REVISION OF *DRACONTIUM* (ARACEAE)¹

Abstract

A taxonomic revision of the genus *Dracontium* L. (Araceae) is presented predominantly from morphological, anatomical, and phytogeographic data. *Dracontium* is treated as comprising 23 species, including 10 new species: *D. amazonense* G. Zhu & Croat, *D. angustispathum* G. Zhu & Croat, *D. asperispathum* G. Zhu & Croat, *D. bogneri* G. Zhu & Croat, *D. grandispathum* G. Zhu & Croat, *D. grayumianum* G. Zhu & Croat, *D. guianense* G. Zhu & Croat, *D. peruvianum* G. Zhu & Croat, *D. plowmanii* G. Zhu & Croat, *na peruvianum* G. Zhu & Croat, *D. plowmanii* G. Zhu & Croat, *na peruvianum* G. Zhu & Croat, *D. plowmanii* G. Zhu & Croat, *na peruvianum* G. Zhu & Croat, *D. pitteri* lectotypified herein: *Amorphophallus nivosus* Lem., *A. papillosus* hort. ex Rafarin, *Dracontium elatum* Masters, *D. pitteri* Engl., and *D. soconuscum* Matuda. The following species are newly synonymized: *D. carderi* Hook, f., *D. costaricense* Engl., *D. dressleri* Croat, *D. lineare* G. S. Bunting & Tillett, *D. loretense* K. Krause, *D. ornatum* K. Krause, *D. trianae* Engl., and *Echidnium regelianum* Engl. All taxa are described and illustrated.

Key words: Araceae, Dracontium, monograph, taxonomy.

The Araceae are a family of herbaceous monocots with 106 genera and approximately 3500 species, the vast majority occurring in the New World tropics (Croat, 1988, 1992). The World Checklist and Bibliography of Araceae (and Acoraceae) lists a total of 2824 recorded species (Govaerts & Frodin, 2002). Members of the family are highly diverse in life form, leaf morphology, and inflorescence characteristics. Life forms range from submerged or free-floating aquatics to terrestrial (sometimes tuberous), epiphytic or hemiepiphytic plants, to climbers. Leaves range from simple and entire to compound and highly divided, and may be basal or produced from an aerial stem. The family is best characterized by its distinctive inflorescence, a spadix with bisexual or unisexual flowers (sometimes with a sterile region) subtended by a solitary pedunculate spathe.

The present study of *Dracontium* L. comprises a taxonomic revision of one of the most poorly known tuberous genera in the Araceae. *Dracontium*, as here recognized with 23 species, represents the most species-rich tuberous genus of the Araceae in the New World. Vegetatively, it shares a great similarity with the Old World genus *Amorphophallus* Blume ex Decne. Plants in both genera usually con-

sist of a single leaf arising from an underground tuber with a more or less mottled, reptilian-patterned petiole up to several meters long with a highly divided, compound, spreading blade reaching as much as three meters or more in diameter. Inflorescences of both genera are notorious for their fetid scents at anthesis. However, *Dracontium* differs sharply from *Amorphophallus* in having bisexual flowers on a uniform spadix.

Accurate identification of Dracontium species has been difficult because of the paucity and inadequacy of herbarium material and their sporadic phenology. Herbarium specimens, though comparatively abundant for some species such as Dracontium spruceanum (Schott) G. Zhu, are frequently sterile and often incomplete since mature adult leaves are almost always too large to be mounted on a single herbarium sheet. Frequently, a single leaf is mounted on several to many herbarium sheets. Hence, intensive study of living material in the field or under cultivation is essential. Though local populations may contain many plants, populations of Dracontium are often widely scattered and single individuals not frequently encountered. Under unfavorable growing conditions, plants of Dracontium may remain vegetative for many years,

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and often go dormant for two to four months in the dry season. Inflorescences of *Dracontium* often arise from the apex of the tuber before or after leaf development. Therefore, matching fertile with sterile herbarium material of the same *Dracontium* species is often problematic.

Live plants of *Dracontium* are not uncommon in cultivation in botanical gardens and aroid nurseries, as they share an ornamental appeal with *Amorphophallus* species and are easy to propagate and maintain. Unfortunately, cultivated material of *Dracontium* is limited to only a few species, such as *D. gigas* (Seem.) Engl., *D. polyphyllum* L., and *D. spruceanum*. Locating these plants in the field is often not difficult since populations of *Dracontium* are usually well known to native people due to the distinctive, reptilian-patterned petioles and medicinal uses.

MATERIALS AND METHODS

This revision was conducted mainly at the Missouri Botanical Garden, where the largest living and herbarium collections of Dracontium in the world are housed. Field research for this study was conducted in Costa Rica, Panama, and Brazil between 1992 and 1995. Trips were made to several botanical gardens to study cultivated plants, including the Marie Selby Botanical Gardens and The New York Botanical Garden in the Unites States, and the São Paulo Botanical Garden and Botanical Garden of Rio de Janeiro in Brazil, as well as to herbaria CR, F, GH, HB, IAN, IBGE, ISC, MG, NY, PMA, R, RB, SCZ, SEL, SP, SPSF, UB, UEC, US, and WSU. Over 670 collections comprising about 3000 herbarium sheets, including loans from 49 major institutions worldwide, were studied (see Appendices 1, 2). Data from all cited specimens are recorded in the Missouri Botanical Garden database TROPICOS.

In this study, we have relied heavily upon live collections, especially the second author's gatherings during his more than 35 years of fieldwork in the Neotropics. Some species, such as *Dracontium guianense* G. Zhu & Croat, are known only from a few herbarium collections. In such cases, descriptions are from herbarium specimens only. Due to the rarity of many *Dracontium* species, all specimens with proper collecting information are cited, including those prepared from cultivated plants. For species determinations, we have also relied on photographs prepared by Croat and many other individuals to reconstruct the natural habits for these plants.

Descriptions of species were prepared using the DELTA (DEscriptive Language for TAxonomy) pro-

gram (Dallwitz et al., 1995). The program TAXA-SOFT (Gouda, 1994) was used for data maintenance of DELTA. The exsiccatal information was prepared by using TROPICOS. Ecological zones are estimated by using the Holdridge Life Zone system (Holdridge et al., 1971).

Material for chromosomal studies was obtained from plants cultivated at the Missouri Botanical Garden. Growing root tips were treated in 0.002M 8-hydroxyquinoline for 4 hr. before being fixed in ethanol-glacial acetic acid-chloroform (6:3:1) at 8°C overnight. Root tips were then rotated through a hydrated 70%–50%–25%–10% ethanol series, were macerated with 1N HCl (room temperature) for 10 minutes, 1N HCl (60°C) for 8 min., and 1N HCl (room temperature) for another 10 min., and rinsed with deionized H₂O for 30 min. before being stained in 0.5% Feulgen for 1.5 hr. (Masahiro Takei, pers. comm.). Finally, the plant material was rinsed with deionized water, and slides with the chromosome squashes were prepared.

TAXONOMIC HISTORY

The first mention of a species referable to Dracontium appeared in Hermann's Paradisi batavi prodromus (1689: 315) as "Arum polyphyllum, dictum Dracontium, caule scabro punicante, surinamense" and "Dracontium americanum caule scabro puniceo radice Cyclaminis." The plant was introduced into the gardens of Holland by the early Dutch plant-hunters from Surinam in the second half of the 17th century. A corresponding plate was later published by Plukenet (1696, t. 149, fig. 1) in his Almagestum under the name "Arum polyphyllum surinamense caule atrorubente glabro et eleganter variegato." This same species was redescribed by Hermann (1698: 93-94) in his Paradisus batavus as "Dracontium americanum scabro puniceo caule radice Cyclaminis," along with a figure (t. 93) under the name "Arum polyphyllum caule scabro punicante." Linnaeus (1737) published the first comprehensive description of this species after he personally studied a flowering specimen in the Clifford Garden at Hartecamp, Holland. Later, he validly published the genus Dracontium with five species in Species Plantarum and established the binominal Dracontium polyphyllum (Linnaeus, 1753), which is the only species still recognized within Dracontium. Under D. polyphyllum, Linnaeus (1753: 967) cited both Plukenet's and Hermann's figures. Hermann's figure was later selected as the lectotype of D. polyphyllum (Hay, 1992). Since D. polyphyllum was referred to as "typical" by Britton and Wilson (1923: 130), it was accepted as the generic type of *Dracontium* (Jarvis et al., 1993: 43).

Rafinesque (1838: 12–13) evidently misidentified a plant as *D. polyphyllum* saying "the scandent sp. appear the type of *Dracontium*, which Anderson changed to Mostera perhaps a better name," and superfluously renamed *D. polyphyllum* as *Eutereia nigricans* Rafinesque. Therefore, the generic name *Eutereia* is a superfluous name for *Dracontium*.

The genus Dracontium remained known only with one species from Surinam until Richard Schomburgk's expedition to Guyana (1840-1844), during which he collected a second species of the genus. Several living tubers of this species were sent to the Botanical Garden of Berlin, Germany, in 1843 (Roth, 1922, 1923; Zhu et al., 1998). This species was later described by Kunth (1844) as D. dubium Kunth. Schott (1857b) transferred this species to his newly described genus Echidnium Schott and created a superfluous name, E. schomburgkii Schott (Zhu et al., 1998). According to Schott (1857b), Echidnium is ostensibly distinguished from *Dracontium* by having a unilocular ovary with two ovules, as opposed to a bi- or pluri-locular ovary in Dracontium.

When describing the single species in his new genus Ophione Schott, Schott (1857a) described a third species of Dracontium as O. purdieana Schott, which differs from *Echidnium* in having an ovary with 4 to 5 locules, and from Dracontium in having a long-acuminate spathe. Later, Schott (1858a) described another Dracontium species as Echidnium spruceanum Schott before publishing the first comprehensive classification of the Araceae in the Prodromus systematis aroidearum in 1860, which laid the foundation for the modern generic concepts within the aroid family. In his Prodromus (1860), Schott recognized four Dracontium species in three genera, namely Dracontium, Echidnium, and Ophione, classified along with Symplocarpus Salisbury in Araceae subtribe Dracontiinae next to subtribe Lasiinae in the tribe Orontieae: Dracontium polyphyllum, Echidnium schomburgkii, E. spruceanum, and Ophione purdieana. The superfluous name E. schomburgkii was used for D. dubium (Zhu et al., 1998). The diagnostic features used by Schott (1860) for his separation of these genera were based exclusively on floral characters such as spathe and spadix shapes, tepal number and shape, stigma lobes, ovary number and shape, and number of ovules per locule. All these characters may be useful for the separation of species within the group, but not for defining generic boundaries.

Unable to confirm the characters of unilocular ovary with two ovules for *Echidnium* and the importance of the floral characters, Engler (1889) transferred Echidnium as a section to Dracontium while recognizing Ophione, but later revived the generic status of Echidnium in his Das Pflanzenreich (1911) and synonymized Ophione within Dracontium. Bogner (1985) and Hay (1988) noted that a unilocular ovary with two ovules cannot be used as a generic character in this group and once again synonymized Echidnium within Dracontium. The supposedly unilocular ovary with two ovules of E. dubium (Kunth) Engl. is erroneous based on its neotype (Zhu et al., 1998), as well as the type of E. spruceanum (Zhu, 1996). Unilocular ovaries do not occur in Dracontium and this genus never has more than one ovule in each locule: these stand as generic traits of the genus (Zhu, 1995, 1996; Zhu et al., 1998). Echidnium spruceanum Schott was recently transferred to Dracontium by Zhu (1996).

Koch (1859) described a fifth species, D. asperum K. Koch, from a plant cultivated at the Berlin Botanical Garden. This plant had been obtained from the Botanical Garden in Amsterdam and originated from Surinam (Koch, 1859). This species was apparently unknown to Schott in 1860. Because of the same country of origin and the ambiguous original descriptions, especially the use of an unreliable diagnostic for petiole texture, D. asperum had been confused with D. polyphyllum for centuries (Zhu & Grayum, 1995). The names have been applied indiscriminately and have been used in different senses by different authors (Schott, 1858b; Engler, 1878, 1911; Jonker-Verhoef & Jonker, 1953). Specimens of the same taxon have been identified with either name in herbaria throughout the world. Through lectotypification and neotypification, Zhu and Grayum (1995) elaborated the concept of these two species. Dracontium asperum has spathe margins broadly overlapping and seed with a strongly interrupted dorsal ridge, while D. polyphyllum has spathe margins rarely overlapping and seed with a continuous dorsal ridge.

In 1865, Schott described the genus *Chersy-drium* Schott on a single species, *C. jararaca* Schott, citing *D. asperum* as a synonym (Schott, 1865: 73). In the protologue, Schott noted that petiole armament is a variable character in *Dracontium*, but failed to provide any diagnostic for his new *Chersydrium*. Because *D. asperum* was cited as a synonym, according to the *Code* (Greuter et al., 2000, Art. 52.1) *Chersydrium jararaca* is superfluous, illegitimate, and to be rejected. Berthold Seemann (1869) described a new genus, *Godwinia* Seem., from Nicaragua with a single species, *G. gigas*, in honor of George Godwin. Masters (1873) later published a drawing of an inflorescence of *G*. gigas and suggested the species would be more properly placed in the genus *Dracontium*, but he did not make the transfer. Engler (1877) agreed, and two years later (1879) established the combination *D. gigas* (Seem.) Engl., which synonymized *Godwinia*. An epitype, an interpretative type when all original material is demonstrably ambiguous (Greuter et al., 2000, Art. 9.7), represented the first taxonomic application of the concept in seed plants and was designated for the species by Zhu (1994a).

In his first classification of the family Araceae, Engler (1877) introduced his subfamily concepts with all presently recognized *Dracontium* species in subfamily Lasioideae, which is defined by assimilated leaves that persist for only one vegetative season. *Dracontium* remains a member of subfamily Lasioideae, although the modern classifications of the Araceae differ radically above the tribal level (Grayum, 1990; Bogner & Nicolson, 1991; Mayo et al., 1997; Keating, 2004). Following Engler (1877, 1920), *Dracontium* has been treated in the tribe Lasieae when tribes are recognized in the subfamily Lasioideae (Hay, 1992).

In his infrageneric classification, Engler (1889) recognized three sections: *Dracontium* sect. *Eudracontium*, including *D. polyphyllum* and *D. asperum*, characterized by a very short peduncle 5–18 cm long above ground and a relatively small spathe (6)10–20 cm long; *Dracontium* sect. *Godwinia*, with the single species *D. gigas*, with its long peduncle to 30–120 cm long and a relatively large spathe to 58–78 cm long; and *Dracontium* sect. *Echidnium*, presumably with a unilocular ovary, which was proven to be erroneous (Zhu, 1996).

Demonstrating his extraordinary knowledge of the Araceae, Engler (1905) described *D. longipes* and *D. pittieri* from Brazil and Costa Rica, respectively. In 1911, he published the only extant revision of the genus synonymizing *Ophione* and reinstating *Echidnium*. Twelve names in three genera were recognized: *Crytosperma spruceanum* (= *D. spruceanum*); *Dracontium asperum*, *D. carderi*, *D. costaricense*, *D. longipes*, *D. polyphyllum*, *D. purdieanum*, and *D. trianae* in section *Eudracontium*; *D. gigas* and *D. pittieri* in section *Godwinia*; and *Echidnium dubium* and *E. regelianum*. Ten of these species remain recognized in *Dracontium*.

Since Engler's landmark work in 1911, eight more names under *Dracontium* have been published. *Dracontium ulei* K. Krause was described from Acre, Brazil (Krause, 1914). *Dracontium soconuscum* Matuda was described from southern Mexico (Matuda, 1949). *Dracontium dressleri* Croat was described from Panama and was named in honor of Robert Dressler (Croat, 1975). *Dracontium* *margaretae* Bogner was described from Mato Grosso, Brazil, and was named in honor of Margarete Emmerich (Bogner, 1981). Three species were described by Bunting in 1986 and 1988, *D. aricuaisanum* G. Bunting, *D. changuango* G. Bunting, and *D. lineare* G. Bunting. Finally, *D. croatii* G. Zhu was described from the Andes in honor of Thomas Croat (Zhu, 1995).

Herein, 10 additional species are described: Dracontium amazonense, D. angustispathum, D. asperispathum, D. bogneri, D. grandispathum, D. grayumianum, D. guianense, D. peruvianum, D. plowmanii, and D. prancei.

MORPHOLOGY AND ANATOMY

TUBERS, TUBERCLES, AND ROOTS

Tubers (Fig. 1). The size, weight, and morphology of tubers vary from one season to the next. Starch accumulates in the tuber to its maximum prior to inflorescence development, and is for the most part utilized during production of the inflorescence and new leaf. Diminution of the tuber is often associated with a change in its vertical depth rather than the horizonal diameter of the tuber. Since the tuber dimensions vary seasonally, hollow spaces in the soil are often seen both above (1-3)cm) and below (3-8 cm) the tuber. This upper space accommodates the growth of tubercles and contractile roots, while the lower hollow allows the tuber to settle deeper into the soil as the contractile roots dry out during dormancy. This settling may gain protection from corm-eating herbivores such as agoutis and peccaries. However, disturbances from these same animals are responsible for distributing the tubercles.

Tubercles (Fig. 1). Tubercles are borne on top of tubers, rarely on the side of irregularly shaped tubers in *D. margaretae*, and often mixed with roots. Tubercles allow *Dracontium* to reproduce vegetatively. They are usually dormant, activated only after disturbance. When a tuber is disturbed or broken off, tubercles start to change in shape, somewhat irregularly shortening, and produce their own shoot and roots.

Roots (Fig. 1). Primary roots of *Dracontium* emanate from the flattened apex of the tuber and grow downward in all directions, completely surrounding the tuber (Fig. 1B). Secondary roots start below the tuber apex and are subdivided into many smaller roots. The strong and often contractile root system functions not only in water and nutrient absorption, but also serves to support the plant. The roots hold the tuber in a position that facilitates the formation of the hollow spaces above and below the tuber.



Figure 1. A–D, *Dracontium* tubers. —A. *D. ploumanii*. Tuber showing more or less flattened top with tubercules and rounded bottom. Photo by G. Zhu. —B. *D. polyphyllum* (*Croat 73867*). Tuber showing roots emerging from the apex of the tuber and clusters of tubercles. —C. *D. polyphyllum* (*Croat 56898*). Cross section of tuber showing typical shape with more or less flattened top and rounded bottom. —D. *D. grayumianum* (*G. Zhu & Croat 1506*). Lower surface of tuber showing rounded, smooth surface with the roots arising from the apical portion.

The tuber naturally assumes a deeper position when the roots dry out after each growing season.

LEAVES

Cataphylls. Cataphylls are the bract-like structures subtending the petiole, and usually completely embracing new growth from tubers after dormancy, often drying long before the leaf blade fully expands, and usually rotting away, becoming barely visible after the leaf blade has fully expanded.

Petioles (Fig. 2). The petioles of Dracontium are thick and aerenchymatous (Fig. 2A), frequently more than 2 m long. The exterior surface is often highly variegated (Fig. 2A, B), dark or purplish green, sometimes brown tinged, mottled with pale green or creamy areas suggesting a reptilian pattern (Fig. 2A, B). The mottled areas often appear as upward brush strokes, which originate from protuberances. Petiole surface texture is variable among species, from smooth textures to heavily beset with protuberances (Fig. 2B). The latter are often accompanied by horizontally elongate, irregular projections bordering two differently colored areas and sometimes also by spiny projections to 2 mm long. The proximal half of the petiole tends to have more protuberances or projections, while the distal half is much smoother. The aerenchyma cells of the petiole are cylindrical, hollow, to 6 cm long and 0.5 cm wide (Fig. 2C). The sheathing of the petiole is convolute, forming a closed space in the center through which the inflorescence or leaf initiates.

Blades (Fig. 2D). The tripartite leaf blade is held horizontally or ascending up to 45° from the petiole apex. Blade rachises may be mottled similar to the petioles but in much paler shades or may be concolored (Fig. 2D). They are usually smooth but may be armed with spiny projections, also similar to those of the petiole. The basal rachis of the middle blade division may be as long as the lateral divisions (D. spruceanum) or twice or more as long as these (D. angustispathum and D. grayumianum). Segments of Dracontium leaf blades can be entire or lobed, and can be distinguished on the basis of their position. Sometimes, there are rounded, triangular, or oblanceolate contrastingly small segments among the basal and medial segments. These small segments may be absent (D. spruceanum) or alternate with the larger segments (D. soconuscum), or more often found near the base of each leaf division (D. polyphyllum). They may be confluent with larger segments (D. gigas) or free (D. spruceanum). Likewise, medial and basal segments may be confluent or free from one another. The basal subdivisions of Dracontium consist of many smaller segments (*D. gigas* and *D. grayumianum*) or sometimes a single segment (*D. angustispathum*). The terminal subdivisions always consist of at least two segments in the lateral division and at least three segments in the middle division.

In the early development of a *Dracontium* leaf blade, all leaf divisions may point upward (*D. gigas*, Fig. 11A; *D. margaretae*, Fig. 16B), or the middle divisions may point upward while the lateral divisions point downward (*D. asperum*; *D. spruceanum*, Fig. 25A). Juvenile leaves of *Dracontium* are usually sagittate or sagittately lobed, rarely linear or trifid (*D. margaretae*).

INFLORESCENCES

Bracteoles (Figs. 4A, 4B, 8A, 16C, 17B, 24B). Bracteoles are the bract-like structure subtending the peduncle of each *Dracontium* inflorescence. The relative length of the innermost (also the longest) bracteole to the peduncle is an important character distinguishing species in *Dracontium*. It ranges from being much shorter than the peduncle (*D. plowmanii*) to longer than the peduncle (*D. prancei*). The bracteoles usually rot away soon after anthesis.

Peduncles (Figs. 7A, 8A, 11B, 13A). Dracontium inflorescences are produced before, or sometimes after, new leaf development. When inflorescences are produced right after a new leaf, they often appear as having developed simultaneously with the leaf, as sometimes in *D. croatii*, *D. pittieri*, and *D. spruceanum* (Fig. 25A). The fertile peduncles of *Dracontium* are usually shorter and thinner than the associated petiole and may be completely underground (*D. dubium*) or nearly as long as the petiole, rarely exceeding the petiole (as sometimes in *D. spruceanum*). Peduncles are much like the petioles in terms of coloration and armament.

Spathe (Figs. 4A, 4B, 7A, 9A, 9B). The shape and size of the spathe distinguish species of *Dracontium*, perhaps more so than any other character. The spathe is marcescent and often disintegrates on a developed infructescence. At anthesis, the length of the spathe in the genus may range from a few cm long and 1 cm wide as in *D. bogneri* to as much as 85 cm long and 20 cm wide as in *D. gigas*. Spathes may be more or less hooded and boat-shaped (*D. asperum*, *D. gigas*, and *D. pittieri*) or suddenly contracted at a certain point and gradually acuminate distally (*D. angustispathum*, *D. dubium*, *D. purdieanum*, and *D. spruceanum*). The spathe margins may be broadly overlapping near the base forming a bell-shaped tube and broadly



Figure 2. A–D, Petioles and blade. —A. Dracontium grayumianum (G. Zhu & Croat 1506). Close-up of petiole showing variegation. —B. D. croatii (Croat 72368). Petioles showing variegation and short spines. —C. D. gigas (G. Zhu 1156). Petioles showing exterior surface and inner surface with aerenchymatous cells. —D. D. croatii (Croat 72368). Lower surface of leaf blade showing the prominently round-raised medial ribs and pinnately lobed lateral veins.

open above as in *D. grayumianum*, *D. purdieanum*, and *D. soconuscum*. They broadly overlap at the lower ¹/₃ to ²/₃ with only a narrow opening above (*D. gigas* and *D. prancei*), or barely overlap (*D. pittieri* and *D. polyphyllum*). The apex of the spathe is variably acuminate and ranges from erect or slightly arching as seen in *D. angustispathum*, *D. polyphyllum*, and *D. spruceanum* to strongly arching to perpendicular in *D. amazonense* and *D. asperum*.

The outer surface of the spathe is often matte, with many elongate clumping projections. The spathe may be maroon, tinged green (D. spruceanum), purplish red or olive-brown (D. polyphyllum), green (D. croatii and sometimes D. spruceanum), or sometimes with a basal paler area on the abaxial side (D. asperum). The inner surface may be glossy (D. angustispathum and D. plowmanii) or semiglossy (D. gigas and D. pittier) or covered with densely overlapping translucent scales (D. dubium and D. purdieanum). Spathe inner surface is maroon (D. polyphyllum), maroon tinged reddish (D. asperum and D. soconuscum), or reddish brown to olivebrown (D. spruceanum). There is usually a creamy white translucent area at the spathe base that may be obscure (D. asperum, D. polyphyllum, and D. ulei) or to 1 to 3 times as long as the spadix in height (D. asperispathum, D. grandispathum, D. pittieri, and D. spruceanum). The inner surfaces of the spathe are often covered with whitish or brownish spotted gland-like structures associated with the stomata. These structures appear to control the emission of scent (see section on Phenology and Pollination).

Spadix (Figs. 3D, 4C, 7B, 11C). The spadix of Dracontium is sessile, or stipitate to 0.5-2.5 cm long. It ranges from 1 to 9 cm long and 0.5 to 2 cm diam. at anthesis, and from 4 to 25 cm long and 4 to 10 cm diam. when fruiting. The color of the spadix corresponds to the color of the tepal apices and styles, which may be dark purple, green, light brown, or rarely gray. The spadix may be hidden at anthesis (D. croatii, Fig. 9A, D. gigas, D. spruceanum, and D. asperum) or exposed naturally (D. polyphyllum, Fig. 21A, D. pittieri, D. soconuscum, Fig. 24A, D. purdieanum, Fig. 23A, and D. dubium). A spadix may be typically cylindric (Fig. 11C), rarely globose, or sometimes cylindroid-tapered (Fig. 22B). Sometimes 1 to 5 tepals at the apex of the spadix are elongated into 0.5-1 cm appendages (D. dubium, D. grayumianum, D. purdieanum, and D. soconuscum, Fig. 3D). The function of these appendages is unknown. The central axis of the spadix consists of aerenchyma, similar to those seen in the petioles and peduncles.

FLOWERS

The flowers of *Dracontium* are arranged spirally on the spadix. Each consists of a perianth, a single pistil, and 4 to 19 stamens (Fig. 3B, C). The perianth consists of 4 to 8 fornicate tepals that envelope the pistil and stamens at anthesis. The apices of the tepals are green to purple and covered with yellow-tinged raphide cells. The lower portion of each tepal is often transluscent, white to light brown, sometimes with red or red-purple dots.

Stamens (Fig. 3C). The filaments are elongate, often slightly dilated, subcompressed, and abruptly contracted at the apex into the connective. The anthers exceed the connective and are linear-elliptic in shape. They are often yellow, turning reddish brown, sometimes with dark purple, especially near the aperture, after anthesis. The anthers are usually hidden before anthesis and dehisce apically by a vertical slit with a more or less rounded aperture at anthesis (Fig. 26B). Pollen emerges from these apertures in a strand that reaches the stigma, and is as long as or longer than the style. The function of these pollen strands is discussed in the section on reproductive biology.

Pistils (Fig. 26A). The ovaries in *Dracontium* are narrowly ovoid, pale green, and incompletely 2to 5-loculed, with axile or basal placentation. The ovules are solitary in the locules and amphitropous or campylotropous. The style is 0.5–5 mm long above the tepals at anthesis. It is dark purple to pale green, and persistent or caducous. The stigmas (Fig. 26A) are unlobed or variably up to 4-lobed, usually covered with a translucent sticky liquid at anthesis but drying out afterward. Ovaries are ovoid, pale green, incompletely 2- to 5(7)-loculed with axile or basal placentation. Ovules are one per locule, amphitropous or campylotropous.

FRUITS AND SEEDS

Fruits. The berries of Dracontium may be globose (D. croatii, Fig. 9C; D. spruceanum), angularly subglobose with three to six angles (D. grayumianum, Fig. 13C; D. longipes, Fig. 15B); or elongate with a projection (D. angustispathum). They range from having one seed (D. angustispathum) to as many as seven seeds (D. polyphyllum). The young berries are usually green, while the mature berries may be orange (D. angustispathum, D. dubium, D. croatii, D. gigas, D. grayumianum, D. peruvianum, D. pittieri, and D. spruceanum), purple tinged (D. asperum), green tinged purple (D. bogneri, D. polyphyllum), red or purple-red (D. margaretae and D. purdieanum), or purple-brown (D. soconuscum and sometimes D. gigas). The berries are usually darker apically and may be depressed around the persistent style (*D. bogneri*, *D. dubium*, and *D. so-conuscum*) or rounded (*D. angustispathum* and *D. spruceanum*). The berries are often covered with small whitish raphide cells and sometimes, red dots.

Seeds. Dracontium shows great diversity in seed morphology, and this is of great value for species distinction in the genus. Seed size ranges from 3 mm wide (D. bogneri) to more than 11 mm wide (D. croatii and D. peruvianum) with only a trace of endosperm present. The seeds may be rounded (D. croatii, D. gigas, and D. pittieri), elongate (D. spruceanum and D. grayumianum), reniform (D. polyphyllum and D. plowmanii), or more or less triangular (D. asperum). They are more or less laterally compressed, with the sides either convex (D. polyphyllum) or depressed (D. asperum). The sides of the seeds may be smooth (D. polyphyllum, D. asperum, and D. bogneri) or decorated with small wart-like projections (D. spruceanum). The seeds typically have three dorsal ridges (D. gigas, D. pittieri, D. peruvianum, and D. spruceanum), but sometimes have only one (D. polyphyllum, D. asperum, and D. plowmanii) or none (D. bogneri). The dorsal ridges may be continuous (D. polyphyllum and D. plowmanii) or strongly interrupted (D. dubium, D. croatii, and D. grayumianum), and either thin (D. grayumianum) or thick (D. croatii, D. gigas, and D. peruvianum).

Chromosome Numbers

All species of Dracontium that were examined are diploids with 2n = 26, the only number known in the tribe Lasieae (Petersen, 1989). These counts of 2n = 26 were confirmed by the first author in D. amazonense (G. Zhu 1454), D. gigas (Bogner 1267), D. polyphyllum (Croat 74210), and D. prancei (Croat 73867), using the method mentioned in Petersen (1989). Counts were made from root tips in all cases. Dracontium has comparatively small chromosomes, similar to those of other members of the same tribe. Petersen (1989) showed that chromosome size and number are highly variable in the Araceae and of great importance for their taxonomy and evolution at the generic level. However, based on the Dracontium chromosomes seen thus far, they appear to be of little taxonomic value at the specific level owing to their similarity in number, size, and shape.

