

THE INDUMENT OF APEIBA AUBL. (TILIACEAE)

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(received June 8th, 1966)

ABSTRACT

The indument on vegetative parts of *Apeiba* is examined. Some taxonomic problems left after Uittien's revision of the genus are reconsidered.

INTRODUCTION

The results presented here were obtained from a study of vegetative characters of the *Tiliaceae* of Suriname. This study was undertaken primarily to provide a key to sterile material of this family. In the course of the examination it was found that the *Apeiba* species possess some interesting features in their indument; at the same time it also became clear that publications by Uittien and Ducke on *Apeiba* had left some taxonomical questions without a satisfactory answer. This prompted me to investigate the trichomes with particular attention to the taxonomy. For practical reasons, however, I restricted myself to the indument on leaves and twigs. The (small) genus was taken in its entirety, thus including taxa outside Suriname as well.

Within *Apeiba* two sections can easily be distinguished: Sect. *Petoumo* Schum. and Sect. *Tibourbou* Schum. Within the first section four or perhaps five species are to be considered. *Apeiba echinata* Gaertn. appears to be very constant. The probably closely related *A. membranacea* Spruce ex Benth. is more variable, but usually it can be well distinguished from the first species. Some confusion has been caused by the presence of a few collections that more or less combine an *echinata*-like leaf indument with fruit characters of *A. membranacea*. One of these specimens seen by me belongs to a syntype collection of *A. macropetala* Ducke; Ducke himself reduced this species to a variety of *A. echinata* about thirteen years later. *A. intermedia* Uittien is known only from one tree in Suriname, several collections from which were made by the former Forestry Bureau. Uittien indicated its possible origin by hybridization between *A. echinata* and *A. glabra* (hence the name). *A. glabra* Aubl. is a well-marked species, very distinct from the others. Turning to Sect. *Tibourbou*, we find Ducke and Uittien against each other on the issue whether *A. albiflora* Ducke should be regarded as a species distinct from *A. tibourbou* Aubl. or not. It is true that the extreme forms are very different from each other and can easily be taken for two different species, but the picture is blurred by a number of collections appearing to be intermediate in one or several respects. *A. schomburgkii* Szyszyl. is easily distinguished from the other (two) species and seems to

be less frequent, at least as far as I could judge from the smaller number of collections made. All other specific names referring to the genus *Apeiba* may be regarded as synonyms (see URTTIEN, 1935).

MATERIAL AND METHODS

Herbarium material largely from the Institute for Plant Taxonomy in Utrecht (Botanical Museum and Herbarium, U) and some from the New York Botanical Garden (NY) was examined. The tip of a dissecting needle was ground on one side and thus converted into a microchisel with which individual hairs could be excised under a dissecting microscope. These hairs could easily be gathered on a small clump of glycerin-gelatin put on the tip of another dissecting needle; this clump was then molten on a warm slide glass and served as the mounting medium. From objects with a very dense and appressed indument a small patch of the epidermis bearing a number of hairs was taken off in the same way; immersion in alcohol sometimes had to be applied prior to mounting in order to expel excess of air remaining among the hairs. Average figures are based on at least 20 measurements made at random on hairs on microscope slides. Not every herbarium specimen was examined this way, but a few samples were taken for each species (or variety), the number of samples depending upon the variability observed. All specimens were checked subsequently, however, by examining them *in toto* under a dissecting microscope, or a compound microscope in case they had very small hairs.

THE INDUMENT

Apeiba is characterized by the stellate hairs common to most representatives of the *Malvales*. These stellate hairs consist of a fascicle of unicellular hairs (called the rays) implanted in the epidermis. The rays are connected to each other at the basal part, where pits may be found too (Fig. 3, G), but are otherwise free. This is the type termed stellate hair ('Stern- oder Büschelhaare') by HUMMEL and STAESCHE (1962), see pp. 212-213, also fig. 7, B on p. 22 and fig. 79 on p. 196 (l.c.). In descriptive literature the term stellate hair is commonly used in a much wider sense, including a variety of hair types such as the unicellular star-shaped trichomes found in *Cruciferae* or various forms of uniseriate and pluriseriate hairs in several families. In some *Malvales* the rays are laterally connected to each other over a greater part of their length: this leads to the (stalkless) scales such as are found in the Tiliaceous genus *Mollia*. Within *Apeiba* a slight tendency towards this may sometimes be seen, especially in the leaf hairs of *A. glabra* (Fig. 2, B). The number of rays within a single stellate hair varies from two to numerous. In the *Tiliaceae* with stellate (or scaly) indument examined (besides *Apeiba*: species of *Luehea*, *Lueheopsis*, *Vasivaea*, *Triumfetta* and *Mollia*, *Heliocarpus popyanensis* H.B.K., *Christiania africana* DC.) the indument of the

lower leaf sides appears to be more or less markedly different from that of petioles and twigs, the indument of large nerves usually being of a transitional type; the upper leaf sides usually have a thinner indument than the lower sides which reflects that of the latter or may be more or less transitional. In *Apeiba*, but this applies to the others mentioned as well, the rays of stellate hairs on the lower leaf sides are positioned at an angle with the epidermis varying from small (in more or less appressed stellae) to about 45–60 degrees, often being nearly equal for all rays within one stellate hair. The ray length usually does not vary much within one stella, and in most cases is not conspicuously variable within the same indument either, whereas the ray number often tends to stay fairly close to the average (usually 10 or less per stella). The whole impresses as a regular type of stellate indument when seen through a hand lens or microscope (Fig. 1, A, B, C, E; Fig. 2, A, B, E; Fig. 3, A, D, E, F; Fig. 4, A, B)¹). The twigs and petioles are covered by a much more irregular type of indument, many of its constituent stellate hairs being tuft- or brush-like with rays oriented at angles with the epidermis varying from small to 90 degrees, often bent or curved in various ways, often variable in size within one stella, their number being equally variable, so that stellate hairs with 3 rays can often be found neighbouring ones with up to 30 (or even more) rays (Fig. 1, F, G; Fig. 2, C, D, G, H; Fig. 3, C, H, I, J; Fig. 4, D, E). It may be added briefly that inflorescence parts as peduncles, pedicels and outer side of sepals usually show the indument type of the twigs, but often in a more luxuriant form (greater density of stellate hairs, these on the average with more and larger rays). The stellate hairs on stipules and bract(let)s often tend towards a comparatively few-rayed type, with rays often irregular in appearance, esp. due to their way of curving or twisting.

The individual cells in all these hairs are usually fairly thick-walled; sometimes cell walls are so thick as to nearly obliterate the cell lumen except for in the basal part (Fig. 3, G).

Besides stellate hairs simple hairs can be found; this is a common feature not only of *Apeiba* but also of other Tiliaceous genera. Their shape is like that of the rays in stellate hairs, but they are often larger. In *Apeiba* Sect. *Petoumo* they are not very numerous, to be found chiefly on young and growing parts (twigs, petioles, large nerves) and fairly soon deciduous, thus often absent from older parts which may still be densely covered by stellate hairs. In Sect. *Tibourbou*, on the other hand, simple hairs are often abundant not only on young but also on adult parts.

