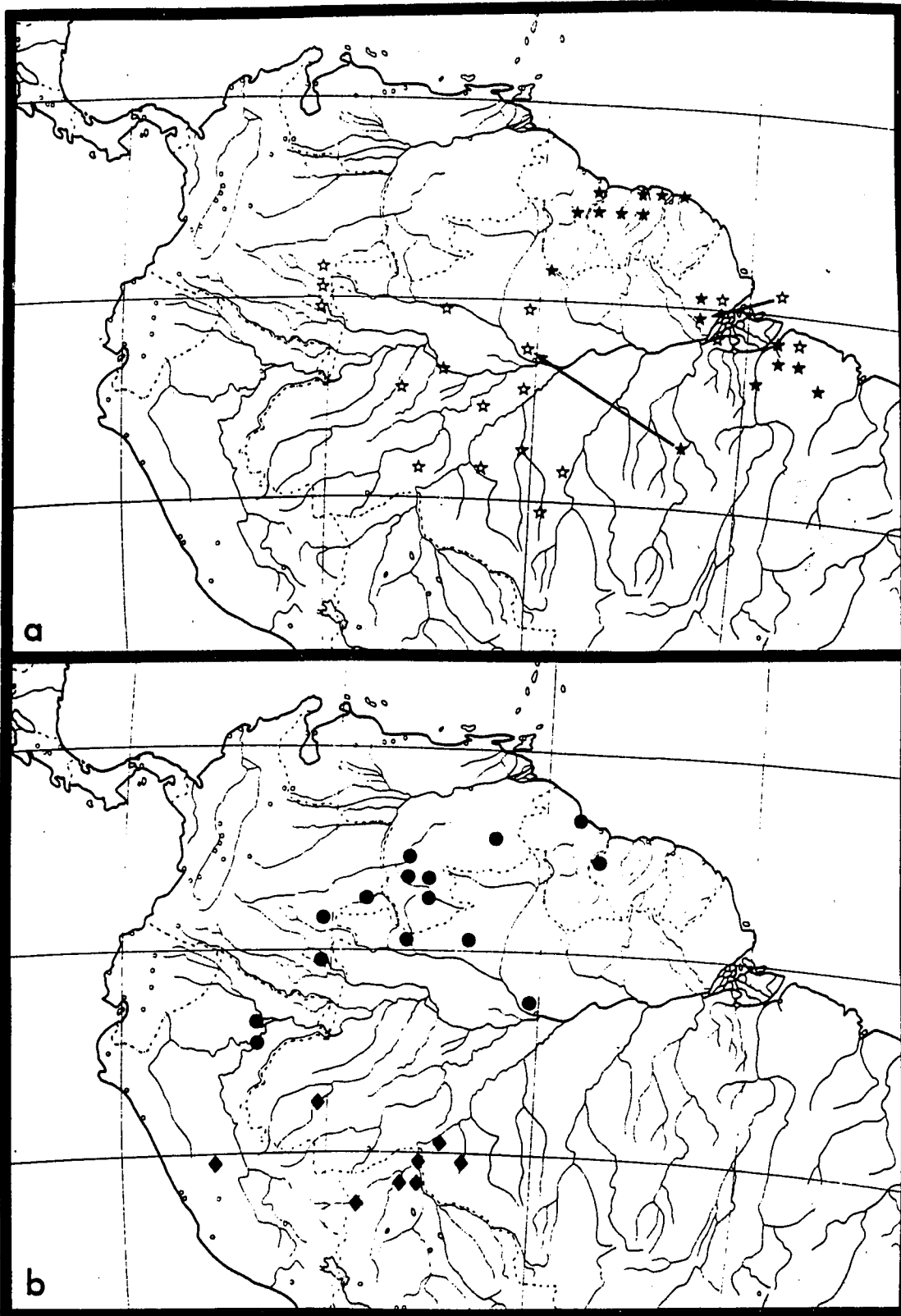


Figure 24.

