

NEW DISCOVERIES OF GNETUM IN TROPICAL AMERICA

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As yet the peculiar gymnospermous genus *Gnetum* in the New World is only known by six species in the Amazon Basin and in the Guyana Highland. These species are differently distributed: 1) *G. urens* (Aubl.) Bl. follows the coastal rain forest from the lower Orinoco River (Catalina) to south of the lower Amazon River (Bragança); 2) *G. nodiflorum* Brongn. inhabits savannahs and wood edges in the Guyana Highland from its eastern border up to the Rio Negro in Venezuela, and similar situations of the Terra Firme in the Amazon region; 3) *G. paniculatum* Spruce is rarer in the Guyana Highland and runs from its eastern border to its southern border, following the Rio Negro valley; 4) *G. venosum* Spruce is found only in the rain forest of the lower and middle Amazon River up to Manáos; 5) *G. Schwackeanum* Taub. has a similar distribution, but seems to extend a little farther up the right tributaries (Rio Madeira, Rio Acre); 6) *G. Leyboldii* Tul. is bound to the wet rain forests, even swampy igapó forest, in the real lowlands along the whole Amazon River, stopping at the tributaries below the rapids (cachoeiras).

By the kindness of several American herbaria specimens of this genus came under my eyes, collected in Panama, and thus extending considerably the area of the genus. Of course now the question arises, where their affinities are to be sought. Morphologically, they stand forth by large, often almost orbicular leaves shining silk-like on the upper surface by means of a dense subepidermal layer of fibres parallel to the secondary nerves. Inflorescences, flowers and fruits correspond to those of *G. Leyboldii* Tul.; now this species is Amazonian. But the large geographical gap is bridged over by a discovery made by Oscar Haught¹ in 1935 in the valley of Rio Magdalena in western Colombia. This sample agrees completely with those from Panama.

In the meantime, Swedish botanists, E. Asplund and F. Fagerlind with G. Wibom, have discovered the genus *Gnetum* even in Ecuador² and R. E. Schultes with G. A. Black and J. Cabrera also in southwestern Colombia. They found two species, *G. nodiflorum* Brongn. and *G. Leyboldii* Tul. In Ecuador the species reach the district of Tunguragua, in Colombia that of Rio Uaupès. On the eastern slope of the Andes, they ascend a little higher up together with the rain forest (to about 250 m above sea level); as maximum altitude Asplund fixed 1200 m on Rio Pastaza. Both species however stop at the lower part of that eastern slope. The taxon of the Rio Magdalena remains separated by the Eastern Cordillera. By this segregation its morphological differentiation from the similar Amazonian *G. Leyboldii* may well

¹ His samples were named by Killip as *Gnetum colombianum* on the herbarium sheets, but this name seems to have never been published.

² An old-mentioned species of Ecuador, *Gnetum trinerve* Spruce (Notes of a botanist in the Amazon and Andes 2 (1908) 279), according to its type specimen at Kew has proved to be a Loranthaceae described by Trelease as the type of his *Phoradendron trisulcatum* (Trelease, the genus *Phoradendron* (1916) 155).

be understood. As the Magdalena Basin had its last regression of the sea only in Pliocene times,³ and thus became accessible for a land Flora not earlier, even the age of differentiation of its taxon from the similar *G. Leyboldii* in the Amazon Basin is made probable. On the other side, between the Magdalena Valley and Panama, since that time there were no mountain obstacles for its distribution. One may expect that the same taxon will be found in the interlying region too.

Its taxonomic position seems nearest to *G. Leyboldii* Tul. The characters of flower and fruit agree so well that it is distinguished only by the shape and fibrousness of the leaves and by the shorter and poorer inflorescences. Thus it is introduced here with the rank of a variety below *G. Leyboldii*.

In order to show it in the whole relationship and to include, at the same time, the other above mentioned discoveries, it may be welcome to have established a conspectus⁴ of all the American species of that genus.

A. Bract collars of inflorescences close to each other (in male ones at the most 2 mm, in female ones at the most 10 mm distant), their margin slightly incurved, their base tapering sinuously into the axis.