In addition to stellate and simple hairs small glandular trichomes are present. HUMMEL and STAESCHE (1962), in their survey of plant

¹) The comparatively large stellate hairs in Sect. *Tibourbou* are always somewhat squeezed between cover glass and slide glass and due to this these drawings, made with a microscope, do not exactly show the position of the rays as it would have appeared, could these hairs have been seen on the leaf surface in true three-dimensional view.

hairs (l.c., p. 237), make mention of uniseriate glandular hairs in *Malvaceae*, *Tiliaceae* and *Bombacaceae*. It was observed by me that in *Tiliaceae* heads of glandular hairs often have vertical cell walls in addition to the horizontal walls (Fig. 1, H; Fig. 4, F). The head always appeared to be thicker than the stalk. The glandular hairs, as far as was seen, were outnumbered and often hidden by stellate hairs, thus making it practically very difficult to assess their taxonomical value. This survey, for that reason, will deal with stellate and simple hairs only.

A SURVEY, WITH CRITICAL REMARKS

Some salient vegetative characters of *Apeiba* are: leaves usually elliptical to oblong-obovate, acute to acuminate, with 3 large primary nerves, the lateral ones usually not much longer than $\frac{1}{2}$ — $\frac{2}{3}$ of the length of the median one and similar in aspect to the secondary nerves of the median primary nerve (arcuate, coming close to the leaf margin and anastomosing with the first pair of secondary nerves), tertiary nerves parallel to each other and at right angles with secondary nerves, quaternary nerves repeating the pattern of the tertiary nerves, but tending towards becoming reticulate, the smallest veinlets reticulate; large nerves prominent below, flat or slightly prominent above; stipules oblong-lanceolate to lanceolate, early caducous in most species; indument of stellate hairs intermixed to a varying degree with simple hairs (esp. in Sect. *Tibourbou*).

Section **Petoumo** Schum.

Leaves entire to sometimes (faintly) dentate-serrate, hairs on lower side on nerves and in intervenular areas, on upper side on nerves only. Conspicuous tufts of (brown) hairs often present at the base of the primary nerves on the lower side, sometimes also in the axils of the secondary nerves of the median primary nerve. Petioles more or less incrassate in their apical part.

Stellate hairs on vegetative parts with a ray length not exceeding 150 (–200) μ (with the exception of the tufted hairs at the base of large nerves). The majority of stellae on lower leaf sides appressed or moderately elevated (notably in *Apeiba echinata*), usually with moderately thick-walled rays having their largest width at or near the base (Fig. 1, A, B; Fig. 2, A, B, E; Fig. 3, A, D). Stellate hairs on large nerves, petioles and twigs more irregular in appearance, their rays curved and oriented in a more variable way and with their largest diameter at or near the base or somewhat higher; brown cell contents also noticeable in dried material (Fig. 1, F, G; Fig. 2, C, D, G, H; Fig. 3, C). Transitional hair forms to be seen on smaller nerves, especially on the upper side (Fig. 1, C, D, E; Fig. 2, F; Fig. 3, B). Stipules on their abaxial side, like bracts, with mostly few-rayed stellate hairs, the rays curved and twisted in a more or less irregular way. Simple hairs often fairly abundant on young, growing

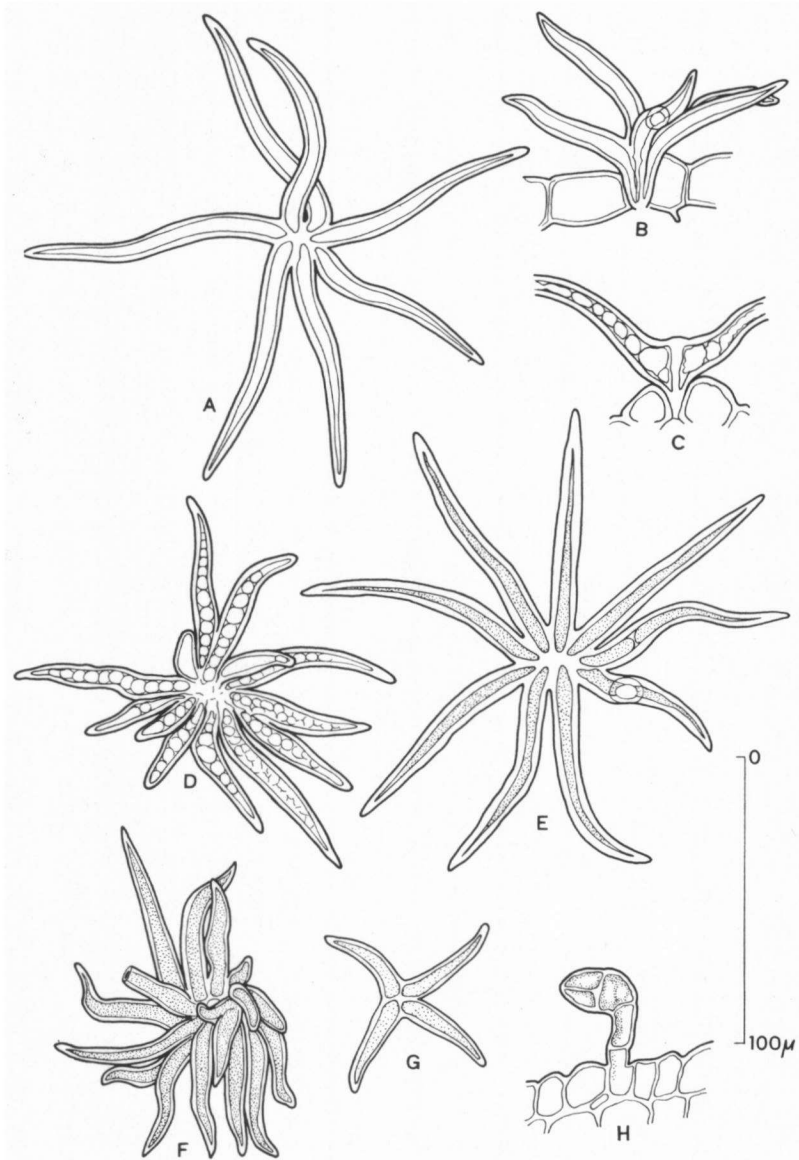


Fig. 1. *A. echinata*. A. Intervenular stellate hair from lower leaf side, top view. B. Same, lateral view, epidermis in sectional view. C. Venular stellate hair from lower leaf side, base in sectional view. D and E. Venular stellate hairs from lower leaf side, top view. F and G. Stellate hairs from petiole, top view. H. Glandular hair from median primary nerve, lower side, sectional view. (A through G from BW 4042; H from Lindeman 6464).

