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A taxonomic revision of neotropical *Discocarpus* (Euphorbiaceae)

Sheila Mae Hayden

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A TAXONOMIC REVISION OF NEOTROPICAL DISCOCARPUS
(EUPHORBIACEAE)

by

SHEILA MAE HAYDEN

B. A., University of Richmond, 1985

A Thesis

Submitted to the Graduate Faculty

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in Candidacy

for the degree of

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in

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Sheila Mae Hayden

The undersigned have read this thesis and find that, in scope and quality, it satisfies the requirements for the degree of Master of Science.

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Preface

This thesis is a taxonomic revision of Discocarpus, a genus of three species of trees from seasonally inundated forests of northern South America. Discocarpus is classified in the family Euphorbiaceae. The Euphorbiaceae or spurge family is a large and diverse taxon of angiosperms consisting of approximately 7000 species placed in 300 genera, comprising 49 tribes and 5 subfamilies (Webster 1994b). The origin of the family is likely Western Gondwanaland, and the earliest fossils identified as Euphorbiaceae date to the Paleocene (Raven & Axelrod 1974). The family is predominately tropical, however, species of Euphorbiaceae are important throughout most of the world except arctic and alpine regions (Raven & Axelrod 1974).

In both temperate and tropical latitudes, many species of Euphorbiaceae are well-known annual or perennial weeds, a number of which can be found in genera such as Acalypha, Croton, Euphorbia, and Phyllanthus. Diverse species of Euphorbia from arid zones of the paleotropics are cactoid succulents, much prized in horticulture. Other important ornamental euphorbs include Acalypha spp., Codiaeum variegatum (croton), Euphorbia pulcherrima (poinsettia), and Ricinus communis (castor bean). Also of considerable economic importance are Hevea brasiliensis (Pará rubber

tree) and Manihot esculenta (cassava). Other euphorbs have local value as sources of timber or medicines. The value of most euphorbs, however, has yet to be appreciated.

Morphological diversity within Euphorbiaceae is tremendous. Because of this diversity it may seem difficult to characterize the family, however, a combination of ovule features is nearly universal within the family. Ovules are anatropous, pendulous from an apical placenta by means of a ventral raphe (funiculus), equipped with an obturator, and occur singly or paired. Ovule features are widely interpreted as synapomorphies that define Euphorbiaceae (Webster 1994a). Other characters that are widespread, but variable, in the family include alternate, stipulate leaves, unisexual flowers with a floral disk and trimerous gynoecium, and six-parted schizocarpous fruits with either 3 or 6 seeds (Webster 1967). The number of ovules per locule, i.e., whether uniovulate or biovulate, seems to reflect an early divergence in the evolutionary history of the family. For example, the three uniovulate subfamilies of Euphorbiaceae, Acalyphoideae, Crotonoideae and Euphorbioideae, have latex throughout the plant while the two remaining biovulate subfamilies, Phyllanthoideae and Oldfieldioideae, do not (Webster 1967).

The genus Discocarpus Klotzsch has traditionally been placed within subfamily Phyllanthoideae which is thought to

be the most primitive subfamily of Euphorbiaceae (Bentham 1878; Pax 1924; Webster 1967, 1994b). The most primitive tribe of Phyllanthoideae is Wielandieae, the tribe in which Discocarpus has been classified most recently (Webster 1994a, 1994b). Other members of tribe Wielandieae include Heywoodia Sim, Savia Willd., Gonatogyne Muell. Arg., Petalodiscus (Baillon) Pax, Blotia Leandri, Actephila Blume, Lachnostylis Turczaninov, Chonocentrum Pierre ex Pax & Hoffmann, and Wielandia Baillon. The genera of Wielandieae occur in tropical America, Africa, and islands of the Indian Ocean (Webster 1967, 1994b).

In Webster's (1994a) opinion, the genera of Wielandieae "appear to represent relics of the original euphorbiaceous complex from the late Cretaceous". The characters which define Wielandieae are 3-colporate, semitectate, reticulate pollen grains (the "Wielandia type" of Köhler 1965), penninerved, eglandular leaves (Levin 1986), and 5 petals (Webster 1967, 1994b). Several other features are common in Wielandieae, however, none of these define the tribe. These plants are monoecious or dioecious trees or shrubs with alternate, entire, stipulate leaves, and simple indumentum; flowers are axillary and usually in glomerules, however, some pistillate flowers are solitary; laticifers are absent (Webster 1994b).

In order to understand the biology and relationships

among the species of Discocarpus it is first necessary to appreciate something of the nature of the rain forest habitats in which they grow. The life-blood of the rain forest, indeed the major ecological influence on northern South America is the Amazon River. Before the rise of the Andes Mountains, the Amazon is thought to have flowed westward to the Pacific Ocean through the Gulf of Guayaquil in Ecuador. By the end of the Miocene epoch, the Andes were fully formed and the Amazon River had reversed its flow (Goulding 1993). Today the Amazon River starts as small tributaries at about 17,000 feet altitude in the Andes Mountains of Peru, Ecuador, and Colombia. At its beginning, it is only about 120 miles from the Pacific Ocean, but flows eastward over 4,000 miles to the Atlantic Ocean. Although it is second to the Nile in length, the Amazon carries the largest volume of water of any river in the world (Kricher 1989). The sediments carried in suspension by this tremendous volume of water turn the Amazon a milky white color, therefore it is referred to as a "white-water river" (Kricher 1989). The Amazon floods during wet seasons, rising up to 10 meters (Goulding 1993; Alexander 1994).

The Amazon River and its 1100 tributaries drain 6 million square kilometers of northern South America; more than one half of this area is within Brazil (Pires & Prance 1977). Many of the larger tributaries are themselves major

rivers, for example the Rio Negro which begins in Colombia and flows southeast into Brazil, joining the Amazon at Manaus. The Rio Negro is a "black-water river," colored dark by large amounts of dissolved tannins (Kricher 1989). The Amazon and its tributaries continue to serve as a highway system to the interior, even as a main access route to cities such as Iquitos, Peru, to which there are no roads (Kricher 1989).

Amazonia is a complex of many habitats, and not, as is commonly assumed, monotonously wet and inundated. Ninety percent of the land is terra firma, well-drained areas above flood level (Pires & Prance 1977). There are even mountain habitats within Amazonia located on the Brazil-Venezuela border (Pires & Prance 1977). The "Amazon Forest" is actually an assemblage of diverse plant communities each associated with a distinctive Amazonian habitat. Some basic types of forest areas include: terra firma forest, lowland forests that are seasonally flooded (Pires & Prance 1977), permanently wet swamp forest or Brazilian igapó, campina or dry upland forest, liana forest dominated by woody plants with vine-like habits, and various dry or inundated upland savannas (Pires & Prance 1977).

Discocarpus species inhabit seasonally inundated lowland forests. This distinctive habitat is called várzea in Brazil (Pires & Prance 1977; Colinvaux 1989; Goulding

1993; Alexander 1994), rebalse in Venezuela (Steyermark 1977), and tahuampal in Peru (Gentry 1977). These special forests occur only in areas where rainfall is above 2000 mm per year (Simpson & Haffer 1978). Floodwaters may inundate the forest for as much as seven months of the year. Although lowland inundated forests occupy only about 3 percent of the total Amazonian forest habitats, it is widely accepted that they are among the world's richest ecosystems (Erwin & Adis 1982; Colinvaux 1989; Goulding 1993).

Fernández-Pérez (1977), Gentry (1977), Steyermark (1977), Pires & Prance (1977), Iltis (1983), Janzen (1986), Colinvaux (1989), Goulding (1993), and Alexander (1994) all clearly express the concerns shared by many biologists working in neotropical rainforests. The concern is that these regions of great, but often still uncataloged biodiversity, are being modified or destroyed at rates that threaten both the survival of hosts of species and, perhaps, the integrity of the ecosystem. Venezuela, for example, has a flora rich in endemic species. The flora of Territorio Federal Amazonas and the Guyana Highland of Venezuela is believed to be composed of 75% endemics; despite decades of relatively intense exploration, many areas in this region have never been explored botanically (Steyermark 1977). Gentry (1977) described Amazonian Peru as a floristically very rich area that is poorly known botanically. Gentry

estimated that 15,000--30,000 species occur in this area, but assessment for endangered species is not yet possible because so little is known of the flora. Nonetheless, development of these forests is proceeding with frightening speed, often with governmental approval, before the forest can be explored. Of the 3 million estimated species of tropical plants and animals (not including an estimated 25 million insects) only about 500,000 have been described and named (Kricher 1989). Unfortunately the situation will likely get worse as the human population continues to grow. It is predicted that 90% of the world's population growth in next 20 years will occur in the tropics (Iltis 1983; Kricher 1989). To support the increasing numbers of people and their economic aspirations without serious change in the distribution of wealth at global levels, forest is being cut, in part, for cattle range and farm land. However, the nutrient poor rainforest soils can support these uses only a few years (Iltis 1983; Goulding 1993). In addition, timber trees are being logged. Dams destroy huge tracts of forest and road building through virgin forest opens these pristine areas to development. Even in sites where national parks and reserves have been established the forest suffers because there are not enough professionally trained managers to make and enforce informed policy (Janzen 1986). Consequently, many potentially important plants and animals

are being threatened with extinction.