I. Adult leaves large, up to 20×15 cm, heavily coriaceous, generally not becoming black when dry. Whole inflorescence much ramified, loose, partial inflorescence on a stalk about 10 mm in length, male one about 15 mm, female about 30 mm long. Male bract collars in anthesis 2 mm distant, female ones 4-8 mm distant, in fruit about 10 mm distant. Sterile female flowers of male inflorescence obovate, fertile female flowers ellipsoidal, acuminate. Fruit oblong, parallel-edged, 45-50 mm long, 20 mm wide, fleshy, its outermost layer thick (1 mm when dry), the innermost solid. *G. Leyboldii* Tul.

a) Leaves broad-elliptic (length to width 1.4-1.7), gleaming silky by means of dense fibres under the epidermis. Inflorescence bearing only 1-2 whorls at the main axis. Colombia to Panama. var. *Woodsonianum* Mgf.
b) Leaves elliptic (length to width 1.7-2), without dense fibres. Inflorescence bearing 3-4 whorls at the main axis. Amazon basin. var. *Leyboldii*.

II. Adult leaves large, up to 17×8 cm, somewhat more tender, often becoming black when dry. Whole inflorescence much ramified, condensed, partial inflorescence almost sessile, about 10 mm long. Male bract collars close to each other even in anthesis, female ones up to 2 mm distant. Sterile female flowers of male inflorescence shortly ellipsoidal, blunt. Fertile female flowers almost globose. Fruit broad-ellipsoidal, 50 mm long, 30 mm wide, its outermost layer very thick (3 mm when dry), the innermost solid. Guyana highland till Rio Negro. *G. paniculatum* Spruce

III. Adult leaves small, up to 12×6 cm, softly coriaceous, yellowish green, gleaming silky by means of dense subepidermal fibres. Whole inflorescence loose, but its lateral twigs mostly not again ramified; partial inflorescence shortly stalked, male one about 10 mm, female one about 20 mm long. Male bract collars 1 mm distant, female ones up to 10 mm distant. Sterile female flowers of male inflorescence cylindric, fertile female flowers oblong, acuminate. Fruit ellipsoidal, slightly obovate, 35-40 mm long, 18-20 mm wide, its outermost layer thin, fibrous, the innermost chartaceous. Coastal forest from Orinoco to Amazon river. *G. urens* (Aubl.) Bl.

B. Bract collars of inflorescences distant (in anthesis 10-20 mm, in fruit mostly 20 mm), dish-like, their margin upright, their base not tapering into the axis.

I. Adult leaves up to 18×9 cm, heavily coriaceous, not gleaming, generally not becoming black when dry. Whole inflorescence very loose, partial inflorescence on a stalk about 20 mm in length, about 100 mm long. Male bract collars in anthesis

³ Buergl, Historia Geologica de Colombia, in Revista de la Academia Colombiana de Ciencias Exactas, Fisicas y Naturales **11** (1961) 173, 170, fig. 40.—Gerth, Der Geologische Bau der Südamerikanischen Kordillere (Berlin 1955) 157, 240.

⁴ Completing that of a monograph in Bull. Jard. Bot. Buitenzorg, 3 sér., **10** (1930) 498.

10 mm distant, female ones 20 mm, fruiting 20 mm. Sterile female flowers of male inflorescence ovate, acuminate; fertile female flowers ellipsoidal. Fruit shortly ellipsoidal, 30-35 mm long, 20 mm wide, its outermost layer thin ($\frac{1}{4}$ mm when dry), the innermost very thin. Guyana Highland and Amazon region.

G. nodiflorum Brongn.

- II. Adult leaves up to 12×6 cm, softly coriaceous, becoming slightly black when dry, slightly gleaming silky by means of parallel subepidermal fibres. Whole inflorescence loose, but only moderately ramified; partial inflorescence on a stalk 10-15 mm in length, 30-50 mm long. Bract collars in anthesis 10-15 mm distant. Sterile female flowers of male inflorescence obovate; fertile female flowers ellipsoidal, acuminate. Fruit oblong-obovate, 35 mm long, 20 mm wide, its outermost layer thin, almost without fibres, the innermost chartaceous. Lower and middle Amazon river. *G. Schwackeanum* Taub.
- III. Adult leaves up to 13×6 cm, softly coriaceous, often obovate, becoming black when dry, gleaming silky by means of dense subepidermal fibres. Whole inflorescence rather loose; partial inflorescence on a stalk 10-15 mm in length, 50-60 mm long. Bract collars in anthesis 5 mm distant. Sterile female flowers of male inflorescence oblong-obovate; fertile female flowers oblong, acuminate. Fruit ellipsoidal, 7 cm long, 4 cm wide, ellipsoidal with acuminate top, its outermost layer fleshy and fibrous, 3 mm thick, the innermost chartaceous. Lower and middle Amazon river. *G. venosum* Spruce.