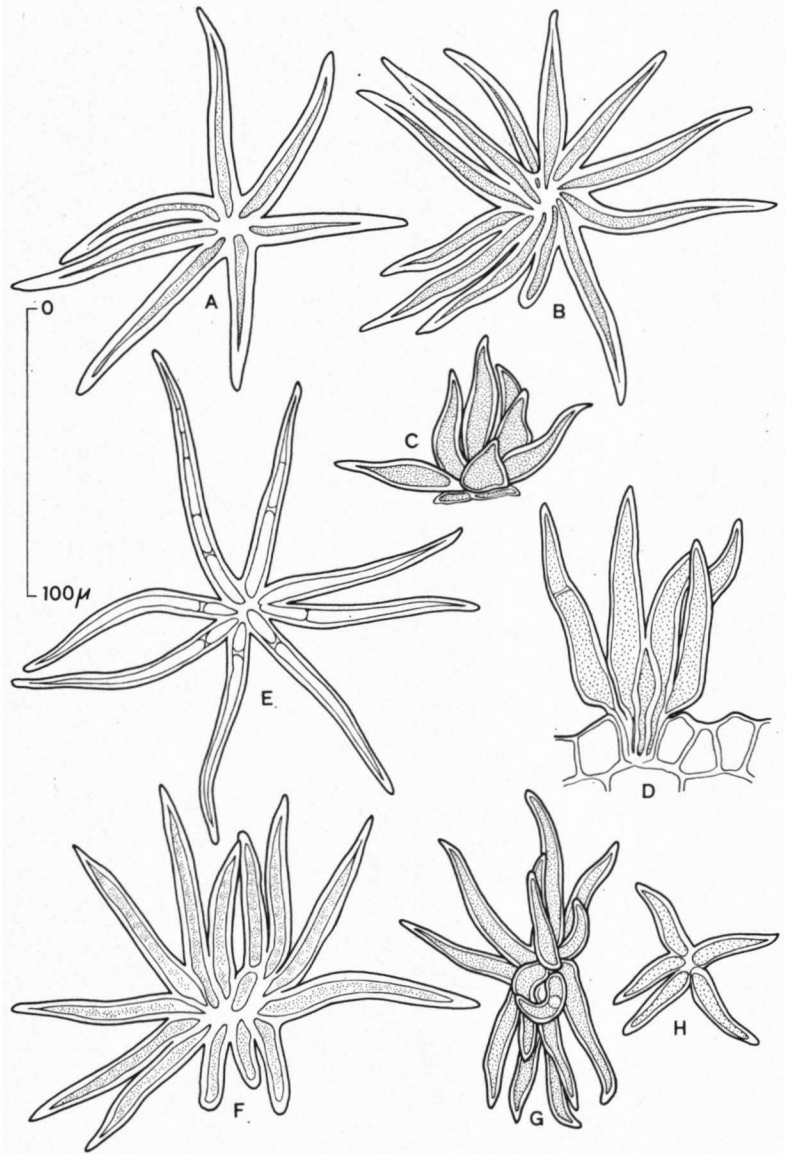


Fig. 2. **A. glabra.** A and B. Stellate hairs from lower leaf side, top view. C. Stellate hair from twig, lateral view. D. Stellate hair from petiole, sectional view. (from BW 6258).

A. intermedia. E. Intravenular stellate hair from lower leaf side, top view. F. Venular stellate hair from lower leaf side, top view. G and H. Stellate hairs from petiole, top view. (from BW 5592).

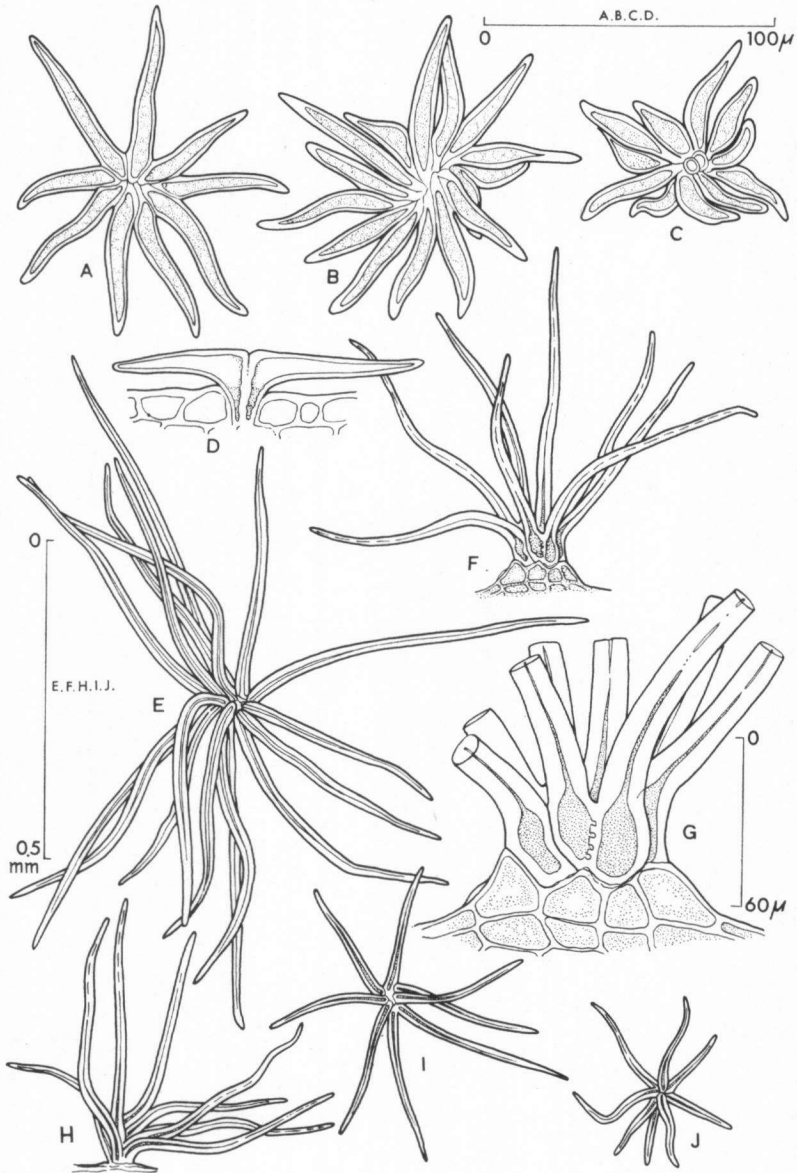


Fig. 3. **A. membranacea.** A. Intervenular stellate hair from lower leaf side, top view. B. Venular stellate hair from lower leaf side, top view. C. Stellate hair from petiole, top view. D. Intervenular stellate hair from lower leaf side, sectional view. (from Kuhlmann HJBR 18075).

A. schomburgkii. E. Stellate hair from lower leaf side, top view. F. Same, lateral view. G. Basal part of F, more enlarged. H. Stellate hair from median primary nerve, lower side, lateral view. I and J. Same, top view. (from Pulle 217).



Fig. 4. *A. tibourbou*. A. Stellate hair from lower leaf side, lateral view, B. Same, top view. C. Simple hair from petiole. D and E. Stellate hairs from petiole, lateral view. F. Glandular hair from petiole head and part of stalk, lateral view. (A through E from Krukoff 1518; F from Krukoff 5291).

parts (large nerves, petioles, twigs), mostly appressed and not exceeding 1 mm in length, soon caducous and thus largely absent from older parts.

***Apeiba echinata* Gaertn.**

Leaves 7–20 cm long and 4–10 cm wide, occasionally up to 30 cm long and 15 cm wide; first pair of lateral primary nerves $\frac{1}{2}$ – $\frac{2}{3}$ of the length of the median one, second pair weakly developed; secondary nerves (3–) 4–7 on each side of the median primary one. Upper leaf sides smooth, the nerves at most only slightly prominent; lower sides covered by a very dense mass of \pm interwoven stellate hairs and nearly always with conspicuous tufts at the base of the primary nerves. Petioles (1–) $1\frac{1}{2}$ – $2\frac{1}{2}$ (–3) cm long, slightly incrassate apically over a length of about $\frac{1}{2}$ –1 cm.