Pires & Prance (1977) propose the following:

"In order to fully understand how best to preserve a natural balance between man and the forest (Amazonian rainforest), intensive study is urgently necessary in the following areas: 1. The identification of and intensive research in those areas most threatened by the interference of man. 2. The collection of vital documentary data such as herbarium material, zoological, and mineralogical specimens, which can then be meticulously studied in the laboratory. 3. The selection and official designation, on the basis of scientific information, of representative areas of forest as biological reserves, the collection of living material for propagation in botanical gardens and zoos and the establishment of more Indian reservations."

Clearly much remains to be done.

This study contributes towards a basic understanding of the systematics of one small genus endemic to the rainforests of northern South America. Ultimately, it will take many projects, large and small, before we understand the extent and value of the biological diversity present in the tropical rainforest. Although considered by some, even other biologists, to be research out of fashion, systematic studies like this thesis, are critical to the identification and documentation of the organisms present in the tropics before they disappear. Systematics is at the core of any biodiversity and conservation effort. The information gained by such studies is urgently needed by field biologists and concerned lay people working to preserve what

remains of these vast forest systems. I feel privileged to make this small contribution.

The study presented herein conforms with precepts stated by the eminent plant systematist Arthur Cronquist (1978):

"Ideally, the comparative studies on which taxonomic conclusions are based should include all characteristics of all species of a group, and of many individuals throughout the geographic range of each species. Morphological comparisons should include not only the obvious floral and vegetative structure, but also the various kinds of micromorphology, as observed both with the light microscope and with the electron microscope."

The information compiled for a revision of a genus includes: history of the nomenclature (scientific names and how they have been applied through time) of the genus and each species, detailed descriptions of the genus and each species, a dichotomous key to species identification, illustrations, habitat information, phenological information (flowering and fruiting times), geographic distribution (including maps), literature, and classification, and thoughts on relationships with other plants (Morin et al. 1989).

The previous taxonomic treatments of Discocarpus are herein regarded as a series of hypotheses involving the definition or limits of individual species, their

relationships to each other, the limits of the genus, and its relationships to other euphorbs. These hypotheses will be evaluated in light of data currently available. These data are derived from examination of herbarium specimens that have been collected and preserved over the past 150 years. Many of these same specimens were studied by past researchers who published on the taxonomy of Discocarpus, and thus provide insight to the historical basis of earlier classifications. Many collections, however, are recent and provide records of the genus which were previously unavailable. In addition, this study employs sources of micromorphological data previously unstudied in Discocarpus. I view taxonomy and classification of Discocarpus as a dynamic process. As our information about any group of taxa increases, and our understanding of the relationships with related taxa develops, the classification is revised to reflect the new knowledge.

Introduction

Discocarpus Klotzsch is a genus of trees found in riparian habitats of northern South America where they are components of the forest canopy in seasonally flooded regions. 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 (see Excluded Species section, below), the next species of Discocarpus to be named was D. spruceanus Muell. 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 Muell. Arg. (1873) was formally named based on a collection of von Martius from the early part of the 19th century. Three taxa were added to the genus in the 20th Century. The first addition was D. hirtus (L.f.) Pax & Hoffmann (1922), a consequence of synonymizing the South African genus Lachnostylis Turcz. with Discocarpus. The two most recently described species, D. mazarunensis Croizat (1948) and D. duckeanus Jablonski

(1967), were based on South American material.

Jablonski (1967) accepted the five South American species as distinct entities comprising Discocarpus. However, Jablonski's treatment reveals several inadequacies and may be considered a preliminary summary of the literature at that time. For example, staminate or pistillate flowers remained undescribed for several species. Furthermore, current knowledge reveals two of the species accepted by Jablonski to have been misplaced in Discocarpus, and presently available collections indicate the existence of a previously unrecognized species.

The generic relationships of Discocarpus also remain uncertain. In this century, Discocarpus was assigned with Chonocentrum Pierre to subtribe Discocarpaceae of the tribe Phyllanthaceae (Pax & Hoffmann 1922). Köhler (1965) suggested placement in Brideliaceae but Webster (1975, 1994b) placed Discocarpus in tribe Wielandieae, an assemblage of primitive mostly petal-bearing phyllanthoid genera. However, placement in Wielandieae has been challenged by Mennega (1987) and references to foliar epidermal sclereids in Discocarpus (Gaucher 1902; Levin 1986) invite detailed comparison with similar structures known to occur in Amanoa Aublet of tribe Amanoeae (Hayden 1990 & unpublished data).

The purpose of this study is to revise the systematics of Discocarpus.

Materials and Methods

A total of 170 herbarium specimens (individual sheets) identified as Discocarpus were borrowed from 27 herbaria in the United States, Europe, and South America (see Appendix I). Specimens were sorted to species as identified on the labels. Label information was recorded on data sheets for each collection. Transcribed label data included: collector and collection number, date collected, collection site, other information on leaf or flower color, gender, phenological information (stage of flower or fruit development), plant size, soil type, and local common names. The preserved plants of each sheet were then studied under the dissecting microscope to record additional characters, for example, size and shape of leaves and terminal buds, vestiture and surface textures, and structural details of flowers, fruits, and seeds. Original descriptions of previously published species were obtained and translated from Latin to aid in understanding past species concepts in the genus. Herbarium sheets were resorted as concepts of species boundaries were refined.

Permission was obtained to remove small samples of leaf tissue from randomly selected collections of each species for anatomical study (see Appendix II). Half of each sample was mounted directly on SEM stubs and sputter coated with a

gold/palladium mixture. 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 μm on a rotary microtome. Paraffin sections were stained in toluidine blue or a combination of safranin and haematoxylin.

Systematic Treatment

Discocarpus Klotzsch. Archiv. Naturg. 7(1): 201. 1841.

TYPE: Discocarpus essequeboensis Klotzsch.

Dioecious trees, (3) 10--20 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 bud acuminate, cylindrical, glabrous to tomentose, 3--7 mm long, often with two basal knob-like protrusions. Leaves alternate, simple, petiolate, glabrous, leathery; petioles 4--8 mm long, wrinkled; margins entire; base obtuse; apex acute to acuminate; venation pinnate. Stipules fugaceous. Inflorescence axillary, 1--several flowers per node; flower clusters subtended by cupulate bracts; bracts ca. 1 mm long, 1 mm wide; staminate clusters essentially sessile, several per node; pistillate clusters sessile or pedicellate, one per node. Staminate flowers sessile, congested, 10--30 per node; sepals 5 (4), 2 mm long, 1 mm wide, pilose; petals 5, delicate, membranous, less than 1 mm long, often lobed or fringed; disk extrastaminal, lobed; stamens 5 (4); filaments fused below the level of the disk; anthers 1 mm long, longitudinally dehiscent, exerted; pistillode segmented into two or three linear, pubescent, membranous filaments. Pistillate flowers short pedicellate, essentially sessile, 1--3 (5) per node;

sepals 5, cupulate, 2--3 mm long, 1 mm wide, pilose, fringed distally; petals 5, membranous, 1 mm long, less than 1 mm wide, fringed apically; disk lobed to nearly entire; ovary 3-carpellate, smooth or sculpted, densely pubescent; styles 3, parted to the base or nearly so, spreading horizontally; stigmas dilated, more or less lobed, reflexed; ovules 2 per locule. Fruits 1--3 seeded, 7--14 mm in diameter, 7--12 mm long, longitudinally dehiscent into 3 or 6 mericarps; pericarp ca. 1 mm thick, hard, brittle; surface smooth to deeply sculpted, densely pubescent. Seeds globose to subglobose; testa thin, shiny.

Three species of Discocarpus occur in the Amazon and Orinoco River basins of Brazil, Colombia, Peru, and Venezuela, plus smaller rivers of Guyana and Surinam (Fig. 1). Habitat is lowland rainforest below 250 m, along seasonally flooded river banks of várzea forests or occasionally inundated fields. Discocarpus species can form canopy trees, however, samples are sometimes collected from specimens described as small shrubs.