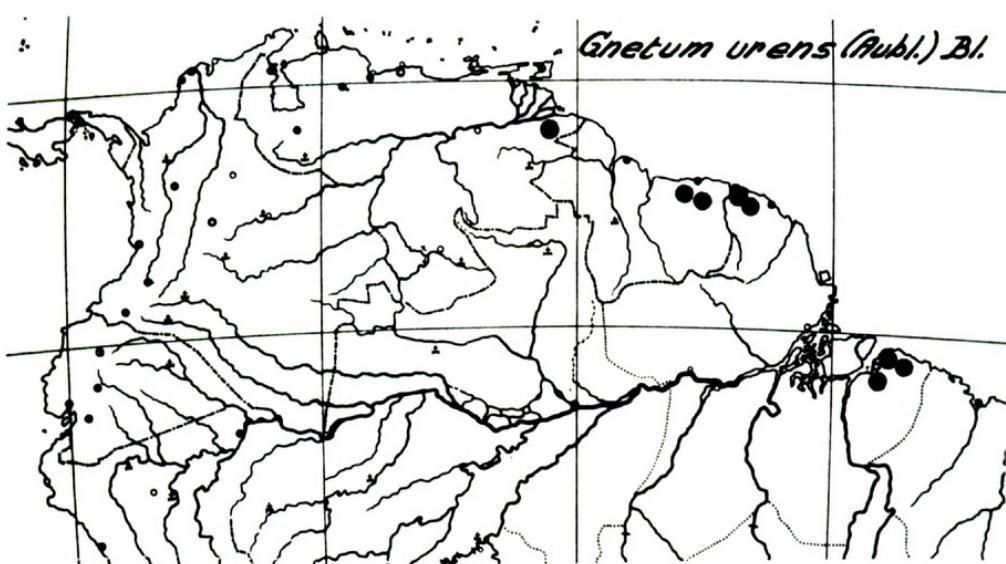
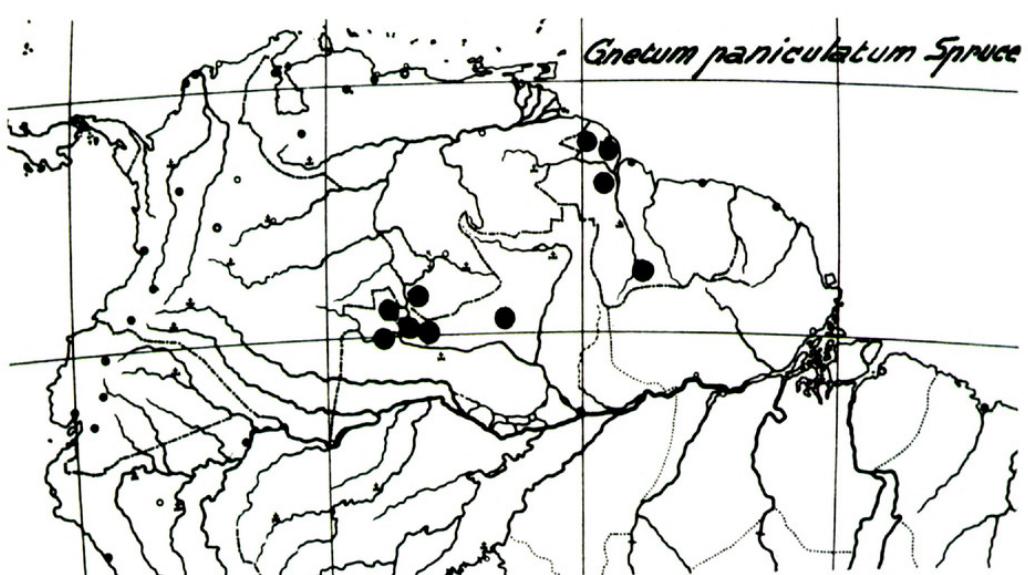
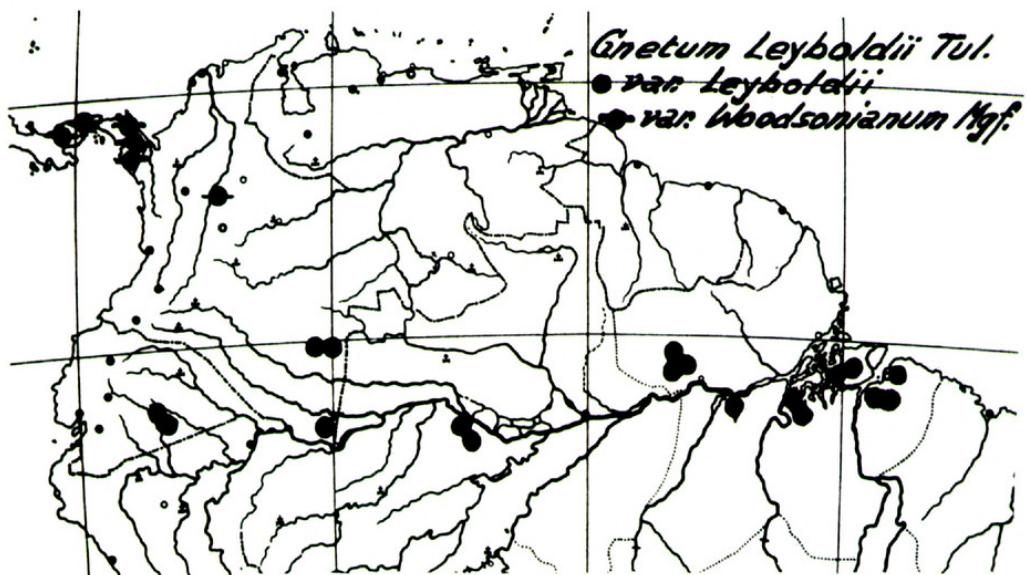
The respective areas of the species are documented by the following localities (see sketch maps).

