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A REVISION OF
DISCOCARPUS
(EUPHORBIACEAE)¹

Sheila M. Hayden and W. John Hayden²

ABSTRACT

As revised here, *Discocarpus* is interpreted to consist of three neotropical species: *D. essequiboensis* Klotzsch, *D. gentryi* S. M. Hayden, which is described and named herein as new to science, and *D. spruceanus* Müll. Arg. One previously accepted name, *D. brasiliensis* Klotzsch ex Müll. Arg., is reduced to synonymy of *D. essequiboensis*. Lectotypes are proposed for the two species previously described. One species is newly excluded from *Discocarpus*, as are three others, following previous literature. Foliar anatomy is described with a focus on epidermal sclereids, which are shown to occur on both epidermides. Evidence presented supports close relationships with *Lachnostylis* Turcz. and *Amanoa* Aubl.; little was found to support previous hypotheses concerning a relationship with *Chonocentrum* Pierre ex Pax & K. Hoffm.

Discocarpus Klotzsch is a genus of trees found in seasonally flooded riparian habitats of northern South America, where they are components of the forest canopy. The plants are dioecious and bear small clusters of flowers in the axils of simple, alternate, entire leaves.

Discocarpus was first described by Klotzsch (1841) who initially named, but did not describe, two species; he subsequently described one of these, *D. essequiboensis* Klotzsch (1843), based on Schomburgk collections from the Essequibo River region of Guayana. Omitting two nettles (Urticaceae) from Mexico and Nicaragua grossly misplaced in the genus, the next species of *Discocarpus* to be

named was *D. spruceanus* Müll. Arg. (1863), based on collections of Richard Spruce from the Rio Negro of Brazil. Some 32 years after being first mentioned by Klotzsch, *D. brasiliensis* Müll. Arg. (1873) was formally named, based on a collection of von Martius from the early 19th century. Three taxa were added to the genus in the 20th century. The first addition was *D. hirtus* (L. f.) Pax & K. Hoffm. (Pax & Hoffmann, 1922), a consequence of synonymizing the South African genus *Lachnostylis* with *Discocarpus*. In current literature, however, *Lachnostylis* is treated as distinct from *Discocarpus* (e.g., Levin, 1986; Menega, 1987; Webster, 1994b). The two most recently described species,

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D. mazarunensis Croizat (1948) and *D. duckeanus* Jabl. (1967), were based on South American material.

Jablonski (1967) accepted the five South American species noted above as distinct entities constituting *Discocarpus*, but his treatment indicated several gaps in the available data on these plants. For example, staminate or pistillate flowers were undescribed for several species. Furthermore, recent studies reveal that two of the species accepted by Jablonski were misplaced in *Discocarpus*, and presently available collections indicate the existence of a previously unrecognized species (Hayden, 1995). In addition, the issue of generic relationships is unresolved. *Discocarpus* was classified most recently in subfamily Phyllanthoideae Asch. tribe Wielandieae Baill. ex Hurus. (Webster, 1994b), but earlier concepts of generic relationships have varied widely (see below). Moreover, reports of foliar sclereids in *Discocarpus* and *Amanoa* (Gaucher, 1902; Levin, 1986) suggest the new possibility of placement in tribe Amanoeae. This paper provides a revision of *Discocarpus*, including detailed descriptions of foliar anatomy and discussion of relationships.

MATERIALS AND METHODS

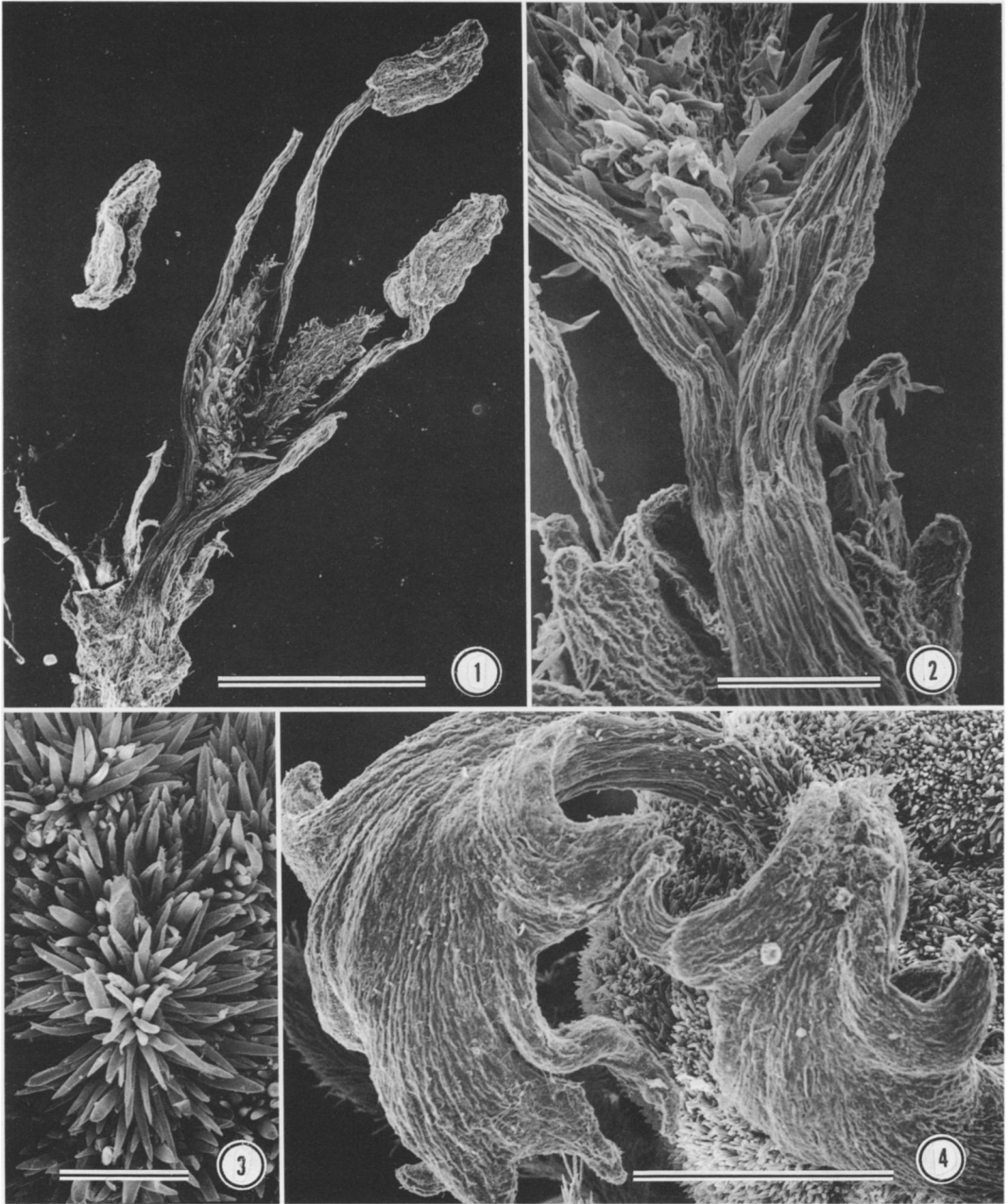
This revision is based on a total of 171 herbarium specimens of *Discocarpus* borrowed from 29 herbaria in the United States, Europe, and South America. Small samples of leaf tissue from the following collections were removed for anatomical study: *Discocarpus essequiboensis* Klotzsch, Jangoux & Bahia 294 (NY), Krukoff & Fróes 11974 (NY), Maas et al. 7395 (U), Schomburgk 659 (U), Silva 4776 (NY), Smith 2692 (F); *Discocarpus gentryi* S. M. Hayden, Encarnación 25065 (F), Vázquez & Jaramillo 5487 (NY); *Discocarpus spruceanus* Müll. Arg., Davidse 27631 (NY), Wurdack & Adelderly 43349 (NY). Half of each sample was mounted directly on stubs and sputter coated with a gold/palladium mixture prior to observation with SEM. The second half of each sample was rehydrated by boiling in water with a few drops of Aerosol OT, dehydrated in tertiary butanol, embedded in paraffin, and sectioned at 10 μ m on a rotary microtome. Paraffin sections were stained in toluidine blue (Berlyn & Miksche, 1976) or a combination of safranin and haematoxylin (Johansen, 1940).

SYSTEMATIC TREATMENT

Discocarpus Klotzsch, Archiv. Naturg. 7(1): 201. 1841. TYPE: *Discocarpus essequiboensis* Klotzsch. Figures 1–4.