DISTRIBUTION AND HABITATS

Distribution. Species of Dracontium occur from 15°22'N latitude in the Mexican district of Socon-

usco in Chiapas State (*D. soconuscum*), south through Nicaragua, Costa Rica, Panama, the Dominican Republic and Puerto Rico, Colombia, Venezuela, Trinidad, West Indies, the Guianas, Ecuador, Peru, Bolivia, and Brazil to the Tropic of Capricorn in Paraguay. In South America, the eastern limit of the collections is 44°28'W longitude in Maranhão, Brazil; *Dracontium* extends west along the Pacific coast of Colombia, Ecuador, and Peru. No collections of *Dracontium* are known from Cuba, Chile, Argentina, or Uruguay.

Five species occur in Mesoamerica: Dracontium gigas, D. grayumianum, D. pittieri, D. soconuscum, and D. spruceanum. Dracontium soconuscum is the only species known from Mexico and the northernmost species of the genus. This species also occurs in Costa Rica and Panama, and is very likely to occur also in Guatemala, El Salvador, and Nicaragua. Dracontium gigas is the only species known from Nicaragua; it is also known from the Atlantic slope of Costa Rica in the provinces of Alajuela, Heredia, and San José. All Mesoamerican species besides D. grayumianum occur in Costa Rica, including D. pittieri, endemic to the Pacific slope in the province of Puntarenas. It has not been collected in adjacent Panama, where three other species occur, D. soconuscum, D. spruceanum, and D. grayumianum. Dracontium soconuscum has its southern geographic limit in the Panama Canal area; to the south it is replaced by D. grayumianum, which has a typical Caribbean/Chocó distribution pattern as encountered in Philodendron species (Grayum, 1996).

Dracontium spruceanum is the most widespread species of the genus, ranging from Costa Rica, through Panama, Colombia, into northwestern Ecuador and along the eastern slope of the Andes through Amazonian Ecuador, Peru, and northwestern Amazonian Brazil. It is the only species of Dracontium that occurs on both slopes of the Andes, having been collected on the western slope of the Andes in Chocó Department, Colombia, and western Ecuador. Species diversity of Dracontium is highest in the Guianas (including the adjacent Venezuelan and Brazilian Amazonian regions), which have seven species (D. amazonense, D. asperum, D. dubium, D. guianense, D. nivosum, D. prancei, and D. polyphyllum). A secondary center of diversity of Dracontium is in Amazonian Peru (Loreto), where five species (D. amazonense, D. angustispathum, D. asperispathum, D. peruvianum, and D. spruceanum) coexist.

Eight of the 23 South American species herein of *Dracontium* appear as narrow endemics, often known only from a few localities (*D. bogneri*, *D.* dubium, D. guianense, D. longipes, D. nivosum, D. polyphyllum, D. prancei, and D. ulei). Some of these relatively narrowly ranging species are slightly more widespread, such as D. amazonense, which ranges from Amazonian Peru to Amazonian Brazil. Only one species, D. asperum, occurs in the Dominican Republic and Puerto Rico; it is also found in the Guianas and the islands of Trinidad and Tobago. In South America, Brazil has the largest contingent of Dracontium species, with 11 plus 2 additional species likely to occur there (D. guianense and D. plowmanii).

Species of *Dracontium* typically occur from near sea level to about 500 m. West Andean *D. croatii* is an Ecuadorian endemic species and is known only from higher elevations, from 800 to 1200 m. A few species may range from quite low elevations to high elevations. These include *D. pittieri* (30– 1000 m), *D. grandispathum* (250–1200 m), and *D. spruceanum* (25–1215 m).

Habitats. Species of Dracontium occur in habitats from Premontane moist forest (P-mf), Tropical moist forest (T-mf), Premontane wet forest (P-wf), and Tropical wet forest (T-wf). Most of the species occur only in one life zone: D. amazonense, D. dubium, D. guianense, D. margaretae, D. prancei, and D. ulei in Tropical moist forest (T-mf); D. gigas and D. grayumianum in Tropical wet forest (T-wf). Some species occur in two life zones (D. angustispathum, D. asperispathum, D. bogneri, D. croatii, D. gigas, D. grandispathum, D. longipes, D. nivosum, D. pittieri, D. plowmanii, D. polyphyllum, and D. purdieanum). Dracontium asperum, D. peruvianum, D. soconuscum, and D. spruceanum are the only ecologically widespread species, all having been collected in three different life zones.

Dracontium plants tend to occur along forest margins and in somewhat disturbed or wasted areas that are usually seasonally wet. Only one species, *D. margaretae*, is found growing in seasonal swamps.

REPRODUCTIVE BIOLOGY

PHENOLOGY AND POLLINATION

Inflorescences in *Dracontium* are often produced before new leaf production (*D. soconuscum*). They may sometimes appear simultaneously with new leaf production as in *D. croatii*, *D. pittieri*, and *D. spruceanum*. Some species produce inflorescences throughout the year (*D. spruceanum*), while others bloom in the wet season (*D. grayumianum* and *D. pittieri*) or in the dry season (*D. gigas*). These inflorescences usually last four to six weeks, then the spadix elongates into an infructescence if pollinated. The berries usually mature in a few to several months, with 9 to 11 months noted in *D. asperum* (J. Boos, pers. comm.).

The flowers of Dracontium are protogynous and mature basipetally (Poisson & Barabé, 1998). For a single flower, the ovary is anthesal usually one to two weeks prior to anther dehiscence. It often takes two to four weeks for all the flowers on a single spadix to reach anthesis. The appearance of the stigmatic fluid signals the receptive maturity of the ovary, often before the anthers of the same flower have dehisced. The disappearance of the stigmatic fluid signals that the stigma is no longer receptive. The anthers of mature stamens dehisce along an apical slit to form more or less rounded apertures. The pollen exits in cohesive strands that contract the stigma and its associated style (Fig. 26). The pollen may be carried away by pollinators or may fall naturally when dry onto a receptive stigma at a lower position on the same spadix. Flowers at the apex of the spadix must have pollen from other plants in order to be pollinated.

This protogyny in Dracontium (common throughout the family) serves to insure cross pollination. Hand pollination for D. asperum was reported in cultivation by Hans Boos in Trinidad, West Indies. In this case the inflorescence produced berries when cross pollinated and withered when there was no pollen from another inflorescence available (J. Boos, pers. comm.). When cultivated in the Missouri Botanical Garden greenhouse, D. polyphyllum developed young berries with only one inflorescence blooming. However, no berries ripened before the infructescence rotted away. Two other species, D. amazoense and D. prancei, have been hand pollinated by the senior author in the Missouri Botanical Garden research greenhouse; both plants failed to form berries. Another attempt at hand pollination between these two species also failed. Future reproductive studies are certainly needed in the genus.

At anthesis, the spathe of *Dracontium* emits a foul odor reminiscent of rotting meat, dead fish, or decomposed vegetables. The timing and duration of scent emission differ among species. Some species release their scent from early in the morning until late in the afternoon (*D. gigas* and *D. polyphyllum*), others from late in the morning until early in the afternoon (*D. soconuscum*), while others emit scent from afternoon to late evening (*D. croatii*) for approximately a six-hour period (Guanghua Zhu, pers. obs.). When the spathe is removed from the inflorescence, the scent vanishes, indicating that the scent is produced by the spathe instead of the spadix, as is commonly believed. Under SEM, there are many structures associated with stomata on the inner spathe surface, sometimes also on its outer surface. These structures may be osmophores responsible for the emission of scent. The stomata may be found opened or closed.

The pollinators of *Dracontium* remain unknown. Croat (1975) suggested that *Dracontium* has a typical fly-pollination syndrome because of the traplike nature of the spathe of some species and the foul scent the plants emit during anthesis, which is typical of other fly-pollinated species in the Araceae. Houseflies and some fruit flies were observed to visit the flowers in the greenhouse; however, these were also the only insects present in the greenhouse. Flies and beetles were reported as visitors of *D. gigas* when it was blooming at La Selva, Costa Rica (M. Grayum, pers comm.). Large metallic blowflies are reported to have visited *D. asperum* in Trinidad as well as in Florida (J. Boos, pers. comm.).

REPRODUCTION AND DISPERSAL

Vegetative reproduction is by tubercles produced at the apex of the tuber or via the production of a tumor-like structure, which is part of the tuber body. Tubercles are the most important means of vegetative reproduction in Dracontium; they typically remain dormant for several years. Tests conducted in North Carolina have shown that they may remain dormant for two years despite different treatments, including wounding, treatment with growth hormones, use of different soils and different temperatures (P. Schmidt, pers. comm.). However, disturbed tubercles may sometimes enlarge and produce a leaf. Concomitantly, the principal tuber usually rots away and is replaced by several smaller plants originating from these tubercles. Sometimes the smaller plants from tubercles may grow simultaneously while still attached to the parent for several seasons before detaching from the principal tuber.

All species of *Dracontium* are known to produce berries and seeds in the wild. However, there is a tradeoff between vegetative and sexual reproduction. When a plant regularly produces inflorescences and leaves (often alternately), its tubercles generally remain dormant. A disturbance to the principal tuber often causes its tubercles to enlarge and to produce a plantlet; the principal tuber ceases inflorescence production and instead produces only leaves.

Populations show high sociability with remarkable densities exhibited by *D. gigas* and *D. grayumianum*. Individual clusters with many small plantlets can be found within a few meters from the parent plant. This suggests that short-distance dispersal via tubercules occurs in these species. Croat (pers. comm.) suggested that Dracontium tubers may be harvested by wild pigs because of their starch content. At La Selva, a clump of D. gigas was found near an agouti nest. The agouti's digging may have been responsible for the short-distance dispersal of this species. However, there was no evidence that this animal was eating the tuber. The tubercles of Dracontium easily detach from the parent tuber when it is harvested or disturbed. Due to their small size, the tubercles can be transported easily in dirt when dug up. This theory is not in conflict with the fact that many plants of Dracontium are found as single individuals before reaching the stage of sexual reproduction. As stated earlier, tubercles remain dormant if the plant is not disturbed, and the long-distance dispersal of seeds by birds and mammals may result in an individual plant growing in a new location away from the mother plant. Long-distance dispersal of Dracontium seeds is still unstudied, but the genus has a typical bird-dispersal syndrome with colorful but non-aromatic fruits and seed, which can be individually pecked out of an infructescence. However, some Dracontium berries, e.g., those of D. grayumianum, have a pleasant fruity scent and sweet taste, which is typical of a mammal-dispersed seed syndrome.

USES

The ethnobotanical uses of Dracontium were summarized by Plowman (1969) and later by Croat (1994). Many Dracontium species are utilized by indigenous people, including those of Hispanic culture, as having edible parts and possessing medicinal uses. One of the most common medicinal uses of these plants is in the treatment of snakebite, documented for D. asperum, D. grayumianum, D. pittieri, D. polyphyllum, and D. spruceanum. The method of aroid medicinal usage varies in different areas. Roots and petioles of D. asperum are crushed with sugar and alcohol yielding a tincture, which is consumed at regular intervals for snakebite in Brazil (Plowman, 1969). The remaining pulp is applied to the area of snakebite by the same people (Croat, 1994). Leaf infusions of D. pittieri were ingested and applied externally as a remedy for the poisonous bite of the bocaraca snake (Bothreichis schlegelii Berthold) by indigenous peoples of Puntarenas, Costa Rica (Pittier, 1957). The Bribri Indians of Costa Rica first boil an infusion of D. pittieri or

D. soconuscum leaves, then apply this to snakebite wounds after cooling (Ginzbarg, 1977).

Dracontium spruceanum has been used extensively by indigenous peoples. Pulp from scraped tubers or split petioles of this plant is used by the Mayna Indians of Peru and applied directly to wounds (Croat, 1994). The scraped tuber and unheated inflorescences (or infructescence) are used by the Achuar Indians of Peru to massage snakebite, while the pulp of the scraped tuber is also applied to boils (Croat, 1994). The Achuar also use the crushed tuber of this plant mixed with equal parts of two Solanum (Solanaceae) species ("untukar" and "syukahuito") to alleviate boils and to make tumors recede (Croat, 1994). Tubers of D. spruceanum are also cooked and eaten to relieve chest pain in Peru (Croat, 1994). Steward and Metraux (1948) reported that leaves of D. spruceanum (as D. longipes Engl.) were rubbed on snakebite wounds by the Amahuaca Indians of Ecuador. Schultes and Raffauf (1990) reported that plants of D. longipes Engl. were cultivated by the Kofán Indians of Colombia and Ecuador and used in a decoction for treating diarrhea. They further reported that in Peru, tubers of these plants are ground into a paste, wrapped in Calathea (Marantaceae) leaves, warmed in a fire, and applied to snakebite.

Other medicinal uses have been reported for Dracontium. The powdered tuber of D. asperum has been used to treat the effects of asthma, anemia, amenorrhea, and whooping cough (Peckolt, 1892; Le Cointe, 1934). Juice from the tubers of this species is used to kill maggots in animals (Plowman, 1969). In Trinidad, D. asperum tubers have been harvested as a substitute for potatoes after a period of drying in storage (Boos & Boos, 1993). Tubers of D. grayumianum are ground with water and used by Chocó Indians in Panama for treating hemorrhaging during childbirth (Croat, 1994). An infusion of the leaves of D. pittieri is used to kill maggots on wounds (Pittier, 1957). In addition to being used as a snakebite remedy (Plowman, 1969), D. polyphyllum is used as a remedy for hemorrhoids (Croat, 1994) and as an antidote for the venom of spiders and stingrays (Levi-Strauss, 1952). The tubers of D. longipes are ground and used as a paste applied to snakebites in Brazil (Plowman, 1969). Tubers of some species of Dracontium, such as D. soconuscum and D. asperum, are edible. They may be boiled and served like a potato or ground with water and consumed as a juice (Croat, 1994).

Some species of *Dracontium* have horticultural value and are favored by tropical gardeners and aroid nurseries because of the snakelike patterning of their petioles and the umbrella-like cut leaf

blades. Most are easy to grow and can be vegetatively propagated by their tubercles. Several species were described from cultivated plants, including D. polyphyllum, D. asperum, D. croatii, and D. gigas. Dracontium gigas has been well known and commonly cultivated in European gardens since its discovery in Nicaragua in 1869. Since then, this species has been repeatedly described and illustrated in gardening publications and featured in plant exhibits (Seemann, 1869; Hooker, 1873; Masters, 1873; Watson, 1901; Macmillan, 1956). Other species, including D. amazonense, D. prancei, D. soconuscum, and D. spruceanum, are in cultivation in botanical gardens in Germany, the Netherlands, the United Kingdom, and the United States, as well as in private nurseries in Florida. The market for these plants is growing with increasing knowledge of the genus.

Relationships

Several general trends can be observed from our study of Dracontium, as well as from unpublished analysis of 58 different character states. Some species pairs share much in common. These include: (1) Dracontium amazonense and D. prancei; (2) D. grayumianum and D. soconuscum; (3) D. dubium and D. purdieanum; (4) D. gigas and D. pittieri; (5) D. angustispathum and D. guianense; and (6) D. asperispathum and D. spruceanum. In addition, Dracontium margaretae is clearly related to D. amazonense and to D. prancei. Dracontium grandispathum is most closely related to D. asperispathum and D. spruceanum. Dracontium grayumianum and D. soconuscum are often grouped together with D. dubium and D. purdieanum. Our studies indicate no infrageneric groups in the genus, but two major clades are suggested. Morphologically, these two clades can be distinguished by their peduncles. All species with subterranean peduncles or with peduncles only a few centimeters above ground level group in one clade (short-peduncle clade), while those with a peduncle more than 30 cm long above ground level, with only one exception, group in the other clade (long-peduncle clade). Our preliminary investigation also suggested an evolutionary trend from long peduncles to short (usually subterranean) peduncles within Dracon*tium.* The most basal members of the genus are D. angustispathum and D. guianense, while the most advanced members are D. amazonense and D. prancei. The member with the most distinctive leaf blade of the genus, D. margaretae, is also among the advanced group.

TAXONOMIC TREATMENT

- **Dracontium** L., Sp. Pl. 967, 1753. TYPE: *Dracontium polyphyllum* L. (lectotype, designated by Britton & Wilson (Scientific Survey of Puerto Rico and the Virgin Islands, 5(1): 7, 1923)).
- Eutereia Raf., Fl. Tellur. 4: 12. 1836 [1838]. TYPE: Eutereia nigricans Raf.
- Echidnium Schott, Oesterr. Bot. Wochenbl. 7: 62. 1857. TYPE: Echidnium schomburgkii Schott.
- Ophione Schott, Oesterr. Bot. Wochenbl. 7: 101. 1857. TYPE: Ophione purdieana Schott.
- Chersydrium Schott, Öesterr. Bot. Z. 15: 72. 1865. TYPE: Chersydrium jararaca Schott.
- Godwinia Šeem., J. Bot. 7: 314, t. 96, 97. 1869. TYPE: Godwinia gigas Seem.

Terrestrial, tuberous, perennial herbs, 1-5 m tall, with 1 leaf (rarely 2) and with 1 (or rarely 2) inflorescences, arising from an underground tuber buried 5–75 cm deep; tuber \pm hemispheric, 2–20 cm diam., 2-10 cm thick; flat above, with a few to many tubercles among many roots; convex below, smooth or strongly wrinkled, without tubercles and roots; tubercles elongate, ovoid to ellipsoid or cylindrical and often laterally compressed, 0.5–3 \times 0.5-1 cm, light brown; cataphylls 3 to 5, the innermost the longest, 2-20 cm long above ground, partially covering the petiole base, white-tinged pink or light brown (especially near the apex). Leaves solitary or sometimes more, arising terminally from tuber apical bud, tripartite; petioles 1-5 m long, 2-8 cm diam. at base, 1-3.5 cm diam. at apex, light to dark or brownish green, sometimes tinged brown near the base, mottled and streaked with whitish or pale green areas forming a reptilian pattern; armament varying from a smooth surface to having heavy protuberances, sometimes with horizontal elongate irregular projections bordering 2 differently colored areas, sometimes with spiny projections to 2 mm long; lower half of the petiole with more protuberances or projections, smoother above; blades with 3 major divisions, each 0.5-1.5 cm long, papyraceous to thinly coriaceous; upper surface green, glossy or less glossy, rarely matte; lower surface semiglossy or matte; sometimes with fenestrations along rachises or major veins; middle division sub-dichotomously divided into 3 sections; lateral divisions sub-dichotomously divided into 2 sections; each section may comprise a single leaf segment or be subdivided into 2 or 3 smaller subsections accordingly; midrib and major veins convex and light green on upper surface and conspicuously round-raised and paler on lower surface; secondary veins \pm parallel and arching apically, forming 2 collecting veins along the margins, with the innermost the strongest; terminal segments 8- $20 \times 3-7$ cm, lanceolate to irregular, free or confluent at base, often strongly decurrent downward along rachises, apically acuminate or caudate gradually into 1, 2, or rarely 3 apices; smaller leaflets oblanceolate or \pm triangular, 1–15 \times 1–6.5 cm, caudate, acute or rounded at apex, free at base, or decurrent downward partly covering the rachises, or confluent completely at base with rachises completely covered by leaf tissue; irregular or often pinnately arranged on the rachises; rachises mottled similar to petiole in a much paler shade or uniformly light green, sometimes tinged brown, smooth or armed as petiole; length from petiole apex to the first terminal subdivision of the middle division as long as or to twice as long as lateral divisions. Inflorescence solitary (rarely 2) arising from apex of tuber before or after leaf development; bracteoles 3 to 5, white-tinged pink to dark brown, acuminate contracting to an apiculate apex; the longest one (the innermost) completely covering the underground part and the base of the peduncle, sometimes longer than the peduncle and partly covering the spathe; peduncle reaching to slightly surmounting ground level, to 2.5 m long, often shorter than petiole, rarely exceeding petiole, 0.5-6 cm diam., much like the petiole in appearance when not covered by cataphylls, but tending to be smoother; coloration similar to that of petiole, sometimes more rose or brown; spathe marcescent, degrading on developed infructescence, narrowly ovate to naviculiform, convolute at base, open above, often hooded to broadly open; margins not overlapping or overlapping at the base and forming a tube, to broadly overlapping with only a small apical opening; \pm acuminate at apex, erect to slightly arching (less than 45°) to strongly arching (45°-90°), externally violet-purple, often tinged green or greenish, with obvious raphide cells, often raised, sometimes with surface somewhat bullate, internally reddish purple to maroon, glossy to semiglossy, sometimes with thin dry scales, often with stomata surrounded by whitish or brownish spotted glands, often with a whitish translucent area 0.5-10 cm high around the base of the spadix, periodically emitting at anthesis a foul scent like decomposing vegetables or meat; spadix at anthesis greenish to purple, cylindric (sometimes thinner at apex), sessile or stipitate with a stipe 0.5-2.5 cm long; spadix of infructescence $4-25 \times 4-10$ cm, often 4 to 15 times longer and 4 to 8 times wider than at anthesis. Flowers perfect, perigoniate, and spirally arranged on spadix, opening basipetally; tepals 4 to 6(8), green to purple, completely covering anthers before anthesis. Stamens (4)5 to

17(19); anthers yellow, open apically, turning redbrown, sometimes with dark purple especially near the opening after anthesis; filaments often slightly dilated, subcompressed and abruptly contracted at the apex into the connective; anthers exceeding connective, linear-elliptic, yellow, turning reddish brown, sometimes with dark purple, especially near the aperture, after anthesis, dehiscing apically by a vertical slit with rounded aperture at anthesis; pollen emerging in strands; ovary of 2 to 5(7) locules each with 1 ovule; style 2–5 mm long above tepals at anthesis, pale green to dark purple, persistent in fruit or not; stigmas 2- or 3-, sometimes 4-lobed, covered with a clear sticky liquid at anthesis. *Berries* green when young, maturing to reddish, purplish, purplish red, purple-brown or orange, covered with small whitish raphide cells, sometimes with red dots (easily visible at $10\times$), darkened apically, somewhat depressed around style when persistent or rounded; *seeds* 1 to 7 per berry, variable in shape from round to reniform to triangular to elongate, 0.5–1.0 cm long, 0.4–1.2 cm wide, smooth or decorated dorsally with warty projections, usually with 1 to 3 dorsal ridges, these continuous or interrupted, thin or thick. Chromosome number: 2n = 26 on all species counted to date.

Key to the Neotropical Species of Dracontium

 Blade segments linear, 1–1.5 cm wide, usually ascending at 45° angle from the petiole; growing in seasonal swamps; Venezuela (Apure and Guárico), Brazil (Mato Grosso do Sul), and Paraguay

13. D. margaretae Bogner
 Blade segments not linear, 3–12 cm wide, spreading horizontally (or ascending at 45° angle from the petiole when young); growing in habitats other than seasonal swamps; southern Mexico to central Paraguay.

2a. Peduncle completely subterranean or not more than 10 cm above ground level; longest bracteole reaching to base of or covering to ½ of the spathe.

3a. Spathe cymbiform (boat-shaped), not at all constricted; spadix lacking appendages at apex.
4a. Spadix often concealed by spathe at anthesis; spathe margins broadly overlapping at the base for at least ½ of the spathe.

 5a. Spathe 28–35 cm long, 6–10 cm wide at anthesis; endemic to Pará and Maranhão, Brazil
 14. D. nivosum (Lem.) G. Zhu

5b. Spathe to 20 cm long and 4.5 cm wide at anthesis; Brazil, Venezuela, and Peru.6a. Inner surface of spathe semiglossy to velvety, never with translucent scales.

- 7a. Spathe usually less than 13 cm long, arching toward apex by 45° to 90°; lacking an apparent translucent area (at base of inner spathe surface); Amazonian Peru, Venezuela, and Brazil
 1. D. amazonense G. Zhu & Croat
- 7b. Spathe usually more than 15 cm long, slightly arching toward apex (by up to 45°); with a translucent area (at base of inner spathe surface) 0.5–1 cm high; known from Brazil (Amazonas and Roraima) ________ 19. D. prancei G. Zhu & Croat
- 6b. Inner surface of spathe semiglossy to velvety, obscured with translucent scales.8a. Seeds reniform, laterally concave, with small cells along dorsal ridge; en-
- 4b. Spadix visible from face view externally at anthesis; spathe margins slightly to hardly overlapping at the base; French Guiana, Suriname, Guyana, Brazil, and Amazonian Venezuela 18. D. polyphyllum L.
- 3b. Spathe not cymbiform, constricted in lower $\frac{1}{5}$ to $\frac{1}{2}$ and differentiated into a proximal tube and a distal lamina; spadix often with one to several appendages (elongated and enlarged tepals) at apex.
 - 9a. Inner surface of spathe never with translucent scales.
 - 10a. Seeds with 5 or 6 thin, strongly discontinuous ridges to 1.5–2 mm high; tropical wet forests, Darién, Panama, to Chocó, Colombia 10. D. grayumianum G. Zhu & Croat 10b. Seeds with 3 thick, continuous ridges to 0.5 mm high; tropical moist forests, southern
 - - 11a. Seeds with 4 or 5 thin, slightly interrupted ridges to 1.5 mm high; Guyana, Venezuela,

 Brazil
 7. D. dubium Kunth

 11b. Seeds with 3 continuous ridges to 0.5 mm high; Caribbean coast of Colombia, and

12a. Peduncle 30–90 cm above ground level, less than half as long as petiole.

- - to subtruncate apically; Central America, French Guiana, or South America as far south as Brazil, but not in Peru.

 - 14b. Spathe 9–20 cm long, 3–5 cm wide, acuminate at apex; seeds light brown, 0.5–0.7 cm diam., with 1 dorsal ridge; Dominican Republic, Puerto Rico, Trinidad, Tobago, Guyana, Surinam, French Guiana, Venezuela, and Brazil.
 - 15a. Spathe 9–10 cm long, acuminate at apex, slightly arching apically up to 45° angle; seeds laterally convex, with many fine pits flanking on both sides of the ridges; French Guiana, near Brazilian border 11. D. guianense G. Zhu & Croat
 - 15b. Spathe 10–20 cm long, often arching apically by 45°–90° angle; seeds laterally concave, with coarse, wart-like protuberences flanking the margins on both sides of the ridges; Dominican Republic, Puerto Rico, Trinidad, Tobago, Guyana, Surinam, Venezuela, and Brazil ______ 4. D. asperum K. Koch
- 12b. Peduncle 100–250 cm above ground level, usually more than half as long as petiole.
- 16a. Spathe cymbiform, never differentiated into a proximal tube and distal lamina.
 - 17a. Spathe obtuse at apex, widest in upper half.

 - 18b. Seeds reniform, dorsal ridge 1, continuous; spathe maroon externally, the margins scarcely overlapping; spadix exposed at anthesis; endemic to the Pacific slopes of Costa Rica 16. D. pittieri Engl.
 - 17b. Spathe acuminate at apex, widest in lower half.

 - 19b. Spadix 4–5 cm long in fruit; petiole 1–2 m long; seeds reniform, with 3 weak continuous ridges to 0.5 mm high; endemic to Acre, Brazil
 - 12. D. longipes Engl. 16b. Spathe usually not cymbiform, constricted near the base to yield a proximal tube and distal lamina.
 - 20a. Seeds 0.4–0.6 cm diam., laterally convex, with 1 dorsal ridge; spathe usually wrinkled or lobed along the margins; endemic to southern Peru
 - 20b. Seeds 0.7–1 cm diam., laterally concave, with 3 dorsal ridges; spathe never wrinkled
 - or lobed along the margins; Colombia, Ecuador, Peru, Brazil, and Surinam. 21a. Inner surface of spathe semiglossy or velvety, densely covered with translucent

 - - 22b. Spathe 20–35 cm long, 3–6 cm wide, gradually acuminate apically; southern Costa Rica to the Pacific slope of Colombia and Ecuador and in the Amazon basin in southern Venezuela, Colombia, Ecuador, Peru, and Brazil (also in Surinam) ______ 22. D. spruceanum (Schott) G. Zhu
- Dracontium amazonense G. Zhu & Croat, sp. nov. TYPE: Peru. Loreto: Iquitos, Altura de Picuruyacu, near confluence of Río Nanay & Río Amazonas, 3°40'S, 73°13'W, 28 Dec. 1979, C. Davidson & J. Jones 9605 (holotype, MO!; isotype, RSA!). Figures 3A, 4.

Herba usque plus quam 2 m alta; petiolus 1.3–2 m longus; pedunculus subterraneanus, 0–2 cm longus; spatha 10–13 cm longa, 3–4.5 cm lata; extus purpurea; intus velutina, purpurea; spadix 2.5–4 cm longus, 0.8–1.2 cm diam.; baccae globosae, 0.5–0.7 cm diam.; semina rubra, suffusa aurantiaca, usque 0.6 cm diam. Tuber hemispherical, 8–12 cm diam., 6–8 cm thick, flat above, rounded and white to brown below, 10–20 cm below ground level; tubercles abundant, cylindrically elongated or rounded, 0.5–1 cm diam., 0.8–2 cm long, borne around the periphery of tuber; roots whitish, 1–3 mm diam.; *cataphylls* 2 or 3, 5–22 cm long, 3–5 cm wide, pink-tinged or light brown, reaching or surpassing ground level. *Leaves* solitary; *petioles* 1.3–2 m long above ground, 2.5–4 cm diam. at midpoint, dark green, contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, usually smooth



Figure 3. A–D, Flowers. —A. Dracontium amazonense (Croat 56898). Spadix with protruding stigmas. —B. D. polyphyllum (Croat 74210). Apex of spadix showing short styles and stamens. —C. D. spruceanum (G. Zhu 1486). Close-up of flower showing weakly protruding style and a ring of stamens. —D. D. soconuscum (G. Zhu 1502). Spadix with a cluster of appendages at apex.