Key to species of Discocarpus

1. Terminal bud of staminate specimens 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 Muell. Arg.

1. Terminal bud of staminate specimens glabrous or only sparsely pubescent; ovary and fruit surface sculpted; fruits 3-seeded, all carpels accrescent.
2. Pistillate flower clusters on pedicels 3--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

2. Pistillate flower clusters sessile or nearly so; ovary and fruit surface weakly sculpted into muricae or short undulate ridges with rounded crests (beneath dense indumentum); fresh staminate flowers cream. Plants of Guyana and northeastern Brazil.

D. essequiboensis Klotzsch

Discocarpus essequeboensis Klotzsch. London J. Bot. 2: 52.

1843. (Figs. 2, 7, 8, 12)

TYPE: GUYANA: On branch of upper Essequibo River,

Schomburgk 35 (LECTOTYPE selected here: BM!;

ISOLECTOTYPES: G!, K!, OXF!, P!, U!, W!).

Discocarpus essequeboensis Klotzsch. Archiv. Naturg.

7(1): 201. 1841. (nomen nudum).

Discocarpus brasiliensis Klotzsch ex Muell. 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 1 m. 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. Staminate flowers 15--20 per node; bracts glabrous (occasionally pubescent); sepals 5, 2 mm long, 1.5 mm wide, cream-colored, pubescent; petals occasionally present, filiform; disk lobed; stamens 5 (4); pistillode as long as calyx. Pistillate flowers 1--5 per node; bracts pubescent (occasionally glabrous); peduncle 0--1 mm; sepals 3 mm long, 2 mm wide, light green, pubescent, fringed apically; petals reduced, occasionally present, 0.5--3 mm long, hyaline, ciliate; disk slightly lobed; ovary subovate, shallowly muricate to reticulate; styles recurved; stigma dilated,

lobed. Immature fruits dark red; mature fruit brown, 3-lobed, 8--9 mm tall, 10--15 mm in diameter, 3-seeded. Seed subglobose, 6--8 mm in diameter; micropylar and basal surfaces somewhat flattened; testa red-brown.

Distribution: central and eastern Brazil, Guyana, Surinam (Fig. 1); 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. (G, L, M). Goiás: Rio Araguaia at mouth of Rio Javaés, Silva 4862 (ILLS, NY); Rio Piranha, Silva 4776 (NY). Maranhão: Rio Alto Turiaçu, Nova Esperança, 2°55'S, 45°45'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,

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, Corantýne, B.W. 2044 (U); Tapanahoni, Kappler 97 (L, U, W), Kappler 2143 (GOET, W); Schomburgk 459 (G).

Notes: Klotzsch's species Discocarpus essequeboensis was originally based upon three collections, Schomburgk 35 (pistillate flowers), Schomburgk 659 (staminate flowers), and Schomburgk 706 (mature fruits). Since staminate material of Discocarpus bears few diagnostic characters and since the fruiting specimen bears only fragmentary label

data, the pistillate collection, Schomburgk 35, is by far the superior choice to typify this species. The BM specimen bears 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).

Discocarpus brasiliensis is here recognized as synonymous with 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 while Brazilian specimens were called D. brasiliensis. Historically, Discocarpus brasiliensis was 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 (Mueller 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, another pistillate syntype 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 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. essequeboensis and D. brasiliensis that delineates two separate species, the decision was made to place Discocarpus brasiliensis in synonymy under Discocarpus essequeboensis. Both names were first published by Klotzsch, however, the name D. brasiliensis, published in 1841, remained a nomen nudum until Mueller provided it with a diagnosis in 1873. Thus D. essequeboensis, published in 1843, is the oldest legitimate name for this species.

In addition to those named D. brasiliensis Klotzsch, other specimens collected by Martius also 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. (Figs. 3, 9, 10)

TYPE: PERU, Loreto: Santa María de Nanay, south west
of Río Nanay, Schunke V. 2443 (HOLOTYPE: F!;
ISOTYPES: G!, GH!, NY!, US!).

Arbor dioecia, 3--14 m; gemma terminalis glabra, acuminata, 3--6 (7) mm, cum umbo duo basalis; folia elliptica, 7--15 cm longa, 3--7 cm lata; fasciculi staminalis cum 20--30 flores; flores subtenta utrimque bractea cupulata, glabra; flores staminati lutei; flores pistillati 1 (2) per nodum; pedicelli florum pistillatum 4 mm longa; fructus subglobosus, 11 mm longa, 15 mm diam; pericarpium undulatum profunde, viride; semina subglobosa, 8 mm diam; testa laevis, tenuis, cinnamomeus.

Trees or shrubs, 3--14 m tall; DBH 35--40 cm. Terminal buds similar in staminate and pistillate specimens, glabrous, with two basal knobs. Leaves 7--15 cm long, 3--7 cm wide; apex acute to acuminate. Staminate flowers 20--30 per node, bright yellow; bracts glabrous (occasionally sparsely pubescent apically); sepals 2 mm long, 1 mm wide, pubescent; petals 0--5, minute; disk with finger-like lobes; filaments 3 mm long; pistillode segments 2. Pistillate flowers 1 (2) per node; bracts glabrous; peduncles 4--5 mm long; sepals 5, 3 mm long, 2 mm wide; petals 5, 2 mm long, 1 mm wide; disk slightly lobed; ovary subovate; surface deeply undulate; styles recurved; stigma dilated, lobed. Fruit

green, subglobose, 3-lobed, 11 mm long, 15 mm in diameter, 3-seeded; outer wall thickness 1 mm, woody, green; columella persistent; seeds subglobose, ca. 8 mm in diameter; micropylar and basal surfaces somewhat flattened; testa golden brown.

Distribution: Amazonian Peru, and western Brazil (Fig. 1); on white sand or clay soil of low, seasonally inundated forest along rivers (varzea or tahuampa); 120--150 m altitude. Flowers have been collected from December through April; fruits, from September through February.

Common Names: "Ucuchahuasi" (Vasquez & Jaramillo 5487); "Loromicuna" (Ayala 1415).

Additional specimens examined: BRAZIL. Amazonas: Rio Negro near Ilha Provedencia, 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 mph motor, Gentry et al. 18419 (F, MO); right margin of de 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 & 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 pedunculate. In contrast, fruits of D. essequiboensis, though still sculpted, are smoother, and pistillate flower clusters are sessile. 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. Further, 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 river banks 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 species name commemorates Alwyn H. Gentry (1945--1993), for his many important contributions to the floristics of Central and northern South America. Gentry's collections of Discocarpus from the region around Iquitos, Peru, were instrumental in recognizing these plants as new to science.

Discocarpus spruceanus Muell. Arg. Linnaea 32: 78. 1863.

(Figs. 4, 5, 6, 11)

TYPE: BRAZIL, Amazonas: Rio Negro above the mouth of the Casiquiare River, Spruce 3527 (LECTOTYPE selected here: BM!; ISOLECTOTYPES: BR!, C!, E!, F!, G!, GH!, GOET!, K!, MO!, NY!, OXF!, P!, TCD!, W!).

Drypetes krukovii Monachino. 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, glabrous with two basal knobs in pistillate trees. Leaves 5--12 cm long, 2--5 cm wide; apex acute to acuminate. Staminate flowers 15--30 per node; bracts pubescent; sepals 4--5, 1.5 mm long, 1 mm wide, pubescent; petals 4--5, filiform; stamens 4 (5); anthers exerted to 3 mm beyond the calyx; pistillode 2(3)-segmented, ciliate. Pistillate flowers 1--3 per node; peduncles of clusters 1--5 mm long; bracts pubescent; sepals 5, 1.5 mm long, 1 mm wide, pubescent; petals 5, 1.5 mm long, 0.5 mm wide, pubescent; disk slightly lobed; ovary subovate, smooth, densely pubescent; styles 3, fused half-way to base.

Fruit brown, subglobose, asymmetrically 3-lobed by abortion of 2 (1) carpels, 6--9 mm in diameter, 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. 1); 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 (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, Dovebros (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: Río Guainia between Comunidad and Santa Rita, Wurdack & Adderley, 43349 (NY, S, US); Caño Adobo, 25 km S of San Cargos of Río Negro, 1° 38'N, 66° 58'W, Liesner 8634 (MO, NY); Departamento Río 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 spruceanus, Spruce 3527 and Spruce 3781, are often curated together and this has led to a potentially confusing situation. Generally, specimens labelled as Spruce 3781 are staminate and those labelled Spruce 3527 bear fruits, but the numbers were apparently reversed 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 have been recognized as the type of a different plant, Chonocentrum cyathophorum (Muell. Arg.) Pax & Hoffmann. For example, one of the two collections of Spruce 3781 received from OXF was a specimen of Chonocentrum, still 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 discussed above, the fruiting collections of Spruce 3527 are by far more diagnostic than the staminate material that constitutes Spruce 3781 and therefore 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.

At this writing there is a single record of Discocarpus spruceanus from Colombia, a flowering staminate specimen collected by Little & Little 9604 in 1945.