Dioecious trees (or shrubs), (3–)10–30 m tall, DBH 25–100 cm. Twigs glabrous to short-pilose, silvery gray to dark purplish red; lenticels raised, elongate, parallel with the axis; terminal buds acuminate, cylindric, glabrous to tomentose, 3–7 mm long, often with two basal knoblike protrusions, sometimes sexually dimorphic. Leaves alternate, simple, petiolate, glabrous, leathery; petioles 4–8 mm long, wrinkled; margins entire; base obtuse; apex acute to acuminate; venation pinnate; ultimate veins reticulate, orthogonal. Stipules fugaceous. Inflorescence axillary, 1–several flowers per node; flower clusters sessile, subtended by cupulate bracts; bracts ca. 1 mm long, 1 mm wide, glabrous to pubescent; staminate clusters several per node; pistillate clusters one per node. Staminate flowers sessile, congested, 10–30 per node; sepals (4) 5, 1.5–2 mm long, 1–1.5 mm wide, pilose; petals (0–)5, delicate, hyaline, glabrous to pubescent, less than 1 mm long, linear, often fringed apically; disk extrastaminal, lobed; stamens (4) 5; filaments fused below the level of the disk, free portions 1.5–3 mm long; anthers elongate, 1 mm long, longitudinally dehiscent, exerted; pistillode segmented into two or three linear, pubescent, membranous filaments. Pistillate flowers 1–3(–5) per node; pedicels essentially lacking to 5 mm long; sepals 5, cupulate, 1.5–3 mm long, 1–2 mm wide, densely pubescent; petals (0–)5, hyaline, 0.5–3 mm long, up to 1 mm wide, pubescent; disk slightly lobed; ovary 3-carpellate, subglobose, smooth or sculpted, densely pubescent; styles 3, parted to the base or nearly so, spreading horizontally, densely pubescent below; stigmas 3, dilated, lobed, horizontal or reflexed; ovules 2 per locule. Fruits symmetrically 3-lobed or asymmetrically subglobose, 6–12 mm tall, 6–15 mm diam., longitudinally dehiscent into 2, 3, or 6 mericarps, 1–3-seeded; pericarp ca. 1 mm thick, hard, brittle; surface smooth to deeply sculpted, densely pubescent; columella persistent. Seeds subglobose, ecarunculate; testa thin, shiny.

Discocarpus can be distinguished from other woody genera of subfamily Phyllanthoideae by the combination of: deciduous stipules; dioecy; minute petal-bearing flowers produced in axillary clusters; lobed extrastaminal disks; finely reticulate exine on pollen grains; and styles that are not bifid, but terminate in three dilated, irregularly lobed stigmas. It is noteworthy that floral merosity and presence of petals are somewhat inconstant. Most flowers are 5-merous, but 4-merous flowers are not infrequently encountered. Most flowers examined showed petals to be present and isomerous with the sepals, but sometimes fewer petals, or even none, will be



Figures 1–4. Floral morphology of *Discocarpus*, SEM. 1, 2, *Discocarpus spruceanus* Müll. Arg., Spruce 3527 (G). — 1. Staminate flower with sepals and petals removed to show fused filaments; bar = 1 mm. — 2. Fused filaments; bar = 250 μm . — 3. *Discocarpus essequiboensis* Klotzsch, Martius s.n. (L). Hair on fruit surface; bar = 250 μm . — 4. *Discocarpus essequiboensis* Klotzsch, Schomburgk 35 (G). Dilated, lobed, reflexed stigmas; bar = 1 mm.

found. Notably, the minute size and flimsy texture of the petals render them easy to overlook. Important clues to recognizing the genus in sterile condition include the elongate terminal buds with paired distinctive basal knobs and fine veins form-

ing highly regular minute areoles that lack free-ending veinlets.

In Webster's (1994b) key to genera of Wielandiaeae, two aspects of morphology of staminate flowers attributed to *Discocarpus* are at variance with

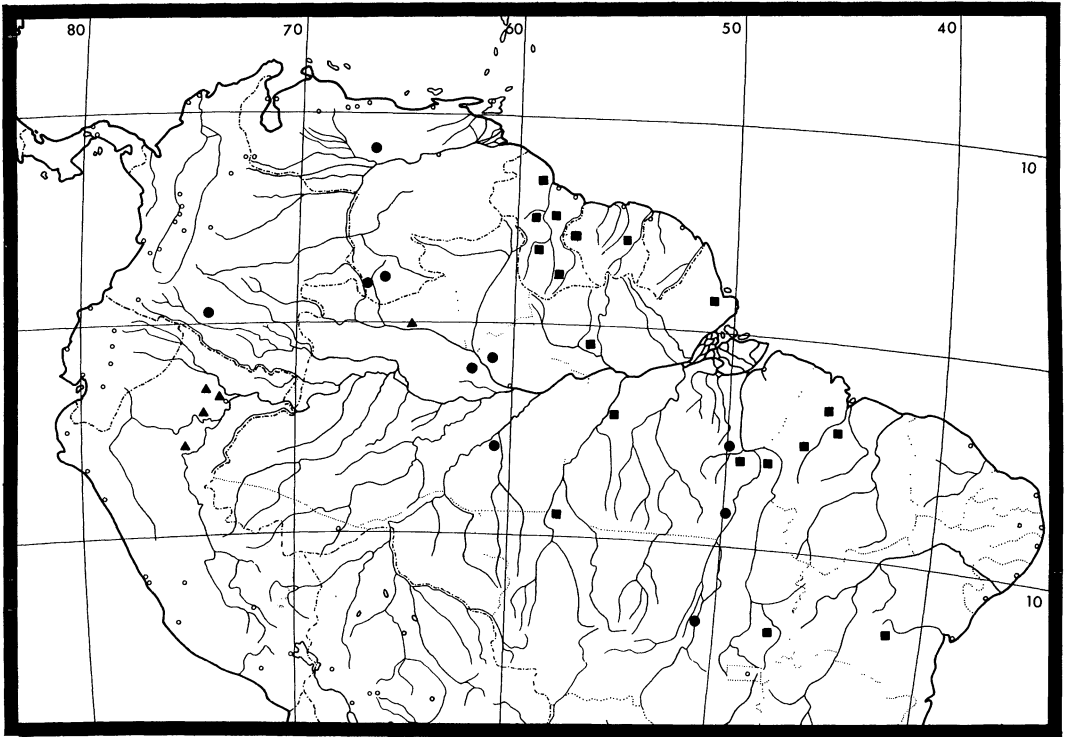


Figure 5. Distribution of *Discocarpus*. Squares = *Discocarpus essequiboensis* Klotzsch; circles = *Discocarpus spruceanus* Müll. Arg.; triangles = *Discocarpus gentryi* S. M. Hayden.

the above description. Staminate flowers are sessile and bear filaments fused to the base of the pistillode, features also noted by Pax and Hoffmann (1922).

Three species of *Discocarpus* occur in the Amazon and Orinoco River basins of Brazil, Colombia, Peru, and Venezuela, as well as smaller rivers of Guyana and Surinam (Fig. 5). Habitat is lowland rainforest below 250 m, along seasonally flooded riverbanks of *várzea* forests or occasionally inundated fields. *Discocarpus* species can form canopy trees, but samples are sometimes collected from specimens described as small shrubs.

KEY TO SPECIES OF *DISCOCARPUS* (FIGS. 6–9)

- 1a. Terminal bud of staminate specimens lacking basal knobs, covered with dense indumentum; ovary and fruit surface smooth; fruits 1(–2)-seeded, 2 carpels usually abortive; widely scattered in the Amazon and Orinoco River basins
..... *D. spruceanus* Müll. Arg.
- 1b. Terminal bud of staminate specimens with two prominent basal knobs, glabrous or only sparsely pubescent; ovary and fruit surface sculpted; fruits 3-seeded, all carpels accrescent.
 - 2a. Pistillate flowers on pedicels 4–5 mm long; ovary and fruit surface deeply sculpted into