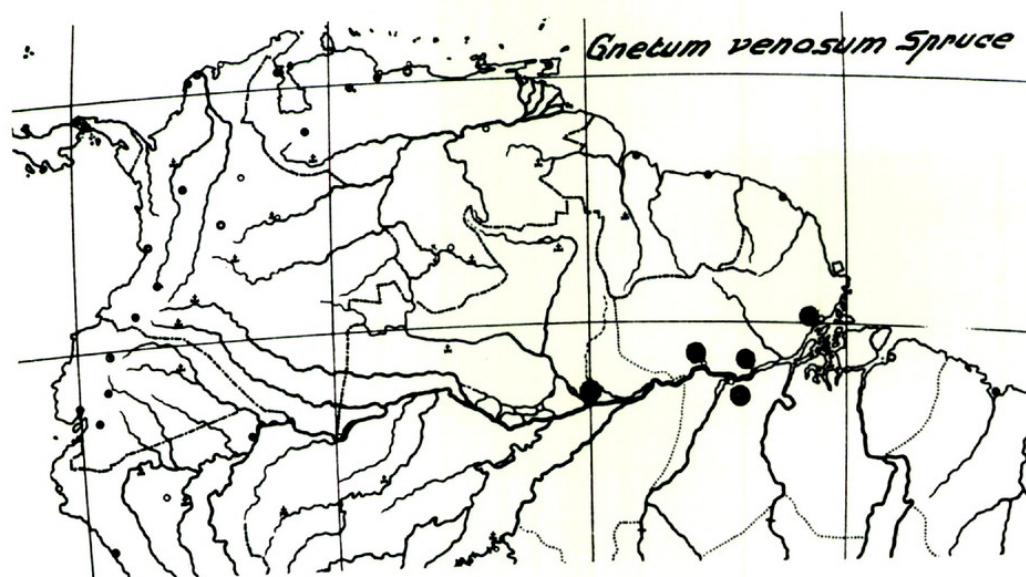
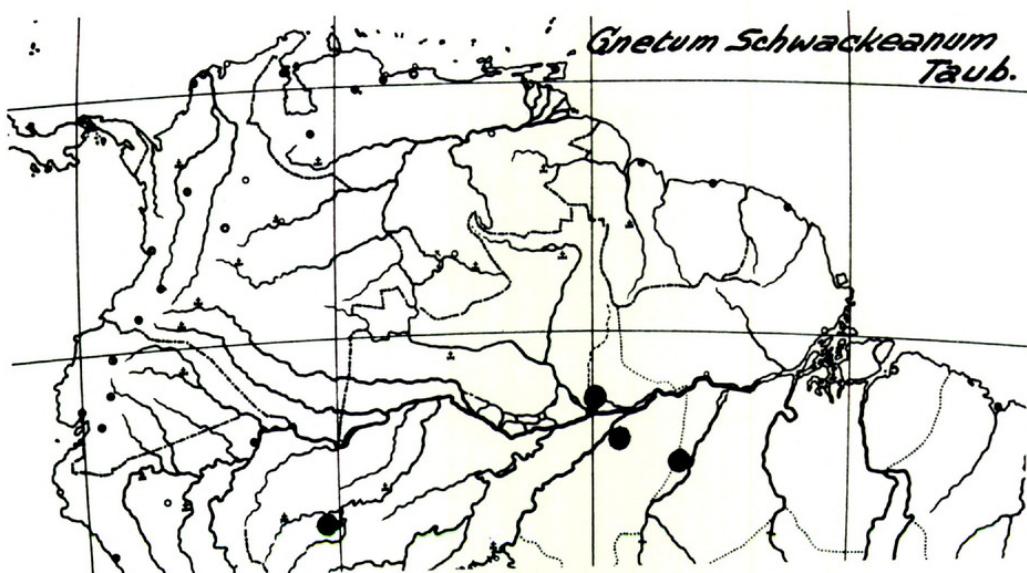
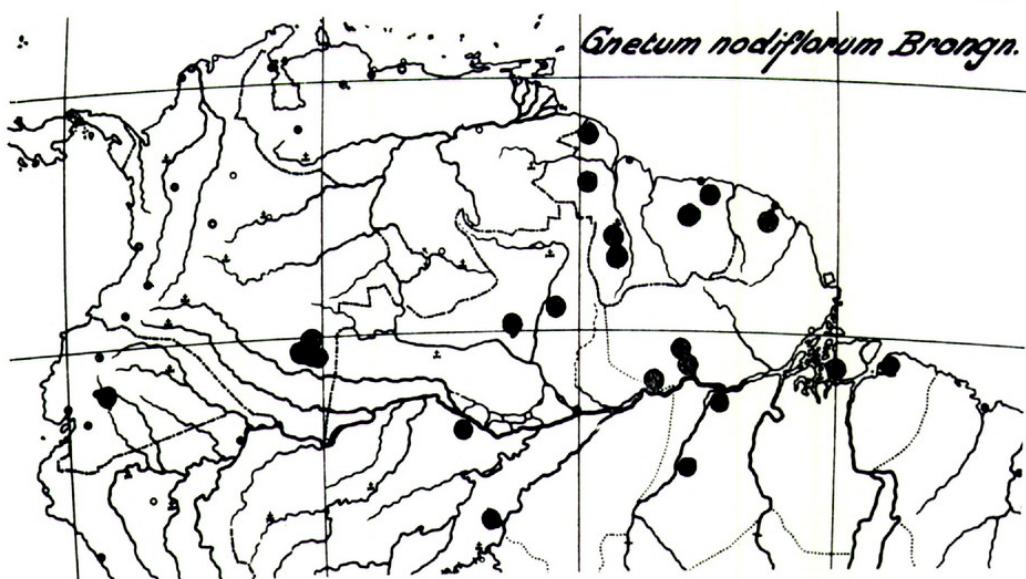
1. *Gnetum urens* (Aubl.) Bl., Tijdschr. Natuurl. Geschied. **1** (1834) 155. (*Thoa urens* Aubl., Pl. Guyane Franç. **2** (1775) 874; *Gnetum Thoa* R. Br. ex Brongn. in Duperrey, Voy. sur la Coquille (1829) 12; *G. Melinonii* Benoist, Bull. Mus. Hist. Nat. Paris 2 Sér. 17 (1945) 66).