Stellate hairs on lower leaf sides with 4–11 (–15), averaging ca. 8, rays of ca. 30–125 μ , averaging ca. 65–85 μ , long and with a largest diameter of 6–10 (–13) μ (Fig. 1, A, B); on small nerves stellae to be observed with a larger number of rays, that can be somewhat wider and sometimes are connate to each other to a little beyond the base (Fig. 1, C, D, E) – these hairs also present (scattered) on the upper side. The tufts consisting of stellate hairs more or less comparable to those on the petioles, but much larger in size, the rays (3–) 4–20, mostly directed upward, to 1– $1\frac{1}{2}$ mm long and 25 (–30) μ wide, often fairly thin-walled in comparison with the surrounding hairs. Large nerves, petioles and twigs (densely) covered by stellate hairs with (3–) 4–20 rays, these directed at often very variable angles, even within one stella (particularly in large hairs), about 20–80 μ , averaging ca. 40–50 μ , long and to 15 μ wide (Fig. 1, F, G). Simple hairs chiefly on very young parts, to $\frac{3}{4}$ mm long. Stellate hairs on stipules, abaxial side, mostly 4–8-rayed; simple hairs there to $\frac{1}{2}$ mm long and 15 μ wide present or absent.

Two collections by Lindeman (nrs. 5428 and 6464, sterile material only) tend towards having a slightly thinner indument on the lower leaf sides than is normally found in this species, and the basal hair tufts are \pm poorly developed in comparison with other collections. This may be due to the fact that those collections were made from young trees, indicated as 7 m and 3 m tall respectively. It should be added, however, that Lindeman 5956, while collected from a tree $4\frac{1}{2}$ m tall, has leaves as observed from mature trees.

Material seen:

VENEZUELA, BOLÍVAR: Sierra Imataca, Rio Toro (Rio Grande) between Rio La Reforma and Puerto Rico, north of El Palmar, Steyermark 88124 (U).

BRITISH GUYANA: Matthews Ridge, Barima River, Northwest territory, Cowan 39373 (U); Essequibo River, Moraballi Creek, near Bartica, Sandwith 430 (U), 622 (U).

SURINAME: Coppename River, near Bitagron, Lindeman 6464 (U); Emma Range, Jonker and Daniels 1095 (U); Watramiri, tree nr. 1618, BW 1937 (U),

3454 (U), 3897 (U), 4042 (U), 4302 (U), 5003 (U), 5153 (U); Zanderij I, Wood Herbarium Surinam 205 (U); Sectie 0, tree nr. 702, BW 1386 (U), 3835 (U), 3949 (U), 4149 (U); Brownsberg, tree nr. 1031, BW 1774 (U), 6356 (U), 6749 (U), 6914 (U); *ibid.*, tree nr. 1185, BW 3221 (U), 3435 (U), 4001 (U), 4702 (U); *ibid.*, BW 3313 (U), 6512 (U); Osembo, Para River, BBS 89 (U); Peninica, BBS 1136 (U); Perica River, Commewijne Distr., Lindeman 5428 (U); Rikanau, near Moengo, Lindeman 5956 (U); Marowijne River, Armina Falls, BW 4177 (U); Tapanahony River, Manlobi, BW 3702 (U); without locality, Hostmann 294 (U, type coll. of *Apeiba hypoleuca* Steud.).

FRENCH GUIANA: Mana River, BAFOG 199M (U), 7007 (U); Cayenne, BAFOG 1052 (U), 1190 (U); Oiapoque River, Pedra Alice, 3° 40' N, 52° 1' W, Irwin, Pires and Westra 47559 (U).

BRAZIL, PARÁ: Upper Cupari River, plateau between the Xingú and Tapajós Rivers, Krukoff 1168 (U), 1186 (U).

Apeiba echinata, var. *macropetala* (Ducke) Ducke

No conspicuous hair tufts at the base of the primary nerves, but instead small tufts in the axils of the secondary nerves of the median primary nerve and also at the base of the primary nerves, or hair tufts totally lacking.

The indument often heavier than in the species (notably on upper sides of leaves and on petioles and twigs). Stellate hairs on lower leaf sides with rays of ca. 40–200 μ , averaging ca. 90–115 μ , long and 6–13 μ in largest diameter; on small nerves stellate hairs of even larger size, these with brown cell contents and thus easily visible among the surrounding mass when seen through a low-power microscope (25–50 \times). Tufts, if present, with rays up to 1 mm long and 20 (–25) μ wide. Large nerves, petioles and twigs also having a greater ray length than in the species, ca. 30–200 μ , averaging about 75–90 μ , with a largest diameter ca. 8–13 (–15) μ . Simple hairs on adult parts observable here and there among the stellate hairs, to ca. $\frac{1}{2}$ mm long and 20 μ wide.

In his revision of the genus UITTEN (1935) leaves some doubt as to how to separate *Apeiba echinata* from *A. membranacea*. His key distinguishes between leaves distinctly grayish tomentellous beneath with very conspicuous brown hair tufts at the base of the lateral primary nerves (called basal nerves) and depressed fruits ('concave top') for *A. echinata*, and leaves indistinctly tomentellous or nearly glabrous beneath with conspicuous brown hair tufts at the base of the lateral primary nerves and smaller tufts in the axils of the other (i.e. secondary) nerves, and fruits with a mammiform apex ('somewhat apiculate at the top') for *A. membranacea*. According to this, Ducke HJBR 24035 would match *A. membranacea* in its fruit shape and the small hair tufts at the base of the large nerves; its dense indument on the lower leaf sides, however, is distinctly 'echinata'-like. Uittien cites this collection under *A. membranacea*. Ducke HJBR 18080 is very similar: the fruit on the sheet in U is almost flat at the top, and as such it comes within the variability range of the *A. membranacea* fruit as observed by me, but it still is very different from the markedly depressed fruits on all the *A. echinata* material

I have seen; there are no hair tufts, but Uittien assumes that those have been eaten by insects, otherwise the dense indument on the lower leaf sides is again very 'echinata'-like. This collection, inconsequently, is cited by Uittien under *A. echinata* because of its leaf indument.

Apeiba macropetala Ducke (1925) was based, among others, on Ducke HJBR 18080; later on (1938) Ducke reduced this species to a variety of *A. echinata* because he considered his collection Ducke HJBR 24035 as an intermediate. However, there is the fruit which is like that of *A. membranacea*, not at all like that of *A. echinata*, and this might indicate that Ducke's taxon should be placed at the specific rather than a lower level. Be it as it is, Ducke's solution apparently is a more consequent and natural one for the moment than that by Uittien, the indument providing an excellent character to distinguish readily between the taxa involved. Whether or not this will hold when more material will have been studied, remains yet to be answered.

Ducke, at first, thought that var. *macropetala* represented the species in the eastern half of the Amazon plain. Its area, however, appears not to be sharply separated from that of *A. echinata*, since it has been collected in British Guiana and since the species is now known from the Xingú and Tapajós Rivers region in Pará.

Material seen:

BRITISH GUIANA: basin of Essequibo River, near mouth of Onoro Creek at about 1° 35' N, A. C. Smith 2775 (U).

BRAZIL, AMAZONAS: Rio Negro, Santa Izabel, Ducke HJBR 24035 (U); basin of Rio Solimões, municipality São Paulo de Olivença, basin of creek Belem, Krukoff 8289 (U); Parintins, Lago José-Assú, Ducke HJBR 34964 (U).

PARÁ: Belém, Ducke HJBR 18080 (U, syntype coll. of *A. macropetala* Ducke).