Distribution patterns of Protium

- a) ◆ = P. ferrugineum
 ● = P. reticulatum
- b) ▲ = P. puncticulatum
 ● = P. macrophyllum

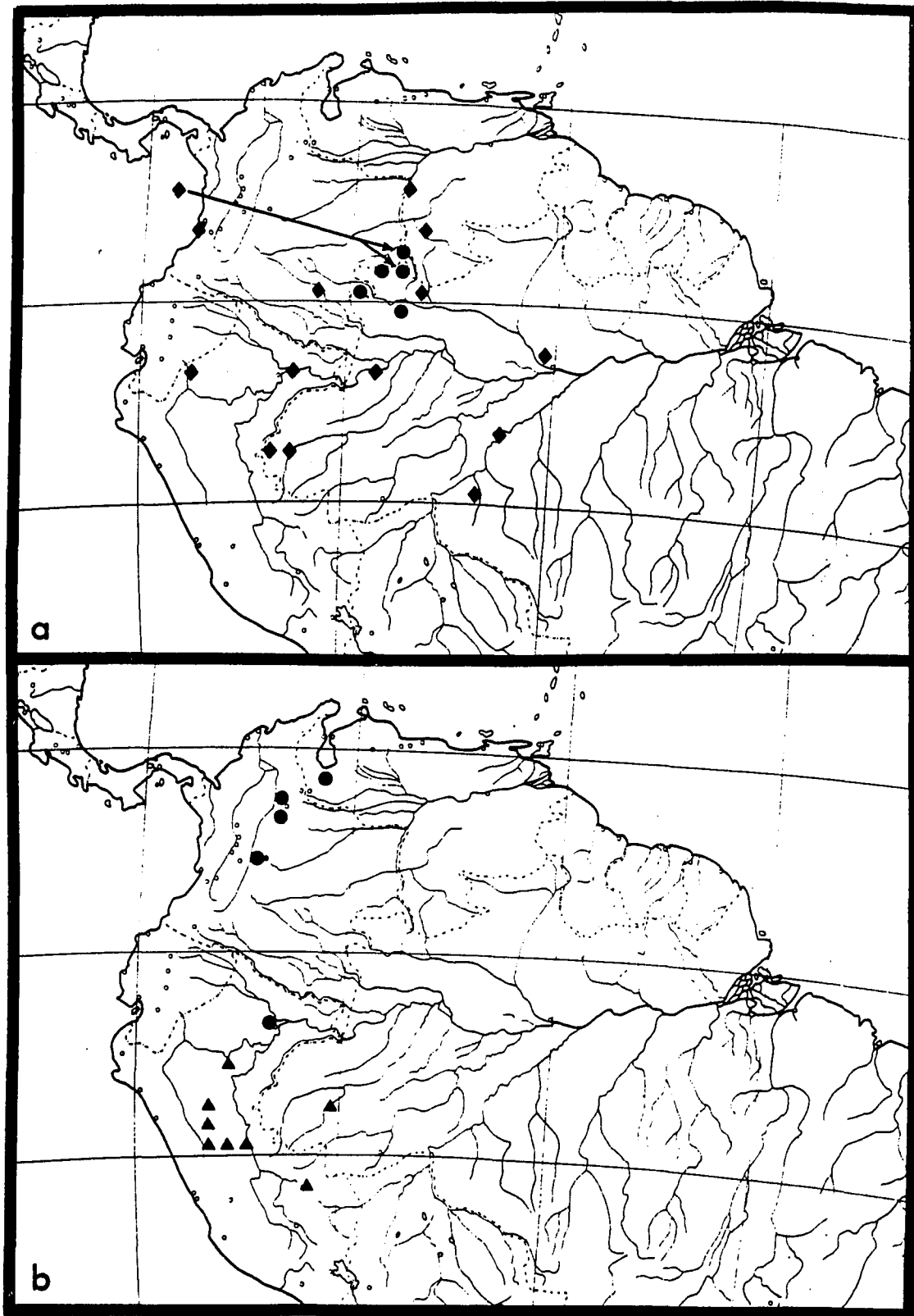


Figure 25.