VENEZUELA: Catalina (lower Orinoco), ♂ fl, May 1896, Rusby & Squires 424 (Z). SURINAME: Bergendal at the Suriname River, ♂ fl, Focke 1314 (U); Saramacca River, ♂ fl, Weigelt ? (G). FRENCH GUIANA: Acarouany (NW), fr, 1855, Mélinon (G), Sagot 493 (P); Maroni, Mélinon (P). NORTHERN BRAZIL: PARÁ: Bragança, Colonia Benjamin, in silva secundaria, fr, 17.11.1908, Ducke 19410 (RB); Estrada de Tracutena, capoeira, fr. 11.6.1952, Fróes 28489 (IAN); Município de João Coelho, estrada de ferro de Bragança, capoeira, fr, 13.5.1956, Ferreira (IAN); Belém. mata do mocambo IAM, fr, Nov 1951, Black 51-14108 (US).

2. *Gnetum nodiflorum* Brongn. in Duperrey, Voy. sur la Coquille (1829) 12. (*G. amazonicum* Tul., Ann. Sc. Nat. 4 Sér. **10** (1858) 116; *G. Cruzianum* Gleas., Bull. Torrey Bot. Cl. **52** (1925) 196.)

BRITISH GUIANA: Amakura River (NW), ♂ fl, De La Cruz 3522 (NY); Kamakusa, Mazaruni River, $59^{\circ}50'W$, ♂ fl, July 1923, De La Cruz 4222 (NY); Sandige Savanne am Demerara, ♂ fl & fr, Apr 1844, Rich. Schomburgk 1013 (W); Rupunini River, Isherton, fr, 1937, A. C. Smith 2420 (K); Moraballi Creek, fr, 1929, Sandwith 531 (K); Kanuku Mts., Wabuwak, 600 m, ♀ fl & fr, Oct 1948, Wilson Browne 5738 (K). FRENCH GUIANA: Cayenne, ♂ fl, 1819/21 Poiteau (G, Isotype); ♂ fl, 1821, Perrotet 176 (G). NORTHERN BRAZIL: PARÁ: Região de Ariramba, Campo do Mutum, á beira do campo, ♂ fl, 28.5.1957, Black, Egler, Cavalcante & Silva 57-19672 (IAN); Ilha de Colares, município de Vigia, Sítio Horizonte, fr, 29.9.1954, Black 54-16935 (IAN); Município de Breves, perto do Igarapé Arapigó, fr. 5.11.1958, Guedes 661 (IAN); Bellavista, lower Tapajoz River, in campis arenosis apertis, Campina do Perdido, unterhalb der Cachoeira Maranhãozinho, fr, 12.9.1916, Ducke 19406 (RB); Cunani, fr, 13.10.1895, Huber 1031 (MG, G); Santarem Alto do Chão, silva non inundata, ♀ fl, 22.6.1910, Ducke 10821 (MG); Obidos, ♀, Jan 1921, unknown collector (RB). AMAZONAS: ad ripam Lago Faro, ♀, 3.9.1907, Ducke 8581 (MG); Vista Alegre, no meio Rio Branco, matas de Savanna, ♂ fl, March 1913, Kuhlmann 2977 (RB); Cachoeira do Rio