Excluded Species

Discocarpus duckeanus Jablonski. Mem. New York Bot. Garden.

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, have petal-less flowers with 8 (or more?) filaments fused into a central column with 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).

Two additional staminate specimens (Rosário 73 from NY, and Davidse & González 16315 from NY and U) were received bearing provisional identifications as Discocarpus duckeanus. Many features prove these specimens to be discordant with both Discocarpus and Chaetocarpus, including: leaves with large, irregular areoles and laticifers; conspicuously jointed peduncles, the lower portion of which persists post-anthesis; stamens 10; and highly lobed, segmented disks. It is likely that these specimens represent a species of some other uniovulate genus

of Euphorbiaceae.

Discocarpus mazarunensis Croizat. Bull. Torr. Bot. Club.

75: 400. 1948. Type: Fanshawe 2124 (NY!). =

Chaetocarpus schomburgkianus (Kuntze) Pax & Hoffmann.

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, types of D. mazarunensis have filaments fused into a prominent staminal column with anthers diverging at different levels. Exclusion from Discocarpus is thus amply 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 towards the surface, thinner towards the mesophyll; outer periclinal walls bearing subcuticular micropapillae (in *D. spruceanus*) (Figs. 14, 15, 16). Adaxial epidermal cells 15 μm thick, uniformly bearing tannin deposits, rarely sclerified in reverse pattern; cuticle 1--2 μm thick. Abaxial epidermal cells average 11 μm thick, occasionally bearing tannin deposits; cuticle < 1 μm thick. Stomata restricted to the abaxial epidermis, densely crowded, oriented randomly, widely elliptic, 18 μm long, 15 μm wide; anticlinal walls forming stomatal pore minutely crenulate (Fig. 17); subsidiary cells brachyparacytic.

Mesophyll stratified, tannin deposits scattered throughout; palisade cells well developed, sometimes lightly sclerified near the adaxial epidermis; spongy layer weakly developed, vertically oriented, intercellular spaces large, druses present (Fig. 13).

Large veins comprised 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 leaves of Discocarpus are true sclerophylls. These are physically tough leaves containing many sclerified cells, thick-walled fibers, prismatic crystals, and druses. In this case, sclerophylly may be an adaptation that discourages herbivory by insects. Little insect damage was observed on leaves of the herbarium specimens studied.

While the anatomical preparations described above conform generally with previously published information, some features described herein are interpreted differently. Although both Gaucher (1922) and Levin (1986) described the sclerified abaxial epidermal cells of Discocarpus, neither mentioned the existence of sclerified cells in the adaxial layer. Levin (1986) also states that most cells in the abaxial epidermis appear to be subsidiary cells or guard cells. Granted, the stomates are densely crowded on the lower epidermis, however, it is not difficult to find ordinary epidermal cells separating the subsidiary cells.

Discussion of Relationships

In his recent paper on the classification of the Euphorbiaceae, Webster (1994a) proposed primitive and derived states for 36 characters important in the taxonomy of this large and diverse group of plants. Of the 36 characters listed in Webster's chart, Discocarpus is known to exhibit 25 characters in the primitive state (Appendix III). Despite the large number of primitive characters, some inferences concerning the relationships of Discocarpus can be made.

Two monotypic genera, Lachnostylis Turczaninow, and Chonocentrum Pierre ex Pax & Hoffmann, have been historically associated with Discocarpus (Pax & Hoffmann 1922) and their close association is maintained in Webster's (1994b) classification; all three genera are classified in Wielandieae, and key out adjacent to each other. In fact, the South African genus Lachnostylis Turczaninow was combined with Discocarpus by Pax & Hoffmann (1922).

The small trees and shrubs of Lachnostylis grow in much drier habitats than neotropical Discocarpus and, thus, the plants present a superficially different aspect. 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 earlier view. To distinguish Lachnostylis from Discocarpus, Webster

(1994b) cites thin styles, pubescent staminate disks, and stamens adnate to the pistillode in the former. However, cursory examination of these characters in Ecklon 34 (W) reveals thick styles in Lachnostylis similar to those of Discocarpus 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. 5, 6), 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 and further study of the former may prove to support Pax & Hoffmann's treatment.

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) considers any possible relationships with this genus to be uncertain. cursory examination of several syntypes of the only species in the genus, C. cyathophorum (Muell. Arg.) Pax & Hoffmann, show the genus to be clearly distinct from Discocarpus. The cup-like fused calyx, absence of petals, and large funneliform

pistillode contrast sharply with Discocarpus and have no counterpart in Wielandieae. Although Webster (1994b) states 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 cup-like calyx of staminate flowers of Hyeronima Allemão (Franco R. 1990) and the funnel-like pistillode of Cyathogyne Muell. Arg. (Pax & Hoffmann 1931), both members of Antidesmineae, are directly comparable to those of Chonocentrum.

Two previously unappreciated characters may serve as synapomorphies that argue for a novel taxonomic placement of Discocarpus (including Lachnostylis?) in tribe Amanoeae. First, 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 the dicots. So, the presence of foliar epidermal sclereids can be considered as a synapomorphy for these genera. Second, Discocarpus, Lachnostylis, and at least two species of Amanoa, A. nanayensis W. J. Hayden and A. steyermarkii Jablonski (Hayden 1990), share the extraordinary feature of an androgynophore-like structure in

staminate flowers (sometimes described as filaments connate to the pistillode); this feature, too, is likely synapomorphic (Webster 1994a). In addition, Amanoa and Discocarpus (as well as Lachnostylis) share the derived state of simple perforation plates in the xylem (Mennega 1987).

Superficially, inflorescences of Discocarpus and Amanoa appear distinctly different, however, their basic architecture may prove to be homologous. As described above, flowers of Discocarpus occur in axillary clusters. Substructure within these clusters is difficult to discern in the dry, 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, the differences between inflorescences of these genera are neither great nor absolute. The cymes of Discocarpus occur in the axils of foliage leaves whereas those of neotropical Amanoa are placed in the axils of reduced bracteal leaves. It is noteworthy, however, that cymes of some African Amanoa are axillary to foliage leaves. Another presumed distinguishing feature between these genera is that Discocarpus is dioecious whereas Amanoa is monoecious; however, Amanoa anomala (Little 1969) matches Discocarpus in this regard. Similarly, although pollen differences with Amanoa exist, Punt (1962) placed Discocarpus as a distinct

type under his "Amanoa configuration."

As discussed in the introduction, arguments against retention of Discocarpus in Wielandieae have been expressed by Punt (1962), Köhler (1965), and Mennega (1987), while Pax and Hoffmann (1922) placed the genus in a separate subtribe. Inflorescence architecture, flower structure, foliar anatomy, wood, and pollen, suggest that Discocarpus is better placed in tribe Amanoeae than Wielandieae.

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Appendix I

Key to the Abbreviations of Herbaria

- BM The Natural History Museum, London, England.
- BR National Botanical Garden of Belgium, Meise,
Belgium
- C Botanical Museum, University of Copenhagen,
Denmark.
- E Royal Botanic Garden, Edinburgh, Scotland.
- F The Field Museum, Chicago, Illinois.
- G Herbarium, Conservatoire et Jardin Botaniques de
la Ville de Genève, Switzerland.
- GH Harvard University Herbarium, Massachusetts.
- GOET Herbarium, Systematisch-Goebotanisches Institut,
Universität Göttingen, Göttingen, Germany.
- ILLS Illinois Natural History Survey, Champaign,
Illinois.
- K Royal Botanic Gardens, Kew, England.
- L Rijksherbarium, Leiden, The Netherlands.
- M Botanische Staatssammlung München, Germany.
- MANCH Manchester Museum, University of Manchester,
Manchester, England.
- MICH The Herbarium of the University of Michigan,
Michigan.
- MO Missouri Botanical Garden, St. Louis, Missouri.

- NY The New York Botanical Garden, Bronx, New York.
- OXF Fielding-Druce Herbarium, Oxford University
Herbaria, Oxford, England.
- P Herbier, Laboratoire de Phanérogamie, Muséum
National d'Histoire Naturelle, Paris, France.
- R Museu Nacional, Universidade Federal do Rio de
Janeiro, Brazil.
- RB Jardim Botânico do Rio de Janeiro, Brazil.
- RSA Rancho Santa Ana Botanic Garden Herbarium,
Claremont, California.
- S Swedish Museum of Natural History, Stockholm,
Sweden.
- TCD Herbarium, School of Botany, Trinity College,
Dublin, Ireland.
- U Projectgroep Herbarium Rijksuniversiteit Utrecht,
The Netherlands.
- UC University Herbarium, University of California,
Berkeley, California.
- URV University of Richmond Herbarium, Richmond,
Virginia.
- US Smithsonian Institution, Dept. of Botany,
Washington, D. C.
- W Naturhistorisches Museum Wien, Austria.