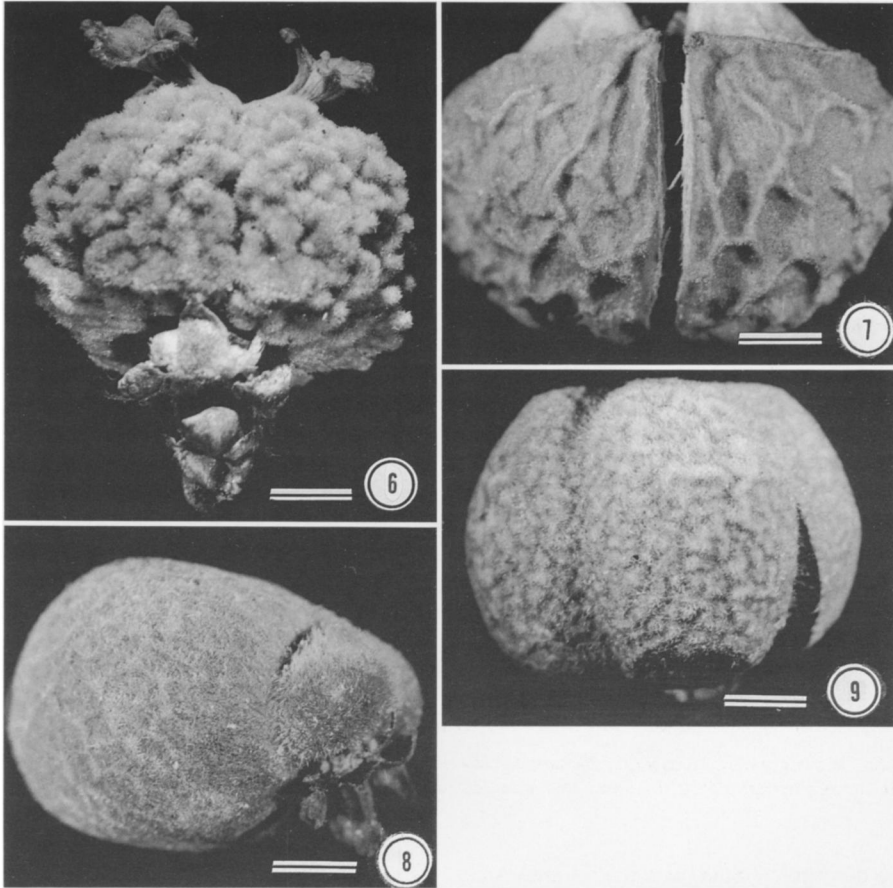
long undulate ridges with sharp crests (beneath dense indumentum); fresh staminate flowers yellow; Amazonian Peru and western Brazil *D. gentryi* S. M. Hayden

- 2b. Pistillate flowers sessile or nearly so; ovary and fruit surface weakly sculpted into muricæ or short undulate ridges with rounded crests (beneath dense indumentum); fresh staminate flowers cream; Guyana, Surinam, and northeastern Brazil
..... *D. essequiboensis* Klotzsch

Discocarpus essequiboensis Klotzsch, London J. Bot. 2: 52. 1843. TYPE: Guyana. On branch of upper Essequibo River, *Schomburgk 35* (lectotype, selected here, BM; isolectotypes, G, K, OXF, P, U, W). Figures 10, 3, 4, 9.

Discocarpus brasiliensis Klotzsch ex Müll. Arg. Mart. Fl. Bras. 11(2), 13: 1873. SYNTYPES: Brazil. Bahia: near Villa do Rio de Contas, *Martius s.n.* (G, L, M, MO); Bahia: *Martius s.n.* (M).

Trees, 10–20 m tall, DBH 25–100 cm. Terminal buds similar in staminate and pistillate specimens, glabrous, with two basal knobs. Leaves 8–22 cm long, 4–8 cm wide; apex acuminate (to 10 mm long) to merely acute. Inflorescence bracts glabrous to pubescent. Staminate flowers 10–30 per node,



Figures 6–9. Ovary and fruit surface features of *Discocarpus*. —6. *Discocarpus gentryi* S. M. Hayden, *Gentry et al.* 18419 (F). Ovary. —7. *Discocarpus gentryi* S. M. Hayden, *Revilla 411* (NY). Mature fruit. —8. *Discocarpus spruceanus* Müll. Arg., *Spruce 3527* (P). Mature fruit with one developed and two aborted lobes. —9. *Discocarpus essequeboensis* Klotzsch, *Schomburgk 706* (G). Mature fruit. All bars = 2 mm.

cream-colored; sepals (4) 5, 2 mm long, 1.5 mm wide; petals (0–)5, pubescent; disk lobed; stamens (4) 5; pistillode segments 3. Pistillate flowers 1–5 per node; pedicel 0–1 mm; sepals 3 mm long, 2 mm wide, light green; petals reduced, (0–)5, 0.5–3 mm long; ovary shallowly muricate to reticulate; stigmas reflexed. Immature fruits dark red; mature fruit brown, symmetrically 3-lobed, 8–9 mm tall, 10–15 mm diam., 3-seeded, surface weakly sculpted into shallow muricae or short undulate ridges with rounded crests. Seed 6–8 mm diam.; micro-
pylar and basal surfaces somewhat flattened; testa red-brown.

Distribution. Central and eastern Brazil, Guyana, Surinam (Fig. 5); on sandy soil in frequently inundated forest along rivers (*várzea*) and periodically flooded fields. Flowers have been collected

from June through December; fruits, from September through December.

Common Names. “Square Wood” (in reference to shape of trunk, *Anderson 408*); “Oity do Campo” (*Fróes & Krukoff 11974*).

Additional specimens examined. BRAZIL. **Amapá:** *Bastos 201* (MO). **Amazonas:** *Martius s.n.* (L); *Maués, Pires 109* (NY, U). **Bahia:** *Villa do Rio de Contas, Martius s.n.* (C, L, M). **Goiás:** Rio Araguaia at mouth of Rio Javães, *Silva 4862* (ILLS, NY); Rio Piranha, *Silva 4776* (NY). **Maranhão:** Rio Alto Turiaçu, Nova Esperança, 2°5'S, 45°5'W, *Jangoux & Bahia 294* (NY, RB); Rio Pindare Basin, Monção, *Fróes & Krukoff 11974* (GH, MICH, NY, US); Rio Mearim-Lapela, municipality de Vitória do mearim, Campo Coberto, *Silva 4191* (RB). **Mato Grosso:** margin of Rio Juruena, *Rosa & Santos 2149* (MO, NY). **Pará:** Marabá, *Fróes & Black 24336* (P, U); Cachoeira Porteria, Rio Trombetas, *Ducke 8953* (BM, G); Rio Trombetas margin, *Ducke 7988* (BM); Rio Trombetas margin,