***Apeiba glabra* Aubl.**

Leaves 9–15 cm long and 4–6 cm wide, first pair of lateral primary nerves $\frac{2}{3}$ – $\frac{3}{4}$ of the length of the median one, second pair weakly developed (up to $\frac{1}{2}$ of the length of the first pair) to nearly obsolete; secondary nerves (2–) 3–4 on each side of the median primary nerve. Leaf surface often somewhat scabrid, the hairs barely visible to the naked eye, but appearing under a hand lens, varying from scattered to very numerous on the lower sides. No hair tufts at the base of large nerves, or only indicated by some stellate hairs of larger size. Petioles 1–2 cm long, somewhat thickened apically over $\frac{1}{2}$ to $\frac{3}{4}$ of their length.

Stellate hairs on lower leaf sides with about 4–20, averaging ca. 8–14, rays of ca. 30–115 μ , averaging ca. 55–80 μ , long and with a largest width of 9–12 μ , the rays often connate to each other somewhat beyond the base, thus making many hairs appear more or less scale-like (Fig. 2, A, B); largest stellate hairs with greatest ray number on small nerves; rays of stellate hairs at the base of large nerves sometimes to $\frac{1}{2}$ mm long and 20 μ wide. All leaf stellae containing brown cell substance, as hairs on other parts of the plant. Petioles and twigs with a dense cover of stellate hairs having 4–20 (–25)

rays directed in very variable ways, particularly in large hairs, measuring ca. 25–110 μ , averaging ca. 40–55 μ , in length and 9–15 μ in largest diameter, sometimes up to 200 μ long and ca. 20 μ wide (Fig. 2, C, D). Simple hairs often quite numerous on younger parts, scattered or lacking on adult parts, up to $\frac{3}{4}$ –1 mm long and 20–25 μ wide; occasionally stellate hairs observable one ray of which much exceeds the others in size and may become about equal to the simple hairs. Stipules with stellate hairs on abaxial surface with 3 to as many as 20 (–25) rays (as far as could be seen).

Material seen:

SURINAME: Wilhelmina Range, Julianatop, Schulz and Elburg LBB 10273 (U); Coppename River, near Bitagron, Lindeman 6465 (U); *ibid.*, Raleigh Falls, Lanjouw 810 (U), BW 6153 (U), 6258 (U); Saramacca River, upper course, Pulle 231 (U); *ibid.*, Jan Basi Gado, J. & P. A. Florschütz 1212 (U); *ibid.*, Jacob Kondre, Maguire 23897 (U); *ibid.*, Kwatta hede, Maguire 23913 (U); *ibid.*, Paka Paka, Maguire 23969 (U); Upper Suriname River, Tresling 98 (U), 210 (U), 383 (U); Gonini River, BW 3707 (U).

FRENCH GUIANA: Beiman Creek, BAFOG 190M (U); Oiapoque River, Pedra Alice, 3° 40' N, 50° 1' W, Irwin, Pires & Westra 47555 (U).

BRAZIL, PARÁ: São Caetano de Odivellas, Ducke HJBR 15277 (U); Belém, Ducke HJBR 11267 (U), Pires 51747 (U); without locality, Burchell 9480 (U, syntype coll. of *Apeiba burchellii* Sprague).

Terr. AMAPÁ: Serra do Navio, Rio Amapari, Cowan 38082 (U).

Apeiba intermedia Uittien

Leaves 10–21 cm long and 5–8 (–9) cm wide, first pair of lateral primary nerves $\frac{1}{2}$ (– $\frac{3}{4}$) of the length of the median one, second pair weakly developed; secondary nerves 5–6 (–7) on each side of the median primary nerve. Leaf surface smooth, the indument appearing under a low-power microscope, consisting of numerous, but still individually distinguishable, stellate hairs on the lower sides, scattered stellate hairs on the upper sides. Hair tufts present at the base of primary nerves and secondary nerves of the median primary nerve below, but not as conspicuous as those of *A. echinata*. Petioles about (1–) $1\frac{1}{2}$ –2 cm long, apically incrassate over a length of ca. $\frac{1}{2}$ –1 cm.

Stellate hairs on lower leaf sides with 4–10, averaging ca. 8, rays of ca. 30–100 μ , averaging ca. 80–85 μ , long and with a largest diameter of ca. 6–9 μ (Fig. 2, E); on small nerves and also on the upper sides stellate hairs with up to 15 (–20) rays to 13 (–15) μ in largest diameter and sometimes connate to somewhat beyond the base (Fig. 2, F). Stellate hairs from tufts with rays to $\frac{1}{2}$ – $\frac{3}{4}$ mm long and 20 (–25) μ in largest diameter. Large nerves, petioles and twigs covered by stellate hairs with about 4–20 (–25) rays oriented at often very variable angles, particularly in larger stellate hairs, with a length of ca. 30–125 μ , averaging ca. 70–80 μ and with a largest diameter of 7–15 μ (Fig. 2, G, H). Simple hairs few, scattered, up to $\frac{3}{4}$ mm long and ca. 20 μ in largest diameter. Stipules on abaxial side with stellate hairs having an average of about 4 (to perhaps slightly more) rays up to ca. 110 μ long and 7–13 μ in largest diameter; also simple and geminate (or

two-rayed stellate) hairs up to $\frac{1}{2}$ mm long and 15μ in largest diameter observable.

This species is known from Suriname only and all collections were made from the same, marked, tree. UITTEN, when publishing it (1925), described it as an intermediate between *A. echinata* and *A. glabra* and thought it possibly might have originated by hybridization between those two species. Fruits were not available at that time. In 1931 twig fragments bearing mature fruits were collected, but they escaped Uittien's notice and thus the fruits remained unknown until recently, when they reappeared after a reorganization of the fruit herbarium in Utrecht. They are exactly like those of *A. echinata*. This does not give support to Uittien's speculation as to the hybrid origin of *A. intermedia*, for in that case a fruit more or less intermediate between that of *A. echinata* and that of *A. glabra* (which has more numerous and more slender spines) was likely to have been expected. *A. intermedia* is not conspecific with *A. membranacea* as suspected by MACBRIDE (1956), who, of course, could not know the fruits of *A. intermedia*. Fruit shape of *A. echinata* and *A. membranacea* is discussed under *A. echinata*, var. *macropetala*: everything said for *A. echinata* also applies to *A. intermedia*.

Apart from the fruits, *A. intermedia* resembles *A. membranacea*, but the foliar stellae (on the type material) of the first are somewhat larger and about equal those of *A. echinata* in size.

Material seen:

SURINAME: Brownsberg, tree nr. 1023 (type tree), BW 1727 (U), 5592 (U), 6370 (U), 6819 (U), s.n. (fruits) (U).

***Apeiba membranacea* Spruce ex Benth.**

Leaves 7–21 cm long and 4–9 cm wide, first pair of lateral primary nerves about $\frac{1}{2}$ of the length of the median one, second pair weakly developed; secondary nerves (4–) 5–7 on each side of the median primary nerve. Leaf surfaces smooth, the indument barely visible to the naked eye, but appearing at a magnification of 25–50 \times and consisting of stellate hairs varying from scattered to (fairly) numerous on the lower sides, sometimes mainly concentrated along the larger nerves. Hair tufts at the base of primary nerves and secondary nerves of the median primary nerve, varying from quite conspicuous (but not as large as those of *A. echinata* to inconspicuous, sometimes almost absent. Petioles about 1–2 $\frac{1}{2}$ cm long, with a slight apical thickening of about $\frac{1}{2}$ –1 cm.