Figure 4. A–D, Dracontium amazonense.—A. (Croat 56898). Spathe showing side view. —B. (Croat 71895). Spathe showing front view. —C. (Croat 65898). Spathe with cut-away view showing spadix at anthesis. —D. (Davidse & Jones 9605). Seeds in side view.

in upper half and with irregular protuberances in lower half; juvenile blades sagittate, or sagittately lobed; mature blades spreading horizontally, 1-1.2 m diam., subcoriaceous, rarely fenestrate, never variegated, often without raphide cells or dark markings, glossy and dark green above, semiglossy and medium green below; middle division once or twice trichotomously branched, 45-60 \times 40-45 cm, with terminal subdivision consisting of three sections, with each basal subdivision consisting of many segments; lateral divisions twice dichotomously branched, $40-55 \times 40-50$ cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections free, each consisting of many segments; leaf segments often entire, broadly oblanceolate, more than 5 cm wide on each side of the major ribs, narrowly elliptic, at least some of the basal segments free from each other, often without contrastingly smaller rounded or triangular segments; apices acuminate; ultimate segments 10-15 cm long, often confluent with penultimate segments; other segments 7-13 cm long; penultimate segments free from subterminal sections; medial segments free from basal subdivisions; basal segments present, free from each other; rachises patterned similar to petiole but in much paler shades, smooth; tertiary veins obscure above and weakly raised below; bracteoles 1 or 2, 6–22 \times 1-2.5 cm, pink tinged, the longest one longer than the peduncle, covering up to 1/3 of the spathe. Inflorescence solitary or two, appearing before new leaf; peduncle 0-2 cm long above ground, 1-1.2 cm diam. at midpoint, often almost completely subterranean, scarcely mottled, whitish tinged pink, smooth; spathe (6–)10–13 \times 3–4.5 cm, cymbiform, cucullate, often arching 90°, apex acuminate; inner surface velvety, violet-purple, with translucent area obvious, 0.5–1.5 cm high, shorter than spadix; outer surface maroon, tinged green, matte; margins entire, slightly overlapping at the base; veins obscure inside, conspicuously darker or paler than the spathe, brown; spadix often hidden, sessile, cylindric, narrower at apex, brownish purple, 2.5–4 \times 0.8-1.2 cm at anthesis, never with appendages at apex; flower tepals 4 to 5, $1.5-2 \times 1-2$ mm, light brown or brownish purple; stamens 6 to 8; filaments 1-2 mm long; anthers 0.5 mm long, completely exserted; ovary 3-locular, white; stigma unlobed, or 3-lobed; style 0.5-2 mm long above tepals, brownish purple, persistent. Infructescence with spadix 3.5 cm long, 1.5 cm diam. in fruit; berries 0.5-0.7 \times 0.6 cm, globose, apically rounded; young berries pale green; mature berries with abundant raphide cells; seeds 0.5-0.6 cm diam., reniform, light brown, laterally depressed; dorsal ridges evident, 3, \pm continuous, more than 1 mm thick, warty along both sides, appearing as strongly reduced lateral ridges. Chromosome number 2n = 26 (*G. Zhu* 1454).

Phenology. Flowering known only in March; mature fruits known only in December.

Distribution and habitat. Dracontium amazonense is known from Amazonian Venezuela (Bolívar), Brazil (Amazonas and Pará), and Peru (Loreto). It occurs in the *Tropical moist forest* (T-mf) life zone, at elevations of 60 to 100 m.

Discussion. Dracontium amazonense is easily confused with D. polyphyllum in both sterile and fertile condition. Mature leaves of both species closely resemble one another, and their inflorescences are superficially similar. However, D. amazonense differs in its laterally concave seeds (vs. laterally convex in D. polyphyllum) and the spathe usually arching 90° apically (vs. arching 45° in D. polyphyllum), as well as by its usually hidden spadix (vs. exposed in D. polyphyllum).

A tuber of the type collection (Davidson & Jones 9605) of D. amazonense was sent to the Missouri Botanical Garden in December 1979. The plant bloomed the following spring, and a fertile specimen (Croat s.n., MO 4369881) was prepared in April 1980. Two years later, two more tubers of this species were brought into cultivation at the Missouri Botanical Garden from Manaus, Amazonas, Brazil (Croat 53561, June 1982). However, when we started to study the genus Dracontium 10 years later in 1992, both Davidson & Jones 9605 and Croat 53561 were missing from the greenhouse. Instead, D. amazonense was represented by two other numbers, Croat 56898 and Croat & Grayum 59844, in the greenhouse, each with several mature plants. These plants must have been mislabeled, since both numbers apparently originated from Costa Rica, where D. amazonense is unknown. Croat 56898 was collected by Helen Young from La Selva, in the province of Heredia, where only D. gigas occurs. Croat & Gravum 59844 was collected from the Osa Peninsula, where only D. pittieri is known. Therefore, the cultivated plants labeled as Croat 56898 and Croat & Grayum 59844 in the Missouri Botanical Garden greenhouse probably originated from the collections Davidson & Jones 9605 and Croat 53561 and represent D. amazonense.

Dracontium amazonense is one of the most easily grown species in the genus. It blooms regularly and propagates easily in the greenhouse by means of tubercles. However, to the authors' knowledge it had never produced fruit by means of either selfor cross-pollination. This species has been widely distributed by the Missouri Botanical Garden, under the number *Croat* 56898 and the name *D. gigas*, to many institutions worldwide and private aroid growers in the United States.

Paratypes. BRAZIL. Amazonas: Manaus, Chacaras de Tarumn, ca. 16 km NW of Manaus, T. Croat 53561, 56898 (MO); Tefé, Lago Tefé, NW shore, T. Plowman et al. 12510 (MG, MO); mouth of Rio Bauana, T. Plowman et al. 12550 (MG, MO, NY). Pará: Rio Juruá, Bom Fim, Ule 5286 (MG). PERU. Loreto: Quebrada Yanamono, Explorama Tourist Lodge, Río Amazonas, P. Maas et al. 8299 (U). VENEZUELA. Bolívar: Santa Elena de Uairén, Gran Sabana, campos del Sr. Fernández Peña, Tamayo 3188 (F, US, VEN).

Cultivated plants. Peru. Loreto: Altura de Pecuruyacu, TYPE: Davidson & Jones 9605, (MO 4369881), cult. at Missouri Botanical Garden (MBG) [represented by G. Zhu 1454, 1456, 1457, 1460, 1461, 1464, 1465, 1489, 1514, 1516 (MO)]. Brazil. Amazonas: Manuas, T. B. Croat 53561 (MO), cult. at MBG. Ecuador. Napo: Puyo, C. McDaniel s.n., T. B. Croat 71895 (MO), cult. at MBG.

 Dracontium angustispathum G. Zhu & Croat, sp. nov. TYPE: Peru. Loreto: Mishuyacu, near Iquitos, 100 m, in forest, *G. Klug 254* (holotype, US!; isotypes, F!, NY!). Figure 5.

Herba usque plus quam 2 m alta; petiolus 1–2 m longus; lamina 35–55 cm longa, 25–35 cm lata; pedunculus 45–65 cm longus, 0.5–1.5 cm diam.; spatha 6–10 cm longa, 1.5–2 cm lata, convoluta basi, apice 20–50 cm longa; extus impolita, sordide purpurea; intus purpurea; spadix 2–5 cm longus, 0.5–1 cm diam.; tepala 5–7; semina brunneola, 0.5–0.65 cm longus, 0.4–0.5 cm lata.

Tuber hemispherical, 6-10 cm diam., 5-6 cm thick, flat above, rounded and white to brown below, 10-15 cm below ground level; tubercles abundant, rounded or cylindrically elongated, 0.5-1 cm diam., 0.6-1 cm long, borne around the periphery of tuber; cataphylls 2 or 3, 2-15 cm long, 1-2.5 cm wide, light brown, reaching or surpassing ground level. Leaves solitary; petioles 1-2 m long above ground, 1.5-3.5 cm diam. at midpoint, dark green or brownish green, contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, usually smooth in upper half and with irregular protuberances in lower half; juvenile blade sagittate, or sagittately lobed; mature blades spreading horizontally, 1-1.2 m diam., thinly coriaceous, rarely fenestrate (sometimes fenestrate in juvenile leaves), never variegated, without raphide cells or dark markings, semiglossy and medium green above, matte and medium green below; middle division once or twice trichotomously branched, $35-55 \times 25-35$ cm, with terminal subdivision consisting of three sections, with each basal subdivision often consisting of an entire segment; lateral

divisions twice dichotomously branched, 35–55 \times 25-35 cm, with terminal subdivision often consisting of an entire segment, with basal subdivision often consisting of an entire segment; terminal and subterminal sections free, each usually consisting of a single segment; leaf segments often entire, broadly oblanceolate, more than 5 cm wide on each side of the major ribs, lanceolate, mostly free from each other in each division, without contrastingly smaller rounded or triangular segments; apices caudate; ultimate segments 20-35 cm long; basal segments absent; rachises patterned similar to petiole but in much paler shades, smooth; tertiary veins prominent above, or weakly raised below; bracteoles 2 or 3, 5-20 cm long, 1-2 cm wide, dark brown or light brown, the longest one much shorter than the peduncle, confined at the base of the peduncle. Inflorescence solitary, appearing before or after new leaf; peduncle (35-)45-65 cm long above ground, 0.5-1.5 cm diam. at midpoint, less than half as long as the petiole, mottled similar to petiole but deeper in color, dark green, smooth in upper half; spathe $6-10 \times 1.5-2$ cm, cymbiform, non-cucullate, erect or slightly arching, apex caudate, 3 to 5 times longer than the remainder of the spathe; inner surface semiglossy, maroon, with translucent area obscure (to 3 mm height); outer surface dark purple, matte; margins entire, broadly overlapping or convolute in the lower two-thirds; veins obscure inside and outside, similar to the spathe in color; spadix hidden, sessile, cylindric, light brown or purple, 2-5 cm long, 0.5-1 cm diam. at anthesis. Flower tepals 5 to 7, $1.5-2 \times 1-1.5$ mm, pale green; stamens 6 or 7; filaments 1.5-2 mm long; anthers 0.5-1 mm long, slightly exserted; ovary bilocular, pale green; stigma unlobed, or 2-lobed; style 1-2 mm long above tepals, green, persistent. Infructescence with spadix 6-9 cm long, 1.5-2 cm diam. in fruit; berries 1.1-1.8 cm diam., 0.8-1 cm thick, obliquely obovoid, apically apiculate; young berry medium green; mature berry orange, with abundant raphide cells; seeds solitary, $0.5-0.65 \times 0.4-0.5$ cm, rounded or reniform, light brown, laterally flattened; dorsal ridges obscure.

Phenology. Flowering from July to April; mature fruits from August to April.

Distribution and habitat. Dracontium angustispathum is found in Loreto Department in Peru, and there is also one collection from Vaupés in Colombia. It occurs in *Tropical moist forest* (T-mf) and *Tropical wet forest* (T-wf) life zones (Holdridge et al., 1971), often in swampy areas, at elevations of 100 to 180 m.

Local names. "Anakaho" (King 416, F); "jer-



Figure 5. A—D, *Dracontium angustispathum*. —A. Cultivated plant by John Banta, originally collected in Peru in 1986 by Josef Bogner. —B. Specimen showing inflorescence, portions of petiole, and tuber (*Plowman et al. 6720, GH*). —C. Herbarium specimen showing close-up of infructescence (*Stein 3999*). —D. Seeds showing dorsal view (top) and side view (bottom) (*Vásquez et al. 8081*).

gón sacha del bajo" (Martin & Lau-Cam 1315, a

ECON). Discussion. Dracontium angustispathum does not resemble any other member of the genus. It is characterized by its thin spathe less than 2 cm wide at anthesis, with a caudate apex 3 to 5 times longer than the body of the spathe (hence its epithet), leafblade divisions usually consisting of a few (3 to 5) segments; and usually 1-seeded berries apiculate apically. This species has been previously identified as the partially sympatric D. loretense [D. spruceanum], which has a much longer peduncle. Cultivated plants of D. angustispathum are only known from John Banta's nursery in Florida.

The new species *Dracontium angustispathum* was previously noted (as nomen nudum) to occur in Peru (Vásquez et al., 2002 [2003]).

Paratypes. COLOMBIA. Vaupés: Río Apaporis, at mouth of Río Pacoa, Schultes 14799 (GH). PERU. Loreto: Maynas, Pebas on Río Ampiyacu, Plowman et al. 6720 (GH); Iquitos, Alpahuayo, Esta. Exp. Inst. Inv. IIAP, Quebrada Brashico, Vásquez et al. 16524 (MO); Almendras, Vásquez & Jaramillo 4938 (MO), 7595 (MO); Iquitos, Mishuyacu, Inchaustegui s.n. (MO), Williams 3756 (F); Maynas, Pebas, Bora Native community of Brillo Nuevo, Plowman et al. 6815 (GH), Treacy & Alcorn 198 (F); Río Ampiyacu, Bora Pucaurquillo, Ramon Castilla, Hahn et al. 17 (MO), Stein 3999 (MO); Río Nanay, Casería Mishana, 30 km SW of Iquitos, Callicebus Biological Reserve, Foster 4389 (F); Pinto-Cocha, Williams 827 (F); Puerto Almendras, Vásquez et al. 8081 (MO). Napo: Río Napo, Negro Urco, Martin & Lau-Cam 1315 (ECON); Río Santa María, trail E of Secova, village of "Vencedor," King 416 (F); Río Blanco, Est. Biol., Vásquez et al. 6761 (MO); Río Itaya, San Antonio, Killip & Smith 29351 (NY, US); Río Yubineto, tributary of Río Putumayo, Bellavista Paujilillo, Haxaire 1757 (MO).

Cultivated plants. Peru. Unknown original locality, *J. Bogner s.n.* (M), cult. in United States, Florida, Alva, John Banta's Nursery, E. Spear; Loreto, Río Sucusari, collected by van der Werff, vouchered, 1 Nov. 1996, *Croat 79428* (MO).

 Dracontium asperispathum G. Zhu & Croat, sp. nov. TYPE: Peru. Loreto: Maynas, Pebas on Río Ampiyacu, 3°10'S, 71°49'W, 10 Apr. 1977, *T. Plowman, R. E. Schultes & O. Tovar* 6729 (holotype, F-1825130!; isotypes, F-1823999!, GH!). Figure 6.

Petiolus 1–2.5 m longus; lamina 50–65 cm longa, 50– 60 cm lata; pedunculus 1–1.45 m longus, 1–2.5 cm diam.; spatha 28–46 cm longa, 4–6 cm lata, cucullata basi; extus impolita, sordide viridis; intus velutina, purpurea; spadix 3.5–6 cm longus, 0.7–1 cm diam.; tepala (4–)5–6(–7); semina rubra, 0.6–0.8 cm diam.

Tuber hemispherical, 5–15 cm diam., 4–8 cm thick, flat or slightly sunken above, rounded and white to brown below, 5–20 cm below ground level. Tubercles few, rounded, 0.8–1 cm diam., borne

around the periphery of tuber; roots 2.5-3 mm diam.; cataphylls 1 to 3, $6-22 \times 1.5-3$ cm, pinkish or light brown, reaching or surpassing ground level. Leaves solitary; petioles 1-2.5 m long, 2.5-4 cm diam. at midpoint, dark green or medium green tinged brown, contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, smooth or sometimes with spiny projections; juvenile blade sagittate, or sagittately lobed; mature blades spreading horizontally, 1-1.4 m diam., subcoriaceous, sometimes fenestrate, never variegated, without raphide cells or dark markings, semiglossy and dark green above, matte and medium green below; middle division twice trichotomously branched, 50–65 \times 50–60 cm, with terminal subdivision consisting of three sections, with each basal subdivision consisting of many segments; lateral divisions twice dichotomously branched, 47–60 \times 45-55 cm, with terminal subdivision consisting of two sections, with basal subdivision consisting of many segments; terminal and subterminal sections free, each usually consisting of a single segment or each consisting of a few segments; broadly oblanceolate, more than 5 cm wide on each side of the major ribs, ovate-oblong or elliptic or lanceolate, mostly free from each other in each division, often without contrastingly smaller rounded or triangular segments; apices acuminate, or rarely acute; ultimate segments 20-32 cm long, free from penultimate segments; other segments 9-20 cm long; penultimate segments free from subterminal sections; medial segments often free from basal subdivisions; basal segments present, free from each other; rachises patterned distinct from petiole, pale green, smooth; tertiary veins prominent above and weakly raised below; bracteoles 1 to 4, 4-24 cm long, 1.5-3 cm wide, light brown, the longest one much shorter than the peduncle, confined to the base. Inflorescence solitary, appearing before or after new leaf; peduncle (56-)100-145 cm long above ground, 1-2.5 cm diam. at midpoint, more than half as long as the petiole or sometimes as long as or longer than the petiole, mottled similar to petiole but deeper in color, dark green, smooth in upper half or with irregular protuberances in lower half or spiny projections; spathe 28-46 cm long, 4-6 cm wide, non-cymbiform, constricted at a certain point and differentiated into a proximal tube and a distal lamina (blade), erect or slightly arching, apex acuminate; 8-12 cm long, 4-6 cm wide at widest point; lamina 3 to 5 times longer than the tube; inner surface covered with dense, translucent scales 1-2 mm long, olive-brown or red-purple, with translucent area obvious, 8-15 cm high, 1.5-3 times longer than spadix; outer surface green or green tinged



Figure 6. A–D, *Dracontium asperispathum (Plowman et al. 6729)*. —A. Herbarium type specimen. —B. Herbarium type specimen showing inflorescence. —C. Herbarium type specimen showing infructescence. —D. Seeds in side view.

brown, matte; margins entire, broadly overlapping at the base; veins obscure inside and raised outside, similar to the spathe in color; spadix hidden, stipitate, cylindric, brown or purple or dark purple, $3.5-6 \times 0.7-1$ cm at anthesis, never with appendages at apex; stipe $0.5-1 \times 0.5-0.8$ cm at anthesis, light brown; flower tepals (4)5 or 6(7), 0.5–2.5 \times 1-2 mm, purple or dark purple; stamens 5 to 7; filaments 0.3-2 mm long; anthers 0.3-0.5 mm long, hidden or slightly exserted; ovary 3-locular, pale green or white; stigma unlobed; style 0.5-1.5 mm long above tepals, purple or green, persistent. Infructescence with spadix 8–16 \times 2–4 cm in fruit; berries 0.7–0.8 \times 0.7–1 cm, 1- or 2-seeded, obliquely obovoid, apically rounded or subtruncate; young berries medium green; mature berry orange, without reddish dots and raphide cells; seeds 0.6-0.8 cm diam., rounded, reddish brown, laterally flattened; dorsal ridges obvious, 3, often strongly interrupted, with the central ridge contrastingly raised, more than 1 mm thick, 0.1-0.2 mm high, warty along ridges.

Phenology. Flowering from January to September; mature fruits from April to August.

Distribution and habitat. Dracontium asperispathum ranges from the Amacayacu area in Colombia (Amazonas) to Amazonian Ecuador (Napo) and along Río Amazonas and Río Napo in Peru (Loreto). It occurs in *Tropical moist forest* (T-mf) and *Premontane moist forest* (P-mf) life zones (Holdridge et al., 1971), at elevations of 100 to 230 m.

Local name. "Jergón sacha" (Williams 1942, F; Plowman & Martin 1661, ECON).

Discussion. Dracontium asperispathum is easily confused with *D. spruceanum* where their ranges overlap in the upper Amazon basin because they have very similar leaves and a long-pedunculate elongated purplish spathe, but the former differs in having the spathe inner surface covered with dense, translucent scales (hence, the name asperispathum).

The new species *Dracontium asperispathum* was previously noted (as nomen nudum) to occur in Peru (Vásquez et al., 2002 [2003]).

Paratypes. COLOMBIA. Amazonas: Amacayacu, Par. Nac. Nat. Amacayacu, Trocha de Matamatá, J. Pipoly 15612 (MO). ECUADOR. Napo: Par. Nac. Yasuní, Pozo Petrolero Conoco-Amo 2, D. Neill et al. 8160 (CM, MO, QCNE). PERU. Loreto: Explorama, Napo Camp, Las Amazonas, Quebrada Sucusari, Gentry et al. 42629 (MO); Explorama Inn, 1 km S of Indiana, Río Amazonas, Gentry et al. 54686 (MO); Yanamono, Díaz et al. 1164 (MO); Explorama Camp, Río Amazonas above mouth of Río Napo, Gentry et al. 29076 (MO); Iquitos, Maare 189 (ECON); Picurugacu, Plowman & Martin 1661 (ECON); Río Ampiyacu at Pebas, Plowman et al. 6728 (F, GH); Río Amazonas at Pebas, Williams 1750, 1942 (F); Río Amazonas, Caballo-Cocha, *Williams 2119* (F, US); Río Napo, Isla Inayuga, *Croat 20550* (F, MO); Río Yaguasyacu, Brillo Nuevo, *Plowman et al. 6820* (GH); Ushpacaño, near Iquitos, *Tina & Tello 2054* (ECON); Varadero de Mazan from Río Amazonas to Río Napo, *Croat 19391* (MO); Río Itaya, *Williams 155* (F).

- 4. Dracontium asperum K. Koch, Wochenschr. 33: 259. 1859. TYPE: Surinam. Nickerie, 12 km N of Lucie River, 3 km S of Juliana Top, 3°36'-41'N, 56°30'-34'W, 300 m, H. S. Irwin et al. 55045 (neotype, designated by Zhu & Grayum (1995: 522), NY!; isotypes, COL!, F!, GH!, K!, US!, VEN!). Figure 7.
- Dracontium elatum Masters, Gard. Chron. 1: figs. 58, 344. 1870. TYPE: Guyana. Distributed by Linden and in cultivation at Sanders's nursery, Sanders 1920 (lectotype, designated here, K!).
- Draconiium foecundum Hook. f., Bot. Mag. 1885: t. 6808. 1885. TYPE: Guyana. Orealla, Corentyne River, near coast, 5°19'N, 57°20'W, 2 Mar. 1882, W. W. E. Im Thurn s.n. [from cultivar] (holotype, K!).

Tuber hemispherical, $4-16 \times 3-8$ cm, flat or slightly convex above, rounded and whitish to brownish below, 15-35 cm below ground level; tubercles abundant, cylindrically elongated, 0.5–1 \times 1-3 cm, borne around the periphery of tuber; roots white, 2–3 mm diam.; cataphylls 1 to 3, 14–35 \times 2-5.5 cm, pinkish or light brown, reaching or surpassing ground level. Leaves solitary or sometimes 2 or more per tuber; petioles 1-2 m long above ground, 2-4 cm diam. at midpoint, gray or whitish green (especially when young) or medium-greentinged brown, scarcely mottled, usually smooth in upper half and with irregular protuberances in lower half; juvenile blade sagittate, or sagittately lobed; mature blades ascending to 45° to the petiole spreading horizontally, 1-1.3 m diam., papyraceous, rarely fenestrate, never variegated, without raphide cells or dark markings, glossy and medium green above, glossy and dark green below; middle division twice trichotomously branched, 1-1.2 cm long, 0.9-1.1 cm wide, with terminal subdivision consisting of three sections, with each basal subdivision consisting of many segments; lateral divisions 3 times or more dichotomously branched, $0.75-0.98 \times 0.8-1$ cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections free, each consisting of many segments; leaf segments bilobed or irregularly lobed, broadly oblanceolate, more than 5 cm wide on each side of the major ribs, ovate or oblanceolate, at least some of the basal segments free from each other, often with contrastingly smaller rounded or triangular segments alternating with larger segments; apices



Figure 7. A–D, *Dracontium asperum*. A, B. Photos taken at Orange Grove Estate, Trinidad, by Hans Boos. —A. Inflorescence at anthesis. —B. Inflorescence with one side removed to expose interior of spathe and the spadix at anthesis. —C. (*G. Zhu 1509*). Cultivated plant by Hans Boos in Trinidad showing base of petiole and infructescence with immature fruits and persistent spathe. Photo by Hans Boos. —D. Seeds from Trinidad sent by Julius Boos.

acuminate, or acute (rarely); ultimate segments 12-20 cm long, free from penultimate segments; other segments 6-15 cm long; penultimate segments not free from subterminal sections; medial segments confluent with the basal subdivisions; basal segments present, free from each other; rachises patterned similar to petiole but in much paler shades, with spiny projections (sometimes); tertiary veins conspicuous above and weakly raised below; bracteoles 1 or 2, 4.5– 37×1.5 –3 cm, dark brown mottled with light brown, the longest one much shorter than the peduncle, confined at the base. Inflorescence usually solitary, rarely 2, appearing before new leaf; peduncle 5-17 cm long above ground, 0.5–0.8 cm diam. at midpoint, less than half as long as the petiole, mottled similar to petiole but deeper in color, brown-green, often with irregular protuberances; spathe (10)13–20 \times 3–5 cm, cymbiform, cucullate, often arching 45°-90°, apex acuminate; inner surface velvety, maroon or purple-red or redpurple, with the translucent area obvious, 1-2 cm high, shorter than spadix; outer surface maroon, tinged green or dark purple, matte; margins entire, hardly overlapping at the base; veins obscure or obvious inside and outside, similar to the spathe in color, marcescent on developing infructescence; spadix exposed, sessile, cylindric, purple, 2.6–4 \times 0.8-1.1 cm at anthesis, never with appendages at apex; flower tepals (4 to)5 or 6(to 7), 3-4 mm long, 1-2 mm wide, dark purple; stamens (5)6 or 7; filaments 3-4.5 mm long; anthers 1-1.5 mm long, completely exserted; ovary 3- or 4-locular, pale green; stigma 2- or 3-lobed; style 1-3 mm long above tepals, dark purple, persistent. Infructescence with spadix $8-15 \times 3-4$ cm in fruit; berries 0.8-1.2 cm diam., 0.8-1 cm thick, subglobose, 3- to 6angular, apically subtruncate; young berry light green; mature berry purplish brown, with abundant reddish dots and raphide cells (dried berries); seeds 1- to 3-seeded, 0.5–0.7 cm diam., triangular (\pm) or rounded, light brown, laterally depressed; dorsal ridges obvious, 3, continuous, more than 1 mm thick, warty along both sides, these appearing as another set of strongly reduced lateral ridges. Chromosome number 2n = 26 (Bogner 1132, M; Petersen, 1989).

Phenology. Flowering mainly from January to March, also in December and from June to August; mature fruits from January to August.

Distribution and habitat. Dracontium asperum is a widely distributed species in the Guyana highlands from coastal Surinam and adjacent Brazil (Amazonas), throughout Guyana, ranging into the West Indies from the islands of Trinidad, Puerto Rico, and Dominican Republic. It is likely to be found in northeastern Venezuela since it is phytogeographically related to Trinidad. It occurs in the *Tropical moist forest* (T-mf) life zone (Holdridge et al., 1971), at elevations of 30 to 330 m. *Dracontium asperum* is also known from Dominica and Martinique (Jo Ann Baptiste & Julius Boos, pers. comm.). Julius Boos (pers. comm.) suggests that some of the distribution of this species in the West Indies is partly the result of its probable distribution by means of its use as a journey food by native peoples moving from island to island.

Discussion. Dracontium asperum is distinguished by its often strongly hooded spathe with the margins broadly overlapping in the lower half at anthesis, hidden spadix, peduncle much longer than the longest bracteole 10-35 cm long above ground level, laterally concave seeds with a single strongly interrupted dorsal ridge coarsely ornamented with wart-like structures flanking the ridge, and usually many tubercles at the tuber apex. One of the most perplexing taxonomic problems in the genus Dracontium was the confusion involving D. asperum and D. polyphyllum, resolved by the designation of a neotype for the former and an epitype for the latter (Zhu & Grayum, 1995). Dracontium asperum is also similar to D. prancei, which differs in having the bracteoles usually longer than the peduncles and covering the base of the spathe.

Dracontium asperum was described by Koch (1859) over a century after *D. polyphyllum* (1753), from a plant introduced from Surinam and cultivated at the Berlin Botanical Garden that had been obtained from the Botanical Garden in Amsterdam. The holotype of *D. asperum* prepared by Koch and presumably deposited at B was either destroyed or lost.

Dracontium polyphyllum differs from D. asperum in having a shorter, slightly broader (6-12.5 cm long, 3-5 cm wide), slightly arching spathe (arching $< 45^{\circ}$ angle) with the margins hardly or slightly overlapping at base at anthesis. The inner surface is violet-purple with a whitish area 0.5 cm high around the spadix at the base. The peduncle is 0-5 cm long above ground level, and the cataphyll is often longer than the peduncle and surpassing the base of the spathe. Berries have 3 seeds that are 0.4-0.7 cm in diameter, convex on both sides with a continuous dorsal ridge. In addition, the tuber usually has only a few tubercles at the apex. The species is known from northern Brazil, French Guiana, and Surinam. In contrast, D. asperum differs from D. polyphyllum in having a spathe 13-20 cm long, 3-5 cm wide, often arching 45°-90° at the apex and which is strongly hooded with the margins

broadly overlapping in the lower half at anthesis, often completely covering the spadix. The inner surface is purple to purplish red with a whitish area 1–2 cm high at base. The peduncle is 14–45 cm long above the ground and the cataphyll is much shorter than the peduncle, never reaching the base of the spathe. The seeds are 1 to 2 (rarely 3) per berry and 0.5–0.7 cm in diameter and are strongly depressed on both sides with a strongly interrupted dorsal ridge. The tuber often has many tubercles at the apex.

About 10 years after the discovery of Dracontium asperum, a plant corresponding to D. asperum was redescribed as D. elatum by Masters (1870), based on a cultivated specimen from William Bull's horticultural establishment in Chelsea, England. In the protologue, the origin of the plant was mistakenly referred to as tropical West Africa, where this strictly Neotropical genus does not occur. This plant was believed by Masters to have been introduced into England from Guyana by the British. It is very likely that the plant was distributed by J. J. Linden, a plant importer and dealer in Brussels, since a fertile specimen (Sanders 1920, K) identified as D. elatum was prepared later in 1870 from a plant cultivated at Sanders's nursery and obtained from Linden under the name "Sauromatum asperum," a name mistakenly used for D. asperum. This collection, Sanders 1920 (K), is designated here as the lectotype of D. elatum because no material exists from the living collections cultivated by Bull and because the specimen is believed to be from the same living plant. Thus, the specimen prepared by Saunders is preferable to the cited figure 58 in the protologue.

Ten years after the discovery of *Dracontium asperum*, another collection of this species was made by W. W. E. Im Thurn at Pomeroonon on the Guyana side of the Corentyne River near the Atlantic Coast and was subsequently redescribed by J. D. Hooker as *D. foecundum* in 1885.