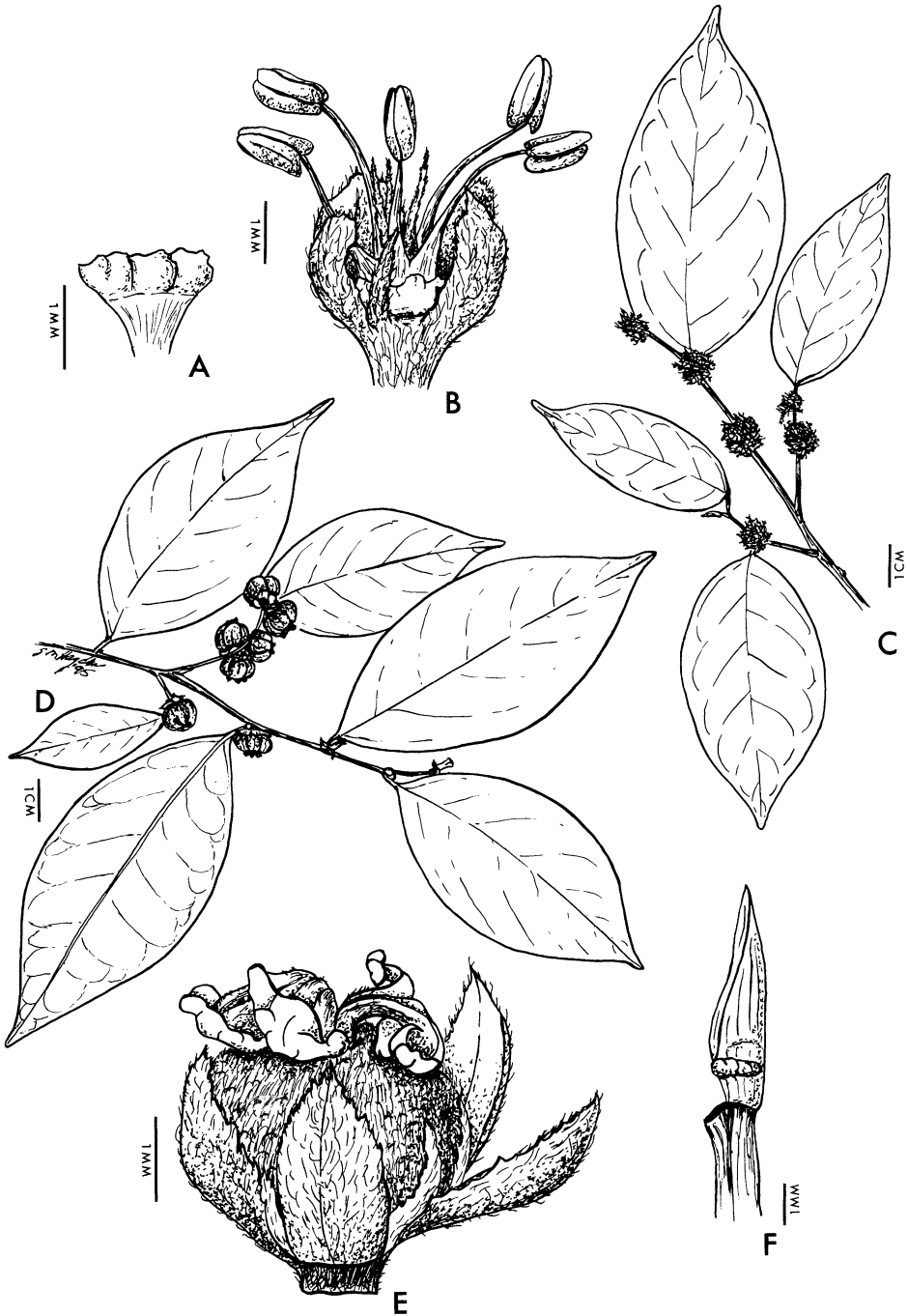


Figure 10. *Discocarpus essequiboensis* Klotzsch. —A. Disk from staminate flower; *Pires 109* (U). —B. Staminate flower, one sepal removed; *Pires 109* (U). —C. Habit, staminate specimen; *Krukoff 11974* (NY). —D. Habit, pistillate specimen; *Rosa & Santos 2149* (MO). —E. Immature fruit; *Schomburgk 35* (W). —F. Terminal bud; *Krukoff 11974* (NY).

Ducke 7993 (BM); National park of Tapajós, 60 km from Itaituba-Jacarecanga at the margin of Rio Tapajós, *Silva & Rosário 3992* (NY). GUYANA. Upper Essequibo River, *Schomburgk 706* (BM, G, K, L, P, U, W); upper Essequibo River, *Schomburgk 659* (BM, E, F, G, K, L, MANCH, OXF, P, U, W); Rupununi Savanna, near Maricouba pond near Karanambo Ranch, 3°45'N, 59°19'W, *Görts-van Rijn et al. 388* (URV); Rupununi District, Kuyuwini Landing, Kuyuwini River, forest along river, 2°5'N, 59°15'W, *Jansen-Jacobs et al. 2903* (URV); Manakobi, Courantyne River, *Anderson 408* (K), *Schomburgk s.n.* (L, U), *Schomburgk 1237* (F), *Schomburgk 920* (F, G, K, P, W); Cuyuni-Mazaruni Region, Essequibo River 6–8 km downstream of Omai, 5°26'N, 58°42'W, *Gillespie 1573* (MO); Rupununi River, Monkey Pond landing SW of Mt. Makarapan, 3°53'N, 58°55'W, *Maas et al. 7395* (P, U); basin of Essequibo River near mouth of Onoro Creek, 1°35'N, *Smith 2692* (F, G, NY). SURINAM. Matappi, Corantyne, *B. W. 2044* (U); Tapanahoni, *Kappler 97* (L, U, W), *Kappler 2143* (GOET, W), *Schomburgk 459* (G).

Notes. Klotzsch's species *Discocarpus essequiboensis* was originally based upon three collections, *Schomburgk 35* (pistillate flowers), *Schomburgk 659* (staminate flowers), and *Schomburgk 706* (mature fruits). Since staminate material of *Discocarpus* reveals few diagnostic characters, and since the fruiting specimen bears only fragmentary label data, the pistillate collection, *Schomburgk 35*, is by far the best choice to typify the species. The BM specimen includes abundant flowers that prove important in defining the species (see below). The spelling of the specific epithet adopted here follows that used by Klotzsch (1843) in contrast to that of the earlier nomen nudum, *Discocarpus essequiboensis* Klotzsch (Archiv. Naturg. 7(1): 201. 1841).

Discocarpus brasiliensis is here placed in synonymy under *Discocarpus essequiboensis*. The two entities are virtually indistinguishable, and it seems that recent practice has been to identify material from the Guianas as *D. essequiboensis* and Brazilian specimens as *D. brasiliensis*. In the past, *Discocarpus brasiliensis* was supposedly distinguished from *D. essequiboensis* by the presence of small bumps or muricae on ovaries and fruits of the former in contrast to the smooth ovaries and fruits of the latter (Müller, 1873; Pax & Hoffmann, 1922). However, the syntypes of *D. essequiboensis* listed by Klotzsch include a fruiting specimen, *Schomburgk 706*, which has a surface texture that is obviously bumpy and identical to other specimens identified as *D. brasiliensis*. Further, the lectotype of *Discocarpus essequiboensis*, *Schomburgk 35*, illustrates a range of developmental stages from very young flowers just emerging from the bud to early fruits. The flowers on this specimen reveal a developmental change in ovary surface from nearly smooth to contoured or bumpy as the ovary matures. On the basis of these observations, and given the lack of

any other consistent character of either pistillate or staminate material of *D. essequiboensis* and *D. brasiliensis* that delineates two separate species, the decision was made to place *Discocarpus brasiliensis* in synonymy under *Discocarpus essequiboensis*. Both names were first published by Klotzsch; however, the name *D. brasiliensis*, published in 1841, remained a nomen nudum until Müller provided it with a diagnosis in 1873. Thus *D. essequiboensis*, published in 1843, is the oldest legitimate name for this species.

In addition to those named *Discocarpus brasiliensis* Klotzsch, other specimens collected by Martius bear the name *D. bahiensis* Klotzsch, but it appears that the latter name has never been published. It is noteworthy that, aside from these nearly 200-year-old collections by Martius, no other collections of *Discocarpus* have been seen from the Atlantic coastal forest of Brazil.

Discocarpus gentryi S. M. Hayden, sp. nov.

TYPE: Peru. Loreto: Santa María de Nanay, SW of Río Nanay, *Schunke V. 2443* (holotype, F; isotypes, G, GH, NY, US). Figures 11, 6, 7.

Arbor vel frutex dioecia, 3–14 m; gemma terminalis glabra; flores staminati lutei; flores pistillati 1 (2) per nodum; pedicellus florum pistillatorum 4–5 mm longus; fructus trilobus symmetricus, seminibus tribus; pericarpium undulatum profunde, viride; testa cinnamomea.

Trees or shrubs, 3–14 m tall, DBH 35–40 cm. Terminal buds similar in staminate and pistillate specimens, glabrous to sparsely pubescent, with two basal knobs. Leaves 7–15 cm long, 3–7 cm wide; apex acute to acuminate. Inflorescence bracts glabrous to somewhat pubescent apically. Staminate flowers 15–30 per node, bright yellow; sepals 2 mm long, 1 mm wide; petals (0–)5, glabrous to sparsely pubescent; disk with fingerlike lobes; stamens 5; pistillode segments 2–3. Pistillate flowers 1 (2) per node; pedicels 4–5 mm long; sepals 3 mm long, 2 mm wide; petals 5, 2 mm long, 1 mm wide; ovary surface deeply undulate; stigmas reflexed. Fruit green, symmetrically 3-lobed, 12 mm tall, 15 mm diam., 3-seeded, surface deeply sculpted into long undulate ridges with sharp crests. Seeds ca. 8 mm diam.; micropylar and basal surfaces somewhat flattened; testa golden brown.

Distribution. Amazonian Peru and western Brazil (Fig. 5); on white sand or clay soil of low, seasonally inundated forest along rivers (*várzea* or *tahuampa*); 120–150 m altitude. Flowers have been collected from December through April; fruits, from September through February.