Stellate hairs on lower leaf sides with 6–20, averaging ca. 8 (–10), rays of 15–85 (–110) μ , averaging ca. (40–) 50–60 μ , long and with a largest width of 6–12 μ (Fig. 3, A, D); largest stellae with greatest ray numbers, with rays sometimes connate to somewhat beyond the base, on small nerves (Fig. 3, B). Stellate hairs from tufts with rays to $\frac{1}{2}$ –1 mm long and 20 (–25) μ in largest diameter. Large nerves, petioles and twigs densely covered by stellate hairs to nearly glabrous,

these stellate hairs with about 4–20 rays ca. 25–140 μ long, averaging ca. 55–80 μ , and ca. 7–12 (–15) μ in largest diameter, directed at often very variable angles, especially in larger hairs (Fig. 3, C). Some simple hairs occurring among the stellate hairs, to $\frac{1}{2}$ – $\frac{3}{4}$ mm long (occasionally up to $1\frac{1}{2}$ mm) and 20–25 (–30) μ wide. Stipules on abaxial side with stellate hairs with 2–10, averaging ca. 5–6, rays with an average length of ca. 80–85 μ and a largest diameter of 7–12 μ ; also with some simple and geminate (or two-rayed stellate) hairs to ca. 350 μ long and 15 μ wide.

See remarks under *A. echinata*, var. *macropetala*, and *A. intermedia*.

Material seen:

PANAMA, DARIEN: Rio Chico, vicinity of Yaviza, P. H. Allen 4578 (U).

COLOMBIA, AMAZONAS: Rio Putumayo, near mouth of Rio Igaraparaná, Schultes 3987 (U).

VENEZUELA, AMAZONAS: Casiquiare, Vasiva, and Pacimoni Rivers, Spruce 3204 (NY, syntype coll.).

BRITISH GUIANA: Bartica-Potaro Road, Forest Dept. F1465–4201 (NY).

BRAZIL, AMAZONAS: basin of Rio Solimões, municipality São Paulo de Olivença, near Palmares, Krukoff 8101 (U), 8170 (U); basin of Rio Juruá, near mouth of Rio Embira (tributary of Rio Tarauacá), 7° 30' S, 70° 15' W, Krukoff 5016 (U); basin of Rio Madeira, municipality Humaitá, near Três Casas, Krukoff 6186 (U); *ibid.*, near Livramento, on Rio Livramento, Krukoff 6580 (U).

Terr. ACRE: basin of Rio Purus, near mouth of Rio Macauá (tributary of Rio Iaco), 9° 20' S, 69° W, Krukoff 5304 (U); between Rio Abunan and Rio Acre, Kuhlmann HJBR 18075 (U).

BOLIVIA, LA PAZ: Larecaja, Tuirí (near Mapiri, on left bank of Rio Mapiri), Krukoff 10736 (U); *ibid.*, Mapiri, Rusby 723 (NY).

Section *Tibourbou* Schum.

Leaves (crenate-) serrate, with hairs on nerves only (the number of hairs per nerve roughly proportional to nerve size on the lower sides, hairs on upper sides more evenly distributed on nerves). No hair tufts at base of nerves. Petioles not or but slightly incrassate in their apical part.

Stellate hairs on vegetative parts with rays up to $\frac{1}{2}$ –1 (–2) mm long, with brown cell contents (in sicco). Those on small nerves with rays mostly directed upward at a fairly large angle, thick- to very thick-walled, the largest width usually at the base, the entire stella sometimes on a slight elevation (Fig. 3, E, F, G; Fig. 4, A, B). Stellate hairs on primary nerves, petioles and twigs with somewhat more irregularly bent or directed rays (Fig. 3, H, I, J; Fig. 4, D, E), the stellate hairs on secondary and tertiary nerves being \pm transitional. Simple hairs on large nerves, petioles and twigs often conspicuous, the petioles and twigs then hirsute by spreading hairs to 2–3 mm long (Fig. 4, C), the nerves with more appressed hairs, at least on the lower sides; simple hairs on secondary and smaller nerves of smaller size, to about as long as the rays. Stipules and bracts on the abaxial side with mostly appressed simple hairs (shorter than

those on the twigs), all or most of them confined to the middle zone, the margin ciliate by simple hairs of somewhat smaller size; comparatively small and few-rayed stellate hairs also present.

***Apeiba schomburgkii* Szyszyl.**

Leaves 12–23 (–24) cm long and 6–11 cm wide, first pair of lateral primary nerves $\frac{1}{3}$ – $\frac{1}{2}$ of the length of the median one, second pair weakly developed; secondary nerves (5–) 6–7 (–8) on each side of the median primary nerve. Large nerves somewhat prominent above, quite prominent below. Both leaf sides stellate hirsutulous-pubescent, the lower more densely so. Petioles 1–2 cm long, very slightly incrassate (over a length of $\frac{1}{2}$ –1 cm) or not incrassate at the apical end.

Stellate hairs on tertiary and smaller nerves on lower sides often on small elevations, with (2–) 4–20 (–25), averaging about 8–12, rays of 0.15–0.80 (–1.00) mm, averaging ca. 0.50–0.60 mm, long and with a largest width of ca. 15–22 μ , with brown-yellow cell walls, the cell lumen nearly obliterated except at the base (Fig. 3, E, F, G). Stellate hairs on upper leaf sides somewhat differing from those below: rays 2–10, averaging about 4–6, ca. 0.10–0.40 mm, averaging ca. 0.20–0.30 mm, long. A few simple hairs similar in size and shape to the rays occurring among the stellate hairs. Large nerves, petioles and twigs with an indument varying from fairly dense to rather sparse: stellate hairs with more variably directed rays than those on the leaves, also somewhat smaller, ca. 0.07–0.70 (–1.00) mm, averaging ca. 0.25–0.40 mm, long (Fig. 3, H, I, J); numerous simple hairs among the stellate hairs, often exceeding them in number and mostly on distinct elevations, to 2 $\frac{1}{2}$ –3 mm long and ca. 40 μ in largest diameter. Stipules on their abaxial side with simple hairs to 2 mm long and with similar hairs to 1 $\frac{1}{2}$ mm long on the margin; stellate hairs with an average of about 4–5 rays, these (30–) 50–200 (–250) μ long and with a largest diameter of ca. 10–13 μ , mostly appressed or slightly elevated.

Material seen:

TOBAGO: Bacolet, Sandwith 1874 (U); valley of Doctor's River, SE of Charlotteville, Webster, Ellis and Miller 9822 (U).

TRINIDAD: Cascade, Beard 138 (U); Botanic Garden, Kostermans A15043 (U).

BRITISH GUIANA: Western extremity of Kanuku Mts., in drainage of Takutu River, A. C. Smith 3111 (U).

SURINAME: Corantijn River, Tramway Falls, Rombouts 155 (U); Voltzberg, Pulle 217 (U, type of *Apeiba surinamensis* Uittien).

BRAZIL, AMAZONAS: Upper Rio Branco, Bôa Vista, Kuhlmann HJBR 3513 (U).