Aracá, subafluente do Rio Negro, ♀ fl, 29.10.1952, *Froes & Addison* 29179 (IAN); Ega (=Teffe), ♀, Sept 1831, *Poeppig* 2601 (W.) ECUADOR: PROV. Tungurahua, Rio Negro, fr, 9.11.1952, *Fagerlind & Wibom* 1238 (LD). COLOMBIA: Amazonas, Río Caquetá, La Pedrera, ♂ fl, July 1948, *Schultes & Lopez* 10220A (US); Amazonas-Vaupés, Rio Apaporis, Raudal Yacayacopí (La Playa), 250 m, 0°5'S, 70°30'W, fr, 18.8.1952, *Schultes & Cabrera* 16909 (US); Río Apaporis, Jinogojé (at mouth of Río Piraparaná) & vicinity, alt about 700 ft, 0°15'S, 70°30'W, fr, 27.2.1952, *Schultes & Cabrera* 15667, 16656 (US); Rio Apaporis, entre el rio Pacoa y el rio Takunema, Cerro de la Hoz, alt ca 250 m, fr, 21.9.1951, *Schultes & Cabrera* 14119 (US); Rio Apaporis Raudal de Jirijirimo (below mouth of Rio Kananarí), Quarzite base, 900 ft, 0°5'N, 70°40'W, fr, 15.3.1952, *Schultes & Cabrera* 15932 (US); Rio Piraparaná (tributary of Rio Apaporis, lower course), between 0°15'S, 70°30'W and 0°25'N, 70°30'W, fr, 9.3.52, *Schultes & Cabrera* 15921 (US).

3. *Gnetum paniculatum* Spruce ex Bentham in Hook., J. Bot. and Kew Gard. Misc. **8** (1856) 357. (*G. microstachyum* Spruce, loc. cit.)

BRITISH GUIANA: Assakatta (NW), fr, *De La Cruz* (NY); Essequibo, ♂ fl, 1928, *Sandwith* (K); Moraballi Creek, *Sandwith* 36, 376, 420, 527 (K); Barabara Creek, ♂ fl, For. Dept 3559 (K); Black Creek, ♂ fl, For. Dept 4525 (K); Demerara River, ♂ fl, *Jenman* 6880 (K). FRENCH GUIANA: Le Monnier (G.). VENEZUELA: Rio Guainia (upper Rio Negro) San Carlos, ♂ fl, 1853/4 *Spruce* 1923 (K, holotype). NORTHERN BRAZIL: upper Rio Negro São Gabriel, capoeiras, ♀, May 1852, *Spruce* 2314 (K); Panuré (=Ipanoré), Rio Uaupés ♂ fl, 1852/3, *Spruce* 2554 (K); Camatina, terra firme, 250 m, ♀ fl, 25.1.1949, *Fróes* 24004 (K); Rio Içana, Estirao Santa Ana, fr, *Fróes* 27982 (IAN); São Felipe, Rio Negro, Igarapé Tourí, igapó, ♂ fl, 27.9.1952, *Fróes* 28780 (IAN); Cachoeira do Rio Acará, subafluente do Rio Negro, à margem do rio, ♂ fl, 29.10.1952, *Fróes & Addison* 29150 (IAN).