Additional specimens examined. BRAZIL. Amazonas: Yanomami, Rio Demini, Watoriketheri, below Serra Demini, Milliken 1717 (K, MO). DOMINICAN REPUB-LIC. Duarte: Caño Azul, Villa Rita, Liogier 19363 (NY). Essequibo: Kuyuwini River, 150 mi. from mouth, Smith 3029 (F, GH, K, NY, U, US). PUERTO RICO. Río Abajo State Forest, ca. 0.7 km due S of Camp Radley, Proctor 46104 (SJ); SW of Vega, Baja Rd. 155, km 53, Woodbury s.n. (NY); San Juan, Barrio Aibonito, Guajataca Rec. area, 0.4-0.9 km SW of Rd. 437 & Rd. 113, Proctor 46460 (SJ), G. Zhu 1445, (MO); Río Tudras, Forest Station, Britton & Britton 10060 (NY). Locality unknown: Demerara River, Jenman 6895 (NY); Wullschlägel 1096 (BR). National District: El Enjuagodor, Jimenez 3420 (US). GUY-ANA. Sierra de Luquillo: Barrio Mameyes, 0.9 km due SSE of La Vega, Proctor 47976 (SJ). SURINAM. Brokopondo: 2.4 km S of Gansee, Feroe Creek, Donselarr 1159 (U). Commewijne: Florschutz & Maas 3162 (NY, U). Nickerie: Zuid River, 2 km above mouth of Lucie River, Irwin et al. 55749 (NY). TRINIDAD & TOBAGO. Trinidad: Buenos Aires, Frin, Broadway 7455 (NY); Cumuto Rd., Kalloo & Gonzales 1358 (TRIN); Manzanilla to Mayaro Rd. at mi. 25, Johnson 243 (TRIN); Nestles Milk Factory, Barnes s.n. (TRIN 18584); Orange Grove, Churchill Roosevelt Hwy., Boos s.n. (TRIN 31296).

Cultivated plants. Guyana: Orealla, left bank of Corentyne River, cult. Royal Botanical Gardens at Kew, Great Britain, Im Thurn s.n. (K), Jenman 491 (K); originally from Leiden Botanical Garden, hort. Saunders, Saunders 1920 (K). Trinidad: cult. Botanic Gardens of St. Avis, Florida, U.S.A., Broadway 5212 (F); originally collected at Orange Grove Estates in Trinidad by J. Boos, 1988, cult. at Royal Botanical Gardens at Kew, Great Britain, G. Zhu 1442, 1444, 1479, 1497, 1515 (MO); collected by H. Boos, Mar. 1993, G. Zhu 1484 (MO); Port of Spain, collected by H. Boos, G. Zhu 1509 (MO). Puerto Rico: cult. Washington, D.C., Barret s.n. (US).

 Dracontium bogneri G. Zhu & Croat, sp. nov. TYPE: Brazil. Goiás: Rio Sobrado, bei der Brücke, cultivated at München Botanical Garden, 1994, *J. Bogner 2097* (holotype, MO-04633684!; isotype, MO-04633683!, RJ!). Figure 8.

Petiolus 1–2 m longus; lamina 50–62 cm longa, 40–50 cm lata; pedunculus subterraneanus, 0–1.5 cm longus; spatha 2.9–7.3 cm longa, 1.4–2.8 cm lata; extus brunneola; intus velutina, purpurea; spadix 1.2–2 cm longus, 0.5–0.7 cm diam.; baccae subglobosae, usque 0.8 cm diam.; semina brunneola, usque 0.5–0.6 cm diam.

Tuber hemispherical, 8 cm diam., 5 cm thick, flat or slightly sunken above, rounded and whitish to pinkish below, 25-30 cm below ground level; tubercles few, rounded or obovoid, 0.6-1.2 cm diam., borne around the periphery of tuber; roots 0.3 cm diam., white, sometimes tinged pink near the base; *cataphylls* 1, 24–25 \times 2–4 cm, pink, reaching or surpassing ground level. Leaves solitary; petioles 1-2 m long above ground, 1.2-2 cm diam. at midpoint, brownish green, contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, usually with spiny projections; juvenile blade sagittate, or sagittately lobed; mature blades spreading horizontally, 0.5-1 m diam., papyraceous, rarely fenestrate, never variegated, without raphide cells or dark markings, semiglossy and medium green above, semiglossy and medium green below; middle division twice trichotomously branched, 50-62 cm long, 40-50 cm wide, with terminal subdivision consisting of 3 sections, with each basal subdivision consisting of many segments; lateral divisions twice dichotomously branched, $0.5-0.6 \times 0.4-0.5$ cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and



Figure 8. A–D, *Dracontium bogneri*. A–C. Photos by J. Bogner from type, *Bogner 2097*. —A. Flowering plant with tuber and inflorescence. —B. Spathe cut away to expose the interior of the spathe and the spadix at anthesis. —C. Leaf blade. —D. Seeds in side view (*Irwin et al. 34730*).



Figure 9. A–D, *Dracontium croatii.* —A. Inflorescence of live type plant voucher at anthesis (*Croat 72368*). —B. Spathe with one side removed to expose interior and spadix at anthesis. —C. Close-up of infructescence. —D. Seeds in side view (from *Dodson & Fallen 7762*).

subterminal sections free, each usually consisting of a single segment; leaf segments often entire or bilobed, broadly oblanceolate, more than 5 cm wide on each side of the major ribs, ovate-oblong and lanceolate, mostly free from each other in each division, often with contrastingly smaller rounded or triangular segments alternating with larger segments; apices acuminate, or caudate; ultimate segments 12-15 cm long, often confluent with penultimate segments; other segments 5-8 cm long; penultimate segments free from subterminal sections; medial segments confluent with the basal subdivisions; basal segments present, free from each other; rachises patterned distinct from petiole, pale green, tinged brown or similar to petiole but in much paler shades, smooth; tertiary veins prominent above and weakly raised below; bracteole 1, $1.8-6 \times 1.2-2.4$ cm, dark brown, the longest one longer than the peduncle, covering up to 1/3 of the spathe. Inflorescence solitary, appearing before new leaf; peduncle 0-1.5 cm long above ground, 0.3-0.6 cm diam. at midpoint, often almost completely subterranean, scarcely mottled, brownish green, smooth; spathe 2.0-7.3 cm long, 1.4-2.8 cm wide, cymbiform, cucullate, arching to 45°, apex acuminate; inner surface covered with dense, translucent scales 1-2 mm long, purple-red and olive-brown, with translucent area obscure; outer surface olivebrown, semiglossy or matte; margins entire, broadly overlapping at the base; veins obscure inside and raised outside, conspicuously darker or paler than the spathe, brown; *spadix* exposed (\pm) , stipitate, cylindric, light brown or brown, $1.2-2 \times 0.5-0.7$ cm at anthesis, never with appendages at apex; stipe $0.2-0.4 \times 0.3-0.6$ cm at anthesis, light brown or brown. Flower tepals 4 or 5, 1.5-2 mm long, 1 mm wide, light brown; stamens (7)8 or 9; filaments 0.3-3.5 mm long; anthers 0.8-1 mm long, completely exserted; ovary bilocular, pale green; stigma 4-lobed; style 1-1.5 mm long above tepals, greenish, persistent. Infructescence with spadix 5.5×2.8 cm in fruit; berries 4-seeded, 0.8 cm diam., 1 cm thick, subglobose, 3- to 6-angular, apically subtruncate; young berry light green, without reddish dots and raphide cells; mature berry yellowish orange; seeds 0.5–0.6 \times 0.5–0.6 cm, reniform, light brown, laterally depressed; dorsal ridges obvious, $3, \pm$ continuous, more than 1 mm thick, finely decorated with small cells on both sides.

Phenology. Flowering in November; mature fruits in January.

Distribution and habitat. Dracontium bogneri is endemic to Brazil in Goiás and adjacent areas in the states of Mato Grosso do Sul and Pará. It occurs in Premontane moist forest (P-mf) and Tropical montane wet forest (TM-wf) life zones, at elevations of 300 to 1000 m.

Discussion. Dracontium bogneri has the smallest spathes in the genus, as small as 2 cm long and 1.4 cm wide. It is characterized by having a completely subterranean peduncle and the inner spathe surface covered with translucent scales. It is superficially close to D. ulei in having an almost completely subterranean peduncle, but that species differs in having laterally convex, smooth seeds (vs. laterally depressed, finely decorated seeds for D. bogneri). This species is named in honor of Josef Bogner, of the Munich Botanical Garden, who independently recognized this taxon as an undescribed species at the time that he collected it. He is one of the foremost aroid specialists in the world, whose significant aroid collections from South America include the type specimen of this species.

Paratypes. BRAZIL. **Goiás:** 14 km S of Niquelândia, 14°25'S, 48°20'W, 1000 m, *H. S. Irwin et al.* 34730 (NY). **Minas Cerais:** Municipo de Itaberiera, road from Itaberiera to Claudio, then side road to Serranha, 900 m, 8°58'S, 72°47'W, in shade of seasonally dry woods, 2 Feb. 1993, *G. Zhu* 1510 (MO) [originally collected, A. Meerow et al.]. *Cultivated plante* Brazil Paré Compaigned of the seasonal of the se

Cultivated plants. Brazil. Pará, Conceição do Araguaia, 20 km W of Redenção, cult. by Allen Fernández, South Miami, Florida, U.S.A., *T. Plowman 12043* (F).

 Dracontium croatii G. Zhu, Novon 5: 301. 1995. TYPE: Ecuador. Lita-San Lorenzo, 15.5 km W of Lita, San Lorenzo Cantón, Esmeraldas, 0°55'N, 78°28'W, 705 m, G. Zhu 1493 (holotype, MO!). [Originally collected, T. B. Croat 72368 (MO), cult. at MBG.] Figures 2B, 9.

Tuber hemispherical, 8-11 cm diam., 6.5 cm thick, flat above, rounded and whitish to brownish below, 4–30 cm below ground level; tubercles few, rounded or cylindrically elongated, 0.5-1 cm diam., 1-2.3 cm long, borne around the periphery of tuber; roots whitish, 2-4 mm diam.; cataphylls 3 to 5, 5–45 \times 3–5 cm, dark brown or pink, 5–15 cm long above ground. Leaves solitary; petioles 1.4-3 m long above ground, 2-4.5 cm diam. at midpoint, dark green or brownish green, contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, usually smooth in upper half and with irregular protuberances in lower half; juvenile blade sagittate, or sagittately lobed; mature blades spreading horizontally, 1-1.5 m diam., thinly coriaceous, rarely fenestrate, never variegated, without raphide cells or dark markings with abundant raphide cells, semiglossy and dark green above to matte and medium green above, semiglos-

sy and medium green below to matte and medium green below; middle division twice trichotomously branched, $0.8-1 \times 0.5-0.8$ cm, with terminal subdivision consisting of 3 sections, with each basal subdivision consisting of many segments; lateral divisions twice dichotomously branched, 0.8–0.95 \times 0.5-0.8 cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections confluent, each consisting of many segments; broadly oblanceolate, more than 5 cm wide on each side of the major ribs, oblanceolate, mostly confluent with each other in each division or at least some of the basal segments free from each other, often with contrastingly smaller rounded or triangular segments alternating with larger segments; apices acuminate, or rarely acute; ultimate segments 20 cm long, confluent with penultimate segments; other segments 3.5-15 cm long; penultimate segments confluent with the subterminal sections; medial segments confluent with the basal subdivisions; basal segments present, free from each other or rarely confluent with each other; rachises patterned similar to petiole but in much paler shades, with irregular protuberances; tertiary veins prominent and conspicuous above; bracteoles 3 or 4, $20 \times 2-$ 4 cm, light or dark brown, the longest one much shorter than the peduncle, confined at the base of the peduncle. Inflorescence solitary, appearing before new leaf; peduncle 80-120 cm long above ground, 1.3-3.5 cm diam. at midpoint, more than half as long as the petiole, mottled similar to petiole but deeper in color, brownish green, with irregular protuberances in lower half and spiny projections; spathe 23-50 cm long, 8-15 cm wide, cymbiform, cucullate, erect or slightly arching, apex obtuse; inner surface velvety, maroon and solid greenish white (4-6 cm along the margin), with translucent area obvious, 3-7 cm high, 1.5 to 3 times longer than spadix; outer surface dark yellowish green, matte; margins entire, broadly overlapping in the lower two-thirds; veins obscure inside, conspicuously darker or paler than the spathe, purple and pale green (on lower half); spadix hidden, sessile, cylindric, narrower at apex, purple, 1.8-6.5 cm long, 0.7-1.5 cm diam. at anthesis, never with appendages at apex. Flower tepals (6)7 or 8(9), 1.8- $2.2 \times 1-2$ mm, brown-purple or dark purple; stamens 6 to 9; filaments 1.5-2 mm long; anthers 1-1.5 mm long, hidden or slightly exserted; ovary bilocular, pale green; stigma 2-lobed, or rarely 3lobed; style 1-1.2 mm long above tepals, purple, persistent. Infructescence with spadix 6-12 cm long, 3.4-5 cm diam. in fruit; berries 2-seeded, 1-1.8 cm diam., globose, apically rounded; young berry light

green; mature berry orange, with or without some reddish dots or raphide cells; *seeds* 0.8–1 cm diam., rounded, reddish brown, laterally depressed; dorsal ridges obvious, more than 3, strongly interrupted, monomorphic, more than 1 mm thick, 1–2 mm high, smooth on both sides.

Phenology. Flowering from November to February; mature fruits from February to July.

Distribution and habitat. Dracontium croatii is known only from the western slopes of the Andes in Ecuador; it may also occur in adjacent areas in Colombia. It occurs in *Premontane wet forest* (P-wf) and *Tropical montane moist forest* (TM-mf) life zones (Holdridge et al., 1971), at elevations of 450 to 1000 m.

Local names. "Papayuëla" (Barfod 41597, MO).

Discussion. Morphologically, D. croatii does not appear to be particularly close to any member of the genus. It is readily distinguished by its showy greenish spathe that is unique in Dracontium, by the matte upper leaf-blade surface (typically semiglossy elsewhere), and globose mature fruits and seeds that are up to 1 cm in diameter, the largest in the genus.

This species was named in honor of Thomas B. Croat of the Missouri Botanical Garden, who served as the chairman for the first author's dissertation committee and laid the foundation of this work through his collections of both herbarium specimens and photographic materials.

Additional specimens examined. ECUADOR. Carchi: For. Res., Awá Ethnic Reserve, Hoover et al. 3279 (QCA); San Marcos-Tobar Donoso, Barfod 41597 (AAU, MO, QCA). Pichincha: bridge over Río Chiguilpe near jct. w Río Baba, 7 km from jct. of entrance rd. at 7 km from Santo Domingo on hwy. to Quevedo, Dodson 5951 (SEL); La Centinela, at crest of Montañas de Ila on rd. 12 km from Patricia Pilar to 24 de Mayo, Dodson & Fallen 7762 (MO, QCNE, SEL); La Centinela, 13 km E of Santo Domingo-Quevedo Hwy. in Patricia Pilar, Croat 73040 (MO, QCNE).

Cultivated plants. Ecuador. Cult. by Dewey Fisk, Florida, U.S.A., G. Zhu 1508 (MO); cult. Marie Selby Botanical Gardens (75-461, vouchered by Dodson 5951), Christenson 1576 (SEL), Madison 4140 (SEL); Marie Selby Botanical Gardens (78-2173), Dodson 7288 (SEL), Christenson 1154 (SEL), Croat 71798 (MO), Plowman 10926 (F), G. Zhu 1453 (MO); cult. MBG (vouchered by Croat 72368), G. Zhu 1459, 1518 (MO); received from the Marie Selby Botanical Gardens (78-2173, vouchered by Dodson 7288), G. Zhu 1453, 1495 (MO).

 Dracontium dubium Kunth, Ind. Sem. Hort. Berol. 1844: 283. 1844. *Echidnium dubium* (Kunth) Engl., Pflanzenr. 4, fam. 23C: 38. 1911. TYPE: Pl. 88 in Schott, Gen. Aroid., 1858: 88 (neotype, designated by Zhu, Boos & Croat (1998: 102)); Venezuela. Carabobo: Caño Paso Ancho, ca. 6 km S of Valencia, near El Paito, *G. S. Bunting 3677B* (epitype, designated by Zhu, Boos & Croat (1998: 102), MY!; isotypes, MO!, NY!). Figure 10.

Dracontium changuango G. S. Bunting, Phytologia 60: 302. 1986. TYPE: Venezuela. Carabobo: Caño Paso Ancho, ca. 6 km S of Valencia, near El Paito, 22 Jan. 1968, G. S. Bunting & Trujillo 2856 (holotype, MY!; isotypes, MO!, NY!).

Tuber hemispherical, 5–17 cm diam., 6–9 cm thick, flat above, rounded and whitish to brown below, 3-36 cm below ground level; tubercles few, rounded or cylindrically elongated, 0.5-0.9 cm diam., 0.5–1.5 cm long, borne around the periphery of the tuber; roots whitish, 1-2 mm diam.; cataphylls 2 or 3, 3-36 \times 1.5-8 cm, pink to light brown, reaching or surpassing ground level. Leaves solitary; petioles 1-2.4 m long above ground, 2-4 cm diam. at midpoint, dark green or tinged brown, contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, smooth or sometimes with spiny projections; juvenile blade sagittate, or sagittately lobed; mature blades spreading horizontally, 1-1.2 m diam., subcoriaceous papyraceous, rarely fenestrate, never variegated, sometimes with abundant dark markings, semiglossy and dark green above, matte and medium green below; *middle division* twice trichotomously branched, $50-72 \times 45-75$ cm, with terminal subdivision consisting of 3 sections, with each basal subdivision consisting of many segments; lateral divisions twice dichotomously branched, 50–70 \times 47-73 cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections confluent or free, each usually consisting of a single segment or a few segments or rarely each consisting of many segments; leaf segments bilobed, broadly oblanceolate, more than 5 cm wide on each side of the major ribs, orbicular-ovate, at least some of the basal segments free, often with contrastingly smaller rounded or triangular segments alternating with larger segments; apices acuminate, or acute; ultimate segments 9-20 cm long, free from penultimate segments; other segments 10-20 cm long; penultimate segments confluent with the subterminal sections; medial segments confluent with the basal subdivisions; basal segments present, free from each other; rachises patterned distinct from petiole, pale green or distinct from petiole, pale green, tinged brown, with irregular protuberances; tertiary veins obscure above and conspicuous below; bracteoles 1 or 2, 5–15(37) \times 1.5–2 cm, white to pink (at apex), the longest one longer than the peduncle, covering up to ¹/₃ of the spathe. Inflorescence solitary or sometimes two, appearing before new leaf; peduncle 3-36 cm long above ground, 0.5-1 cm diam. at midpoint, often almost completely subterranean (to a few cm above ground level), mottled similar to petiole but lighter in color, white tinged pink, smooth; spathe 4-15 cm long, 2-5 cm wide, noncymbiform, broadened at a certain point and differentiated into a proximal tube and a distal lamina (blade), non-cucullate or cucullate (slightly), arching to 45°, apex acuminate; $1-4 \times 1.8-3.5$ cm at widest point; lamina 2 or 3 times longer than the tube; inner surface covered with dense, translucent scales 1-2 mm long, olive-brown or red-purple, with translucent area obscure; outer surface maroon, matte; margins entire, broadly overlapping in the lower third; veins obscure inside and outside, similar to the spathe in color; spadix exposed (often extending above the spathe tube), stipitate, cylindric, brownish purple, $1.2-4.2 \times 0.5-1.3$ cm at anthesis, often with several appendages at apex, 0.2–0.5 cm long when present; stipe 0.2–0.8 \times 0.4-0.5 cm at anthesis. Flower tepals 6 or 7, 1-2 mm long, 0.5-1 mm wide, brown-purple; stamens 6 or 7; filaments 0.5-1.5 mm long; anthers 0.8-1 mm long, slightly exserted; ovary bilocular or 3- to 5-locular, pale green; stigma 3-lobed, or 4-lobed; style 0.2-0.5 mm long above tepals, greenish, not persistent. Infructescence with spadix 4–6.5(10) \times 2.6-3.5 cm in fruit, berries (1)3- or 4(5)-seeded, 1-1.5 cm diam., 1.2-1.7 cm thick, subglobose, 3- to 6-angular, apically truncate; young berries dark green; mature berries orange (or yellow), with or without some reddish dots or raphide cells, seeds 0.8-1 cm long, 0.5-0.7 cm diam., elongated or rounded, red-brown, laterally flattened; dorsal ridges obvious, more than 3, strongly to slightly interrupted, monomorphic, less than 0.5 mm thick, 0.8-1 mm high, smooth on both sides. Chromosome number 2n = 26 (Aristeguieta 12734; Petersen, 1989).

Phenology. Flowering from late January to April; mature fruits from May to July.

Distribution and habitat. Dracontium dubium ranges from the Amazon basin to the Atlantic coast in Venezuela and is expected to be found in adjacent areas in Colombia and Guyana. It occurs in the *Tropical moist forest* (T-mf) life zone (Holdridge et al., 1971), at elevations of 80 to 500 m.

Local names. "Changuango" (Bunting 4432, MY); "cuma pan" (Liesner & González 5773, MO). Discussion. Dracontium dubium is character-



Figure 10. A–D, Dracontium dubium. —A. Leaf of cultivated plant at Munich Botanical Garden (Aristeguieta 12734). —B. Seeds in various positions (Huber 1826). —C. Inflorescence at anthesis (Aristeguieta 12734). —D. Type specimen of D. changuango G. S. Bunting (Bunting & Trujillo 2856).

ized by having the inner surface of the spathe covered with dense, translucent scales (1–2 mm long) and a spadix that often has apical appendages. *Dracontium purdieanum* is very similar in terms of its leaf, the relatively short inflorescences, the noncucultate spathe, and the occasional presence of appendages on the end of the spadix; it differs in having usually shorter peduncles (less than 5 cm above the soil) and in having seeds with three continuous ridges to 0.5 mm high.

Dracontium dubium Kunth was first collected by Richard Schomburgk during an expedition to British Guiana (Guyana) in 1840-1844 at the base of Mt. Curassawaka of the Kanuku Mountains, south of Nappi, and several living tubers were sent to the Botanical Garden of Berlin in 1843 (Roth, 1922: 387-388; 1923: 103). One plant bloomed in the Garden and was described by Kunth in the following year (Kunth, 1844). Schott (1860: 481) noted that there were fertile collections of this species at the Berlin Herbarium (B). However, no specimen of D. dubium was seen by Engler (in 1911: 39), who only cited "Bluehte im Bot. Garten zu Berlin Sept. 1844" (flowered in Berlin Botanical Garden in September 1844) under the species. Schott (1860) might very likely have only seen live specimens of the species since at Kunth's time, garden plants were often described and illustrated without preparing herbarium specimens (Paul Hiepko, pers. comm.). Kunth had apparently made a drawing of the inflorescences and some floral details of the species, which was deposited in the Berlin herbarium (Engler, 1911: 38, fig. 14A-F). More than a decade after the discovery of D. dubium, Schott (1857b), based on unspecified ovary and stigma details of the species, described the new genus Echidnium, giving the single species a new name, E. schomburgkii. In the following year, Schott (1858b: pl. 88) published a plate that included the inflorescence and floral details of this species under the name E. schomburgkii, which copied Kunth's drawing adding an inflorescence at anthesis and other floral details. Later, when he published the first comprehensive classification of the Araceae, Schott (1860) accepted the name E. schomburgkii, citing D. dubium as a synonym. Under contemporary rules of the ICBN (Greuter et al., 2000), E. schomburgkii is a superfluous name, since Schott should have used the name E. dubium for the transfer. Engler (1911) rectified this situation by publishing the combination E. dubium (Kunth) Engl.

Echidnium is ostensibly distinguished from *Dracontium* by having a unilocular ovary with two ovules (Schott, 1857b), as opposed to a bi- or plurilocular ovary in *Dracontium*. However, these

characters have been shown to be either spurious (Zhu, 1995) or not to be good generic characters in this group (Bogner, 1985; Hay, 1988; Zhu, 1996). The two plates originated from the typical material of D. dubium (Genera aroidearum, pl. 88, Schott, 1858b; Das Pflanzenreich, 4 (23C): p. 38, fig. 14A-F, Engler, 1911) clearly demonstrated a plant of at least two locules. Schott's statement of a unilocular ovary was evidently erroneous based on his own illustration. Zhu (1995, 1996) noted that unilocular ovaries do not occur in Dracontium and this genus never has more than one ovule in each locule; these stand as generic traits of the genus. Therefore, Echidnium was accepted as a synonym of Dracontium, and D. dubium is the accepted name for the treated species (Zhu et al., 1998).

Additional specimens examined. VENEZUELA. Amazonas: alrededores de San Juan de Manapiare, Girardi 16 (VEN); Atabapo, Canaripo, lower Río Ventuari, 20 km E of confluence w Río Orinoco, Huber 1826 (MO); Santa Bárbara del Orinoco, near confluence of Río Orinoco and Río Ventuari, Stevermark et al. 117171 (MO, VEN); Atures, Isla Castillito-San Fernando de Atabapo on Río Orinoco, outskirts of Siquita, Bunting 3677A (MY, NY); Caño Wedidi, upper Río Ventuari, Lister 461 (K). Apure: Río Orinoco to Piedra La Villa, opposite Raudal Marimare, Wurdack & Monochino 41392 (NY). Barinas: Res. For. Caparo, 26 km E of El Cantón, Meier 435 (VEN). Bolívar: 1 km N of Paragua, Liesner & González 5773 (MO, VEN); 1 km S of Quebrada La Flore, tributary Río Parguaza, Stevermark et al. 131647 (MO). Carabobo: Caño Paso Ancho, 5-6 km S of Valencia on rd. to El Paito, Bunting & Trujillo 2856 (MO, MY, NY). Cojedes: Quebrada Chumeo, Fundo La Leona, Delascio 6818 (VEN). Guárico: Río Orituco, S of Calabozo, Castillo 260 (VEN); Calabozo, Aristeguieta 5381 (VEN). Portuguesa: Guanare, Fundo "El Chaparral," 16 km NW of Guanaré, Aymard & Stergios 3807 (MO, PORT, VEN); Río María, NE of Boca de Monte, 28-32 km NNE of Guanaré, Steyermark et al. 127097 (MO, PORT, VEN); Río Tucupido, Rodriguez 158 (MY); Turen, Esta. de Silvicultura, Ortega & Aristeguieta 1554 (MO, PORT); Pozo Blanco, Est. Biol., Ortega 748 (MO, PORT).

Cultivated plants. Venezuela. Portuguesa, Turén (Villa Bruzual), cult. Munich Botanical Garden, Germany, Aristeguieta 12734 (M); Amazonas, Atures, Aragua, Maracay, along the Río Orinoco, collected by G. S. Bunting, Bunting 3677A, Bunting 3677B (NY).

 Dracontium gigas (Seem.) Engl., Monogr. Phan. 2: 284. 1879. Godwinia gigas Seem., J. Bot. 7: 313. t. 96, 97. 1869. TYPE: Fig. 1 in J. Bot. 7: t. 96 & 97, 1869 (lectotype, designated by Zhu (1994a: 407)); Nicaragua. Chontales: betw. Javalí Gold Mine & Quebrada de Las Lajas, 19 Mar. 1884, Brown s.n. (epitype, designated by Zhu (1994b: 407), K!). [Cult. at K, originally collected by B. Seemann.] Figures 2C, 11, 14D.

Tuber hemispherical, up to 20 cm diam., 12 cm



Figure 11. A–D, *Dracontium gigas.* —A. Plant in natural habitat at La Selva in Costa Rica (photo by G. G. Dimijian). —B. Flowering plant at anthesis with M. H. Grayum at La Selva (*Grayum 7911*). —C. Inflorescence at anthesis showing interior of spathe with spadix at anthesis. —D. Seed showing side view (*Beach 1490*).

thick, flat above, rounded and white to brown below, 5-60 cm below ground level; tubercles few, cylindrically elongated, $0.5-1 \times 1-2$ cm, borne around the periphery of tuber; roots 0.4 cm diam., white; cataphylls 4 to 7, up to 40 cm long (to 5 cm long above ground level), 4-10 cm wide, pink to light brown (when dry). Leaves solitary or sometimes two or more per tuber; petioles up to 3.4 m long above ground, up to 9.5 cm diam. at midpoint, dark green, contrastingly mottled with dirty white or pale green blotches, usually smooth in upper half and with irregular protuberances in lower half; juvenile blade sagittate, or sagittately lobed; mature blades spreading horizontally, 1.5-2.5 m diam., subcoriaceous, rarely fenestrate, never variegated, without raphide cells or dark markings, glossy and medium green above, semiglossy and medium green below; middle division 3 times or more trichotomously branched, 1.4×1.8 cm, with terminal subdivision consisting of 3 sections, with each basal subdivision consisting of many segments; lateral divisions 3 times or more dichotomously branched, 1.3×1.6 cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections confluent, each consisting of many segments; leaf segments often bilobed or rarely trilobed, oblanceolate or triangular, mostly confluent with each other in each division, often with contrastingly smaller rounded or triangular segments alternating with larger segments; apices often caudate, or sometimes acute; ultimate segments 10-16(-20) cm long, confluent with penultimate segments; other segments 10-20 cm long; penultimate segments confluent with the subterminal sections; medial segments confluent with the basal subdivisions; basal segments present, confluent with each other; rachises patterned similar to petiole but in much paler shades, smooth; tertiary veins conspicuous above and obscure below; bracteoles 3 or 4, 10-60 \times (sometimes 5-10 cm above ground level) 4-6 cm, light brown, the longest one much shorter than the peduncle, confined at the base of the peduncle. Inflorescence solitary, appearing before new leaf; peduncle 30-120 cm long above ground, 3.5-6 cm diam. at midpoint, less than half as long as the petiole, mottled similar to petiole but deeper in color, dark green or brownish green, with irregular protuberances in lower half; spathe 58-78 \times 13-15(-21) cm, cymbiform, cucullate, erect or slightly arching, apex obtuse; inner surface semiglossy, redpurple or purple-red, with a translucent area obvious, 4-6.5 cm high, shorter than spadix; outer surface maroon tinged brown, matte; margins entire, broadly overlapping in the lower two-thirds; veins purple, obscure inside and outside (slightly impressed inside), conspicuously darker or paler than the spathe on top; spadix hidden, sessile or stipitate, cylindric, brown-purple, $9-16 \times 1.5-1.8$ cm at anthesis, never with appendages at apex. Flower tepals 6 to 8(9), 3.5-5 mm long, 1.5-2 mm wide, light brown tinged green; stamens 8 to 17(19); filaments 1-3.5 mm long; anthers 1-1.5 mm long, completely exserted; ovary 3- to 4-locular, pale green; stigma 3-lobed; style 4-6 mm long above tepals, dark purple, persistent. Infructescence with spadix 20-30 cm long, 4-6 cm diam. in fruit; berries often 2-seeded, 1.8×1.5 cm, 4- to 5-angular or globose (rarely), apically truncate; young berry unknown; mature berry orange or purple-brown, with or without some reddish dots or raphide cells; seeds 1-1.2 cm diam., rounded, reddish brown, laterally raised; dorsal ridges obvious, 3, continuous, less than 0.5 mm thick. Chromosome number 2n =26 (Bogner 1267; Petersen, 1989).