***Apeiba tibourbou* Aubl. (including *A. albiflora* Ducke)**

Leaves 14–35 (–40) cm long and 6–15 (–17) cm wide, first pair of lateral primary nerves $\frac{1}{3}$ – $\frac{1}{2}$ of the length of the median one, second pair varying from weakly developed to manifest, up to ca. $\frac{1}{3}$ of the length of the first pair, a third pair often discernible. Secondary

nerves 8–12 (–13) on each side of the median primary nerve. Lamina slightly rugose (almost flat only in Wurdack and Guppy 113) to very rugose, stellate-pubescent to hirsutulous on both sides. Petioles 1–3½ cm long, not incrassate or (in comparatively long-petioled specimens) faintly incrassate at the apical side over a length of ½–1½ cm. Stipules often fairly persistent, remaining much longer than in other *Apeiba* species, 1½–3 cm long, 4–8 mm wide.

Stellate hairs on lower leaf sides on small elevations or not, with 4–15 (–20), averaging about (6–) 8–10, rays 0.2–1.0 (–1.2) mm, averaging ca. 0.6–0.7 (–0.8) mm, long and with a largest diameter of 12–17 μ , with colorless to faintly brown-yellow cell walls, the cell lumen widest at the base, narrow elsewhere; densest indument, along with greatest ray numbers, observed on tertiary nerves, greatest ray lengths (often) on quaternary nerves (Fig. 4, A, B). Stellate hairs on upper leaf sides with ca. 2–10, averaging ca. 4–5, rays of ca. 0.2–0.8 (–1.0) mm, averaging ca. 0.3–0.5 mm, long and with a largest diameter up to 20 μ , the stellae with most rays again on tertiary nerves; specimens with very rugose leaves bearing very few hairs on quaternary and smaller nerves on upper side. Simple hairs on upper leaf sides mostly of same size as rays, sometimes up to 1½–2 mm long and 25 μ in largest diameter. Indument of primary and secondary nerves more or less transitional.

Indument of petioles and twigs showing two extremes, in combination with certain other characters, viz.:

I. Petioles and twigs densely villous with predominantly stellate hairs having less than 8 (–10) rays on the average, these rays to 2 mm long, averaging ca. ¾–1 mm, and usually directed upward at an angle close to 90 degrees (compare Fig. 4, E). Simple hairs on twigs not exceeding stellate hairs in length and also (far) less in number than those, on petioles (and large nerves) sometimes more evident. Leaves strongly rugose, commonly oblong and mostly shorter than 20 cm; petioles ca. 1–1½ cm long, not incrassate.

II. Petioles and twigs hirsute with a great number of spreading simple hairs up to 3 mm long and 30–40 (–50) μ in largest diameter (Fig. 4, C), furthermore covered in somewhat variable degree by stellate hairs with rays up to 2 mm long (fig. 4, E), but averaging not more than about ½ mm (often much less), the average ray number usually 10 or more per stella (largest numbers in small ones), the rays directed at very variable angles even within one stellate hair (Fig. 4, D). Leaves mostly somewhat rugose, elliptic to elliptic-oblong, mostly longer than 20 cm; petioles ca. 2–3½ cm long, slightly incrassate apically or not.

Stellate rays in both groups from ca. 50 μ to ca. 2 mm long and with a largest diameter of ca. 10–20 (–25) μ . Stipules on abaxial side with simple hairs to 2–2½ mm long, the margin with (often comparatively thin-walled) simple hairs up to 1 mm long; stellate hairs more or less covering the entire abaxial surface or largely confined to the middle zone, with 2–10, averaging ca. (5–) 6 (–7), rays to 0.2 mm long and ca. 12 μ in largest diameter.

Most of the specimens examined can be placed in one of the two groups just described, hence to be referred to as group I and group II respectively. The material collected in the Guiana's largely comes within group I. The typical collections may be enumerated:

I. Breteler 3867, Fanshawe in Forest Dept. 3438, Fanshawe s.n., Fanshawe in Forest Dept. 3354, Schulz and Elburg LBB 10124, Lindeman 4750, Schulz 8513, Exp. Wilhelmina Geb. 71, BAFOG 7280, Sagot s.n., Black 47-1901, Lisbôa HJBR 4730.

II. Holm and Iltis 247, Dodge *et al.* 16631, Johnston 8, Harris 6506, Schulz 35, Vogl 702, Wurdack and Guppy 113, Krukoff 5291, 1074, Huber Herb. Mus. Goeldi 9333, Fróes 1807, Krukoff 1518, Klug 4213.

Group I conforms to *Apeiba albiflora* Ducke (1922); Lisbôa HJBR 4730 is one of the collections on which Ducke based his species; see also remarks by BURRET apud DUCKE (1938), p. 51. Group II, then, is *A. tibourbou* in the proper sense. White flowers and more globular fruits with very long and softer spines are mentioned as characters to distinguish *A. albiflora* from *A. tibourbou*. UITTEN, in his revision of the genus (1935), concludes that the fruit shape is variable and cannot be relied upon and states that the white flower color is of no importance at all for the taxonomy of a genus which includes species with white flowers (*A. schomburgkii*) and yellow flowers as well. One may object to this statement, taken in its absolute sense, but in *Apeiba tibourbou/albiflora* collector's data on flower color are too scarce and sometimes vague and cannot have much conclusive force yet. Uittien, for those reasons, puts *A. albiflora* under synonymy with *A. tibourbou*.

As to vegetative characters examined by me, specimens intermediate in one or more respects were found. These will be commented upon now. Steinbach 6707 has very rugose, elliptic leaves with petioles to 2 cm long and slightly incrassate apically, the indument being conform to that of group I (petals indicated as white); Lanjouw 935 agrees in its leaf shape and size with group I, but the lamina is less rugose than in the collections cited above, the indument, with simple hairs clearly in evidence, tending towards that of group II; Dumortier 18 conforms to group I except for its elliptical leaves; also largely belonging to group I are Maas and Tawjoeran LBB 10902 and Lindeman 6197, the indument in the first somewhat tending towards that of group II, as also does to some extent that in the second, the leaves of which, in addition being less rugose than average in group I. On the other side there are two collections belonging to group II in most respects, but one, BAFOG 7840, has petioles only $1\frac{1}{4}$ – $1\frac{1}{2}$ cm long and a lamina more rugose than is normally seen in group II, and the other, Breteler 3910, has an indument tending towards that of group I. A short glance I could take at the herbarium material in NY (not cited, because lack of time kept me from a more extensive microscopical examination) made me suspect that several other collections could augment this series.

It seems wisest, in view of this, to stick to Uittien's decision now

and regard the whole *A. tibourbou* complex as a single, variable, species. Ducke's concept certainly has some appeal, and eventually may still prove to be right, but extensive investigation of more material must be carried out first.

Material seen:

COSTA RICA, PUNTARENAS: vicinity of Cascajal, 25 km ESE of Puntarenas, Holm and Iltis 247 (U).

PANAMA, PANAMA: along road between Panamá and Chepo, Dodge *et al.* 16631 (U).

PERLAS ARCHIPELAGO: San José Island, Johnston 8 (U).

JAMAICA: Hope, Harris 6506 (NY).

VENEZUELA, BARINAS: Pedraza, Ticoporo, Rio Bumbum, Schulz 35 (U); Ticoporo Forest Reserve, bank of Rio Bumbum, 8° 15' N, 70° 45' W, Breteler 3910 (U).

SUCRE: Las Penas, Vogl 702 (U).

BOLÍVAR: Hato de la Vergarena, Rio Saca, Wurdack and Guppy 113 (NY).

Near the border (= Rio Grande o Toro) between Edo. BOLÍVAR and Terr. DELTA AMACURO, ca. 8° 4' N, 61° 44' W, Breteler 3867 (U).