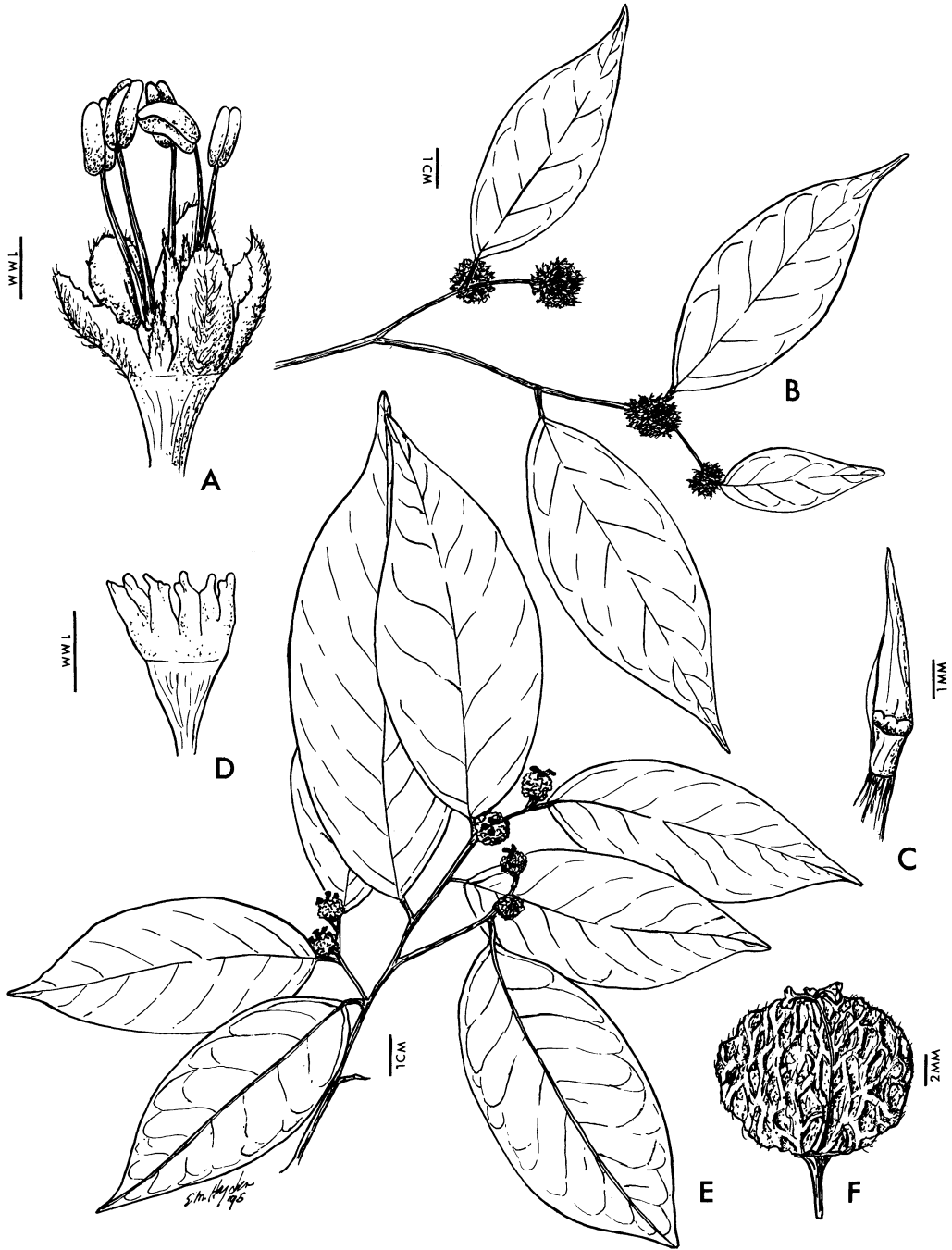


Figure 11. *Discocarpus gentryi* S. M. Hayden. —A. Staminate flower; *Rimachi Y. 3300* (NY). —B. Habit, staminate specimen; *Rimachi Y. 3300* (MO). —C. Terminal bud; *Rimachi Y. 3300* (MO). —D. Disk from staminate flower; *Rimachi Y. 3300* (NY). —E. Habit, pistillate specimen; *Gentry et al. 18419* (F). —F. Fruit; *Revilla 411* (F).

Common Names. "Ucuchahuasi" (*Vásquez & Jaramillo 5487*); "Loromicuna" (*Ayala 1415*).

Additional specimens examined. BRAZIL. **Amazonas:** Rio Negro near Ilha Provedença, *Steward et al. 516* (NY). PERU. **Loreto:** Maynas, Iquitos, Río Nanay, Quebrada de Morropon, *Rimachi Y. 3281* (F, MO, NY, RSA); Río Nanay, 03°51'S, 73°32'W, *Vásquez et al. 7528* (F, NY); Río Nanay at Almendras, 03°48'S, 73°25'W, *Vásquez & Jaramillo 5487* (F, MO, NY); Iquitos, in the gorge of the small settlement of San Pablo de Cuyana above Santa Clara de Nanay, *Rimachi Y. 3300* (F, MO, NY, RSA); Caño Iricahua, below Jenuro Herrera, on the left margin of Río Ucayali, *Encarnación 25065* (F); Iquitos, Río Nanay, 8 bends in the river above de Morona Cocha, *Revilla 411* (F, MO, NY); vicinity of Iquitos, *Revilla 3598* (F, MO); Río Itaya below San Juan de Muniches, 40 mins. above Iquitos with 40 hp motor, *Gentry et al. 18419* (F, MO); right margin of Zungarococha, primary forest, *Ayala 1415* (MO).

Notes. Peruvian specimens of *Discocarpus* referred here to *D. gentryi* have only been collected within the last 30 years. The genus was not treated in MacBride's (1951) earlier compilation of Euphorbiaceae for the *Flora of Peru*, although the presence of *D. brasiliensis* was predicted. When specimens from Peru with sculpted fruit surfaces first came to light they were identified as *D. brasiliensis*, and they are referred to as such in Brako and Zarucchi's (1993) checklist. However, *D. brasiliensis* is herein synonymized with *D. essequiboensis*, and, further, the Peruvian collections prove to be distinct both morphologically and geographically from this species. As noted in the key, fruits of *D. gentryi* have pronounced surface relief, and pistillate flowers are distinctly pedicellate. In contrast, fruits of *D. essequiboensis*, though somewhat sculpted, are smoother, and pistillate flowers are sessile or nearly so. Additionally, mature capsules of *D. essequiboensis* are brown and the seeds are dark brown, in contrast to the mature capsules of *D. gentryi*, which are green and contain golden brown seeds. Careful dissection of staminate flowers of *D. gentryi* reveals disk lobes much more elongate than those of the other two species. *Discocarpus gentryi* has been collected most frequently along riverbanks near Iquitos, Peru, especially in the vicinity of Río Nanay, a blackwater river. There is one additional record of the species from western Brazil, along the Rio Negro, another blackwater river.

The specific epithet commemorates Alwyn H. Gentry (1945–1993), for his many important contributions to the floristics of Central America and northern South America. Gentry's collection of *Discocarpus* from the region around Iquitos, Peru, was instrumental in recognizing these plants as new to science.

Discocarpus spruceanus Müll. Arg., *Linnaea* 32: 78. 1863. TYPE: Brazil. Amazonas: Rio Negro above the mouth of the Casiquiare River, *Spruce 3527* (lectotype, selected here, BM; isotypes, BR, C, E, F, G, GH, GOET, K, LD, MO, NY, OXF, P, TCD, W). Figures 12, 1, 2, 8.

Drypetes krukovii Monach., *Phytologia* 3: 34. 1948. TYPE: Brazil. Amazonas: Municipality Humayta, near Livramento, on Rio Livramento, *Krukoff 6703* (holotype, NY; isotypes, G, US).

Trees, 10–30 m tall, DBH 30–60 cm. Terminal buds sexually dimorphic, densely pubescent with very small to no basal knobs in staminate trees, usually glabrous to sparsely puberulent and with two basal knobs in pistillate trees. Leaves 5–12 cm long, 2–5 cm wide; apex acute to acuminate. Inflorescence bracts pubescent. Staminate flowers 15–30 per node, pale yellow; sepals 4–5, 1.5 mm long, 1 mm wide, pubescent; petals 4–5, glabrous to sparsely pubescent; disk irregularly lobed; stamens 4–5; pistillode segments 2–3. Pistillate flowers 1–3 per node; pedicels 1–5 mm long; sepals 1.5 mm long, 1 mm wide; petals 5, 1.5 mm long, 0.5 mm wide; ovary smooth; stigmas horizontal. Fruit brown, subglobose, asymmetrically 3-lobed by abortion of 2 (1) carpels, 6–9 mm tall, 6–7 mm diam., 1(–2)-seeded, surface smooth. Seed shape and dimensions unknown (usually shriveled in herbarium specimens); testa brown.

Distribution. Widely scattered in the Amazon and Orinoco River basins of Brazil, Colombia, and Venezuela (Fig. 5); in *várzea* or *rebalse* vegetation of frequently inundated forest along rivers; often locally abundant. Flowers have been collected from January through August; fruits, in November and December.