Phenology. Flowering from December to April; mature fruits from April to August.

Distribution and habitat. Dracontium gigas ranges from central Nicaragua (Chontales), along the Atlantic slope to central Costa Rica (Heredia, Limón). It occurs in *Tropical moist forest* (T-mf) and *Premontane wet forest* (P-wf) life zones (Holdridge et al., 1971), at elevations of 15 to 100(-450) m.

Discussion. Dracontium gigas has the largest spathes in the genus, ranging from 58 to 78 cm long and 13 to 15(-21) cm wide. It is the most wellknown species horticulturally, especially in Europe. It regularly blooms in European gardens and private nurseries, but has never been reported flowering in gardens of the New World. This species propagates rapidly by means of tubercles. It is also a fast grower, capable of growing a couple of inches in height overnight. It is often a big attraction when it blooms.

Dracontium gigas is easily confused with D. pittieri in sterile condition. The mature leaves of these species are almost identical. However, leaves of D. pittieri tend to have more raphide cells, especially when young, and less leaf tissue along the rachis and at the branching points. The upper half of the petiole is often smooth and unicolored in D. pittieri, while often mottled and with projections in D. gigas. Despite strong vegetative similarities, these two species are distinct in their inflorescence morphology. Dracontium gigas has a large spathe and a short peduncle, which is always less than twice as long as the spathe. Dracontium pittieri has a much longer peduncle, 5 to 8 times longer than the spathe. The spathe of D. gigas is more or less hooded at the apex, with the margins broadly overlapping and completely covering the spadix. The spathe of *D. pittieri* is open at the apex with the margins scarcely overlapping, such that the spadix is exposed. The translucent area at the base of the inner spathe surface extends much higher than the spadix in *D. pittieri*, while it never exceeds the height of the spadix in *D. gigas* (Zhu, 1994a).

Since there is no type designated in the protologue of *Godwinia gigas* Seem., the basionym of *Dracontium gigas* (Seem.) Engl., a plate from the original material, fig. 1 in J. Bot. 7: t. 96 & 97, 1869, was designated as the lectotype of *Godwinia gigas* (Zhu, 1994a). Since this lectotype does not contain enough information to identify *D. gigas* from *D. pittieri*, a fertile specimen prepared by N. E. Brown (*Brown s.n.*, K) was designated as an epitype for *D. gigas* to ensure the accurate application of these names (Zhu, 1994a).

Additional specimens examined. COSTA RICA. Valerio 678 (MO). Alajuela: Canas-Upala, Río Zapote, 1.8-5 km S of Río Canalete, Burger & Baker 9999 (F, MO, US); San Carlos, Roig 11 (CR, F). Heredia: Braulio Carrillo, Rara Avis, trail El Atajo and Catarata, G. Zhu 1154 (MO); La Selva, Beach 1490 (DUKE, MO); Río Sarapiquí at Chilamate, Croat 68381 (B, M, MO); Sarapiquí, near Puerto Viejo, Valerio 24 (USJ), 15 Aug. 1993, G. Zhu 1519 (MO). Limón: 10 km NW of Guápiles, Gómez 18513 (MO); Río Reventazón below Cairo, Standley & Valerio 48885 (US): Hacienda Tapezco-Hda., La Suerte, 29 air km W of Tortuguero, Davidson 8624 (MO, RSA); Siquirres, Dodge 5622 (F); Bataau, Lehmann 246619 (CR). NIC-ARAGUA. Chontales: received from Mr. Fitch in spirits (on sheet #6 of Brown s.n., 30 Dec. 1878), Bull s.n. (K). Río San Juan: Caño Chontaleño, 20 km NE of El Castillo, Neill & Vincelli 3512 (MO); Res. Indio-Maiz, San Juan del Norte, Río Indio, Rueda et al. 8615 (MO); El Castillo, Sábalos, comarca Las Maravillas, Rueda et al. 2869 (MO), 5225 (MO). Zelava: Cerro Saslava-San José Hormiguero, Caño Sucio-Loma Mollejones, Stevens 7007 (M, MO); Stawas, 1 km N of Río Grande de Matagalpa, 8 km N of La Cruz, Neill 4336 (MO); drainage of Ríos Punta Gorda, Alemán and Zapote, Shank & Molina 4953 (GH, US); É of comarca del Salto del León, Rueda et al. 3390 (MO); Mun. Nueva Guina, Res. Indio-Maiz, Rueda et al. 10190 (MO); este del poblado de Nueva Atlanta, Rueda et al. 3295 (MO).

Cultivated plants. Nicaragua. Cult. at Berlin Botanical Garden, Germany, Anonymous s.n. (M); Chontales, originally collected by Seemann, W. Bull's establishment, between the Javalí Gold Mine and the Quebrada de Los Lajas, cult. Royal Botanical Gardens at Kew, Great Britain, Brown s.n. (GH, K), Brown s.n. (GH), Brown s.n. (K). Costa Rica. Limón, originally collected by M. Birdsey, cult. at Robert and Catherine Wilson Botanical Garden at Las Cruces, G. Zhu 1156 (MO); originally collected by Clarence Horich, Alajuela, between San Carlos & San Pedro Cutris, cult. at Munich Botanical Garden, Bogner 1267 (M); originally collected by John Banta, Llanuras de San Carlos, betw. Vasconia and San Pedro Cutris, cult. MBG, Croat 71840 (MO), vouchered by G. Zhu 1156, 1517 (MO); vouchered by *G. Zhu* 1159, 1467 (MO); vouchered by *Croat* 68381, *G. Zhu* 1481 (B, M, MO).

9. Dracontium grandispathum G. Zhu & Croat, sp. nov. TYPE: Ecuador. Napo: Cañon de los Monos, 15 km N of Coca near Río Coca, Hacienda of Hector Noboa, 0°20'S, 77°01'W, 250 m, 9 Apr. 1985, W. Palacios, D. Neill, M. Baker & J. Zaruma 311 (holotype, MO!). Figure 12.

Petiolus 1.25–2.75 m longus; lamina 55–75 cm longa, 55–60 cm lata; pedunculus 1–1.35 m longus, 1.5–2 cm diam.; spatha 45–50 cm longa, 10–15 cm lata, cucullata basi; extus impolita, olivacea; intus velutina, purpurea; spadix 3–5.5 cm longus, 0.5–1 cm diam.; tepala 5–6; semina rubra, 0.6–0.7 diam.

Tuber hemispherical, 10-18 cm diam., 6-10 cm thick, flat above, rounded and white to brown below, 12-20 cm below ground level; cataphylls 3 to 4, 12–21 \times 2–3 cm, light brown, reaching or surpassing ground level. Leaves solitary; petioles 1.25-2.75 m long above ground, 2-3.5 cm diam. at midpoint, dark green, contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, usually smooth in upper half and with irregular protuberances in lower half; juvenile blade sagittate, or sagittately lobed; mature blade spreading horizontally, 1-1.2 m diam., subcoriaceous, sometimes fenestrate, never variegated, without raphide cells or dark markings, glossy and medium green above, semiglossy and medium green below; middle division twice trichotomously branched, 55- $75 \times 50-60$ cm, with terminal subdivision consisting of three sections, with each basal subdivision consisting of many segments; lateral divisions twice dichotomously branched, 55–75 \times 55–60 cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections often confluent, each consisting of many segments; leaf segments often entire, broadly oblanceolate, more than 5 cm wide on each side of the major ribs, ovate or lanceolate, mostly free from each other in each division, often without contrastingly smaller rounded or triangular segments; apices acuminate; ultimate segments 25-30 cm long, often free from penultimate segments; other segments 15-20 cm long; penultimate segments free from subterminal sections; medial segments confluent with the basal subdivisions; basal segments present, free from each other; rachises patterned similar to petiole but in much paler shades, smooth; tertiary veins conspicuous above and weakly raised below; bracteoles 3 or 4, $12-22 \times 2-3$ cm, light brown, the longest one much shorter than the peduncle, confined to


Figure 12. A–D, Dracontium grandispathum. A, B. (Croat 75207). —A. Inflorescence, side view. —B. Close-up of inflorescence showing front view of spathe with spadix. —C. (Pinkley 60-B). Immature infructescence. Photo by H. Pinkley. —D. (Cerón & Cerón 3070). Seeds in side view.

the base. Inflorescence solitary, appearing before or after new leaf; peduncle 100-135 cm long above ground, 1.5-2 cm diam. at midpoint, more than half as long as the petiole, mottled similar to petiole but deeper in color, brownish green, smooth or spiny projections; spathe 45–50 \times 10–15 cm, non-cymbiform, constricted at a certain point and differentiated into a proximal tube and a distal lamina (blade), cucullate or non-cucullate, erect or slightly arching, apex acuminate (very broadly); 10–15 \times 10-15 cm at widest point; lamina 2 to 3 times longer than the tube; inner surface semiglossy, maroon or purple-red or olive-brown, with translucent area moderately conspicuous, 12-15 cm high, 1.5 to 3 times longer than spadix; outer surface olive-brown or green or green tinged brown, matte; margins entire, broadly overlapping at the base; veins conspicuous inside and raised outside, conspicuously darker or paler than the spathe, purple; spadix hidden, stipitate, cylindric, pale green or light brown, $3-5.5 \times 1-1.5$ cm at anthesis, never with appendages at apex; stipe $0.5-1 \times 0.5-0.7$ cm at anthesis, light brown or dark purple. Flower tepals 5 to 6, 1-3 mm long, 1-2 mm wide, light brown or purple; stamens 7 to 11; filaments 1-2 mm long; anthers 0.5 mm long, hidden or slightly exserted; ovary 3locular, pale green; stigma unlobed, or 3-lobed; style 0.5-1 mm long above tepals, dark purple, persistent. Infructescence with spadix $12-18 \times 2.5-3.5$ cm in fruit; berries 1- or 2-seeded, 0.5-0.6 cm diam., 0.8-1 cm thick, obliquely obovoid, apically rounded; young berry light green; mature berry orange, without reddish dots and raphide cells; seeds 0.6-0.7 cm diam., rounded, red-brown, laterally flattened; dorsal ridges obvious, 3, often strongly interrupted, with the central ridge contrastingly raised, more than 1 mm thick, 0.1-0.2 mm high, warty along ridges.

Phenology. Flowering from November to May; mature fruits from March to December.

Distribution and habitat. Dracontium grandispathum is known only from Amazonian Ecuador (Morona-Santiago, Napo, and Pastaza). It occurs in Premontane moist forest (P-mf) and Tropical montane moist forest (TM-mf) life zones (Holdridge et al., 1971) at 250 to 1200 m.

Local names. "Nantaymo" (Aulestia 1823, MO); "pitalala para" (Jipa et al. 968, F).

Discussion. Dracontium grandispathum is vegetatively similar to the sympatric D. spruceanum, but differs in having a much a larger (hence, the name grandispathum) and usually hooded spathe $45-50 \times 10-15$ cm versus $20-35 \times 3-6$ cm in D. spruceanum. The spathe of D. grandispathum is often abruptly acuminate apically and that of *D. spruceanum* is gradually acuminate apically.

Paratypes. ECUADOR. Morona-Santiago: Méndez-Morona, km 45-63, Dodson et al. 17756 (MO), Napo: Baeza-Tena, 5 km N of Jondachi, Harling & Andersson 16404 (GB); Narupa-Coca, 18 km E of Narupa, Hammel & Wilder 17283 (MO); Cantón Lago Agrio, Parroquia Dureño, Cofán-Dureno, Cerón & Cerón 3070 (MO, QCA); Dureño. Pinkley 60 (ECON); Cantón Tena, Jatún Sacha, Palacios 4242 (MO); Par. Nac. Yasuní, Carretera Maxus, km 1, Pompeya, Aulestia 1823 (MO, QCNE); Yasuní, Añangu, Luteyn et al. 9021 (MO, QCA); Río Tiputini, NW of confluence of Río Tivacuno, Romoleroux 2110 (QCA), 2135 (QCA), 2360 (QCA), 2649 (QCA); San José de Payamino, 40 km W of Coca, Jipa et al. 968 (F). Pastaza: Montalvo, Río Bobonaza, Løjtnant & Molau 13549 (AAU). Pichincha: Cantón-Santo Domingo de los Colorados, Cerón et al. 29051 (QAP).

Cultivated plants. Ecuador. Napo, Tena, 27 May 1993, collected by Scott Hyndman, vouchered as T. B. Croat 75207 (MO); G. Zhu 7528 (MO); vouchered by Pinkley 60, Pinkley 294 (ECON), cult. at MBG.

 Dracontium grayumianum G. Zhu & Croat, sp. nov. TYPE: Panama. Darién: near Par. Nac. Darién, 4 km NE of Piji Vasal village, trail W of ANCON Agricultural Station, 8°04'N, 77°46'W, 100 m, 27 July 1994, G. Zhu & T. B. Croat 1506 (holotype, MO!; isotypes, B!, F!, GH!, K!, M!, NY!, PMA!, SCZ!, SEL!, UC!, US!). Figures 1D, 2A, 13.

Petiolus 1–2.2 m longus; lamina 0.8–1 cm longa, 0.7–1 cm lata; pedunculus 1–10(–30) cm longus, 1–1.8 cm diam.; spatha (6)9–15 cm longa, 2.5–4 cm lata, cucullata basi; extus impolita, purpurea; intus velutina, purpurea; spadix 2–3.5 cm longus, 0.8–1.3 cm diam.; baccae 1–2 cm diam.; semina brunneola, 0.8–1 cm longus, 0.6–0.7 cm diam.

Tuber hemispherical, 10-18 cm diam., 6-10 cm thick, flat above, rounded and white to brown below, 10-20 cm below ground level; tubercles few, cylindrically elongated, 0.8-1.2 cm diam., 1-3 cm long, borne around the periphery of tuber; roots white to 0.4 cm diam.; cataphylls 3, 10-30 \times 5-8 cm, white or pink and light brown, 5-15 cm long above ground. Leaves solitary; petioles 1-2.2 m long above ground, 2-6 cm diam. at midpoint, dark green, contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, usually smooth in upper half and with irregular protuberances in lower half; juvenile blade sagittate, or sagittately lobed; mature blade spreading horizontally, 1-1.5 m diam., papyraceous, sometimes fenestrate, never variegated, sometimes with abundant raphide cells and dark markings, glossy and dark green above, semiglossy and medium green below; middle division 3 times or more trichotomously branched, $0.8-1 \times 0.7-1$ cm, with terminal



Figure 13. A–D, *Dracontium grayumianum*, type specimen (*G. Zhu & Croat 1506*). —A. Inflorescence at anthesis in side view. —B. Tuber, petiole base, and cluster of immature infructescences. —C. Spadix with mature berries, mostly already fallen. —D. Seeds in side view.

subdivision consisting of 3 sections, with each basal subdivision consisting of many segments; lateral divisions 3 times or more dichotomously branched, $0.85-1 \times 0.7-1.1$ cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections free, each consisting of many segments; leaf segments bilobed, broadly oblanceolate, more than 5 cm wide on each side of the major ribs, lanceolate, mostly free in each division, often with contrastingly smaller rounded or triangular segments alternating with larger segments; apices acuminate, or acute, or caudate (rarely); ultimate segments 12-15 cm long, confluent with penultimate segments (often); other segments 6-16 cm long; penultimate segments free from subterminal sections; medial segments free from basal subdivisions; basal segments present, free from each other; rachises patterned similar to petiole but in much paler shades, with spiny projections; tertiary veins conspicuous above, or weakly raised below; bracteoles 5-15(-35) cm long, 2-3(-5) cm wide, light brown, the longest one longer than the peduncle, covering the basal half or more of the spathe (often). Inflorescences solitary or sometimes two, appearing before new leaf; peduncle 1-10(-30) cm long above ground, 1-1.8 cm diam. at midpoint, often almost completely subterranean, scarcely mottled, whitish tinged pink or gray or whitish green, smooth; spathe $(6-)9-15 \times 2.5-4$ cm, non-cymbiform, constricted at a certain point and differentiated into a proximal tube and a distal lamina (blade), cucullate, arching $45^{\circ}-90^{\circ}$, apex acuminate; $2.5-3 \times 2-3$ cm at widest point; lamina similar to the tube in length, or 3 to 5 times longer than the tube; inner surface semiglossy, maroon, with translucent area obscure; outer surface maroon or olive-brown, matte; margins entire, broadly overlapping at the base; veins obscure inside and raised outside (slightly), conspicuously darker or paler than the spathe, purple; spadix exposed, stipitate, cylindric, brown or purple, $2-3.5 \times 0.8-1.3$ cm at anthesis, sometimes with one to a few appendages at apex, 0.3-0.5 cm long when present; stipe 0.5-2 cm long, 0.5-1.5 cm diam. at anthesis, brown. Flower tepals 5 to 7, 1-4 mm long, 0.5-1 mm wide, light brown; stamens (5)6 to 8; filaments 3 mm long; anthers 1 mm long, slightly exserted; ovary bilocular, pale green; stigma 2-lobed; style 1-2 mm long above tepals, dark purple, persistent. Infructescence with spadix 8-15 cm long, 3.5-5.5 cm diam. in fruit; berries 4-seeded, 1-2 cm diam., 1-1.2 cm thick, narrowly clavate, apically truncate; young berry light green; mature berry orange, with or without some reddish dots or raphide cells; seeds 0.8-1 cm long, 0.6-0.7

cm wide, reniform, light brown, laterally flattened; dorsal ridges obvious, 5 to 6, strongly interrupted, monomorphic, less than 0.5 mm thick, 1.5–2 mm high, smooth on both sides.

Phenology. Flowering from March to April (June); mature fruits from March to August.

Distribution and habitat. Dracontium grayumianum ranges from southern Panama (Darién and San Blas) to the central Pacific coastal region in Colombia (Chocó and Valle). It occurs in the *Tropical wet forest* (T-wf) life zone (Holdridge et al., 1971) at elevations of 5 to 100 m.

Discussion. Dracontium grayumianum is closest in appearance to D. soconuscum, especially in leaf size, shape, and form as well as a similar inflorescence; however, D. soconuscum differs in having seeds with 3 very short (0.1–0.5 mm high), dorsal ridges instead of 5 to 6 strongly interrupted (1.5–2 mm high) dorsal ridges.

The species honors Michael H. Grayum of the Missouri Botanical Garden, an aroid specialist, and one whose familiarity with the many aspects of plant taxonomy helped immeasurably with the completion of this work on *Dracontium*.

Paratypes. COLOMBIA. Chocó: Río Bicordó, above Noanamá, Forero et al. 4718 (COL); Río Cacarica, Romero 6357 (COL); Río San Juan, near Palestina, Forero et al. 3800 (COL); Zona de Urabá, Cerros do Cuchillo, Camino Cuchillo Negro a Cumbre Noroeste rd., Cárdenas 1805 (JAUM). Valle: Chocó region, Río Calima, La Trojita, Cuatrecasas 16474 (F); Finca La Cabaña, camino a la Patricia, Rentería 4314 (JAUM); Finca La Cabaña, Camino al Río León, Rentería 4220 (JAUM). PANAMA. Darién: Piji Vasal, G. Zhu & Croat 1507 (MO); Pinogana, E of El Real, Pittier 6546 (US); Río Chucunaque, Yaviza, Quebrada Barbua, Stern 93 (GH, MO); km 16 to Yaviza along Q Uvital off Río Chucunaque, Duke 5103 (GH, MO). San Blas: Río Cangandí, Pueblo Cangandí, Herrera 252A (MO).

 Dracontium guianense G. Zhu & Croat, sp. nov. TYPE: French Guiana. Haut Oyapock, Ouest de Trois Sauts Crique Euleupousing, Saut Beco, 15 July 1975, *J. de Granville & Cremers 1129* (holotype, CAY!). Figure 14A, B, C.

Petiolus usque 2.5 m longus; lamina 40–50 cm longa, 35–40 cm lata; pedunculus 30–40 cm longus, 0.5 cm diam.; spatha 9–10 cm longa, 4–5 cm lata; extus impolita, purpurea; intus velutina, purpurea; spadix 2.8 cm longus, 0.6 cm diam.; baccae 0.7–1 cm diam.; semina fusca, 0.65 cm diam.

Tuber hemispherical, 10-15 cm below ground



Figure 14. A-C, Dracontium guianense. —A. Holotype specimen, leaf and inflorescence (de Granville & Cremers 1129, CAY). —B. Close-up of inflorescence from de Granville & Cremers 1129 (CAY). —C. Infructescence with mature fruits (Grenand 1277). —D. D. gigas. Leaf of plant at La Selva, Heredia Prov., Costa Rica.

level; petioles 2.5 m long above ground, 1.2 cm diam. at midpoint, dark green, contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, smooth; mature blades 80-100 cm wide, subcoriaceous, rarely fenestrate, never variegated, without raphide cells or dark markings, glossy and dark green above, semiglossy and medium green below; middle division once or twice trichotomously branched, 40–50 \times 35–40 cm, with terminal subdivision never divided into sections, with each basal subdivision consisting of many segments; lateral divisions twice dichotomously branched, 40-45 \times 35-40 cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections free, each consisting of many segments; broadly oblanceolate, more than 5 cm wide on each side of the major ribs, oblanceolate, mostly free from each other in each division, often with contrastingly smaller rounded or triangular segments alternating with larger segments; apices acuminate; ultimate segments 15-17 cm long, free from penultimate segments; other segments 3-15 cm long; penultimate segments free from subterminal sections; medial segments free from basal subdivisions; basal segments present, free from each other; rachises patterned similar to petiole but in much paler shades, smooth; tertiary veins obscure above and weakly raised below; bracteoles 1, 10-15 cm long, 0.5-1 cm wide, light brown, the longest one much shorter than the peduncle, confined at the base of the peduncle. Inflorescence solitary, appearing after new leaf; peduncle 30-40 cm long above ground, 0.5 cm diam. at midpoint, less than half as long as the petiole, mottled similar to petiole but deeper in color, brownish green, smooth; spathe 9–10 \times 4–5 cm, cymbiform, non-cucultate, erect or slightly arching up to 45° angle, apex acuminate; inner surface semiglossy, maroon, with translucent area obscure; outer surface maroon tinged brown, matte; margins entire, hardly overlapping at the base; veins obscure or conspicuous inside, conspicuously darker or paler than the spathe; spadix sessile, cylindric, brown or brown-purple, 2.8×0.6 cm at anthesis, never with appendages at apex. Flower tepals 4 to 5, 2-3 mm long, 1-2 mm wide, light brown; stamens 4 to 6; filaments 2-3 mm long; anthers 0.5 mm long, completely exserted; ovary bilocular, pale green; stigma 2- or 3-lobed; style 0.5 mm long above tepals, green, persistent. Infructescence with spadix 4.3 cm long, 3.2 cm diam. in fruit; berries 2-seeded, 0.7-1 cm diam., 1 cm thick, subglobose, 3- to 6-angular, apically truncate; young berries medium green; mature berries orange, without reddish dots and raphide cells; *seeds* ca. 0.65 cm diam., rounded, dark brown, laterally convex; dorsal ridges obvious, 3, continuous, more than 1 mm thick, 0.1 mm high, finely decorated with small cells (pits) on both sides.

Phenology. Flowering known only in July; mature fruits are known only in May.

Distribution and habitat. Dracontium guianense is known only from the type locality in French Guiana near the border with Brazil (Pará); it will likely be found in Brazil. It occurs in the *Tropical moist forest* (T-mf) life zone (Holdridge et al., 1971) at ca. 100 m.

Local names. "M y kala" (de Granville & Cremers 1129, CAY).

Discussion. Dracontium guianense is very similar to *D. polyphyllum*, but differs in having a much longer peduncle (more than 30 cm above ground level).

Paratypes. FRENCH GUIANA. Haut Oyapock, Ouest de Trois Sauts Crique Euleupousing, saut Beco, 10 May 1996, Grenand 1277 (CAY); Piste de St. Elie, 6 Nov. 1982, Riera 415 (CAY).

 Dracontium longipes Engl., Bot. Jahrb. Syst. 37: 122. 1905. TYPE: Brazil. Acre: Belem at Juruá Miry, 8°S, 72°59'W, Sep. 1901, *E. Ule 5781* (holotype, B!; isotype, B!). Figure 15.

Tuber hemispherical, 10-15 cm diam., 6-10 cm thick, flat or slightly sunken above, rounded and whitish to brownish below, 10-25 cm below ground level; tubercles abundant, borne around the periphery of tuber; roots strong; cataphylls 1 to 3, 10- $25 \times 1-3$ cm, light brown, reaching or surpassing ground level. Leaves solitary; petioles 1-2 m long above ground, 3-4 cm diam. at midpoint, dark green, contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, usually smooth in upper half and with irregular protuberances in lower half; juvenile blade sagittate, or sagittately lobed; mature blades spreading horizontally, 1-1.2 m diam., papyraceous, sometimes fenestrate, never variegated, sometimes with abundant raphide cells, semiglossy and dark green above, matte and medium green below; middle division 3 times or more trichotomously branched, $0.6-0.75 \times 0.5-0.6$ cm, with terminal subdivision consisting of 3 sections, with each basal subdivision consisting of many segments; lateral divisions 3 times or more dichotomously branched, 0.45-0.7 \times 0.5–0.6 cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections



Figure 15. A–D, *Dracontium longipes.* —A. Inflorescence with the lower portion cut away to expose the spadix. —B. Live plant with portion of leaf and infructescence with persistent spathe. —C. Lower portion of spathe cut open showing close-up of spadix (*Croat 85460*). —D. Seeds in side view (*Croat 72368*).

free; leaf segments often entire, broadly oblanceolate, more than 5 cm wide on each side of the major ribs, ovate, mostly free from each other in each division, often with contrastingly smaller rounded or triangular segments alternating with larger segments; apices caudate; ultimate segments 10-15 cm long, confluent with penultimate segments; other segments 9-16 cm long; penultimate segments free from subterminal sections; medial segments free from basal subdivisions; basal segments present, free from each other; rachises patterned similar to petiole but in much paler shades, sometimes with spiny projections; tertiary veins obscure above and weakly raised below; bracteoles 1 or 2, $10-25 \times 1-$ 2 cm, dark brown, the longest one much shorter than the peduncle, confined at the base. Inflorescence solitary, appearing before new leaf; peduncle 60-100 cm long above ground, 1-2 cm diam. at midpoint, less than half as long as the petiole, mottled similar to petiole but deeper in color, dark green, smooth or with irregular protuberances and spiny projections; spathe 23-25 cm long, 5-6 cm wide, cymbiform, cucullate, erect or slightly arching, apex acuminate; inner surface velvety, maroon, with translucent area obvious, 2-4 cm high, as long as spadix; outer surface violet-purple tinged green, matte; margins entire, broadly overlapping in the lower half; veins conspicuous inside, conspicuously darker or paler than the spathe, brownish; spadix hidden, stipitate, cylindric, light brown or purple, $2-3.5 \times 0.5-0.7$ cm at anthesis, never with appendages at apex; stipe 0.5-1 cm long, 0.4-0.5 cm diam. at anthesis. Flower tepals 4 to 6, 1-1.5 mm long, 0.5-1 mm wide, light brown; stamens 7 or 8; filaments 0.5 mm long; anthers 0.5 mm long, hidden; ovary bilocular, pale green; stigma 2- or 3lobed; style 1-1.5 mm long above tepals, brownish purple, persistent. Infructescence with spadix 4-5 cm long, 2-2.5 cm diam. in fruit, berries 1-seeded, 0.4-0.6 cm diam., 0.5-0.8 cm thick, obliquely obovoid, apically rounded; young berries medium green; mature berries color unknown, without reddish dots and raphide cells, seeds 0.6-0.7 cm diam., reniform, reddish brown, laterally depressed; dorsal ridges obvious, 3, continuous, monomorphic, more than 1 mm thick, 0.5 mm high, smooth on both sides (sometimes with a few warts).

Phenology. Flowering from May to September; mature fruits are known only in August.

Distribution and habitat. Dracontium longipes is limited to the area near the border of Acre, Brazil, and Madre de Dios, Peru. It occurs in *Tropical* moist forest (T-mf) and *Premontane wet forest* (P-wf) life zones (Holdridge et al., 1971), at elevations of 150 m.

Discussion. Dracontium longipes is easily confused vegetatively with *D. plowmanii* and *D. spruceanum*, but is distinguished from those species by having a cymbiform rather than an erect or arching spathe. Dracontium plowmanii also differs from *D.* longipes in having a spathe with undulate or lobed margins and small seeds with a single continuous ridge. In contrast, the spathe of *D. longipes* has straight margins and the seeds have three obvious dorsal ridges. Dracontium spruceanum differs in having seeds with more than three dorsal ridges.

Additional specimens examined. BRAZIL. Acre: IN-CRA at ca. 4 km S of main rd. Cruzeiro do Sul to Rio Branco, Croat 62349 (MO); Rio Juruá Miry, Ule 5272 (B); Vista Alegre, Rio Jurua Miry, Croat 85460 (HPZ); Rio Juruá to Mirim at Porangaba, Maas et al. 13201 (NY); Santa Rosa, Rio Purus, Daly et al. 10000 (NY). PERU. Madre de Dios: Manu Park, Cocha Cashu, Río Manu, Foster 6978 (F, MO, QCA), Núñez et al. 14420 (MO).