Appendix II
Anatomical Specimens

Discocarpus essequiboensis Klotzsch

Krukoff & Froes 11974 (NY)

Schomburgk 659 (U)

Jangoux & Bahia 249 (NY)

Maas et al. 7395 (U)

Smith 2692 (F)

Encarnación 25065 (F)

Discocarpus gentryi S. M. Hayden

Vázquez & Jaramillo 5487 (NY)

Discocarpus spruceanus Muell. Arg.

Davidse 27631 (NY)

Silva 4776 (NY)

Wurdack & Adderly 43349 (NY)

Appendix III

Character States of Euphorbiaceae (after Webster 1994a;
if known, * indicates condition found in Discocarpus)

Character	Primitive State	Derived State
1. Habit	*Trees/shrubs	Herb/vines
2. Branching	*Monopodial	Sympodial
3. Phyllotaxy	*Alternate	Opposite
4. Leaf Shape	*Simple	Lobed; compound
5. Leaf venation	*Pinnate	Palmate
6. Stipules	*Present	Absent
7. Vessel Perferation	Scalariform	*Simple
8. Vascular rays	*Multiseriate	Uniseriate
9. Internal Phloem	*Absent	Present
10. Laticifers	*Absent	Present
11. Trichomes	*Simple	Stellate; lepidote
12. Foliar glands	*Absent	Present
13. Inflorescence	*Axillary	Terminal
14. Calyx aestivation	*Imbricate	Valvate
15. Petals	*Present; free	Absent
16. Disk	*Present	Absent
17. Stamen number	*5-10	1-4, over 10
18. Filaments	Free	*Connate

19. Anther dehiscence	*Longitudinal	Horizontal
20. Pollen nuclei	*2-nucleate	3-nucleate
21. Pollen exine	Semitectate	*Tectate; intectate
22. Pollen apertures	*Colpi	Pores; inaperturate
23. Aperture number	3	*4 or more
24. Pistillode	*Present	Absent
25. Carpel number	*3-5	1-2; 6 or more
26. Style branches	*Bifid	Unlobed; multifid
27. Style union	*Free	Connate
28. Ovary number	*2/locule	1/locule
29. Ovule configuration	*Anatropous	Hemitropous
30. Embryo sac	Monosporic	Disporic; tetrasporic
31. Fruit	*Dehiscent	Indehiscent
32. Seeds	*Ecarunculate	Carunculate
33. Seed testa	*Dry	Fleshy
34. Endosperm	Present	Scanty or absent
35. Cotyledon/radicle length	2+	less than 2
36. Cotyledon/radicle width	2+	less than 2

Figure 1. Distribution of Discocarpus. Squares = Discocarpus essequeboensis Klotzsch; circles = Discocarpus spruceanus Muell. Arg.; triangles = Discocarpus gentryi S. M. Hayden.

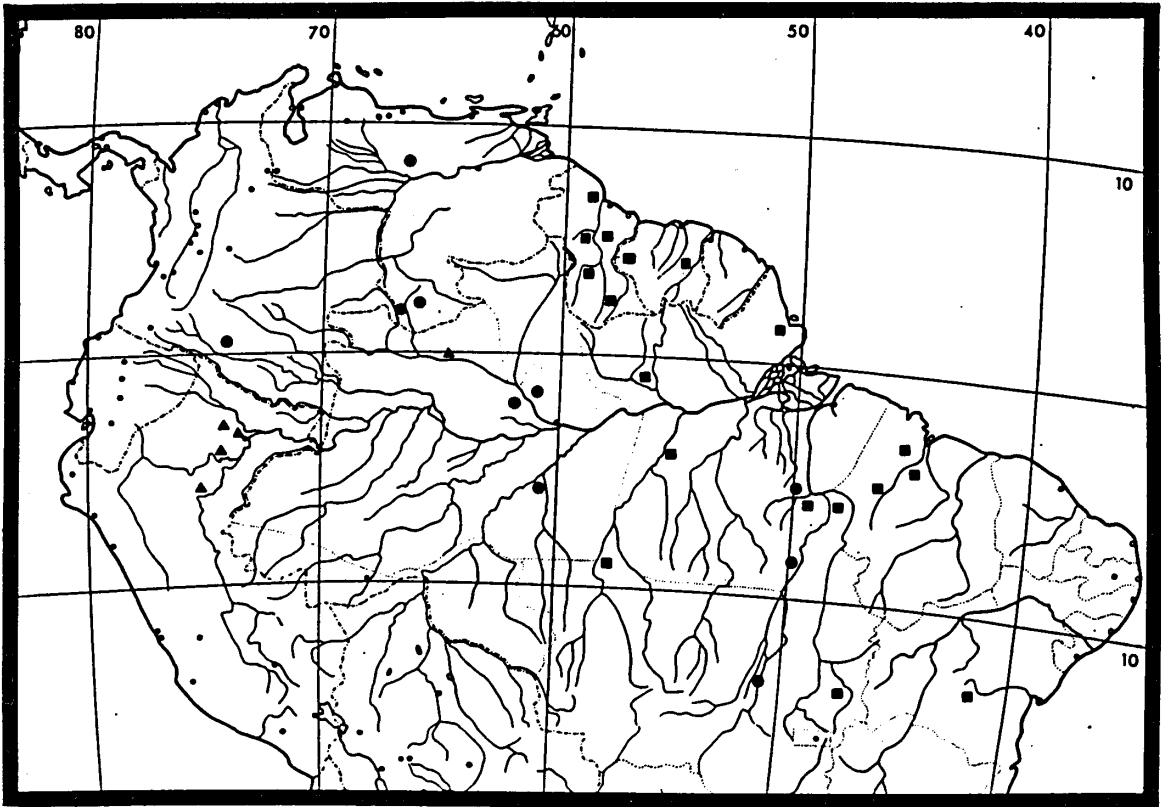


Figure 2. Discocarpus essequeboensis Klotzsch. A. Disk from staminate flower, perianth removed; Pires 109 (U). B. Staminate flower; Pires 109 (U). C. Habit, staminate specimen; Krukoff 11974 (NY). D. Habit, pistillate specimen; Rosa & Santos 2149 (MO). E. Immature fruit; Schomburgk 35 (W). F. Terminal bud; Krukoff 11974 (NY).

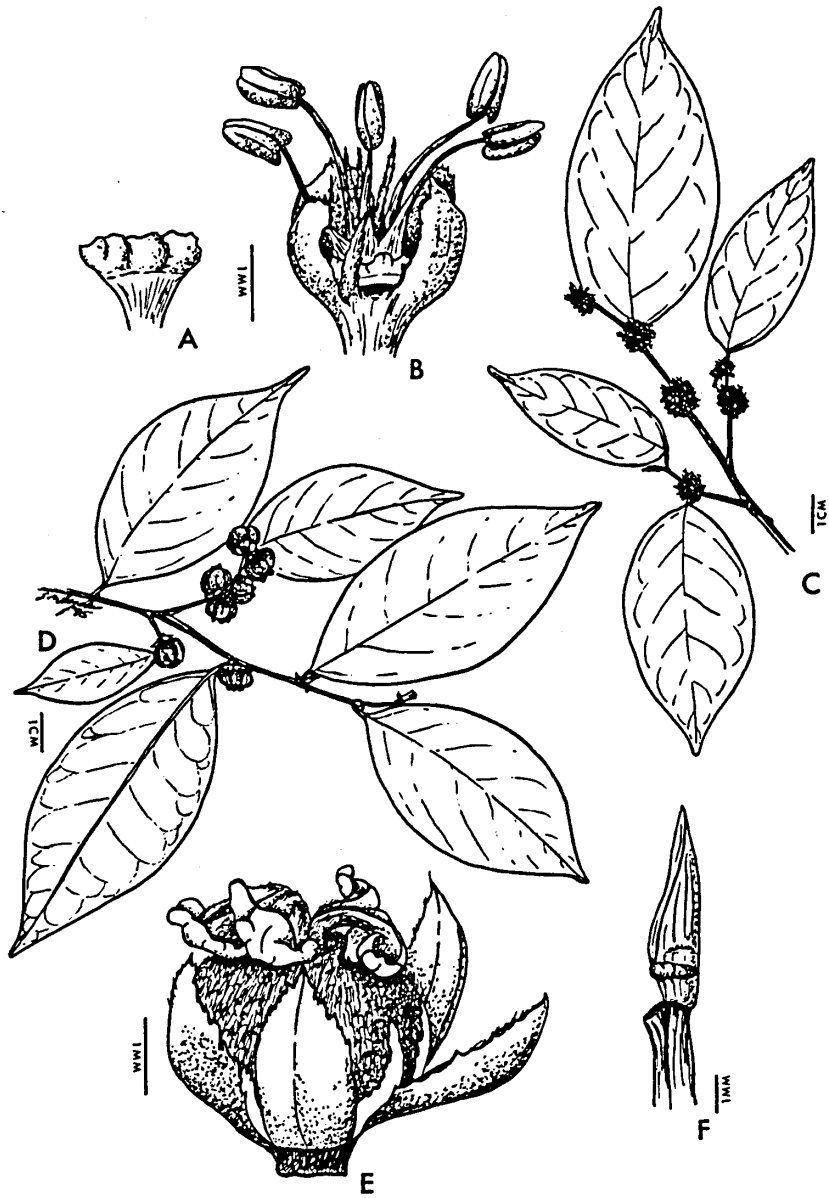


Figure 3. Discocarpus gentryi S. M. Hayden. A. Staminate flower; Rimachi Y. 3300 (NY). B. Habit, staminate specimen; Rimachi Y. 3300 (MO). C. Terminal bud; Rimachi Y. 3300 (MO). D. Disk from staminate flower, perianth removed; Rimachi Y. 3300 (NY). E. Habit, pistillate specimen; Gentry et al. 18419 (F).