BRITISH GUIANA: Mazaruni Station, Fanshawe in Forest Dept. 3438 (U), Fanshawe s.n. (NY); Essequibo River, Tiger Creek, Fanshawe in Forest Dept. 3354 (NY).

SURINAME: between Lucie River and Wilhelmina Range, Schulz and Elburg LBB 10124 (U); Nickerie River, near Blanche Marie Falls, Maas and Tawjoeran LBB 10902 (U); Voltzberg, Lanjouw 935 (U); Suriname River, Jodensavanne, Mapane Creek area, Lindeman 4750 (U), Schulz 8513 (U); *ibid.*, upper course, near Goddo, Exp. Wilhelmina Geb. 71 (U); between Moengo Tapoe and Coermotibo Creek, Lindeman 6197 (U); without locality, Dumortier 18 (U).

FRENCH GUIANA: St. Laurent, BAFOG 7280 (U); Tampoc River, BAFOG 7840 (U); Acarouany, Sagot s.n. (U).

BRAZIL, Terr. ACRE: near mouth of Rio Macauã (tributary of Rio Iaco), 9° 20' S, 69° W, Krukoff 5291 (U).

PARÁ: Belterra, Black 47-1901 (U); Upper Cupari River, plateau between Xingú and Tapajós Rivers, Krukoff 1074 (U); Belém, Huber Herb. Mus. Goeldi 9333 (U).

MARANHÃO: Maracassumé River region, Fróes 1807 (U); Cururupá, Lisbôa HJBR 4730 (U, syntype coll. of *Apeiba albiflora* Ducke).

MATTO GROSSO: near Tabajara, Upper Machado River region, Krukoff 1518 (U).

PERU, SAN MARTÍN: Juan Jui, Alto Rio Huallaga, Klug 4213 (U).

BOLIVIA, SANTA CRUZ: Sara, Buena Vista, Steinbach 6707 (U).

***Apeiba tibourbou*, var. *krukoffii* Uittien**

Leaves 20–30 cm long, 6–9 cm wide, with 5–7 (–8) secondary nerves on each side of the median primary nerve; lamina oblong to oblong-obovate, very rugose and thin. Petioles 1–1½ cm long, not incrassate. Stipules as with the species, 1–1½ (–2) cm long and 2–3 (–4) mm wide.

Leaves more sparsely hairy (except for large nerves) than in the species; stellate hairs on lower leaf sides with 2–8, averaging ca. 5, rays up to 1¼ mm long, averaging ca. 0.7–0.8 mm, on upper leaf sides with 2–6, averaging ca. 3 (–4), rays often directed upward at a large angle, up to 1½ mm long, averaging ca. ¾–1 mm, with a largest diameter to ca. 20 µ; a few simple hairs among the stellae, equal in size and shape to the rays. Large nerves, petioles and twigs with a dense indument (that of the twigs slightly thinner than that of the

petioles, otherwise similar); stellate hairs as described for group I under *A. tibourbou*, but simple hairs present as in group II, to 3-3½ mm long and 40-50 μ wide.

The above description applies to the type specimen which was the only one known to Uittien. Uittien's citation of Harris 6506 from Jamaica must be a mistake: the material seen by me in NY agrees with *A. tibourbou*, group II, and BURRET (in DUCKE, 1938) rightly calls it 'a typical tibourbou'. More recently, Lindeman collected sterile twigs in Surinam (Lindeman 6149) with leaves conspicuously resembling those of var. *krukoffii*; they are slightly smaller and somewhat less rugose. The indument on the lower leaf sides is similar to that of the type, but the hairs are somewhat smaller on the average; on the upper leaf sides simple hairs are slightly more numerous than in the type. The indument of petioles and twigs, however, is that of group II.

BURRET (l.c.) reckons the type collection of var. *krukoffii* to *A. albiflora*. Although it indeed seems to come closest to group I (or *A. albiflora*), it is certainly not perfectly identical with that, as Burret would have it. Scarcity of material does not warrant any conclusions as to the status of var. *krukoffii* at this moment.

Material seen:

SURINAME: between Moengo Tapoe and Coermotibo Creek, Lindeman 6149 (U) (provisionally placed here).

BRAZIL, MATTO GROSSO: source of the Jatuarana River, Machado River region, Krukoff 1567 (U, type).

KEY TO THE SPECIES OF APEIBA, BASED ON VEGETATIVE CHARACTERS

The foregoing may be summarized in the following key:

- 1. Leaves entire or (faintly) serrate-dentate near the apex, with stellate hairs with rays not or rarely more than 150 μ long, the stellae thus barely discernible by the naked eye, with the exception of hair tufts often present at the base of large nerves; simple hairs on petioles and twigs few, inconspicuous, or lacking (Sect. **Petoumo**) 2
 - Leaves (crenate-)serrate, with stellate hairs with rays to ¼-1½ mm long, the stellae thus easily discernible by the naked eye; no hair tufts at the base of nerves; simple hairs often many, conspicuous (Sect. **Tibourbou**) 6
- 2. First pair of lateral primary nerves ¾ or more of the length of the median one, the latter with 3-4 secondary nerves on each side; stellate hairs on leaves often somewhat scale-like **A. glabra**
 - First pair of lateral primary nerves about ½ (to ¾ at the most) of the length of the median one, the latter usually with 5 or more secondary nerves on each side; stellate hairs on leaves (some venular stellae excepted) not scale-like 3
- 3. Lower leaf sides covered by a dense tomentum of stellate hairs so close together as to be undistinguishable individually (a few venular stellae excepted) 4
 - Stellate hairs on lower leaf sides distinguishable individually or the majority of them so; hair tufts at the base of large nerves on lower sides present, sometimes inconspicuous 5

4. Nearly always conspicuous hair tufts at the base of lateral primary nerves on lower sides, no tufts elsewhere; average ray length of stellate hairs on lower leaf sides (usually) less than 90μ **A. echinata**
(Very) inconspicuous hair tufts at the base of secondary nerves of the median primary nerve on lower side present or absent; average ray length of stellate hairs on lower leaf sides more than 90μ **A. echinata**, var. **macropetala**
5. Stellate hairs on lower leaf sides with an average ray length more than 70μ **A. intermedia**
Stellate hairs on lower leaf sides with an average ray length less than 70μ **A. membranacea**
6. Leaves without raised mesophyll, stellate hairs on small nerves below with rays $15-22 \mu$ in largest diameter, with brown-yellow cell walls **A. schomburgkii**
Leaves slightly to strongly rugose; stellate hairs on small nerves below with rays $12-17 \mu$ in largest diameter, with colorless to, at most, faintly brown-yellow cell walls 7
7. Leaves slightly to strongly rugose with an obvious to quite dense stellate indument, stellate hairs on small nerves below with up to $15(-20)$, averaging mostly $8-10$, rays **A. tibourbou** (s.l.: 8)
Leaves strongly rugose, quite glabrous in appearance, with scattered stellate hairs, rays on small nerves below to 8 per stella, averaging ca. 5 **A. tibourbou**, var. **krukoffii**
8. Leaves strongly rugose, mostly shorter than 20 cm; simple hairs, at least on twigs, not exceeding stellate hairs in length. **A. albiflora**
Leaves slightly rugose, mostly longer than 20 cm; simple hairs on twigs conspicuously exceeding stellate hairs in length **A. tibourbou** s.s.)

ACKNOWLEDGEMENT

The author is much indebted to Dr. A. M. W. Mennega for her assistance during the work and for critically reading the manuscript.

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