- Dracontium margaretae Bogner, Aroideana
 4: 87, figs. 1–6. 1981. TYPE: Brazil. Mato Grosso do Sul: Parque Indigena do Xingu, Posto Leonardo, 23 Nov. 1973, *M. Emmerich* 4053 (holotype, R!; isotype, M!). Figure 16.
- Dracontium lineare G. S. Bunting & Tillett, Phytologia 64: 464. 1988. Syn. nov. TYPE: Venezuela. Apure: Achaguas y Rómulo Gallegos, Río Capanaparo, poco arriba de El Porvenir, en las cercanías del Hato San Joaquín, en varios pequeños asentamientos Pumé Santa Bárbara, Los Mangos, Las Maravillas y Las Campanas, 6°48–52′N, 68°45–48′W, 80 m, 10 July 1986, T. Gragson & G. Gragson 13 (holotype, US!; isotypes, MYF not seen, MCA not seen, UCV not seen).

Tuber hemispherical or irregular-shaped, 10-12 cm diam., 8-10 cm thick, flat or slightly sunken above, rounded or flat and whitish to light brown below, 10-15 cm below ground level; tubercles abundant, cylindrically elongated, 0.5-0.8 cm diam., 1-2.5 cm long, borne around the periphery and the side of tuber. Roots whitish sometimes tinged brown, to 3.5 mm diam.; cataphylls 1 or 2, 10-30 cm long, 2-4 cm wide, pinkish or reddish brown, 5-15 cm long above ground. Leaves solitary or sometimes 2 or more per tuber; petioles 0.3-0.9 m long above ground, 2-3 cm diam. at midpoint, light green (in upper half) or brown-green (in lower half), weakly mottled, smooth (often); juvenile blade linear or trifid; mature blade ascending to 45° to the petiole, 0.5-0.7 m diam., thinly coriaceous, never fenestrated, never variegated, without raphide cells or dark markings, semiglossy and medium green above, semiglossy and medium green below;



Figure 16. A–D, Dracontium margaretae. —A. Tuber, petioles, cataphylls, and an inflorescence (Catharino 1832). —B. Potted plant with tuber bearing tubercles, a fully formed leaf, and an opening leaf (G. Zhu 1533). —C. Tuber with infructescence, type specimen (Emmerich 4053). —D. Seed in side view (T. G. Gragson 4).

middle division twice trichotomously branched, 37- 45×30 -40 cm, with terminal subdivision consisting of three sections, with each basal subdivision consisting of many segments; lateral divisions twice dichotomously branched, $35-45 \times 30-40$ cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections free, each usually consisting of a single segment; leaf segments often entire, linear, less than 1 cm wide on each side of the major ribs, linear, mostly free from each other in each division, without contrastingly smaller rounded or triangular segments; apices acuminate; ultimate segments 10-20 cm long, free from penultimate segments; other segments 10-30 cm long; penultimate segments free from subterminal sections; medial segments free from basal subdivisions; basal segments absent, free from each other; rachises patterned distinct from petiole, pale green, smooth; tertiary veins conspicuous above and weakly raised below; bracteoles 2 or 3, 6-25 cm long, 1-3 cm wide, dark brown or pinkish, the longest one shorter than the peduncle, reaching the spathe. Inflorescence solitary, appearing after new leaf; peduncle 3-10 cm long above ground, 0.5-1 cm diam. at midpoint, often almost completely subterranean (or under water), scarcely mottled, whitish tinged pink, smooth; spathe 4-8 cm long, 1-2.5 cm wide, cymbiform, cucullate, arching 90° (or more), apex acuminate; inner surface covered with dense, translucent scales to 1 mm long, olive-brown, with translucent area obscure; outer surface maroon tinged brown, matte; margins entire, slightly overlapping at the base; veins obscure inside and raised outside, conspicuously darker or paler than the spathe; spadix exposed, stipitate, cylindric, brown, $1.3-2 \times 0.6-1$ cm at anthesis, often with several appendages at apex; stipe $0.4-0.5 \times 0.3-0.4$ cm at anthesis. Flower tepals 5 to 6, 1-2 mm long, 0.5-1 mm wide, brownish purple; stamens 6; filaments 1-2 mm long; anthers 0.5 mm long, completely exserted; ovary bilocular, pale green; stigma 2-lobed; style 1-2 mm long above tepals, brownish purple, persistent. Infructescence with spadix $2-4 \times 1.5-2.5$ cm in fruit; berries 2- or 3-seeded, $0.5-0.9 \times 0.7-0.8$ cm, globose or subglobose, 3- to 6-angular, apically rounded or subtruncate, drying ca. 7 mm thick, 2- or 3lobed; young berries medium green; mature berries reddish or purplish red, with abundant raphide cells; seeds 0.4-0.6 cm diam., reniform, light brown, laterally depressed, 2.2-2.3 cm thick; sparsely beset with irregular warts dorsally, dorsal ridges obscure.

Phenology. Flowering from May to November; mature fruits are known only in May.

Distribution and habitat. Dracontium margaretae is known only from a few localities in Brazil (Mato Grosso do Sul), Paraguay, and Venezuela (Apure and Guárico). It occurs in seasonal swamps in the *Tropical moist forest* (T-mf) life zone (Holdridge et al., 1971), at elevations of ca. 100 m.

Discussion. Dracontium margaretae is an atypical member of the genus, recognized by its linear blade segments and by occurring in seasonally swampy habitats. Other distinguishing features include the linear or trifid juvenile leaf blades and tubercles borne at the apex and sides of the tuber. It is confused with no other species. This species grows well as an aquatic in cultivation.

The species described under the name *Dracontium lineare* G. S. Bunting & Tillett (Bunting, 1988) is identical to *D. margaretae*; therefore, the former name is treated as a synonym of the latter.

Additional specimens examined. BRAZIL. Palmas, Estrada para Tocantinia, *Gonçalves 97* (UB). **Mato Grosso do Sul:** Parque Indigena do Xingu, Posto Leonardo, *M. Emmerich 4598* (K, M); Puerto João André-Brasilândia, ca. 7 km before Brasilândia, *Catharino et al. 1832* (SP). PARAGUAY. Estero Laguna, Est. Keicus, *Hassler 10960* (G, MO). VENEZUELA. **Apure:** Dist. Achaguas y Rómulo Gallegos, Río Capanaparo, El. Porvenir, *Gragson & Gragson 4* (US), *13* (MYF, VEN). **Guárico:** Santa Rita, near the rd. to Cabruta, *Susach 251* (VEN), *Trujillo 12633* (MY).

Cultivated plants. Brazil. Mato Grosso do Sul, vouchered as *Catharino 1832*, cult. at Jardim Botânico de São Paulo, *G. Zhu 1533* (MO, SP).

- Dracontium nivosum (Lem.) G. Zhu, World Checklist & Bibliogr. Araceae, 301. 2002. *Amorphophallus nivosus* Lem., Ill. Hort. 12: 1, fig. 424. 1865. TYPE: figure 424 in Ill. Hort. 12: 1865 (lectotype, designated here). Figure 17.
- Amorphophallus papillosus hort. ex Rafarin, Rev. Hortic. 43: 476, fig. 65. 1871. TYPE: figure 65 in Rev. Hortic. 43: 477, 1871 (lectotype, designated here).

Tuber hemispherical or rounded, 6–12 cm diam., 4–8 cm thick, flat above, rounded and white to brown below, 6–27 cm below ground level; tubercles few, rounded, 0.8–1.5 cm diam., borne around the periphery of tuber, roots white, 2–3 mm diam.; *cataphylls* 1 to 3, 9–28 × 2–3 cm, light brown, reaching or surpassing ground level. *Leaves* solitary; *petioles* 1–2 m long above ground, 2.5–3 cm diam. at midpoint, dark green, contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, usually smooth in upper half and with irregular protuberances in lower half; juvenile



blade sagittate, or sagittately lobed; mature blade spreading horizontally, 0.8-1 m diam., often thinly coriaceous, rarely fenestrate, sometimes variegated (along the veins), without raphide cells or dark markings, matte and medium green above, matte and pale green below; middle division twice trichotomously branched (often), 30–45 \times 20–40 cm, with terminal subdivision consisting of 3 sections, with each basal subdivision consisting of many segments; lateral divisions twice dichotomously branched, $28-45 \times 30-45$ cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections free, each consisting of many segments; broadly oblanceolate, more than 5 cm wide on each side of the major ribs, ovate or oblanceolate, mostly free from each other in each division, often with contrastingly smaller rounded or triangular segments alternating with larger segments; apices acuminate; ultimate segments 6-8 cm long, often confluent with penultimate segments; other segments 5-12 cm long; penultimate segments free from subterminal sections; medial segments free from basal subdivisions; basal segments present, free from each other; rachises patterned similar to petiole but in much paler shades, with spiny projections; tertiary veins obscure above, or conspicuous below; bracteoles 3 or 4, $2-28 \times 1-2$ cm wide, light brown, the longest one \pm as long as the peduncle, reaching the spathe. Inflorescence solitary, appearing before new leaf; peduncle 0-2 cm long above ground, 1-1.5 cm diam. at midpoint, often almost completely subterranean, scarcely mottled, whitish tinged pink, smooth; spathe 28-35 \times 6–10 cm, cymbiform, cucultate, arching to 45°, apex acuminate; inner surface semiglossy, maroon, with translucent area obscure; outer surface maroon, matte; margins entire, broadly overlapping in the lower half; veins obscure inside and raised outside, similar to the spathe in color; spadix hidden, stipitate, cylindric, purple or brown-purple, (3-)5-6.5 cm long, 1.2-1.5 cm diam. at anthesis, never with appendages at apex; stipe 0.6-1.2 cm long, 0.5-1 cm diam. at anthesis. Flower tepals 5 to 8, 2.5–3 mm long, 1–2 mm wide, purple; stamens 6 to 8; filaments 2-2.5 mm long; anthers 0.5-1 mm long, slightly exserted; ovary 3-locular; stigma 3lobed; style 4-5.5 mm long above tepals, purple, persistent. Infructescence with spadix 12-18 cm long, 3-3.5 cm diam. in fruit; berries 3- or 4-seeded or sometimes 2-seeded, 0.8-1 cm diam., 0.8-1 cm thick, subglobose, 3- to 6-angular, apically truncate; mature berries orange (tinged red), with abundant raphide cells; seeds 0.5-0.7 cm diam., reniform or rounded, light brown, laterally raised; dorsal ridges obvious, 3, continuous, less than 0.5 mm thick, 0.1 mm high, finely decorated with small cells on both sides.

Phenology. Flowering May to July; mature fruits from December to March.

Distribution and habitat. Dracontium nivosum is endemic to Pará and Maranhão, Brazil. It occurs in *Tropical moist forest* (T-mf) and *Tropical wet forest* (T-wf) life zones (Holdridge et al., 1971) at elevations of 30 to 150 m.

Local names. "Tajá de cobra" (Black 47-2084, MG); "jararaca-taja" (Schott, 1865: 73).

Discussion. Dracontium nivosum is characterized by its subterranean peduncle with a strongly hooded and cymbiform spathe, a spathe much larger than that of any other member of the genus possessing subterranean peduncles. Other species with peduncles at least sometimes subterranean such as D. amazonense, D. bogneri, D. dubium, D. grayumianum, D. polyphyllum, D. prancei, D. purdieanum, D. soconuscum, and D. ulei have spathes only 3-15(18) cm long, whereas the spathe is 28-35 cm long for D. nivosum. Other species that, like D. nivosum, have the spadix hidden at anthesis owing to the broadly overlapping spathe base include D. amazonense, D. bogneri, D. prancei, and D. ulei, but none of them have ranges overlapping that of D. nivosum.

Common names attributed to snakes obviously refer to the reptilian pattern exhibited by the petioles. Perhaps for the same reason many species of *Dracontium* are used by native populations for snakebite remedies (Croat, 1994). This species is known in cultivation at the Instituto Agronomico do Norte (IAN) at Belém, Pará State, Brazil. A plant of the species, collected from Santarem, Brazil, flowered in John Banta's nursery in Florida in 1993.

Since no type was chosen for *Amorphophallus ni*vosus Lem., the only plate from the protologue (III. Hort. 12: 1, fig. 424. 1865) is designated here as a lectotype for the name. Two figures of this species appeared earlier before its publication under the name *D. polyphyllum* (Bot. Reg. 9: fig. 700 A&B, 1823).

Apparently based on a cultivated plant, another name, *Amorphophallus papillosus* hort. ex Rafarin (Rev. Hortic. 43: 476, 1871), was published for the same species. In the protologue of *A. papillosus*, no type was designated and one illustration (fig. 65 in Rev. Hortic. 43: 477, 1871) was included with a caption mistakenly noted as *A. nivosus*. For the integrity of nomenclatural citation, the illustration (fig. 65 in Rev. Hortic. 43: 477, 1871) is designated here as a lectotype for the name *A. papillosus*. Dracontium nivosum was previously noted (as nomen nudum) to occur in Peru (Vásquez et al., 2002 [2003]).

Additional specimens examined. BRAZIL. Maranhão: Monção, P. I. Guajá, Río Turiaçu, Guajá Indianas, Balée 3476 (NY). Pará: "Taperinha, bei Santarem," 16 June 1927, Ginzberger 3109 (WU); Barcarena, Itupanema, Gély 234 (MG); Mpo. Tucuruí, Río Tocantins, 1–5 km from Represa Tucuruí, Plowman et al. 9895 (MG); Rio Cupari, Ingatuba capoeira, Black 2084 (IAN, RB); BR-423, Machiel & Rosário 534 (MG); Vigia, Campina do Palha, Black 18814 (IAN); Paraenfis, 1911, Martius 282 (M); Belém-São Caetano, km 12, Lobato et al. 60 (MG).

Cultivated plants. Brazil. Para, Belém, Museu Paraense Emilio Goeldi, Botanical Garden, May 1901, *Huber 2036, 3667* (MG); Instituto Agronomico do Norte (IAN) at Belém, *Lima 108* (IAN, MG), *Pires 6594* (IAN).

 Dracontium peruvianum G. Zhu & Croat, sp. nov. TYPE: Peru. Loreto: Maynas, Allpahuayo, 4°10'S, 73°30'W, 150–180 m, 4 Dec. 1990, *R. Vásquez & N. Jaramillo 15226* (holotype, MO). Figure 18.

Herba usque plus quam 6 m alta; petiolus 2–6 m longus; lamina 0.6–1 m longa, 0.6–0.9 m lata; pedunculus 60–115 cm longus, 1.5–6 cm diam.; spatha (25)30–50 cm longa, 6–10 cm lata; extus impolita, purpurea; intus velutina, purpurea; spadix 8–10.5 cm longus, 1–1.3 cm diam.; baccae 0.7–1 cm diam.; semina fusca, 0.7–1 cm diam.

Tuber hemispherical, 10-30 cm diam., 8-15 cm thick, flat above, rounded and white to brown below, 15-45 cm below ground level; tubercles few, rounded or cylindrically elongated, borne around the periphery of tuber; roots white, to 0.4 mm diam.; cataphylls 1 or 2, $10-50 \times 2.5-4$ cm, reaching or surpassing ground level. Leaves solitary; petioles 2-6 m long above ground, 3.6-5 cm diam. at midpoint, dark green (paler toward the apex), contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, usually with spiny projections (especially in upper half or at the apex); juvenile blade sagittate, or sagittately lobed; mature blade spreading horizontally, 1.2-2 m diam., thinly coriaceous, rarely fenestrate or sometimes fenestrate throughout the blade (in young leaves), never variegated, lacking raphide cells or dark markings, semiglossy and dark green above, matte and medium green below; middle division twice trichotomously branched, 60–100 \times 60-90 cm, with terminal subdivision never divided into sections, with each basal subdivision consisting of many segments; lateral divisions twice dichotomously branched, 55–95 \times 55–90 cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections confluent, each consisting of many segments; broadly oblanceolate, more than 5 cm wide on each side of the major ribs, oblanceolate, at least some of the basal segments free from each other, without contrastingly smaller rounded or triangular segments; apices acute or acuminate; ultimate segments 20-27 cm long, often confluent with penultimate segments; other segments 10-15 cm long; penultimate segments free from subterminal sections; medial segments free from basal subdivisions; basal segments present, free from each other; rachises patterned similar to petiole but in much paler shades, smooth; tertiary veins obscure above and weakly raised below; bracteoles 1, 15-50 cm long, 2-4 cm wide, light brown, the longest one much shorter than the peduncle, confined at the base of the peduncle. Inflorescence solitary, appearing before new leaf; peduncle 60–115 \times 1.5–6 cm diam. at midpoint, less than half as long as the petiole, mottled similar to petiole but deeper in color, brownish green, with irregular protuberances in lower half and spiny projections (in upper half, especially at the apex); spathe (25-)30-50 \times 6-10 cm, cymbiform, noncucullate, erect or slightly arching, apex acuminate; inner surface semiglossy, maroon, with translucent area obvious, 5-8 cm high, shorter than spadix; outer surface maroon tinged brown, matte; margins entire, slightly overlapping at the base; veins obscure inside and raised outside, conspicuously darker or paler than the spathe; spadix hidden, stipitate, cylindric, brown or brown-purple, 8-10.5 \times 1–1.3 cm at anthesis, never with appendages at apex; stipe $0.5-2 \times 0.5-1$ cm at anthesis. Flower tepals 5 to 7, $1-2 \times 1-2.5$ mm, light brown or brown-purple; stamens 7 to 11; filaments 1-1.5 mm long; anthers 0.5 mm long, hidden; ovary 3-locular, pale green; stigma 2- or 3-lobed; style 1-1.5 mm long above tepals, brownish purple, persistent or not. Infructescence with spadix $23-35 \times 2.8-3$ cm in fruit; berries 1- to 3-seeded, 0.5-1 cm diam., 0.7-1 cm thick, obliquely obovoid or globose, apically rounded or subtruncate; young berries medium green; mature berries orange, without reddish dots and raphide cells; seeds 0.7-1 cm diam., rounded, dark brown, laterally raised; dorsal ridges obvious, 3, continuous or rarely strongly interrupted, with the central ridge contrastingly raised, more than 1 mm thick, 1-2 mm high, smooth on both sides.

Phenology. Flowering April to November; mature fruits July to March, with a peak in December.

Distribution and habitat. Dracontium peruvianum is known only from Amazonian Peru and Brazil. It occurs in Tropical moist forest (T-mf), Premontane



Figure 18. A–D, *Dracontium peruvianum*. —A. Inflorescence in Ucayali Department, Peru. Photo W. Staeck. —B. Flowering plant in Parque Nacional Alexander von Humboldt, near Pucalpa, Ucayali Department, Peru. Photo by A. Salazar. —C. Infructescence with persistent spathe type specimen (*Vásquez & Jaramillo 15226*). —D. Seeds in lateral view (*Gentry & Daly 18798*).

moist forest (P-mf), and *Tropical montane moist for*est (TM-mf) life zones (Holdridge et al., 1971), at elevations of 180 to 900 m.

Local names. "Jergón sacha" (Plowman & Schunke 11536, MO).

Discussion. Dracontium peruvianum has the longest leaves of any species in the genus, up to 6 m long. The inflorescences of this species are superficially similar to those of *D. pittieri*, but are distinct by the more elongate fruiting spadix (to 23–35 cm long vs. 10–20 cm long for *D. pittieri*), more strongly ridged seeds (vs. less ridging in *D. pittieri*), and basal leaf segments that usually are free from the rachis.

In having such a long peduncle *D. peruvianum* is similar to *D. asperispathum*, *D. croatii*, *D. grandispathum*, *D. longipes*, *D. plowmanii*, and *D. spruceanum*, but only *D. croatii*, *D. longipes*, and *D. pittieri* also have a cymbiform spathe that is not differentiated into a proximal tube portion and a distal lamina. *Dracontium croatii* and *D. pittieri* differ in having the spathe obtuse at the apex (vs. acuminate for *D. peruvianum* and *D. longipes*). *Dracontium longipes* differs from *D. peruvianum* in having a much shorter infructescence (only 4–5 cm long vs. 23–35 cm long for *D. peruvianum*).

Paratypes. BRAZIL. Amazonas: Rio Juruá basin, near mouth of Rio Embira (tributary of Rio Tarauaca), Krukoff 4987 (GH, NY). PERU. Huánuco: Pachitea, Honoria, Río Pachitea, Schunke-Vigo 1775 (F); Tingo María, Gentry & Daly 18798 (F, MO). Loreto: Río Amazonas, Isla de Iquitos, Rimachi 5304 (IBE); Nauta, Vásquez & Jaramillo 8562 (MO); Fernando Lores, Quebrada Tamshiyacu, Grández et al. 2629 (MO), Rimachi 4043 (IBE); Iquitos, L. Williams 7916 (F); Río Itaya just below mouth of Río Ucavali, Gentry et al. 30026 (MO); San Antonio, Río Itaya, Vásquez & Jaramillo 3598 (MO); Río Ucayali, Santa Rosa, Jong 20 (MO); Yurimaguas, NCSU Exp. Station, near headquarters, Gentry et al. 52159 (MO); lower Río Huallaga, L. Williams 4631 (F); San Salvador on the Amazon River, L. Williams 1561 (F). Pasco: Palcazu Valley, Iscozacin, above PEPP Project Camp, Salick 7370 (MO). San Martín: 12 km W of Tocache Nuevo, Gentry et al. 25597 (MO); Tarapoto-Yurimaguas, km 40, trail to Río Tiriyacu and Río Cashiyacu, Knapp & Mallet 7210 (MO); Tocache Nuevo, Tocache Nuevo-Puerto Pizana, km 23, Río Cañuto, Plowman & Schunke 11536 (F, MO, SEL); Lamas Convento, Tarapoto-Yurimaguas, km 68, Alcorn & Mallet 8 (MO); Mariscal Cáceres, Dtto. Tocache Nuevo, Quebrada de Huaquisha, Schunke 7140 (MO); Puerto Huicte, Río Huallaga, Schunke 6428 (UCLA); Yorongos-La Florida near Rioja, van der Werff et al. 16538 (AAU, B, CAS, K, MEXU, MO, US, USM).

Cultivated plants. Peru. Humboldt National Park between Pucallpa and Tingo María, collected by Angel Salazar, cult. at MBG, *T. B. Croat* 53539 (MO).

 Dracontium pittieri Engl., Anales Inst. Fis.-Geogr. Nac. Costa Rica 9: 209. 1896. TYPE: Costa Rica. Puntarenas: Río Naranjo, 200 m, *H. Pittier & A. Tonduz 7515* (lectotype, designated here, CR!; isotypes, B!, BR!). Figure 19.

Tuber hemispherical, 14-20 cm diam., 6-8 cm thick, flat above, rounded and white to brown below, 20-40 cm below ground level; tubercles abundant, irregular-shaped, 0.3-1.5 cm long, borne around the periphery of tuber; roots white, to 3 mm diam.; cataphylls 3 to 5, 4–40 \times 4–7 cm, light brown, reaching or surpassing ground level. Leaves solitary; petioles 1.8-4 m long above ground, 5-8 cm diam. at midpoint, dark green or brownish green, contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, smooth or usually with spiny projections; juvenile blade sagittate, or sagittately lobed; mature blade spreading horizontally, 1.2-2 m diam., subcoriaceous or thinly coriaceous, rarely fenestrate, never variegated, with abundant raphide cells (sometimes), glossy and dark green above, semiglossy and medium green below; middle division 3 or more times trichotomously branched, $80-120 \times 50-100$ cm, with terminal subdivision consisting of 3 sections, with each basal subdivision consisting of many segments; lateral divisions 3 or more times dichotomously branched, 70–120 \times 55–90 cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections confluent, each consisting of many segments; leaf segments bilobed or trilobed, broadly oblanceolate, more than 5 cm wide on each side of the major ribs, oblanceolate or lanceolate-ovate or triangular, mostly confluent with each other in each division, often with contrastingly smaller rounded or triangular segments alternating with larger segments; apices narrowly acuminate, or caudate; ultimate segments 10-20 cm long, confluent with penultimate segments; other segments 10-30 cm long; penultimate segments confluent with the subterminal sections; medial segments confluent with the basal subdivisions; basal segments present, confluent with each other; rachises patterned distinct from petiole, pale green, smooth; tertiary veins obscure above, or conspicuous below; bracteoles 3 or 4, 4–40 cm long, 5–7 cm wide, pinkish, the longest one much shorter than the peduncle, confined at the base. Inflorescence solitary, appearing before new leaf; peduncle 150-250 cm long above ground, 4-6 cm diam. at midpoint, more than half as long as the petiole, mottled similar to petiole but deeper in color, dark green, smooth or with irregular protuberances; spathe 30-50(70) cm long, 8-12 cm wide, cymbiform, non-cucullate, erect or slightly



Figure 19. A–D, Dracontium pittieri. A–C, (Croat & Hannon 79217). —A. Habit of flowering plant with Dylan Hannon. —B. Close-up of spathe with one side removed to expose spadix. —C. Infructescence with premature berries. —D. (Burger 12266). Seeds in side view.

arching, apex obtuse; inner surface semiglossy, maroon or olive-brown or red-purple, with translucent area obvious, (5)10-17 cm high, 1.5 to 3 times longer than spadix; outer surface maroon, matte; margins entire, hardly overlapping at the base; veins obscure inside or raised outside, similar to the spathe in color; spadix exposed, sessile, cylindric, brown-purple (tinged green) or purple, $4-9 \times 1-$ 1.5 cm at anthesis, never with appendages at apex. Flower tepals (4)5 or 6(9), 3-4 mm long, 1-1.5 mm wide, brownish purple or dark purple; stamens 12 to 15; filaments 2-3 mm long; anthers 1 mm long, slightly exserted; ovary bilocular, whitish; stigma (2)3(4)-lobed; style 3-4 mm long above tepals, purple, persistent. Infructescence with spadix 10-20 cm long, 3-4 cm diam. in fruit; berries 2-seeded, 0.6-1.2 cm diam., 0.9-1.3 cm long, subglobose, 3- to 6-angular, apically truncate; young berries medium green; mature berries orange, with abundant raphide cells; seeds 0.9-1.1 cm diam., reniform or triangular, light brown, laterally flattened; dorsal ridges obvious, 1, continuous, more than 1 mm thick, 0.5-1 mm high, warty along both sides, appearing as strongly reduced lateral ridges.

Phenology. Flowering from May to November; one inflorescence was also collected in February; mature fruits in November and February.

Distribution and habitat. Dracontium pittieri is endemic to the Pacific slope in Puntarenas Province and adjacent San José Province in Costa Rica. It occurs in *Tropical moist forest* (T-mf) and *Premontane moist forest* (P-mf) and *Tropical wet forest* and transition forest to *Premontane wet forest* life zones (Holdridge et al., 1971). It is often found along river banks, roadsides, secondary growth, and other disturbed areas, at elevations of 30 to 1000 m.

Discussion. Dracontium pittieri is characterized by having the longest peduncles in the genus. It is easily confused with D. gigas in sterile condition, but differs strikingly in inflorescence morphology (see also discussion of *D. gigas*). Dracontium gigas has a large spathe and a short peduncle, which is always less than twice as long as the spathe, whereas D. pittieri has a much longer peduncle, 5 to 8 times longer than the spathe. The spathe of D. gigas is more or less hooded at the apex, with the margins broadly overlapping and completely covering the spadix. The spathe of D. pittieri is open at the apex with the margins scarcely overlapping, such that the spadix is exposed. The translucent area at the base of the inner spathe surface extends much higher than the spadix in D. pittieri, while it never exceeds the height of the spadix in D. gigas.

Aside from the fact that they are widely separated geographically, *D. pittieri* could also easily confused with *D. peruvianum*; they differ, however, in the features of infructescences, seeds, and leaf blades (see discussion of *D. peruvianum*). A few plants of this species have been brought into cultivation in the United States, but no report of flowering is known. Several plants of *D. pittieri* are known from John Banta's Nursery (Alva, Florida).

In the protologue, two specimens, *Pittier & Tonduz 7515* and *Pittier 11985*, were cited without indication of a holotype (Engler, 1896). Therefore, one of them needs to be designated as the holotype. The *Pittier & Tonduz 7515* collection has three duplicates that are deposited in three different herbaria (B, BR, CR) and are in much better condition than the unicate *Pittier 11985*; therefore, the former collection is designated here as lectotype for the name *D. pittieri*. A description of this species was published at a later date (Engler, 1905).

Additional specimens examined. COSTA RICA. Puntarenas: Boca Culebra, Pittier 11985 (CR); Fila de Cal, betw. San Vito & Ciudad Neily, Grayum et al. 6046 (MO); Cantón de Osa, 2.5 mi. SW of Rincón, Croat & Grayum 59844 (CM, MO), Kennedy 1646 (MO); Fila Retinto, cerros N Palmar Norte, Hammel 17713 (CR); Rancho Quemado, Rincón, Marín 285 (CR, MO), Quesada 259 (CR, INB, MO); above Palmar Norte, Allen 5318 (EAP, MO, US), Croat 35104 (CM, F, MO); vic. Rincón, Hammel et al. 15204 (MO); 5 km W of Rincón de Osa W of airfield, Burger & Stolze 5551 (F, NY); Quebrada Orito & Quebrada Baneguitas, Herrera 4529 (MO); Corcovado Nat. Park, Sirena, Liesner 2867 (CR, MO); Los Patos Forest, Kernan & Phillips 648A (MO); Los Patos, Cerro de Oro, Aguilar & Guzmán 2849 (CR); Coto Brus, Sabanillas de Limoncito, Gómez 22029 (B, F, K, RSA, US); Esquinas forest, along Panamerican Hwy., McAlpin 85-34 (SEL); Finca El Edén, km 183, R 2, E of Santa Marta, Gómez 22935 (CM, MO); Golfito-San Isidro de General, Kress 76585 (DUKE, F); E of Quepos, Burger et al. 10587 (F, PAM); Río Agua Buena, 4 km above airport, Liesner 2017 (MO); Río Naranjo, near Londres & Villa Nueva, Burger et al. 12266 (F); vic. of Boscosa, Aguabuena, Croat & D. Hannon 79217 (MO, NY, WU); Golfito, PN Corcovado, Angulo 273 (INB, MO), San José: R. Ocampo S. 2573 (CR): La Cangreja, Cerros de Puriscal, Santa Rosa de Puriscal, Morales 546 (CR); Playa, Dominical/Baru/Tinamastes, along rd. to San Isidro del General, Burger & Baker 10131 (F, MO).

 Dracontium plowmanii G. Zhu & Croat, sp. nov. TYPE: Peru. Cuzco: Paucartambo, Pilcopata, Villa Carmen, 720 m, 7 Feb. 1975, *T. Plowman & W. Davis 5054* (holotype, GH!; isotype, US!). Figures 1A, 20.