Additional specimens examined. BRAZIL. **Amazonas:** Rio Negro, northern Brazil, *Spruce 3781* pro parte (BM, BR, C, E, F, G, GH, GOET, K, MO, NY, OXF, TCD, W); Airão, *Ducke 904* (F, MO, NY, R, UC, US). **Mato Grosso:** proximity of Rio Cristalino, 13°13'S, 50°51'W, *Dovebrós* (RB). **Pará:** Rio Itacaiuna, cachoeira Grande, *Fróes & Black 24513* (U); proximity of Conceição do Araguaia, 8°44'S, 49°26'W, *Mileski 120* (RB). COLOMBIA. **Caquetá:** 2 km S of Solano, 8 km SE of Tres Esquinas on Río Caquetá below mouth of Río Ortequaza, *Little & Little 9604* (US). VENEZUELA. **Amazonas:** Rio Guainia between Comunidad and Santa Rita, *Wurdack & Adlerley, 43349* (NY, S, US); Caño Adobo, 25 km S of San Cargos of Rio Negro, 1°38'N, 66°58'W, *Liesner 8634* (MO, NY); Departamento Rio Negro, lower part of the Río Baria, 1°27'–1°10'N, 66°32'–66°25'W, *Davidse 27631* (F, MICH, MO, NY); Departamento Atabapo, Riverina del Caño Yagua, 03°37'N, 66°35'W, *Marin 479* (MO).

The syntype collections of *Discocarpus spru-*

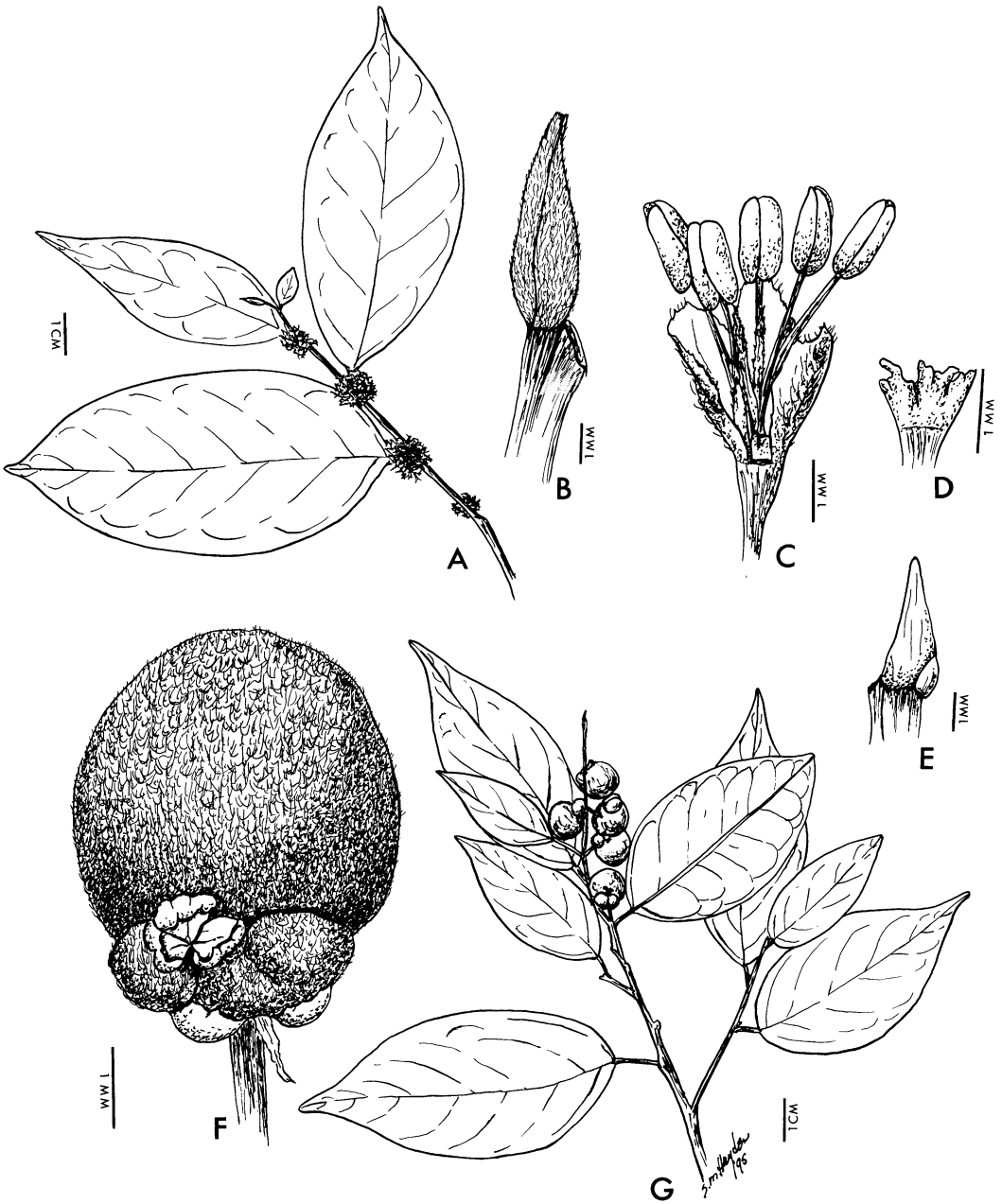


Figure 12. *Discocarpus spruceanus* Müll. Arg. —A. Habit, staminate specimen; *Ducke 904* (F). —B. Terminal bud, staminate specimen; *Mileski 120* (RB). —C. Staminate flower, one sepal removed; *Ducke 904* (F). —D. Disk from staminate flower; *Ducke 904* (F). —E. Terminal bud, pistillate specimen; *Spruce 3527* (BM). —F. Immature fruit; *Davidse 27631* (F). —G. Habit, pistillate specimen; *Spruce 3527* (BM).

ceanus, *Spruce 3527* and *Spruce 3781*, are often curated together leading to potential confusion of the two. Generally, specimens labeled as *Spruce 3781* are staminate and those labeled *Spruce 3527* bear fruits, but the numbers were apparently re-

versed at G. Further, in many herbaria both *Spruce* collections are mounted on the same sheet, and fragments from the two are often mixed together in the same packet. An additional confounding factor is that a portion of the duplicates

of *Spruce 3781* has been recognized as the type of a different plant, *Chonocentrum cyathophorum* (Müll. Arg.) Pax & K. Hoffm. (Indeed, one of the two collections of *Spruce 3781* received from OXF was a specimen of *Chonocentrum* misidentified as *Discocarpus spruceanus*; types of *Chonocentrum cyathophorum* have been seen from OXF, G, and NY, confirming that these plants are not *Discocarpus*.) Of the two syntypes, the fruiting collections that constitute *Spruce 3527* are by far more diagnostic than the staminate collection, *Spruce 3781*, and therefore the former serves better as the type. This selection also avoids possible confusion with *Chonocentrum*. Of the several duplicates seen, the specimen from BM is particularly representative.

The sexual dimorphism in terminal buds of *D. spruceanus* is remarkable given that species of *Discocarpus* are otherwise so similar to each other vegetatively. The question whether staminate and pistillate material cited here truly pertain to the same species cannot be dismissed lightly. In southern Venezuela near the Casiquiare–Negro confluence, pistillate plants with the characteristic smooth-surfaced partially aborted fruits occur with staminate plants with hairy buds. No pistillate material of other species has been collected from this area. Further, staminate plants with densely hairy buds do not occur in the Guianas and eastern Brazil, where all pistillate specimens prove to be *D. essequiboensis*, and they are similarly absent from Peru, where pistillate specimens are *D. gentryi*. We therefore interpret staminate specimens with hairy buds and pistillate material with smooth fruits and just a single fertile carpel to be conspecific.

At this writing, we have seen one record of *Discocarpus spruceanus* from Colombia, a flowering staminate specimen, *Little & Little 9604*, collected in 1945.

EXCLUDED SPECIES

Discocarpus ducleanus Jabl., Mem. New York Bot. Gard. 17: 85. 1967. TYPE: *Ducke 33825* (NY) = *Chaetocarpus echinocarpus* (Baill.) Ducke.

Jablonski (1967) based his species on a single collection bearing staminate flowers that, unlike genuine *Discocarpus*, has consistently petal-less flowers with eight (or more?) filaments fused into a central column, and subglobose anthers diverging at various levels. Although present in *Discocarpus*, fusion of filaments is restricted to the base of the flower; the filaments, never more than five, diverge at the same level and terminate in distinctly elongate anthers positioned at approximately the same

height. In all respects, Jablonski's species matches *Chaetocarpus echinocarpus* (Acalyphoideae).

Discocarpus mazarunensis Croizat, Bull. Torr. Bot. Club 75: 400. 1948. TYPE: *Fanshawe 2124* (NY) = *Chaetocarpus schomburgkianus* (Kuntze) Pax & K. Hoffm.