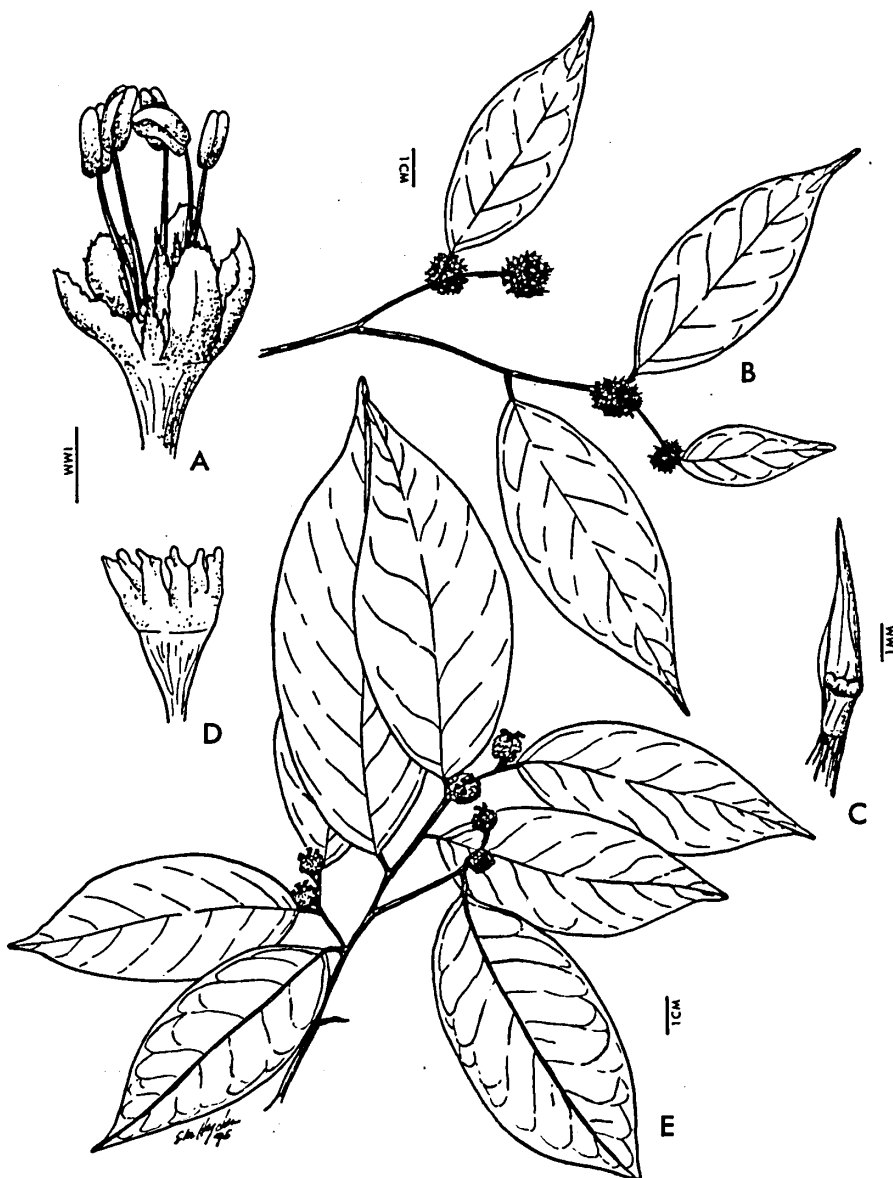
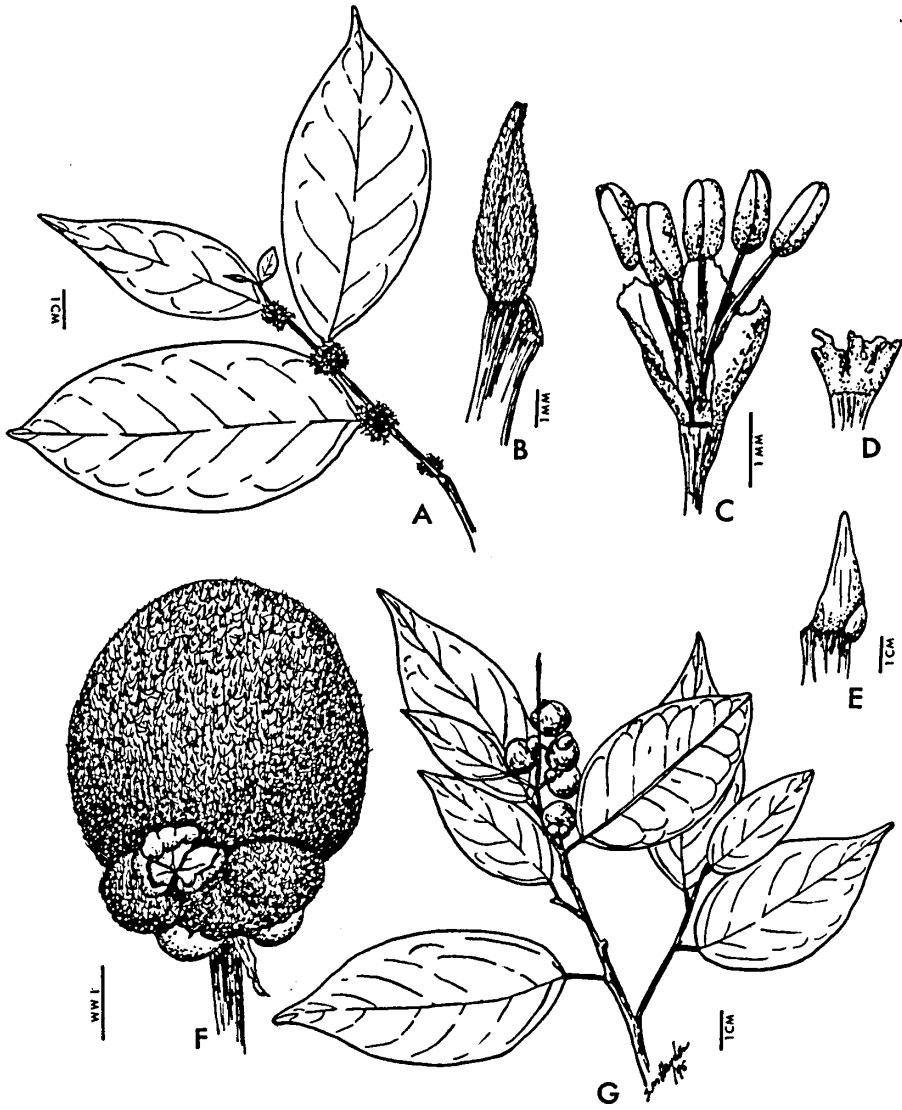
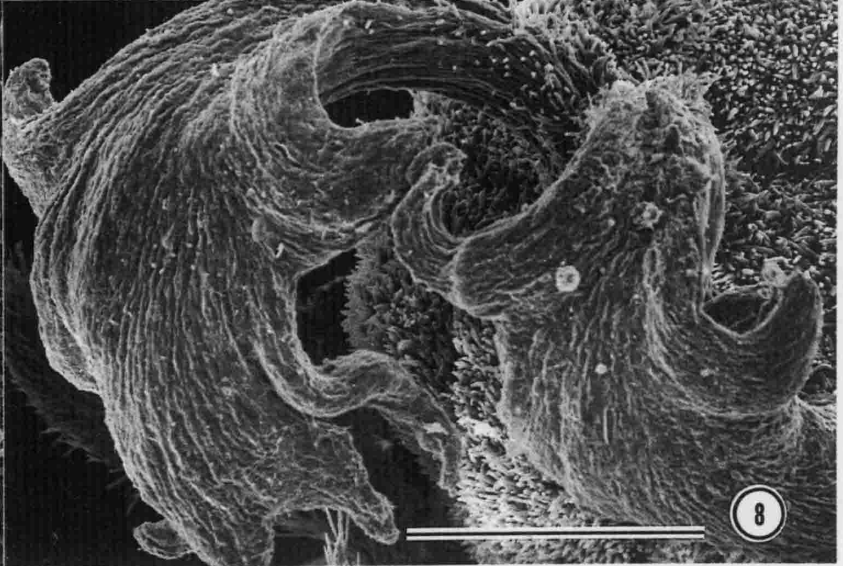
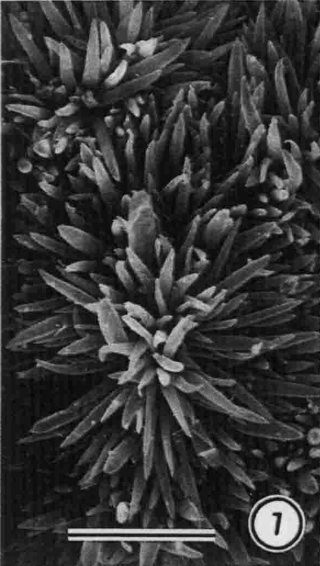
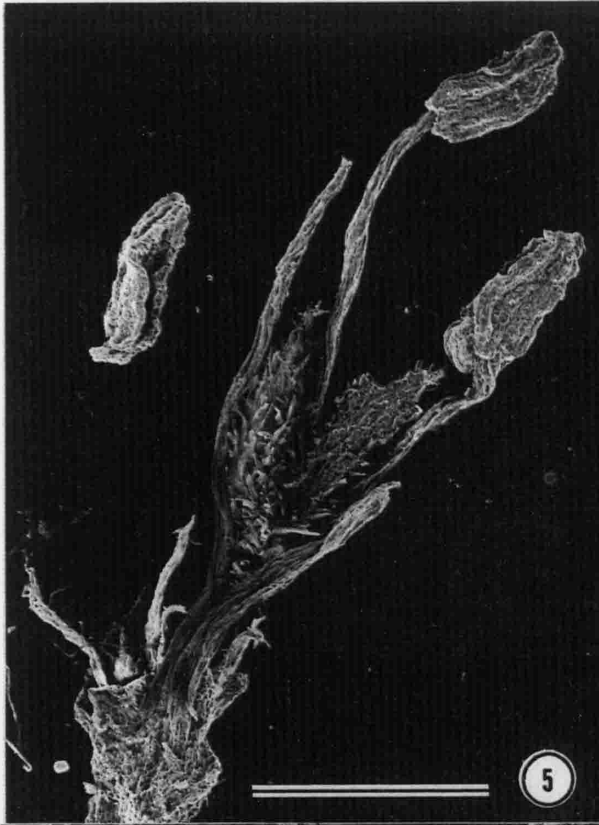