4. *Gnetum venosum* Spruce ex Bentham in Hook., J. Bot. and Kew Gard. Misc. **8** (1856) 358.

NORTHERN BRASIL: PARÁ: Rio Maicurú, município de Monte Alegre, terreno baixo, à beira do rio, fr, 15.9.1953, *Fróes* 30236 (IAN); Macapá, silva riparia ad flumen Matopy, fr, 30.4.1926, *Ducke* 19414 (RB); Santarem, Varzea forest nr Tapeirinha, fr, Dec 1938, *Markgraf* 3898; Lago Salgado, Rio das Trombetas, margem da mata, fr, 20.3.1924, *Kuhlmann* 19044 (RB). AMAZONAS: Manáos, on river Solimões, ♂ & ♀ fl, 12.7.1882, *Schwacke III* 567 (=Glaziou 14284!); Manáos, S bank of Rio Negro, ♂ fl, May 1851, *Spruce* 1579 (K, holotype).

5. *Gnetum Schwackeanum* Taubert ex Markgraf, Bull. Jard. Bot. Buitenzorg 3 Ser. **10** (1930) 450.

NORTHERN BRAZIL: PARÁ: Furnas (middle Tapajoz River), silva non inundata, fr, 11.9.1916, *Ducke* 16474 (MG). AMAZONAS: Manáos, forest Cua reté, ♂ fl, 15.7.1882, *Schwacke III* 788 (=Glaziou 14285, type); Manáos, capoeira Cachoeirinha, ♀ fl, 3.8.1900, *Ule* 5310; Manáus, mata da terra firme em direção ao Rio Tarumá, fr, 8.3.1946, *Ducke* 1927 (K); Rio Madeira, Rio Canumã, cipó sobre árvores isoladas na campina-rana, fr, 5.11.1957, *Fróes* 33762 (IAN). ACRE: mouth of Rio Embira, fr, 1933, *Krukoff* 5065 (K).

6. *Gnetum Leyboldii* Tul., Ann. Sc. Nat. 4 Ser. **10** (1858) 115. (*G. paraense* Hub., Bot. Museu Paraense **3** (1902) 403.)

a) var. *Leyboldii*.

NORTHERN BRAZIL: PARÁ: Collares, silva riparia ad flumen Pará, ♂ fl, 19.8.1913, *Ducke* 19409 (RB). Marajó: in silva igapó ad flumen Anajaz, ♀ fl, 21.8.1926, *Ducke* 19407 (RB); Breves, Furo Macuyubim, ♂ fl, 30.8.1901, *Guedes* 2214 (MG); Rio Acará, Thomé assú, 45 m, fr, 27.7.1931, *Mexia* 6000 (Z); Rio Jaraucu (Xingú), Porto de Móz, à beira do rio, fr, 11.10.1955, *Fróes* 32191 (IAN); Beira do Rio Curuaúna, várzea, região do planalto de Santarém, ♀ fl, Oct 1954, *Fróes* 31343 (IAN); Região de Anapú, Rio Maparaúá, Portel, à beira do rio, ♀ fl, 5.8.1956, *Fróes* 32935 (IAN); Região de Anapú, Rio Flexal, Portel, à beira do