Petiolus 1–2 m longus; lamina 45–55 cm longa, 40–55 cm latis; pedunculus 29.5–70 cm longus, 1–2 cm diam.; spatha 13–20 cm longa, 2.5–3.5 cm lata, cucullata vel non cucullata basi; extus impolita, purpurea; intus velutina, purpurea; spadix 3–4.9 cm longus, 0.8–1.2 cm



Figure 20. A–D, *Dracontium plowmanii*. Photos A–C by P. Schmidt. —A. (Selby Gardens 76-575). Inflorescence (*G. Zhu 1446*). B, C, (Selby Gardens 77-2421). —B. Spathe in side view with petiole. —C. Leaves of potted plant. — D. Seeds in lateral view. Note: each line on left of photo represents 1 mm (*Cornejo 2049*).

diam.; tepala 4–6; baccae $0.7{-1}~{\rm cm}$ diam.; semina brunneola, $0.4{-}0.6~{\rm cm}$ diam.

Tuber hemispherical, 10-20 cm diam., 6-9 cm thick, flat above, rounded and white to brown below, 5-18 cm below ground level; tubercles few, rounded or cylindrically elongated, 0.5-0.8 cm diam., 0.8-1 cm long, borne around the periphery of tuber; roots white, strong; cataphylls 2 to 3, 5.5- $18 \times 2-4$ cm, light brown, reaching or surpassing ground level. Leaves solitary; petioles 1-2 m long above ground, 3-4 cm diam. at midpoint, brownish green, contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, smooth or usually with spiny projections; juvenile blade sagittate, or sagittately lobed; mature blades spreading horizontally, 1-1.2 m diam., thinly coriaceous, sometimes fenestrate throughout the blade, never variegated, without raphide cells or dark markings, glossy and dark green above, semiglossy and medium green below; middle division twice trichotomously branched, $45-58 \times 40-60$ cm, with terminal subdivision consisting of 3 sections, with each basal subdivision consisting of many segments; lateral divisions twice dichotomously branched, $45-55 \times 40-55$ cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections free, each consisting of a few segments; leaf segments bilobed, broadly oblanceolate, more than 5 cm wide on each side of the major ribs, ovate or oblong, at least some of the basal segments free from each other, often with contrastingly smaller rounded or triangular segments alternating with larger segments; apices acuminate, or acute; ultimate segments 10-20 cm long, confluent with penultimate segments; other segments 6.5-19 cm long; penultimate segments confluent with the subterminal sections; medial segments free from basal subdivisions; basal segments present, free from each other; rachises patterned similar to petiole but in much paler shades, smooth; tertiary veins obscure above and conspicuous below; bracteoles 2 or 3, $4-20 \times 2.5-4$ cm, pink to dark brown, the longest one much shorter than the peduncle, partially covering the base of the peduncle. Inflorescence solitary, appearing before new leaf; peduncle 30-70 cm long above ground, 1-2 cm diam. at midpoint, less than half as long as the petiole, mottled similar to petiole but deeper in color, brownish green, smooth; spathe (10-)13-20(-28) cm long, (1-)2.5-3.5(-6) cm wide, cymbiform or non-cymbiform, constricted at a certain point and differentiated into a proximal tube and a distal lamina (blade), cucultate or non-cucultate, erect or slightly

arching, apex acuminate; inner surface glossy, purple-red, with translucent area obvious, 3-4 cm high, shorter than spadix or as long as spadix; outer surface maroon, matte; margins wrinkled and sometimes lobed on each side, broadly overlapping at the base; veins conspicuous inside and raised outside, similar to the spathe in color; spadix hidden, stipitate, cylindric, brown or brown-purple, 3-4.9 \times 0.8–1.2 cm at anthesis, never with appendages at apex; stipe 0.5-0.7 cm long, 0.4-0.6 cm diam. at anthesis. Flower tepals 4 to 6, $1-2.5 \times 0.5-1$ mm, light brown tinged green or brown-purple; stamens 6 to 9; filaments 0.7-2.2 mm long; anthers 0.5 mm long, slightly exserted; ovary 3-locular, pale green; stigma 3-lobed; style 1-2 mm long above tepals, purple, persistent. Infructescence with spadix 6-15 cm long, 2-2.5 cm diam. in fruit; berries 1to 3-seeded, 0.7-1 cm diam., 0.5-0.7 cm thick, subglobose, 4- to 5-angular, apically truncate; young berries dark green; mature berries' color unknown, drying with abundant reddish dots; seeds 0.4-0.6 cm diam., reniform, light brown, laterally raised; dorsal ridge 1, obvious, continuous, more than 1 mm thick, 0.5 mm high, smooth on both sides.

Phenology. Flowering from June to August, sometimes in February; mature fruits collected in January and February.

Distribution and habitat. Dracontium plowmanii is endemic to Peru, ranging from Junín through Cuzco to the Tambopata area in Madre de Dios. It occurs in *Tropical moist forest* (T-mf) and *Premontane moist forest* (P-mf) life zones (Holdridge et al., 1971), at elevations of 200 to 720 m.

Discussion. Dracontium plowmanii is characterized by the often undulate or lobed spathe margins and small seeds with a single continuous dorsal ridge. It is easily confused with *D. spruceanum*, which differs in having larger seeds to 0.7 cm long, with three dorsal ridges, and usually entire and non-wavy spathe margins. It is also superficially similar to *D. longipes*, which differs by having a straight non-wavy margined spathe and seeds that have three obvious dorsal ridges. This species is in cultivation at the Missouri Botanical Garden, Marie Selby Botanical Gardens, and the Dewey Fisk Nursery in Florida.

This new species is named in honor of the late Timothy Plowman, whose numerous collections of Araceae include many live collections introduced to horticulture as well as the type specimen of this species.

Paratypes. PERU. Cuzco: Atayala, Vargas 13433 (US). Junín: San Luíz de Shuara, Plowman & Kennedy 5654 (F, GH). **Loreto:** Yarina at Río Tapiche, Vásquez et al. 4841 (MO). **Madre de Dios:** Cocha Cashu, Parque Manu, Nuñez 1885 (F); Manu, Par. Nac. del Manu on Río Manu, Cocha Cashu Station, Foster 9558 (F, MO); 12 km E of Puerto Maldonado, Gentry & Núñez 69383 (MO); Tambopata ca. 30 air km or 70–80 river km SSW of Puerto Maldonado, Cornejo 1520 (MO, MOL).

Cultivated plants. Peru. Lima, sent by Anderson, cult. Fairchild Tropical Garden, Miami, Florida, (same as Selby 77-2421), M. Madison 4229 (SEL); Madre de Dios, collected by O. Phillips, 5 Sep. 1994, cult. at MBG, G. Zhu 1512 (MO); from Selby Gardens (76-575), cult. at MBG, [vouchered as T. Plowman 5654], Croat 73989 (MO), G. Zhu 1482, 1498 (MO); from Selby Gardens (77-2421), cult. at MBG [vouchered as M. Madison 4229], G. Zhu 1446, 1447, 1480, 1487, 1496, 1496A (MO); from Selby Gardens (76-575), cult. at MBG [vouchered as T. Plowman 5654], Christenson 1287, 1490, 1491 (MO), G. Zhu 1466 (MO).

- 18. Dracontium polyphyllum L., Sp. Pl. 967. 1753, non Dracontium polyphyllum Houtt., Handl. Pl.-Kruidk. 11: 199. 1773-1783, hom. illeg. [= Amorphophallus giganteus Blume]; nec Dracontium polyphyllum Forst. f., Diss. Pl. Esc. 61, n. 29. 1786, hom. illeg. [= Amorphophallus paeoniifolius (Dennst.) Nicolson]; nec Dracontium polyphyllum Dennst., Schluess. Hort. Malab. 38. 1818, hom. illeg. [= Amorphophallus dubius Blume]; nec Dracontium polyphyllum A. Cunn. ex A. DC., in DC., Prod. 16(2): 534. 1866, hom. illeg. [= Bowenia spectabilis Hook. f.]. TYPE: plate 93 in Herm., Parad. Bat. 1698 (lectotype, designated by Hay (1992: 189)); French Guiana. Saül, 13 Feb. 1993 (T. B. Croat 74210) [cultivated plant at MBG], G. Zhu 1462 (epitype, designated by Zhu & Grayum (1995: 521), MO!). Figures 1B, 1C, 21.
- Dracontium asperum K. Koch var. wallisii Engl. in Mart., Fl. Bras. 3(2): 126. 1878. Syn. nov. Amorphophallus wallisii Regel, Gartenfl. 322. 1861, nom. invalid. TYPE: Brazil. Pará: Martius s.n. (holotype, not seen, probably B or M).
- Echidnium regelianum Engl., in DC., Monogr. Phan. 2: 286. 1889. Syn. nov. Dracontium regelianum (Engl.) Bogner, Aroideana 8: 78. 1985. Echidnium spruceanum Regel, Gartenfl. 15: 98, t. 503. 1866, non Schott. TYPE: tab. 503 in Gartenfl., 1866: 98 (lectotype, designated by Bogner (1985: 78)).

Tuber hemispherical or rounded, 6–10 cm diam., 5–8 cm thick, flat above, rounded and white to brown below, 5–15 cm below ground level; tubercles few, cylindrically elongated or irregularshaped, 0.5 cm diam., 1 cm long, borne around the periphery of tuber; roots white, to 0.3 cm diam.; *cataphylls* 3 to 5, 3–16 cm long, 1–2 cm wide, light brown, reaching or surpassing ground level. *Leaves* solitary or sometimes two or more per tuber; *petioles*

1-2 m long above ground, 2-3.5 cm diam. at midpoint, dark green or brown-green, contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, usually smooth in upper half and with irregular protuberances in lower half; juvenile blade sagittate, or sagittately lobed; mature blade spreading horizontally, 0.8-1 m diam., papyraceous, sometimes fenestrate, sometimes variegated, with abundant raphide cells (sometimes), glossy and dark green above, semiglossy and medium green below; middle division twice trichotomously branched, 50–80 \times 50–75 cm, with terminal subdivision consisting of three sections, with each basal subdivision consisting of many segments; lateral divisions twice dichotomously branched, 50–80 \times 45-70 cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections confluent or free, each consisting of a few segments or each consisting of many segments; leaf segments bilobed or trilobed, broadly oblanceolate, more than 5 cm wide on each side of the major ribs, oblanceolate or elliptic, at least some of the basal segments free from each other, often with contrastingly smaller rounded or triangular segments alternating with larger segments; apices caudate or acuminate; ultimate segments 12-20 cm long, free from penultimate segments or rarely confluent with penultimate segments; other segments 5-15 cm long; penultimate segments free from subterminal sections; medial segments free from basal subdivisions, or rarely confluent with the basal subdivisions; basal segments present, free from each other; rachises patterned similar to petiole but in much paler shades, with spiny projections (sometimes); tertiary veins obscure above and weakly raised below; bracteoles 3 or 4, 6–18 \times 1.5–2 cm, dark brown to pink, the longest one \pm as long as the peduncle or shorter than the peduncle, covering up to 1/3 of the spathe. Inflorescence solitary or rarely two, appearing before new leaf; peduncle 5-18 cm long above ground, 0.5-0.8 cm diam. at midpoint, often almost completely subterranean (less than 10 cm above ground level), scarcely mottled, gray or whitish green, with irregular very weak protuberances; spathe 6-12 cm long, 3-5 cm wide, cymbiform, cucullate, arching to 45°, apex acuminate; inner surface semiglossy, violet-purple, with translucent area obvious, 0.5-1 cm high, shorter than spadix; outer surface maroon, tinged green, matte; margins entire or sometimes wrinkled, scarcely to slightly overlapping at the base; veins obscure to conspicuous inside, conspicuously darker or paler than the spathe, purple; spadix exposed, stipitate, cylindric, narrower at apex, purple, 2.5-



Figure 21. A–D, *Dracontium polyphyllum*. —A. Inflorescence at anthesis in face view (*G. Zhu 1462*). —B. Infructescence with persistent spathe (*Croat 74210*). —C. Habit of plant with leaf and infructescence (*Croat 74284*). — D. Seeds in side view (*Croat 74210*).

4.2 cm long, 1-1.2 cm diam. at anthesis, never with appendages at apex; stipe 0.5-0.8 cm long, 0.4-0.8 cm diam. at anthesis, pale green or light brown. Flower tepals 4 to 5(to 6), 2-4 mm long, 1-2 mm wide, purple or light brown; stamens 5 or 6 to 7; filaments 2-3 mm long; anthers 1-2 mm long, slightly exserted; ovary 3-locular or 3- or 4-locular (rarely), pale green; stigma 2-lobed or often 3lobed; style 0-2 mm long above tepals, purple, persistent. Infructescence with spadix 5-16 cm long, 3-4 cm diam. in fruit; berries 3-seeded, 0.5-0.7 cm diam., 1-1.5 cm thick, subglobose, 3- to 6-angular, apically subtruncate; young berries pale green; mature berries greenish purple; seeds 0.5-0.7 cm diam., reniform, light brown, laterally raised; dorsal ridges obvious, 1, continuous, with the central ridge contrastingly raised, more than 1 mm thick, 0.5-1 mm high, warty along both sides, appearing as strongly reduced lateral ridges. Chromosome number 2n = 26 (*Croat* 74210).

Phenology. Flowering from December to June, with the peak probably from December to January; mature fruits are only collected in February.

Distribution and habitat. Dracontium polyphyllum ranges from the Atlantic coast of Surinam and French Guiana to northern Brazil (Pará State) and Amazonian Venezuela (Bolívar and Portuguesa States). It occurs in *Tropical moist forest* (T-mf) and *Premontane wet forest* (P-wf) life zones (Holdridge et al., 1971), at elevations of 0 to 220 m.

Local names. "Mai-eri" (Balée 2106, NY); "kao aj" (Sauvain 175, K).

Discussion. Dracontium polyphyllum is distinguished by its often subterranean peduncle, usually broadly opened spathe with a glossy inner surface, and smooth, laterally convex seeds. Historically, it has been confused with *D. asperum* (see discussion of *D. asperum*). It is also similar to *D. guianense*, which differs in having the above-ground portion of the peduncle much longer than the spathe. The shape of the spathe of *D. polyphyllum* is similar to that of *D. dubium*, but the inner surface of the spathe is semiglossy in the former and is covered with translucent scales in the latter.

Dracontium asperum K. Koch var. wallisii Engl. is synonymized here under D. polyphyllum for the first time. The name Dracontium asperum var. wallisii had been synonymized with D. asperum previously (Engler, 1911). However, D. asperum var. wallisii has a variegated blade, which shows that it belongs to D. polyphyllum.

Under the name *Echidnium spruceanum* Schott, Regel (1866: 98, t. 503) described a species based on a plant collected by Appun, presumably in Venezuela, with a plate. This species was later named as *E. regelianum* Engl. (1879: 286) in memory of E. Regel, citing the plate of the plant published by Regel (1866: t. 503). In the protologue of *E. regelianum*, Engler (1879: 287) only mentioned the collector's name "Appun" and did not designate a type. The plate (Regel, 1866: t. 503) was designated as a lectotype of *E. regelianum* by Bogner (1985: 78) when he made the combination *Dracontium regelianum* (Engl.) Bogner. No herbarium material related to the original description has been found. All characters from the description and the lectotype suggest it is conspecific with *D. polyphyllum*.

Wallis (1861) collected a plant he called "Amorphophallus dubius (Dracontium polyphyllum)" on an exploration trip to Pará in northern Brazil, and published a sketch of the plant in its natural habitat along with his field notes. Regel (footnote in Wallis, 1861: 332) suggested that the plant might be a new species and later published a color illustration of the same plant received from Wallis under the name A. wallisii, with a clear statement that the name was provisional and that it might end up being a "form" of an already described species (Regel, 1862). Thus, according to Article 34 of the current International Code of Botanical Nomenclature (Greuter et al., 2000), the name A. wallisii Regel is of no taxonomic value. Engler (1878) intended to use the name A. wallisii as the basionym of a new combination, D. asperum var. wallisii, but this name is no longer considered published, so actually Engler published a new name for his variety. Engler provided a description and cited one specimen he saw for this variety. Because Regel's name is not validly published, this specimen must be considered the type.

Additional specimens examined. BRAZIL. Pará: Lageira, airstrip on Rio Maicuru, Strudwick et al. 3987 (MG, NY); Altamira, Igarapé Ipixuna, affluent of Rio Xingu, Araweté Indian Reserve, Balée 2106 (MO, NY); Barcarena, Itupanema, São Caetano, km 12, Gély 60 (MG); Conceição do Araguaia, ca. 20 km W of Redenção, near Côrrego São João & Troncamento Santa Teresa, Plowman et al. 8616 (MG, MO, NY); Oriximiná, Campos do Ariramba, Serra da Preciosa, 20 km N of Ponte do Rio Cuminá-Mirim, Martinelli et al. 6815 (MG, NY); Rio Xingu, Altamira, Dias 513 (MG). FRENCH GUIANA. Locality unknown: Leprieur s.n. (P), Richard s.n. (P), Broadway 407 (GH, NY, US); Chemin de la source de Baduel, Jacquemin 2191, 2194 (CAY); Colline du Montabo, Riera 415 (CAY); Montagne des Nouragues, Bassin de l'Approuague, Arataye, Larpin 998 (CAY); village Boni de Locu, Bassin du Maroni, Lawa, Fleury 802 (CAY, MO, P, U); Mont Cabassou, Cremers & Crozier 14308 (CAY). Acarouany: Sagot 608 (P); Bassin de l'Approuague, Crique Kapiri, Cremers 11618 (CAY); Montagnes de Kaw, Cremers 7682 (BR, CAY, K, P, US); S of Cayenne, along Route de Montagne Trésor, along side trail to Placer Trésor, Feuillet 3993 (CAY, K, NY, P, U, US); Montagne du Mahury, Sentier du Rorota, Cowan 38843 (NY, P); Piste Sophie, La Gréve, Hallé 790 (CAY, P, U, US); Route du Rorota, Paris 36 (CAY); Petit Tukuchi, Grenand 1913 (CAY); Saül N of Eaux Claires along rd. to Béllizon, Croat 74210 (CAY, MO, K, US); Saül, Saint Laurent du Maroni, Moretti 122 (CAY). Saut Mapaou: bassin de L'Approuague, Cremers 12734 (CAY). SURINAM. Jodensavanne-Mapane creek area, Bosbeheer 9845 (U); Sectie O, Pulle 161 (U). Brokopondo: Banafokonde on Surinam River, Sauvain 175 (BBS, CAY, K, P); Browns Berg Nature Reserve, Kastelein 16153 (BBS). Commewijne: Akinto Soela, Mapanegebied, Sang 16866 (BBS); Mapanegebied, Elburg 9845 (BBS). Paramaribo: Rijsdijkeg, ca. 25 km S Paramaribo, Lindeman 4608 (U); achter Cultuurtuin, Stahel s.n. (B). VENEZUELA. Bolívar: Río Caura, Caño La Ceiba (Caño Cumaca), Stergios & Delgado 12940 (MO, PORT). Portuguesa: Est. Biol. Pozo Blanco, Mori et al. 9666 (NY).

Cultivated plants. French Guiana. Cult. Paris Museum, France, Mélinon s.n. (P); collected by Joep Moonen in March 1993, received from J. Boos, cult. MBG, G. Zhu 1440, 1441 (MO); Cayenne, cult. MBG [vouchered as Croat 74210], G. Zhu 1462, 1513 (MO). Brazil. Espírito Santo, cult. MBG [vouchered as Croat 71785], Zhu 1483, 1488 (MO); originally collected by H. van der Werff, cult. MBG [vouchered as Croat 71785] (MO). Singapore. Behind repair shed, Nicolson 1119 (US).

 Dracontium prancei G. Zhu & Croat, sp. nov. TYPE: Brazil. Amazonas: Pico Rondon, km 211, Perimetral Norte Hwy., 1°32'N, 62°48'W, 2 Feb. 1984, G. Prance, I. L. do Amaral, J. Pipoly, A. Tavares, C. D. A. la Mota & A. Cress 28732 (holotype, NY!). Figure 22.

Petiolus 1.6–2.5 m longus; pedunculus subterraneanus, 1–5 cm longus; spatha (10)15–18 cm longa, 3.2–4 cm lata; extus purpurea; intus velutina, purpurea; spadix (2.5)4–5 cm longus, 0.9–1.2 cm diam.; tepala 5; baccae globosae, 1–1.2 cm diam.; semina brunneola vel fusca, 0.5–0.6 cm diam.

Tuber hemispherical, 8-14 cm diam., 6-9 cm thick, flat above, rounded and white to brown below, 10-15 cm below ground level; tubercles abundant, rounded, 0.5-1 cm diam., borne around the periphery of tuber; roots whitish, to 0.3 mm diam.; cataphylls 4 or 5, 4-20 cm long, 2.5-4 cm wide, pink to light brown, 5-15 cm long above ground. Leaves solitary or sometimes two or more per tuber; petioles 1.6-2.5 m long above ground, 2.5-3.5 cm diam. at midpoint, dark green, contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, usually smooth in upper half and with irregular protuberances in lower half; juvenile blade sagittate, or sagittately lobed; mature blade spreading horizontally, 1-1.2 m diam., papyraceous, sometimes fenestrate, never variegated, without raphide cells or dark markings, glossy and medium green above, semiglossy and medium green below; middle division twice trichotomously branched, 55–65 \times 50–60 cm, with terminal subdivision consisting of 3 sections, with each basal subdivision consisting of many segments; lateral divisions once or twice dichotomously branched, 50- $60 \times 55-60$ cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections free from each other, each consisting of many segments; leaf segments often entire, broadly oblanceolate, more than 5 cm wide on each side of the major ribs, oblanceolate, mostly free from each other in each division, without contrastingly smaller rounded or triangular segments; apices acuminate; ultimate segments 10-13 cm long, free from penultimate segments; other segments 3-12 cm long; penultimate segments free from the subterminal sections; medial segments free from basal subdivisions; basal segments present, free from each other; rachises patterned distinct from petiole, pale green, smooth; tertiary veins conspicuous above and weakly raised below; bracteoles 3 or 4, 7-14 cm long, 3-5 cm wide, pink and light brown, the longest one longer than the peduncle, slightly covering the base of the spathe. Inflorescence solitary or sometimes two, appearing before new leaf; peduncle 1-5 cm long above ground, 1-1.2 cm diam. at midpoint, often almost completely subterranean, scarcely mottled, brownish green or whitish tinged pink, smooth; spathe (10-)15-18 cm long, 3.2-4 cm wide, cymbiform, cucullate, arching up to 45°, apex acuminate; inner surface semiglossy or velvety, maroon or blackish purple, with translucent area obvious, 0.5-1 cm high, shorter than spadix; outer surface maroon (sometimes tinged green), matte; margins entire, broadly overlapping in the lower two-thirds; veins obscure inside and raised outside, conspicuously darker or paler than the spathe; spadix hidden, stipitate, cylindric, narrower at apex, purple or brownish purple, (2.5–)4–5 \times 0.9-1.2 cm at anthesis, never with appendages at apex; stipe 0.5-0.8 cm long, 0.5-0.7 cm diam. at anthesis, purple. Flower tepals 5, 1.5-2.5 mm long, 1-2 mm wide, purple or brownish purple; stamens 6 or 7; filaments 1-2.5 mm long; anthers 0.5 mm long, completely exserted; ovary 3-locular, pale green; stigma 3-lobed; style 1-2 mm long above tepals, purple, persistent. Infructescence with spadix 5.5 cm long, 2.4 cm diam. in fruit; berries 1-seeded, 1-1.2 cm diam., 0.8-1 cm thick, subglobose, 3- to 6-angular, apically truncate; young berries light green; mature berries color unknown, with abundant raphide cells; seeds 0.5-0.6 cm diam., reniform, light brown or dark brown, laterally flattened; sparsely beset with irregular warts dorsally, dorsal ridges obscure. Chromosome number 2n = 26(Croat 73867).



Figure 22. A–D, Dracontium prancei. —A. Inflorescence in side view (Croat 73867). —B. Inflorescence with spathe cut away to expose spadix. —C. Apical portion of leaf blade (G. Zhu 1455). —D. Close-up of stigma (G. Zhu 150).

Phenology. Flowering known only in February; mature fruits are known only in May.

Distribution and habitat. Dracontium prancei is known only from Brazil in the states of Amazonas and Roraima. It occurs in the *Tropical moist forest* (T-mf) life zone (Holdridge et al., 1971), at elevations of 50 to 150 m.

Discussion. Dracontium prancei may be confused with D. asperum because of the similar sizes and shapes of the spathe, but the latter species differs in having bracteoles much shorter than the peduncles and never reaching the spathe (in contrast to elongate bracteoles that subtend the entire peduncle, even over the base of the spathe in D. prancei). Dracontium prancei has a short peduncle up to 5 cm above ground while D. asperum has a peduncle 5 to 17 cm above ground. Live plants of this species of unknown origin were widely distributed by the Munich Botanical Garden under the name D. polyphyllum, which differs from D. prancei in having a much shorter spathe 6–12 cm long versus (10-)15-18 cm long in D. prancei. The spadix is usually exposed in *D. polyphyllum* and completely embraced by the spathe in D. prancei. Dracontium prancei is another species that is easily grown and has great horticultural value. It grows rapidly, propagates easily by tubercles, and blooms regularly in cultivation. A plant of D. prancei is cultivated in the Climatron® at the Missouri Botanical Garden.

Dracontium prancei is named in honor of Ghillean Prance, whose many collections throughout the Amazon basin of Brazil include the type specimen of this species.

Paratype. BRAZIL. Roraima: SEMA Ecol. Res., S of Cachoeira de FumaHa, 24 July 1987, *Milliken et al.* 511 (K).

Cultivated plants. Origin unknown. Collected by J. Bogner, cult. at Munich Botanical Garden, Germany, 28 May 1994, J. Bogner 1132 (M), G. Zhu 1501 (MO). Originally from Munich Botanical Garden, Germany, received from W. Hetterscheid in Holland, cult. MBG, T. B. Croat 73867 (MO), G. Zhu 1458, 1463 (MO).

- 20. Dracontium purdieanum (Schott) Engl., Pflanzenr. IV. 23C (Heft 48): 45. 1911. Ophione purdieana Schott, Oesterr. Bot. Wochenbl. 7: 101. 1857. TYPE: Colombia. Magdalena: Santa Marta, 1845, W. Purdie s.n. (holotype, K!). Figure 23.
- Dracontium aricuaisanum G. S. Bunting, Phytologia 60: 301–302. 1985. TYPE: Venezuela. Zulia: Dtto. Perijá, outskirts of Est. Hidrol. Aricuaisá-Pie de Monte, 9°35'30"N, 72°53'55"W, 100–250 m, 25 Feb.–3 Mar. 1982, G. S. Bunting, G. Panapera & H. Lobo 10866 (holotype, NY!; isotype, VEN!).

Tuber hemispherical, 4-6 cm diam., 3.5-4 cm

thick, flat above, rounded and white to brown below, 9-16 cm below ground level; tubercles abundant, obovoid, 0.5-0.9 cm diam., 1-1.5 cm long, borne around the periphery of tuber; roots white, to 3 mm diam.; cataphylls 3 to 4, (3-)9-17 cm long, 2-3 cm wide, whitish to light brown, reaching or surpassing ground level. Leaves solitary; petioles 1-1.8 m above ground, 2.5-4 cm diam. at midpoint, dark green or brownish green (tinged gray), contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, smooth; juvenile blade sagittate, or sagittately lobed; mature blade spreading horizontally, 0.8-1.2 m diam., papyraceous, sometimes fenestrate, sometimes variegated, with abundant raphide cells and dark markings (1-2 mm long), semiglossy and medium green above, glossy and dark green below; middle division twice trichotomously branched, 50–65 \times 40–55 cm, with terminal subdivision consisting of 3 sections, with each basal subdivision consisting of many segments; lateral divisions twice dichotomously branched, 50-60 \times 45-50 cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections free, each usually consisting of a single segment; broadly oblanceolate, more than 5 cm wide on each side of the major ribs, oblanceolate, mostly free from each other in each division, without contrastingly smaller rounded or triangular segments; apices acuminate, or acute, or caudate (sometimes); ultimate segments 9-20 cm long, free from penultimate segments; other segments 1.5-10 cm long; penultimate segments free from subterminal sections; medial segments free from basal subdivisions; basal segments present, free from each other; rachises patterned distinct from petiole, pale green, smooth; tertiary veins obscure above and weakly raised below; bracteoles 3 to 4, 9-25 cm long, 2-3 cm wide, light brown, the longest one \pm as long as the peduncle, reaching the spathe. Inflorescence solitary, appearing before new leaf; peduncle 0-5 cm long above ground, 0.8-1 cm diam. at midpoint, often almost completely subterranean (0-5 cm above ground level), scarcely mottled, brownish green, with irregular protuberances or spiny projections (sometimes); spathe 6- 15×1.8 -3.5 cm, non-cymbiform, broadened at a certain point and differentiated into a proximal tube and a distal lamina (blade), non-cucullate, arching to 45°, apex acuminate; $1.5-3 \times 1.8-3.5$ cm at widest point; lamina 2 to 3 times longer than the tube; inner surface covered with dense, translucent scales 1-2 mm long, violet-purple or olive-brown, with translucent area obscure; outer surface violetpurple, tinged green, matte; margins entire, broadly



Figure 23. A–D, *Dracontium purdieanum*. A, B, (*Aristeguieta s.n.*). —A. Inflorescence at anthesis. Photo by J. Bogner. —B. Cultivated plant with leaf at Munich Botanical Garden. —C. Type specimen of *D. aricuaisanum* G. S. Bunting. —D. Seeds in lateral view (*Bunting 11463*).

overlapping at the base; veins conspicuous inside, conspicuously darker or paler than the spathe, purple; *spadix* exposed, sessile or stipitate, cylindric, brownish purple, 2-4 cm long, 0.5-1 cm diam. at anthesis, often with one to a few appendages at apex, 0.2-0.5 cm long when present; stipe 0.8 cm long, 0.5 cm diam. at anthesis, light brown. Flower tepals 4 to 6(to 7), 1-2 mm long, 1 mm wide, green or light brown; stamens 6 or 7; filaments 1-2 mm long; anthers 0.5 mm long, slightly exserted; ovary 3- to 5-locular, pale green; stigma 3- or 4-lobed; style 0.5-1 mm long above tepals, greenish, not persistent. Infructescence with spadix 4.5-5 cm long, 3.5-4 cm diam. in fruit; berries (1)3- to 4(5)seeded, 1-1.2 cm diam., 1-1.3 cm thick, subglobose, 3- to 6-angular, apically truncate; young berries dark green; mature berries purplish red, sometimes with abundant raphide cells; seeds 0.5-0.7 cm diam., reniform, dark brown, laterally depressed; dorsal ridges obvious, 3 continuous ridges (sometimes with 1-2 strongly intermediate interrupted dorsal ridges), less than 0.5 mm thick, 0.3 mm high, warty along ridges. Chromosome number 2n = 26 (Aristeguieta s.n.; Petersen, 1989).