Four phytogeographic subdivisions of Amazonia:

- a) Ducke & Black (1953)
- b) Rizzini (1963)
- c) Hueck (1972)
- d) Prance (1977)

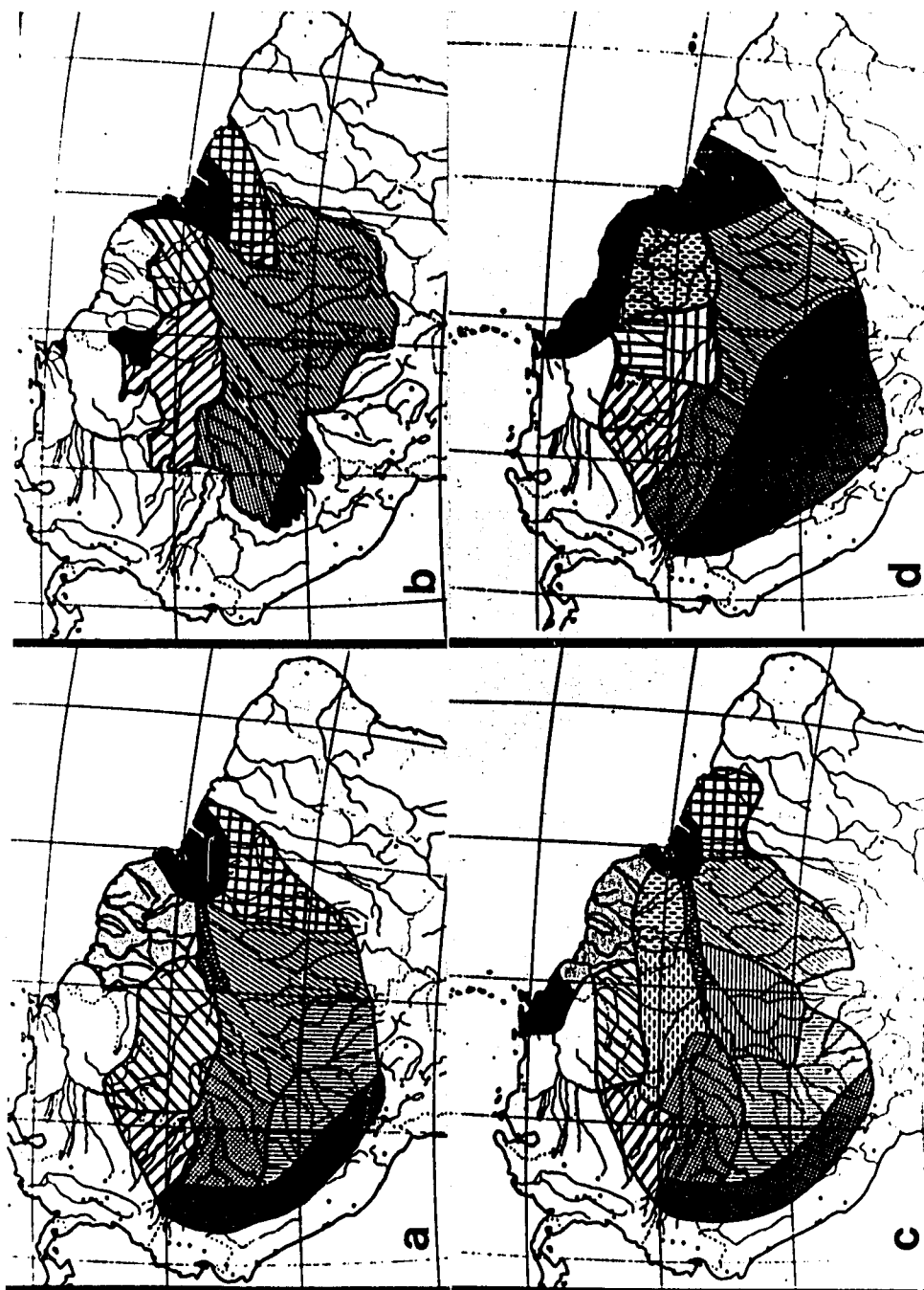