rio, young fr, 30.9.1956, Fróes 32758 (IAN) Região de Anapú, Rio Pracajaí, Portel, á beira do rio, young fr, 14.9.1956, Fróes 32746 (IAN); Beira do Rio Mapuá, várzea, entre Vila Emilia e Bôca do Mapuá, ♂ fl, 18.7.1950, Black, Fróes & Ledoux 50-9801 (IAN); Antonio Lemos, várzea, Igarapé Pixuna, muito comun, ♂ fl, 18.7.1948, Black 48-2967 (IAN); Rio das trombetas, Mittellauf, am Ufer der Stromschnellen des Flusses Jaramacarú, ♀ fl, 11.10.1913, Ducke 19408 (RB); Rio das Trombetas, Unterlauf, am Ufer der Stromschnellen des Flusses Mapuera, fr, 5.12.1907, Ducke 9044 (MG). AMAZONAS: Humaytá, border of Rio Ipixuna between Monte Christo and Santa Victoria, fr, Krukoff 7264 (K); Ega (=Teffe), im feuchten Urwald, ♂ fl, Nov 1819, Martius (M, type); In Wäldern bei Nogueira (westl. Ega) fr, Dec 1819, Martius (M); In den Wäldern am Fluss Yapurá (bei Ega) fr, Jan 1820, Martius (M); Rio Caipurá, fr. Spruce (K). ECUADOR: Prov Tungurahua, Rio Negro, forest on shore of Rio Pastaza, 1200 m, ♂ fl, 25.8.1939, Asplund 8558 (S); Prov Tungurahua, Rio Negro, Uferwald am Rio Pastaza, 1200 m, ♂ fl, 26.9.1955, Asplund 18638 (S); Prov Tungurahua, Rio Negro, ♂ fl, 9.11.1952, Fagerlind & Wibom 1236a & b (LD). COLOMBIA: Amazonas, Rio Mirití-Paraná, 0°30'S, 70°40'W, 200 m, fr, 8.5.1952, Schultes & Cabrera 16412 (US); Amazonas-Vaupés, Rio Apaporis, Cachivera de Jirijirimo, 250 m, fr, 7.7.1951, Schultes & Cabrera 12973 (US); Amazonia, Ufer des Rio Loreto-Yaco, Várzea-Wald, fr, 1.11.1946, Schultes & Black 46-268 (US); Vaupés, Lobo Igarapé, Oberlauf des Caño Teemeeña (Rio Pira-paraná, Nebenfluss des Rio Apaporis), zwischen 0°15'S, 70°30'W & 0°25'N, 70°30'W) fr, 10.9.1952, Schultes & Cabrera 17339 (US).

b) var. **Woodsonianum** Mgf., var. nov.

COLOMBIA: Dept Santander, vic of Porto Berrio, Carare valley, 100-700 m, ♂ fl, 22.4.-1935, Haught 1662 (US). PANAMA: High hills back of Puerto Obaldéa, San Blas coast, 50-200 m, fr, Aug 1911, Pittier 4317 (US); Bismarck, above Penonome, fr, 18.3.1908, Williams 608 (US), vic of La Palma, southern Darien, 0-50 m, fr, Jan/Febr 1912, Pittier 5488 (US); Boco de Panarandó, on Sambú River, southern Darien, alt 20 m, fr, Febr 1912, Pittier 5685 (US); NW Canal Zone, W of Limon Bay, Gatun Locks & Lake, IWTC headquarters, ♂ & ♀ fl, fr. 5.4.1956, Johnson 1786 (MO).

Frutex alte scandens dioicus. Truncus lignosus, ad 10 cm crassus, ligno ex anulis annorum 5 mm latis latiporis constructo, cortice griseo, aspero, lenticellis magnis percusso obtectus. Ramuli teretes, graciles, laeves. Folia opposita, petiolus 1 cm longus, lamina late ovata, acuta vel breviter acuminata, 9-15 cm longa, 5-10 cm lata, plerumque 10 cm longa, 6 cm lata, laete viridis, fibris crebris oblique parallelis, supra conspicuis sericeo-nitens, nervi laterales 1 cm inter se remoti, arcuati, 5-7 in utroque latere, 6-8 mm ante marginem coniuncti, subtus prominuli. Inflorescentiae ♂ axillares, semel vel bis ramificatae, uni- vel binodae internodiis gracilibus, primi ordinis ad 4 cm longis, e bracteis nodalibus 2 oppositis ovato-acuminatis, 3-5 mm longis spicas 2-4(-5) emittentes, spica una apicali terminatae. Spicae adultae 2 cm longae, 6-7 collibus cyathiformibus, basin versus angustatis, 3 mm altis et 2 mm latis, 2 mm inter se distantibus ornatae. In quoque collo multi flores lutei masculini et nonnulli feminini steriles pilis immersi. Perianthium masculinum obconicum, angulatum, 0.7 mm longum, 0.3 mm latum; stamen unicum 1 mm longum, exsertum, filamentum a dorso compressum, antherae 2 apicales, oblongae, rima brevi apicali apertae. Florum femineorum sterilium involucrum externum clavatum 0.7 mm longum 0.3 mm latum, involucrum internum brevius, tenerum, supra medium latissimum. Inflorescentiae ♀ graciles, semel ramificatae, internodiis apicem versus cito brevioribus (ab 1 cm ad 2 mm) collibus 3-5, iuvenilibus cyathiformibus, adultis dilatatis et tum vix 1 mm altis, 2 mm latis ornatae. Flores feminei fusco-lutei, subglobosi, perianthium ½ mm altum et latum, involucrum medium crassiusculum, intimum globosum, minus (tantum medium altitudinem involuci medii attingens), in tubulum apicalem brevem, vix exsertum



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