When Croizat (1948) named his new species, based strictly on staminate material, he noted that its vegetative features were discordant with those of *Discocarpus*. Jablonski (1967) accepted *D. mazarunensis* without comment. In recent years, Michael Huft annotated several specimens of *Discocarpus mazarunensis* as *Chaetocarpus schomburgkianus*, and Gillespie (1993), following his lead, excluded this species from *Discocarpus*. As in the case described above, the flowers in the type of *D. mazarunensis* have filaments fused into a prominent staminal column with anthers diverging at different levels. Exclusion from *Discocarpus* is thus justified.

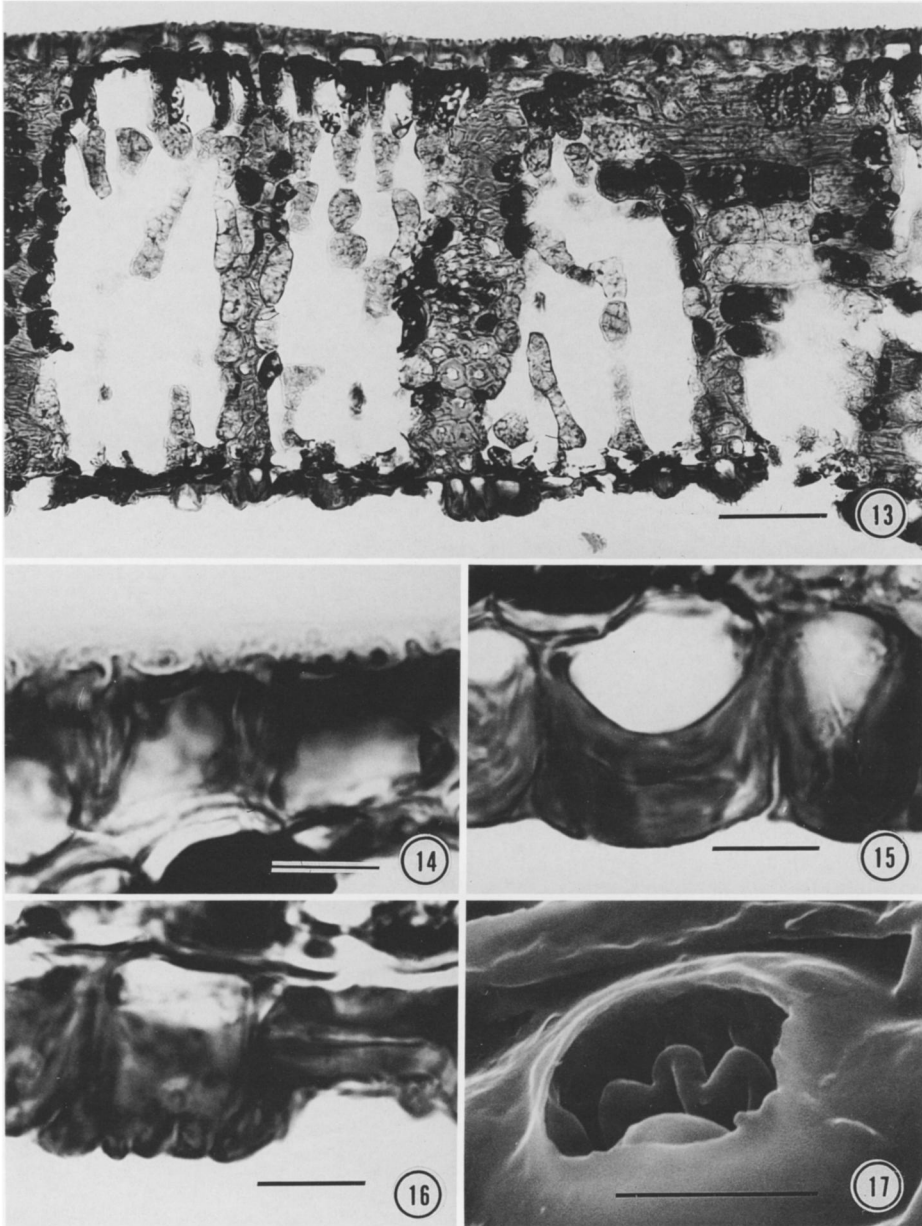
Discocarpus mexicanus Liebm., Skr. Vidensk.-Selsk. Christiana, Math.-Naturvidensk. Kl. 5: 309. 1851 = *Laportea mexicana* (Liebm.) Wedd. (Urticaceae) (as per Pax & Hoffmann, 1922).

Discocarpus nicaraguensis Liebm., Skr. Vidensk.-Selsk. Christiana, Math.-Naturvidensk. Kl. 5: 309. 1851 = *Laportea nicaraguensis* (Liebm.) Wedd. (Urticaceae) (as per Pax & Hoffmann, 1922).

FOLIAR ANATOMY

Leaf anatomy was found to vary little from species to species, hence the following descriptions pertain to all three species. Dimensions cited are average values based on 10 measurements of each feature per specimen.

Epidermis (both adaxial and abaxial) uniseriate; cells irregular, partially sclerified; outer periclinal walls sclerified; anticlinal walls wavy, sclerified unevenly, thicker toward the surface, thinner toward the mesophyll (occasional cells of adaxial epidermis sclerified on inner periclinal wall, thinner along anticlinal wall outward); outer periclinal walls bearing subcuticular micropapillae (best seen in *Discocarpus spruceanus*, Figs. 14, 15, 16). Adaxial epidermal cells 15 μm thick, uniformly bearing tannin deposits; cuticle 1–2 μm thick. Abaxial epidermal cells 11 μm thick, occasionally bearing tannin deposits; cuticle <1 μm thick. Stomata restricted to the abaxial epidermis, densely crowded,



Figures 13–17. Foliar anatomy of *Discocarpus*. 13–16, *Discocarpus spruceanus* Müll. Arg., Wurdack & Adderly 43349 (NY). —13. Leaf cross section; bar = 50 μ m. —14. Sclerified adaxial epidermis with micropapillae; bar = 10 μ m. —15. Sclerified abaxial epidermis below vein; bar = 10 μ m. —16. Sclerified abaxial epidermis with micropapillae; bar = 10 μ m. —17. *Discocarpus gentryi* S. M. Hayden, Rimachi Y. 3281 (NY). SEM of stomate with crenulate anticlinal wall of guard cell; bar = 5 μ m.

oriented randomly, widely elliptic, 18 μ m long, 15 μ m wide; anticlinal walls forming stomatal pore minutely crenulate (Fig. 17); subsidiary cells brachy-paracytic.

Mesophyll stratified, tannin deposits scattered throughout; palisade cells well developed, some-

times lightly sclerified near the adaxial epidermis; spongy layer weakly developed, vertically oriented, intercellular spaces large, druses present (Fig. 13).

Large veins composed of concentric arcs of xylem and phloem bounded above and below with groups of fibers; small veins vertically percurrent

by fibrous bundle sheath extensions sheathed with a single layer of parenchyma (Figs. 13, 20); cells of the parenchyma sheath frequently bearing prismatic crystals (Fig. 19). Areoles well developed, quadrangular, oriented (Fig. 18).

The combined presence of many sclerified cells, thick-walled fibers, prismatic crystals, and druses render leaves of *Discocarpus* physically tough and durable. While the anatomical preparations described above conform generally with previously published information, neither Gaucher (1902) nor Levin (1986) mentioned the existence of sclerified cells in the adaxial layer.

DISCUSSION OF RELATIONSHIPS

In this century, *Discocarpus* has been assigned to subtribe Discocarpaceae of tribe Phyllanthaceae (Pax & Hoffmann, 1922, 1931). Köhler (1965) suggested placement in Brideliaceae. Hutchinson (1969) did not include the genus in any of his proposed tribes. Most recently, Webster (1975, 1994b) has placed *Discocarpus* in tribe Wielandieae, an assemblage of primitive mostly petal-bearing phyllanthoid genera. At the generic level, *Discocarpus* has been most closely associated with *Lachnostylis* and *Chonocentrum*; in Webster's (1994b) classification, all three genera are placed in Wielandieae and key out adjacent to each other. In fact, the South African genus *Lachnostylis* was combined with *Discocarpus* by Pax and Hoffmann (1922).