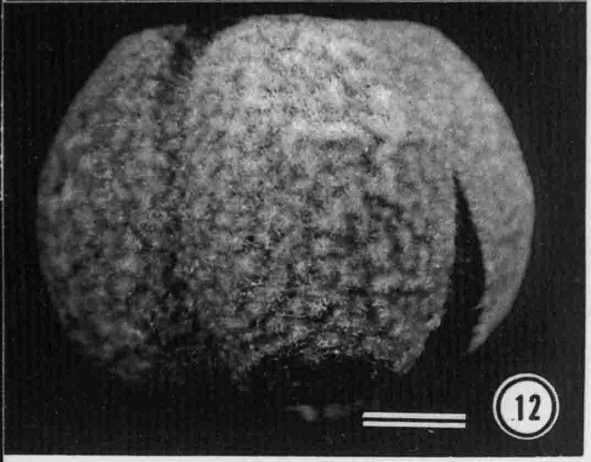
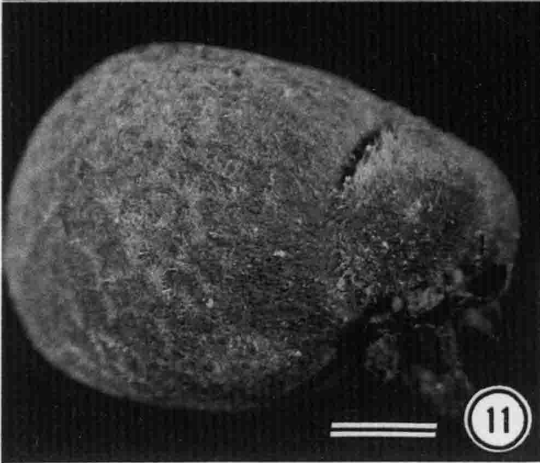
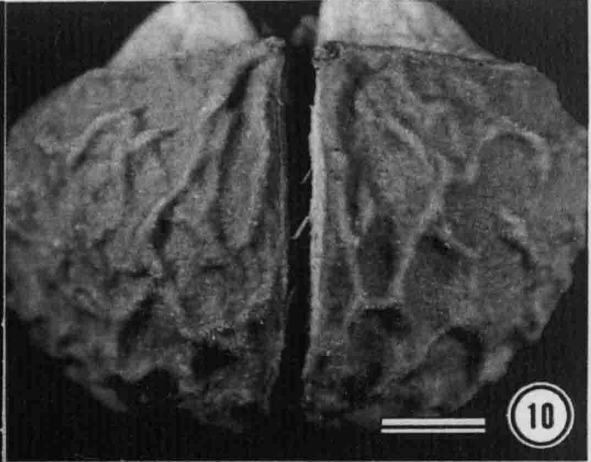
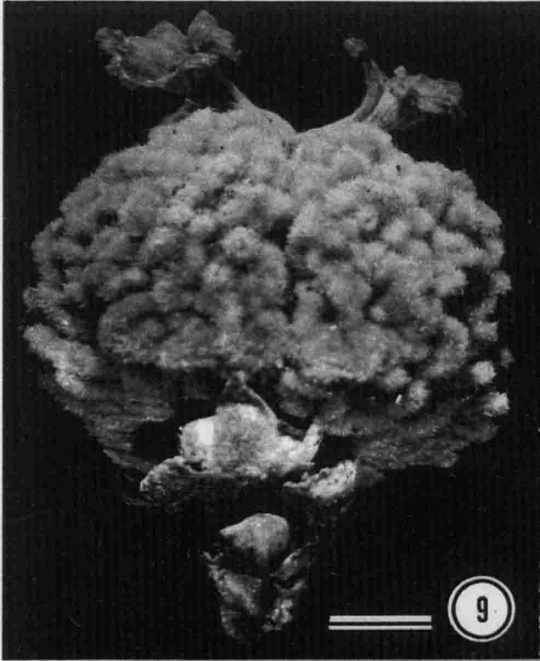
Figure 4. Discocarpus spruceanus Muell. Arg. A. Habit, staminate specimen; Ducke 904 (F). B. Terminal bud, staminate specimen; Mileski 120 (RB). C. Staminate flower; Ducke 904 (F). D. Disk from staminate flower, perianth removed; Ducke 904 (F). E. Terminal bud, pistillate specimen; Spruce 3527 (BM). F. Immature fruit; Davidse 27631 (F). G. Habit, pistillate specimen; Spruce 3527 (BM).