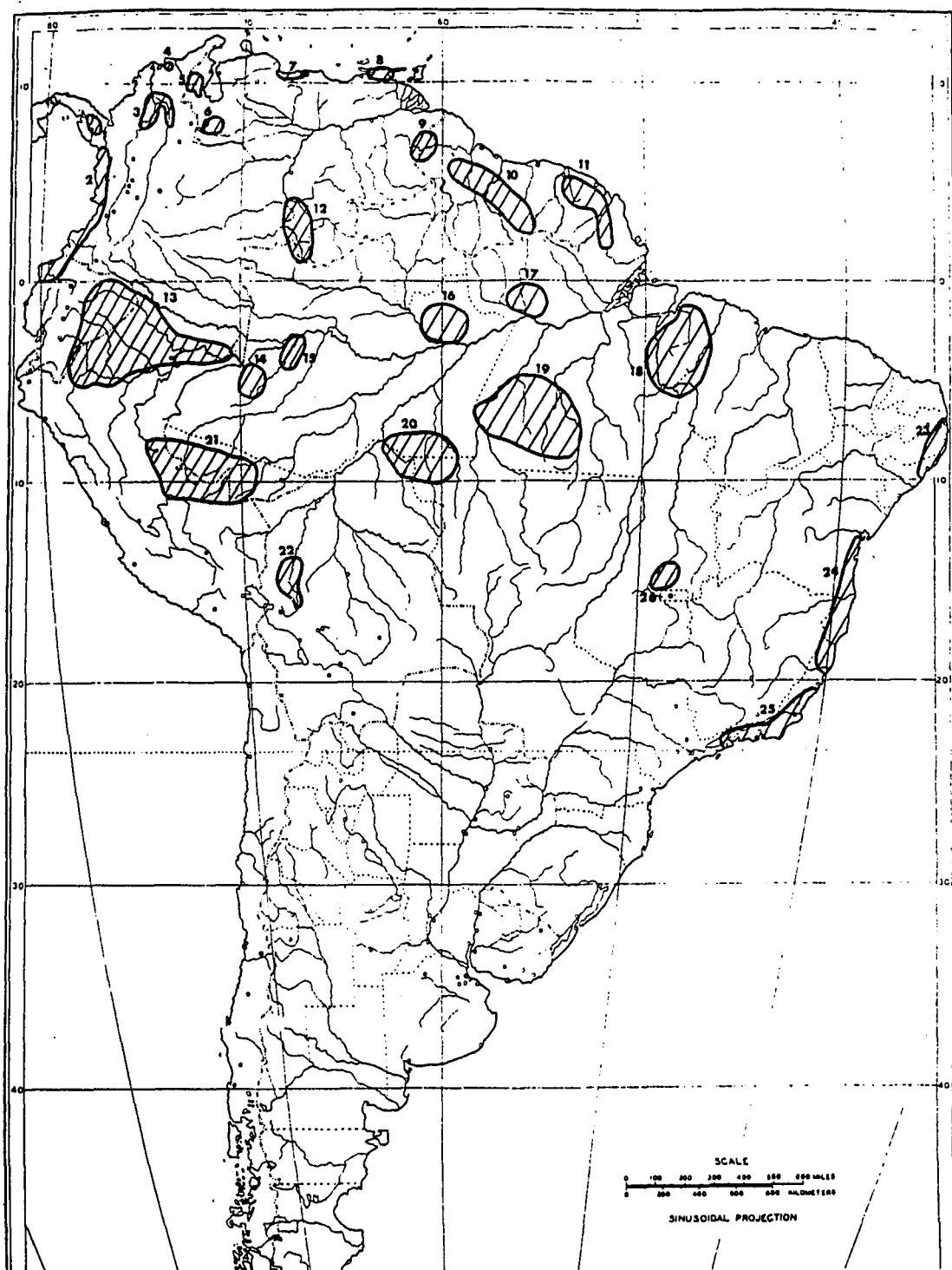


Figure 26.

Locations of proposed Pleistocene refuges
of moist forest (from Prance, 1982)



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