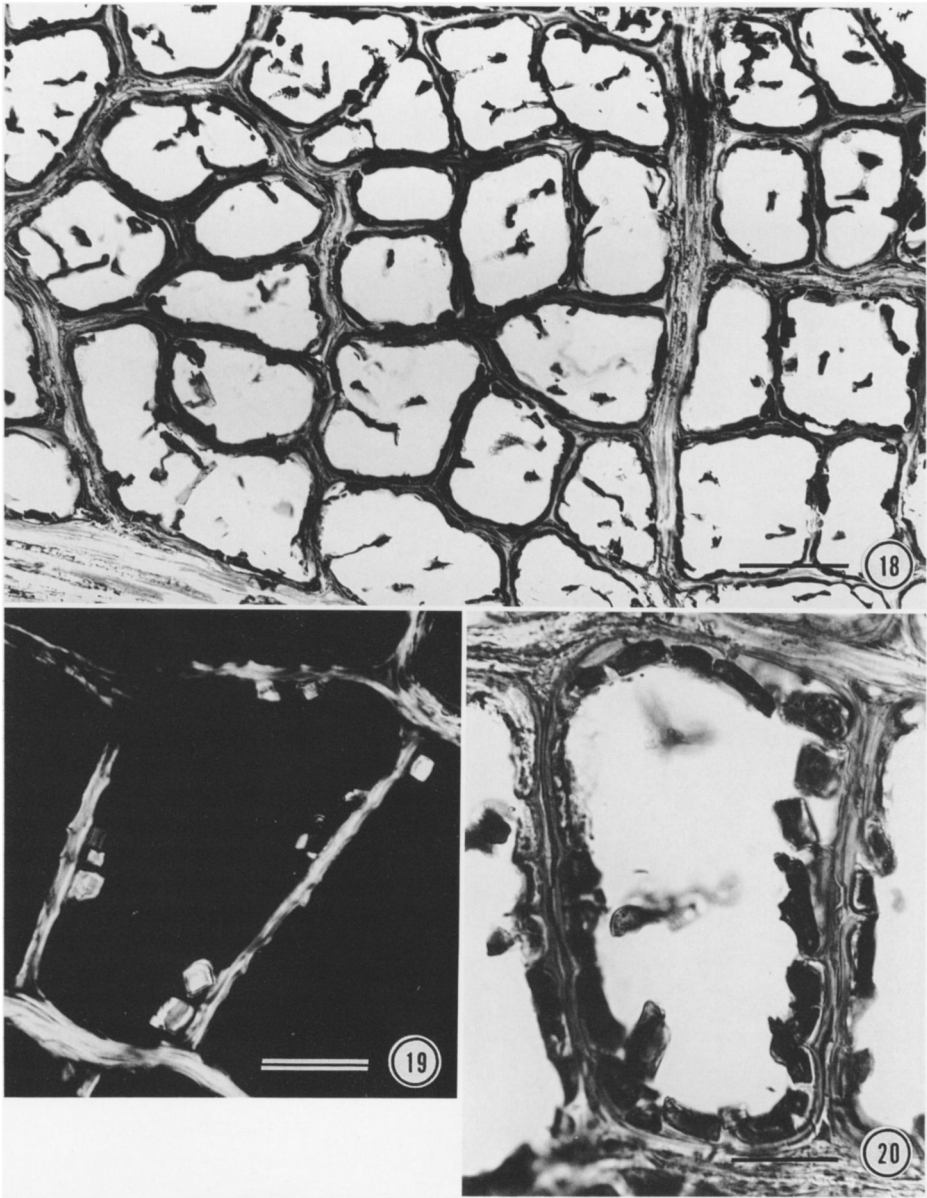
The small trees and shrubs of *Lachnostylis* grow in much drier habitats than neotropical *Discocarpus* and, thus, the plants appear different superficially. However, when one looks beyond the much smaller leaves and highly branched stems, details such as flowers, areolation, and shape of terminal buds support Pax and Hoffmann's (1922) earlier view. To distinguish *Lachnostylis* from *Discocarpus*, Webster (1994b) cited thin styles, pubescent staminate disks, and stamens adnate to the pistillode in the former. However, cursory examination reveals thick styles in *Lachnostylis* similar to those of *Discocarpus* in at least some specimens, and pubescence of the disk may be little more than a reflection of the overall hairier aspect of *Lachnostylis*. Most importantly, as documented herein for *Discocarpus* (Figs. 1, 2), staminate flowers of both genera have connate filaments adnate to the base of the pistillode. Hence, the relationship between *Lachnostylis* and *Discocarpus* seems extremely close.

In contrast, relationship with *Chonocentrum* is much less likely. *Chonocentrum* first became associated with *Discocarpus* by accident. As discussed above, type collections of *Discocarpus spruceanus*

and *Chonocentrum* bear the same collection number, *Spruce 3781*, as a result of mixing these clearly distinct plants. *Chonocentrum* is still known only from the type collection, so comparative data are scarce, and Webster (1994b) considered any possible relationships with this genus to be uncertain. Cursory examination of several isotypes of the only species in the genus, *C. cyathophorum*, shows this plant to be clearly distinct from *Discocarpus*. The cuplike fused calyx, complete absence of petals, and large funnelliform pistillode contrast sharply with *Discocarpus* and have no counterpart in Wielandieae. Although Webster (1994b) stated that the pollen of *Chonocentrum* is unknown, Punt (1962) placed the genus in his "*Antidesma* type," noting that the grains are "quite different" from those of *Discocarpus*. Given its ament-like staminate inflorescence, fused calyx, and absence of petals, *Chonocentrum* keys readily to Webster's (1994b) tribe Antidesmeae, a context within which further comparative studies should prove fruitful. The cuplike calyx of staminate flowers of *Hyeronima* Allemão (Franco R., 1990) and the funnel-like pistillode of *Cyathogyne* Müll. Arg. (Pax & Hoffmann, 1931), both members of subtribe Antidesmineae, appear directly comparable to structures found in *Chonocentrum*.

Two previously unappreciated characters may serve as synapomorphies that argue for a novel taxonomic placement of *Discocarpus* (including *Lachnostylis*?) near *Amanoa* (tribe Amanoeae). First, neotropical *Discocarpus* and *Amanoa* share the unique feature of sclereids in the epidermis, which is otherwise unknown in the Euphorbiaceae (Gaucher, 1902; Levin, 1986) and extremely rare among dicots. Presence of foliar epidermal sclereids is likely synapomorphic for these genera. Second, staminate flowers of *Discocarpus*, *Lachnostylis*, and at least two species of *Amanoa*, *A. nanayensis* W. J. Hayden and *A. steyermarkii* Jabl. (Hayden, 1990), share an androgynophore-like structure (sometimes described as filaments connate to the pistillode); this feature, too, is likely synapomorphic for these genera (Webster, 1994a). In addition, while several genera of Wielandieae possess scalariform perforation plates in the wood, *Amanoa* and *Discocarpus* (as well as *Lachnostylis*) share the derived state of simple perforation plates (Mennega, 1987; Hayden et al., 1993). Based on wood features, Mennega (1987) argued for the exclusion of *Discocarpus* from Wielandieae.

Superficially, inflorescences of *Discocarpus* and *Amanoa* appear distinctly different; however, their basic architecture may prove to be homologous. As described and illustrated here, flowers of *Discocar-*



Figures 18–20. Foliar anatomy of *Discocarpus*. —18. *Discocarpus gentryi* S. M. Hayden, Vázquez & Jaramillo 5487 (NY). Areoles between veins in paradermal section; bar = 100 μm . 19, 20, *Discocarpus essequeboensis* Klotzsch, Smith 2692 (F). —19. Prismatic crystals associated with parenchyma cells lining the areoles; polarized light micrograph; bar = 40 μm . —20. Parenchyma cells lining areoles; bar = 40 μm .

pus occur in axillary clusters. Substructure within these clusters is difficult to discern in the dried, pressed specimens available for study; however, their placement appears to be consistent with the sessile cyme diagrammed for *Amanoa* by Pax and Hoffmann (1922). Thus, while the cymes of *Discocarpus* occur in the axils of foliage leaves and those of neotropical *Amanoa* are placed in the axils of

reduced bracteal leaves, the differences between these genera are neither great nor absolute in this regard. It should be noted that cymes of some African *Amanoa* are axillary to foliage leaves. While *Amanoa* is largely monoecious, *Amanoa anomala* Little (Little, 1969) is dioecious, as is *Discocarpus*. It is also noteworthy that Punt (1962) and Köhler (1965) distinguished the pollen of *Discocarpus* from

that of other Wielandiaeae. Although pollen differences with *Amanoa* exist, Punt (1962) included *Discocarpus* as a distinct type under his "*Amanoa* configuration." Thus, inflorescence architecture, flower structure, foliar anatomy, wood, and pollen, all support classification of *Discocarpus* in tribe Amanoeae as superior to its present placement in Wielandiaeae.

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