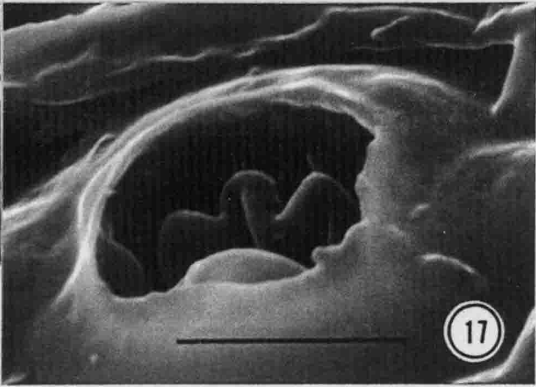
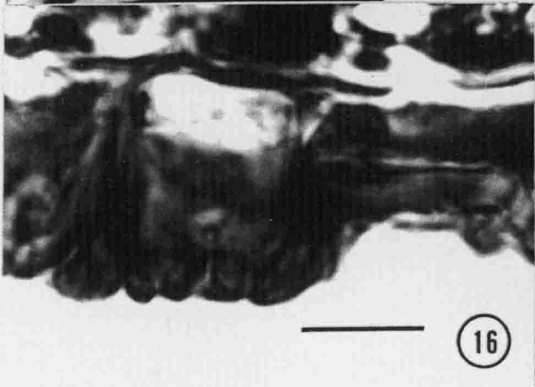
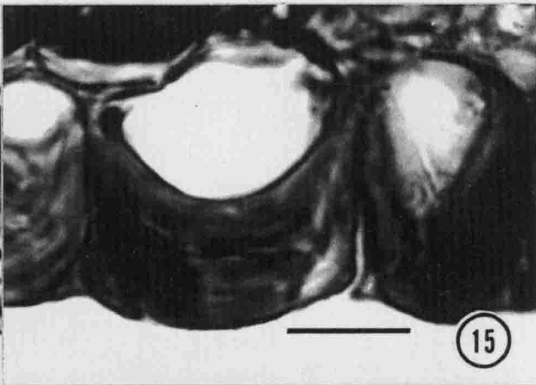
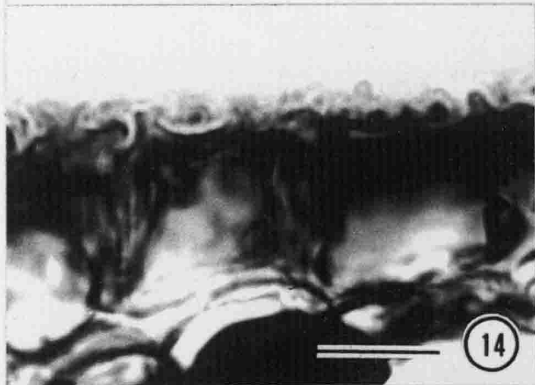
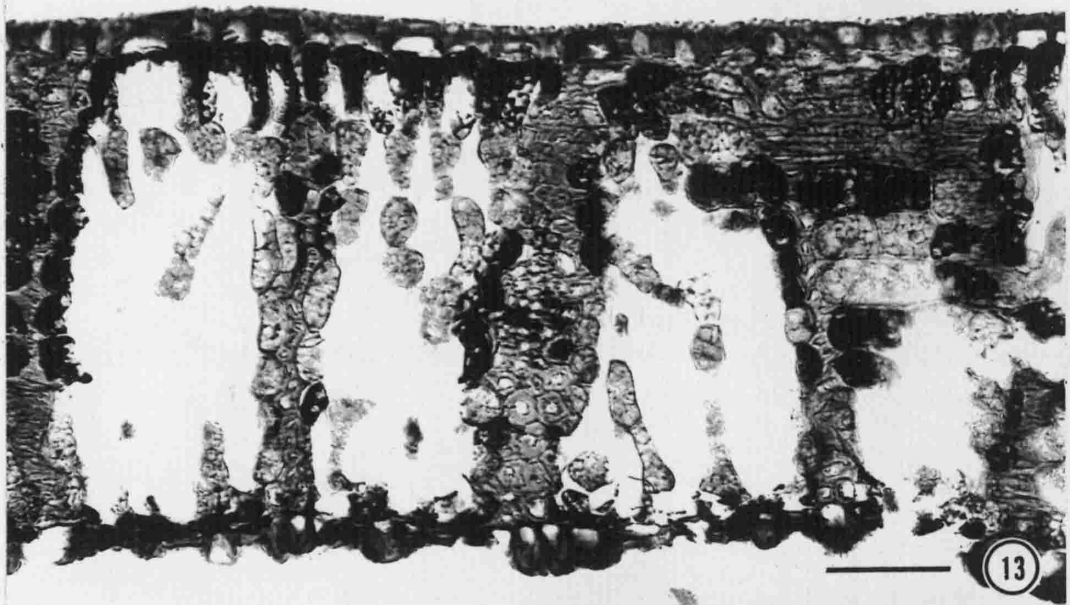
Figures 5--8. Floral morphology of Discocarpus, SEM. 5--
6, Discocarpus spruceanus Muell. Arg., Spruce 3527 (G). 5.
Staminate flower with sepals and petals removed to show
fused filaments; bar = 1 mm. 6. Fused filaments; bar = 250
 μm . 7. Discocarpus essequiboensis Klotzsch, Schultes
903157 (L); Hair on fruit surface; bar = 250 μm . 8.
Discocarpus essequiboensis Klotzsch, Schomburgk 1839 (G);
Dilated, lobed, recurved stigmas; bar = 1 mm.



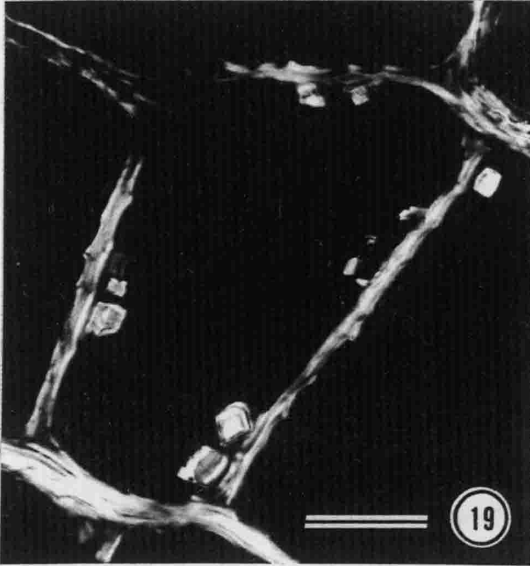
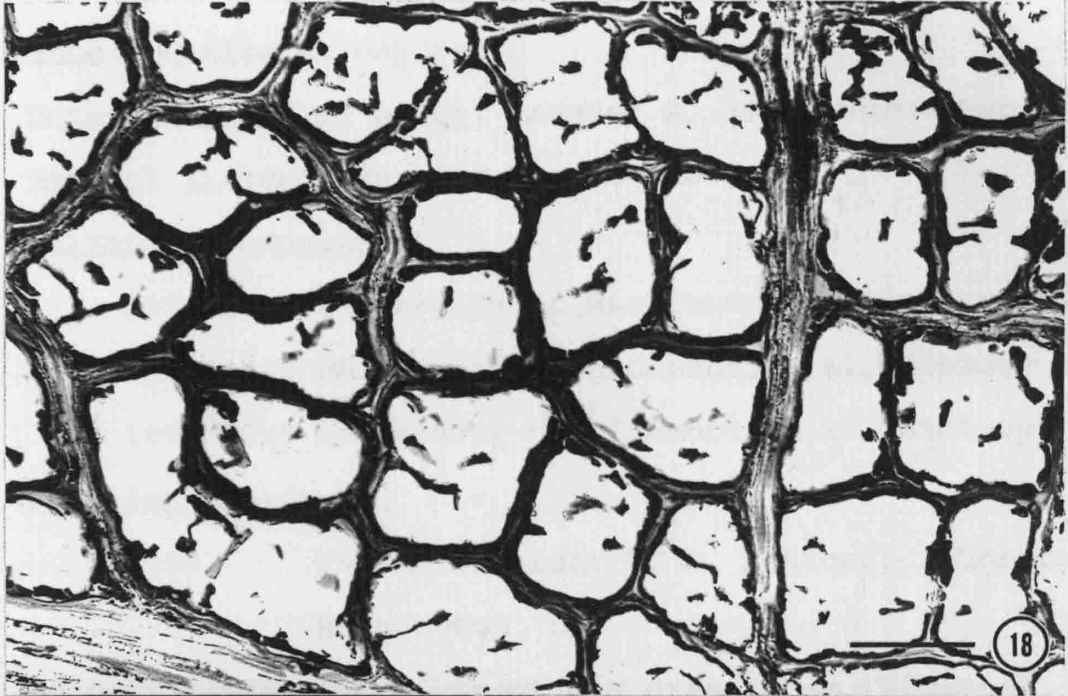
Figures 9--12. Ovary and fruit surface features of Discocarpus. 9. Discocarpus gentryi S. M. Hayden, Gentryi et al. 18419 (F); ovary. 10. Discocarpus gentryi S. M. Hayden, Revilla 411 (NY); mature fruit. 11. Discocarpus spruceanus Muell. Arg., Spruce 3527 (P); mature fruit with one developed and two aborted lobes. 12. Discocarpus essequiboensis Klotzsch, Schomburgk 706 (G); mature fruit. All bars = 2 mm.



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



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



Curriculum Vitae

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1974-1979 University of Maryland, horticulture major

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1978 Herbarium aide, U. S. National Arboretum,
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1980-1982 Clerk, Great Big Greenhouse, Richmond, VA

1982 Laboratory research assistant, Dept. of
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1985-1987 Education coordinator, Lewis Ginter Botanical
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1985-1986 Teacher, botany course "Exploring Our Green
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1987-1993 Free-lance garden columnist (weekly),
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1987-1989 Medical billing clerk, Dr. Robert Mitchell
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- 1991-1992 Laboratory teaching assistant
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- 1994-1995 Adjunct faculty, botany, zoology, and
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Publications:

- Hayden, S. M., & W. J. Hayden. 1994. Stem
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of Croton glandulosus var. septentrionalis
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