Phenology. Flowering from February to March; mature fruits from April to May.

Distribution and habitat. Dracontium purdieanum is known only from the Caribbean coastal departments of Atlántico, Magdalena, and Bolívar in Colombia, and Zulia, Venezuela. It occurs in *Tropical moist forest* (T-mf) and *Premontane moist forest* (P-mf) life zones (Holdridge et al., 1971) along the coast, at elevations from sea level to 250 m.

Discussion. Dracontium purdieanum is characterized by having the inner surface of the spathe densely covered with translucent scales $(1-2 \text{ mm} \log)$, and a spadix that often has appendages at the apex. This species is vegetatively similar to *D*. *dubium* but differs from that species in having seeds with 3 continuous ridges (sometimes with 1– 2 strongly intermediate interrupted dorsal ridges).

In 1845, a year after Schomburgk's expedition to British Guiana (Guyana), William Purdie collected a second plant presently included in *Dracontium* from the vicinity of Santa Marta, Magdalena Department, Colombia. This collection was named *Ophione purdieana* Schott as a new unispecific genus, which differs from *Dracontium* in having a long-acuminate spathe (Schott, 1857a). Later, Engler (1911) placed this species in *Dracontium*, citing "*D. purdieanum* (Schott) Hook. f. in Bot. Mag. (1873) in observatione ad tabulam 6048." However, no such combination was made by J. D. Hooker in that publication. Instead, Engler himself validly published the combination (1911: 45), citing the basionym after *D. purdieanum*, which combination must therefore be attributed to "(Schott) Engler" according to the *Code* (Art. 46, Greuter et al., 2000).

In the protologue of *Ophione purdieana* Schott (1857a: 101), there is no explicit type designation, but it was clearly stated that the name, which honors the collector, was based on a gathering made by "Purdie" from "St. Marta." This constitutes mention of a single gathering as indication of the type (Art. 37.3, Greuter et al., 2000). A specimen (*Purdie s.n.*, K, 1845) collected near Santa Marta in Colombia is evidently the same one used by Schott when describing *O. purdieana*. Schott (1858b: t. 89) published an illustration of the species a year after its original description. The spathe in the illustration matches that of *Purdie s.n.* in great detail. *Purdie s.n.* can therefore be regarded as the holotype of *O. purdieana* Schott.

More than a century after its discovery, *Dracontium purdieanum* was re-collected and redescribed by Bunting (1986) as *D. aricuaisanum* from Aricuaisá–Pie de Monte in Zulia State, Venezuela. Bunting's new species differed from *D. purdieanum* in no significant way.

Additional specimens examined. COLOMBIA. Atlántico: along trail from Luruaco to Piñar de Candelaria, Dugand 1161 (F). Bolívar: lands of Loba, Caño Papayal, vic. of Estrella, Curran 349 (GH, US). VENEZUELA. Zulia: betw. Aricuaisá [Ariguaisá] & Pie de Monte on Río Aricuaisá, 55 km SW of Machiques by air, Liesner & González 13060 (MO, VEN).

Cultivated plants. Venezuela. Zulia, Aricuaisá, cult. at Munich Botanical Garden, Germany, Aristeguieta s.n. (M).

- 21. Dracontium soconuscum Matuda, Amer. Midl. Naturalist 41: 494. 1949. TYPE: Mexico. Chiapas: Soconusco, Santa Elena, 16 km W of Acapetagua, 30 m, Jan. 1947, *E. Matuda* 17780 (lectotype, designated here, MEXU 85137! pro parte, inflorescence; isotypes, MEXU!, NY!). Figure 24.
- Dracontium dressleri Croat, Selbyana 1: 168. 1975. Syn. nov. TYPE: Panama. Canal Zone: Barro Colorado Island, near end of Zetek trail, 30 June 1972, *R. Dressler s.n.* (holotype, MO!).

Tuber hemispherical or rounded, 4–7 cm diam., 5–9 cm thick, flat above, rounded and white to brown below, 4–45 cm below ground level; tubercles few, cylindrically elongated, 0.5–0.8 cm diam., 0.5–1 cm long, borne around the periphery of tuber; roots whitish or sometimes tinged green, to 3 mm diam.; *cataphylls* 3 or 4, 3–47 cm long, 2–3.5 cm wide, pink or light brown (when dried), reaching



Figure 24. A-D, *Dracontium soconuscum*. —A. Cultivated by J. Bogner. Inflorescence at anthesis in face view. Photo by Bogner. B, C, (*G. Zhu 1502*). —B. Inflorescence side view. —C. Leaf blade adaxial surface. —D. Seeds in lateral view (*Bartlett & Lasser 16831*).

or surpassing ground level. Leaves solitary or sometimes two or more per tuber; petioles 1-1.8 m long above ground, 3-5 cm diam. at midpoint, dark green or gray or whitish green, sometimes tinged brown or red-brown, weakly mottled, usually smooth in upper half and with irregular protuberances in lower half; juvenile blade sagittate, or sagittately lobed; mature blade ascending to 45° to the petiole spreading horizontally, 1-1.2 m diam., subcoriaceous papyraceous, sometimes fenestrate, never variegated, without raphide cells or dark markings, semiglossy and dark green above, matte and medium green below; middle division 3 times or more trichotomously branched, 0.8–1.5 \times 0.6–1 cm, with terminal subdivision consisting of 3 sections, with each basal subdivision consisting of many segments; lateral divisions 3 times or more dichotomously branched, $0.8-1 \times 0.5-0.8$ cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections free, each consisting of many segments; leaf segments bilobed, broadly oblanceolate, more than 5 cm wide on each side of the major ribs, oblanceolate or orbicularovate, at least some of the basal segments free from each other, often with contrastingly smaller rounded or triangular segments alternating with larger segments; apices acuminate, or acute; ultimate segments 7-17 cm long, free from penultimate segments or rarely confluent with penultimate segments; other segments 5-15 cm long; penultimate segments free from subterminal sections; medial segments free from basal subdivisions; basal segments absent, free from each other; rachises patterned similar to petiole but in much paler shades, similar to petiole but in a much paler scale; tertiary veins obscure above and weakly raised below; bracteoles 1 to 3, 5-45 cm long, 1.5-2.5 cm wide, pink to light brown, the longest one longer than the peduncle, covering the basal half or more of the spathe. Inflorescence solitary or rarely two, appearing before new leaf; peduncle 4-45 cm long above ground, 0.8-1.2 cm diam. at midpoint, often almost completely subterranean (0-5 cm above ground level), scarcely mottled, whitish tinged pink, smooth; spathe 6-8(10) cm long, 3-4(6) cm wide, non-cymbiform, constricted at a certain point and differentiated into a proximal tube and a distal lamina (blade), cucullate, arching 45°-90°, apex acuminate; 1-3 cm long, 2.5-4(5) cm wide at widest point; lamina similar to the tube in length (or slightly longer); inner surface glossy, violet-purple or maroon, with translucent area obscure; outer surface olive-brown or maroon, semiglossy; margins entire, broadly overlapping in the lower half; veins obscure

inside or raised outside, similar to the spathe in color, purple; spadix exposed, stipitate, cylindric, violet-purple, $1-4 \times 0.5-1$ cm at anthesis, often with several appendages at apex, 0.5-0.8 cm long when present; stipe $0.3-0.7 \times 0.5-0.6$ cm at anthesis, light brown. Flower tepals (4)5 or 6(8), 2-2.5 mm long, 1 mm wide, dark purple; stamens (5)6 or 7(9); filaments 1-1.5 mm long; anthers 1-2 mm long, slightly exserted; ovary 2- to 5-locular, pale green; stigma 3-lobed; style 0-1 mm long above tepals, dark purple, not persistent. Infructescence with spadix 4-10 cm long, 2-3.5 cm diam. in fruit; berries 4-seeded, 0.8-1.4 cm diam., 1-1.5 cm thick, subglobose, 4- to 5-angular, apically truncate; young berries dark green; mature berries purplish brown, with abundant reddish dots; seeds 0.6-0.9 cm long, 0.5-0.6 cm diam. (wide), reniform or triangular (\pm) , dark brown, laterally depressed; dorsal ridges obvious, 3, continuous, monomorphic, more than 1 mm thick, 0.1-0.5 mm high, warty along both sides, appearing as strongly reduced lateral ridges.

Phenology. Flowering from October to April; mature fruits from April to August.

Distribution and habitat. The northernmost species of the genus, Dracontium soconuscum is known from the Pacific slope in southern Mexico (Chiapas) and northern Costa Rica (Guanacaste, Alajuela, Puntarenas), and on the Caribbean slope in central Panama (Canal Zone). It occurs in costal lowland thicket or bushes of the Tropical moist forest (T-mf) life zone (Holdridge et al., 1971), from sea level to about 1100 m.

Local names. "Cola de tigre" (E. Matuda 17780, MEXU, NY).

Discussion. Dracontium soconuscum is easily confused vegetatively with *D. grayumianum*, but that species differs in having seeds with five or six strongly interrupted dorsal ridges, whereas *D. soconuscum* has seeds with three obvious and continuous dorsal ridges.

According to the protologue, the type of *Dracontium soconuscum, E. Matuda 17780,* consists of a holotype in the Matuda Herbarium (CHIS) and two isotypes (MEXU 6739, F). The holotype was later transferred to MEXU (MEXU 85137) and the isotype intended for F was evidently sent to NY instead. The type is a mixed collection of two gatherings prepared by the same collector in January and May, 1947, respectively. Since a type can only be a single gathering (Art. 8, Greuter et al., 2000), the inflorescence on MEXU 85137 is designated here as the lectotype of *D. soconuscum.*

There are three other gatherings existing under

the same collection number: *Matuda 17780* (MEXU 47893) collected from Cruz do Piedra, January and May 1947; *Matuda 17780* (MEXU 85107) collected from Nandolopez, January and May 1947; and *Matuda 17780* (MEXU 141842) collected from Santa Teresa, Acapetagua, on 14 July 1947.

Additional specimens examined. COSTA RICA. Alajuela: Finca Carlos Gómez, Orotina, Chacón 1414 (MO); La Balsa de Río Grande, Pittier 3650 (US). Guanacaste: Río Higuerón, near Taboga, Liesner et al. 2720 (MO). Puntarenas: rd. to Monteverde, Luteyn 3394 (DUKE); Garabito Canton, Res. Biol. Carara, along S side of Río Grande de Tárcoles, from Carretera Constanera to Río Carara, Grayum et al. 11108 (MO). MEXICO. Chiapas: Mazapa, 10 km E of Motozintla, Garcia et al. 1527 (BM). PANAMA. Canal Zone: Pittier 3429 (US); Barro Colorado Island, Zetek Trail, Croat 27795 (MO); Juan Mina, Chagres River, Bartlett & Lasser 16831 (F, MO, NY); vic. Summit Hills Golf Course, Croat 27794 (MO). Coclé: Camp Piña, Allen 3427 (MO). Colón: Achiote, 1974, Dressler s.n. (DUKE, PMA); Gamboa Country Club Marina, Garwood 1639A (F). Panamá: Río Agua Clara, Icantí, Gentry 2598 (MO).

Cultivated plants. Panama. Barro Colorado Island, cult. Munich Botanical Garden [vouchered as Croat 27795], Bogner s.n. (M); Colón, Achiote, STRI [vouchered as Dressler s.n.], G. Zhu 1502 (MO); Canal Area, cult. Fairchild Tropical Garden, Miami, Florida, U.S.A., Fantz 4115, 4249 (FTG); cult. Selby Gardens, Madison 3764 (SEL); cult. by Dewey Fisk, Florida (received from J. Boos), G. Zhu 1485 (MO).

- 22. Dracontium spruceanum (Schott) G. Zhu, Novon 6: 308. 1996. Echidnium spruceanum Schott, Oesterr. Bot. Z. 8: 350. 1858. Cyrtosperma spruceanum (Schott) Engl., Martius, Fl. Bras. 3(2): 118. 1878. TYPE: Brazil. Amazonas: São Gabriel, May 1852, R. Spruce 2406 (holotype, K!). Figures 3C, 3D, 25, 26.
- Dracontium carderi Hook. f., Bot. Mag. t. 6523. 1880. Syn. nov. TYPE: Colombia. Apr. 1879, N. E. Brown s.n. (holotype, K! [3]). [Cultivated plant by Mr. Bull, originally collected by Carder in Colombia, locality unknown.]
- Dracontium costaricense Engl., Pflanzenr. 4, Fam. 23C(44). 1911. Syn. nov. TYPE: Costa Rica. Limón: Talamanca, forest of Shirones, 100 m, Feb. 1895, H. Pittier 9232 (holotype, BR!; isotype, B!).
- Dracontium trianae Engl., Pflanzenr. 4, Fam. 23C(44). 1911. Syn. nov. TYPE: Colombia. Meta: Villavicencio, 400 m, Jan. 1856, J. J. Triana 691 (lectotype, designated by Zhu (1996: 309), BM!; isotype, COL!).
- Dracontium loretense K. Krause, Notizbl. Bot. Gart. Berlin-Dahlem 11: 617. 1932. Syn. nov. TYPE: Peru. Loreto: lower Río Huallaga, 155–210 m, Oct.–Nov. 1929, L. Williams 5144 (holotype, F!; isotype, US!).
- Dracontium ornatum K. Krause, Notizbl. Bot. Gart. Berlin-Dahlem 15: 40. 1940. Syn. nov. TYPE: Ecuador. Pastaza: above Mera, 1100 m, 16 Nov. 1938, A. Schultze-Rhonhof 2998 (holotype, B! [on sheet with Schultze-Rhonhof 3031]).

Tuber hemispherical, 4–18 cm diam., 3–10 cm

thick, flat or slightly convex above, rounded and white to brown below, 15-40 cm below ground level; tubercles abundant, rounded, 0.5-2 cm diam., borne around the periphery of tuber; roots to 4 mm diam.; cataphylls 1 to 3, 10-40 cm long, 2-4 cm wide, pink to light brown, reaching or surpassing ground level. Leaves solitary; petioles 1-3 m long above ground, 1.2-4 cm diam. at midpoint, dark green, contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, usually smooth in upper half and with irregular protuberances in lower half; juvenile blade sagittate, or sagittately lobed; mature blade spreading horizontally, 0.9-1.5 m diam., subcoriaceous to thinly coriaceous, rarely fenestrate, never variegated, without raphide cells or dark markings (often), semiglossy and dark green above, matte and medium green below; middle division once or twice trichotomously branched, $47-60 \times 45-55$ cm, with terminal subdivision never divided into sections, with each basal subdivision consisting of many segments; lateral divisions twice dichotomously branched, $45-62 \times 50-60$ cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections often free, each consisting of many segments; broadly oblanceolate, more than 5 cm wide on each side of the major ribs, oblanceolate or elliptic, mostly free from each other in each division, without contrastingly smaller rounded or triangular segments (often); apices caudate; ultimate segments 12-35 cm long, confluent with penultimate segments or free from penultimate segments; other segments 4.5-30 cm long; penultimate segments free from subterminal sections; medial segments free from basal subdivisions; basal segments present, free from each other; rachises patterned similar to petiole but in much paler shades, smooth; tertiary veins obscure above and weakly raised below; bracteoles 1 to 3, 4-45 cm long, 1-3 cm wide, pinkish or light brown, the longest one much shorter than the peduncle, confined at the base. Inflorescence solitary, appearing before or after new leaf; peduncle 60-150 cm long above ground, 2-3.5 cm diam. at midpoint, more than half as long as the petiole or sometimes as long as or longer than the petiole, mottled similar to petiole but deeper in color, dark green or brownish green, smooth or with irregular protuberances in lower half; spathe (20-)25-35 cm long, 3-6 cm wide, non-cymbiform, constricted at a certain point and differentiated into a proximal tube and a distal lamina (blade) or cymbiform (rarely), non-cucullate, erect or slightly arching, apex acuminate; 5-10 cm long, 3-6 cm wide at widest point; lamina 3 to 5



Figure 25. A-D, *Dracontium spruceanum*. —A. Habit showing flowering plant (*G. Zhu 1503*). —B. Spathe at anthesis split open to show the pale basal portion and the spadix (*G. Zhu 1486*). —C. Cultivated by Luis Bueno, Miami. Petioles and juvenile infloresence. —D. Seeds in lateral view (*Cerón 72368*).



Figure 26. A, B, *Dracontium spruceanum (G. Zhu 1486)*. —A. Side view of pistil showing unopened anthers. — B. Apex of flower showing tip of pistil with emerging threads of pollen.

times longer than the tube; inner surface semiglossy, maroon or olive-brown, with translucent area obvious, 4-8 cm high, 1.5 to 3 times longer than spadix; outer surface maroon, tinged green, or green, matte; margins entire, broadly overlapping at the base; veins obscure inside or raised outside, similar to the spathe in color; spadix hidden, stipitate, cylindric, purple or brownish purple or brown, (2.5- $)3-4(-6.5) \times 0.6-1$ cm at anthesis, never with appendages at apex; stipe $0.5-0.8 \times 0.4-0.6$ cm at anthesis, pale green or light brown. Flower tepals 4 to 5, 1.5-2 mm long, 1-2 mm wide, purple; stamens 6 to 11; filaments 1-1.5 mm long; anthers 0.5 mm long, slightly exserted; ovary 3-locular, pale green; stigma unlobed, or 2- to 3-lobed; style 0.5-1 mm long above tepals, purple, persistent. Infructescence with spadix $8-16 \times 2.5-3.5$ cm in fruit; berries 1- or 2-seeded, 0.5-0.7 cm diam., 0.7-1 cm thick, globose or obliquely obovoid, apically rounded (sometimes slightly concave around the persistent style); young berries medium green; mature berries orange, without reddish dots and raphide cells; seeds 0.5-0.7 cm long, 0.4-0.5 cm diam., elongated or rounded, reddish brown, laterally depressed; dorsal ridges obvious, more than 3, strongly interrupted (often), with the central ridge contrastingly raised, more than 1 mm thick, 0.1-0.3 mm high, warty along ridges.

Phenology. Flowering throughout the year; mature fruits throughout the year.

Distribution and habitat. Dracontium spruceanum ranges from the Caribbean coastal plain of Costa Rica (Limón) to Colombia and Ecuador (on both sides of the Andes) and Amazonian Ecuador, Peru, Venezuela, and Brazil. It has also been collected from Surinam. It occurs in *Tropical moist forest* (Tmf), *Premontane wet forest* (P-wf), and *Tropical wet forest* (T-wf) life zones (Holdridge et al., 1971), at elevations of 25 to 1215 m.

Local names. "Tamá kida bari" (La Rotta 586, COL); "chupadera" (Archer 1729, US); "papayuëla" (Idrobo & Cuatrecasas 2685, COL); "machaqui mandi" (Alarcon 62, QCA); "jergón sacha" (Vásquez & Jaramillo 4938, MO).

Discussion. Dracontium spruceanum is the most morphologically plastic and widely distributed species in the genus. It is characterized by its usually erect or slightly arching (non-cymbiform) spathe, which differentiates into a proximal tube and distal lamina (blade), with the translucent area of the inner spathe surface 1.5 to 3 times longer than the spadix, and by having the rachises of the leaf blades usually naked.

Dracontium carderi, D. costaricense, D. loretense,

D. ornatum, and *D. trianae* are synonymized here for the first time. The differences among the type specimens are slight. They closely resemble each other and the type of *D. spruceanum*, especially in spathe shape and peduncle length.

Dracontium spruceanum was first described by Schott (1858b) as Echidnium spruceanum in honor of Richard Spruce, who collected the holotype (Spruce 2406, K) at São Gabriel along the Rio Negro in Amazonas, Brazil. This name was later transferred to the genus Cyrtosperma by Engler (1878), and subsequently not considered to be a Dracontium based on Engler's inference of a unilocular ovary. This is a misinterpretation, since anatomical study indicates that the specimen is too young to yield accurate information (Richard Keating, pers. comm.). Further, specimens collected near the type locality usually have a single ovule in each of two or three locules per ovary.

Dracontium spruceanum shares a long peduncle with D. asperispathum, D. croatii, D. grandispathum, D. longipes, D. peruvianum, D. pittieri, and D. plowmanii. Dracontium croatii, D. pittieri, and D. peruvianum differ in having a cymbiform spathe that is not differentiated into a proximal tube and a distal lamina, whereas the others listed above have a non-cymbiform spathe that is constricted at the base to form a proximal tube and distal lamina. Dracontium plowmanii differs from D. spruceanum (as well as *D. asperispathum* and *D. grandispathum*) in having smaller seeds with a single dorsal ridge and a spathe usually wrinkled along the margins. Dracontium asperispathum also differs from D. spruceanum in having the inner spathe surface densely covered with translucent scales (vs. the inner spathe surface semiglossy in D. spruceanum). Finally, D. grandispathum differs from D. sprucean*um* in having a much larger spathe that is abruptly acuminate at the apex (45-50 cm long and 10-15 cm wide vs. 20-35 cm long and 3-6 cm wide and gradually acuminate for *D. spruceanum*).

Additional specimens examined. BRAZIL. Amazonas: basin of Rio Purus, Capoeira on Rio Cunhuá at Canahuá, Prance et al. 16400 (INPA, NY, U, US); Benjamim Constant, Alto Solimões, Duarte 6909 (MO, RB); Manaus, km 18 da BR-17, Luiz 2996 (INPA, MG); Río Solimões, Tonantins, Froes 12233 (NY). COLOMBIA. Caquetá, San Vicente del Caguán, Neiva-San Vicente, Betancur et al. 1874 (COL). Amazonas: Río Amazonas, 2 km downriver from Puerto Nariño, Plowman et al. 2412 (COL, ECON, GH); Mun. Leticia, PN Amacayacu, Rudas et al. 3724 (MO). Antioquia: Maceo, hacienda Santa Bárbara, parcela de don Cipriano, Quebrada "Guarda sol," Fonnegra et al. 7738 (HUA, K, MO, US); Corr. Providencia, above hydroelectric plant, Soejarto & Villa 2750 (GH); Par. Nac. Nat. "Las Orquídeas," Cogollo et al. 4063 (JAUM), Cogollo et al. 3583 (JAUM); 2 km S of Chigorodó, Haught

4585 (COL); San Luís, Cañón del Río Claro, Cogollo et al. 1455 (JAUM); Segovia, km 15 via Zaragoza Cerro Cabezas, Río Pocuné, Cardona et al. 52 (COL). Chocó: Bolívar-Quibdó, km 67, Grayum et al. 7638 (MO); Alto Río Baudó, Resguardo Indígena Emberá, La Rotta 586 (COL); La Mojarra, near Istmina, Juncosa 1307 (JAUM, MO); La Oveja-Quibdó, Archer 1729 (US); Pueblo Rico-Istmina, Quebrada Antón, 15 km W of Santa Cecilia, Croat 70886 (MO, TULV); Quibdó-Río Atrato, Idrobo & Cuatrecasas 2685 (COL); Río Fujiadó, tributary of Río San Juan, Forero et al. 4823 (COL). Meta: Honoria, Bosque Nac. Iparia, toward El Parrao, Pittier 1775 (F); Río Duda near the mouth of Río Guayabero, Pérez 7191 (COL); Llanos de San Martín, Madison 848 (GH); La Serranía, Río Ariari at Aguasucia Lake, Jaramillo 1036 (COL); Río Guatiquia, André 1025 (K); Sabanas de San Juan de Arama, Río Ghejar, near Los Micos airport, Idrobo 1193 (COL); Sierra de la Macarena, Caño Entrada, Philipson 2203 (COL); Villavicencio, Cuatrecasas 4633 (F, US), Triana 289 (BM). Nariño: Fumaco, resguardo indígena Alto Albí, M. S. González 125 (COL); Tumaco, Llorente, Albí, Cuasambí, M. S. González 13 (COL). Santander: Landazuri, Cerro de Armas, 70 km N of Velez, Fassett 25426 (NY, US); Puerto Berrio, Haught 2203 (US); Barranca bermeja, Haught 1575 (US). Valle: Cordillera Occidental, W slope, Río Sanquininí, La Laguna, Cuatrecasas 15697 (F). Vaupés: Mitú, Río Vaupés, base of Cerro de Mitú, Zarucchi 1916A (COL); Mitú-Javareté, Schultes & Cabrera 17184 (GH); Río Piraparaná Caño Teemeeña, Schultes & Cabrera 17184 (GH). COSTA RICA. Limón: BriBri on Río Sixaola, Río Catarata, Baker & Burger 111 (F, MO); Fila Carbón, 6 km E of Home Creek, Hammel et al. 18119 (CR); Quebrada Mata de Limón, Grayum et al. 4461 (MO); E of Puerto Viejo de Sarapiquí, Gravum 4417 (MO); 2 km S of Manzanillo de Talamanca, Grayum et al. 4388 (MO); Res. Indígena Talamanca, Amubri-Cachabri, Chacón 1 (MO); 1.5 km above jct. of Río Urén and Río Sukut, Herrera 3189 (CR). ECUADOR. Manabí: Machalilla Nat. Park near Puerto López, Gentry & Josse 72402 (MO). Napo: 8 km E of Puerto Misahuali, Hedin 144 (MO); Jatun Sacha, Cerón 1046 (MO, QCNE); Limón Cocha, Madison et al. 5343 (SEL); Nueve Rocafuerte, Alarcon 62 (QCA); Reserva Faunistica Cuyabeno, Río Aguarico, Palacios et al. 7660 (QCNE); Río Arajuno, Sola Cocha, Neill et al. 6978 (F, MO, QCA); 6 km NNW of Ahuano, Kohn 1193 (MO, WIS); Añangu, Lawesson et al. 39334 (AAU); San José de Payamino, 40 km W of Coca, Irvine et al. 968 (F); Res. Ecol. Antisana, Shamato, J. L. Clark et al. 5014 (MO, QCNE); Hollín-Loreto, N of Archidona, Whitten et al. 93091 (MO); Río Shiripuno, Huantime, J. S. Miller & P. Yépez, Bai 562 (QCA); Laguna Limoncocha, Jaramillo & Grijalva 11555 (QCA); Chiro Isla, Río Napo, R. Bensmab 189 (QCA). Pastaza: Lorocachi, 3 km from Río Curaray, Jaramillo et al. 30780 (AAU, MO); S of Río Curaray, mouth of Río Querano, Neill & Palacios 6760 (MO); Mera, Plowman 4490 (GH, S); 19 km S of Puyo, Croat 50533 (MO, QCA). Sucumbios: Parroquia Gonzalo Pizarro, 8 km SW of Recinto Amazonas, Yánez & Shuigra 854 (QCA). Zamora-Chinchipe: between La Saquea and Yacuambí, 1 km N of Chapintza, Harling & Andersson 23856 (GB); Pachicutza, trail to Hito, Palacios et al. 8309 (MO). PANAMA. Bocas del Toro: trail to Quebrada Rabo de Puerco, Santamaría et al. 803 (PMA); Santa Rosa on Río Changuinola, G. Zhu 1503 (MO). Coclé: Distrito Olá, Potrero Llano-Volteadera via La Pintada and Llano Grande. 16 Feb. 2000, Guerra & Wong 1036 (PMA); Alto Calvario, 5-7 km N of El Cope, Thompson 4733 (CM). Colón: Guasimo, Croat 9925 (MO); Santa Rita Ridge, Croat 34334 (MO). Darién: upper Río Tuquesa, Clezio 25 (MO). Panamá: Campo Tres, 3 mi. NE of Altos de Pacora, Croat 22756 (MO); Altos de Pacora NE of Cerro Azul, Dressler 4608 (PMA); Cerro Jefe area, Dressler 3397 (PMA); Parque Nacional Altos de Campana, Serrania del Llorón, Galdames et al. 4382 (PMA); El Llano-Cartí Rd., mi. 6-10, Churchill 3824 (MO). San Blas: vic. Cangandí, de Nevers & Herrera 5668 (MO); Cerro Brewster, de Nevers et al. 6283 (MO); El Llano-Cartí rd., Nusagandí, G. Zhu 1504 (MO); SW of Puerto Obaldía, Croat 16799 (MO). Veraguas: Santa Fe area, N Alto de Piedra, Croat 23126 (MO). PERU. Amazonas: Río Huampami, Kayap 1327 (MO); Galilea, Río Santiago, Berlin 3579 (MO); Quebrada Caterpiza, Río Santiago, 65 km N of Pinglo, Huashikat 428 (MO); Río Cenepa, Ancuash 129, 164 (MO); Huampami, ca. 5 km E of Chávez Valdivia, Ancuash 1415 (MO). Loreto: Iquitos, Alpahuayo, Vásquez 15226 (MO); Andoas, Vásquez 3005 (MO); Yanamono Exp. Camp, 50 km by river from Iquitos, J. P. Hedin & M. C. Hedin 107 (MO); Río Momon, trib. of Río Nanay, near Iquitos, Gustafson 1972 (MO); Pto. Almendras, Yurimaguas, Croat 17986 (MO); San Antonio, Río Itaya, Jaramillo 3598 (MO); Río Macusari, McDaniel 11018 (IBE). SURINAM. Nickerie: Nabij Kamp Koewinikreek, Elias 17317 (BBS). VENEZUELA. Amazonas: 1 km S of San Carlos de Río Negro, Liesner 9047 (MO, VEN).

Cultivated plants. Cult. Great Britain, Chelsea, William Bull's, Carder s.n. (K). Ecuador. Napo, Limón Cocha, 240 m, coll. by Madison, Plowman, and Besse, cult. at Kew (162-80-1627), from Selby 1978-2038, Mayo 130 (K); Napo, cult. at MBG, from Selby 76-95-4, G. Zhu 1499, 1490 (MO); Coca, 0°28'S, 76°58'W, cult. by B. Feuerstein, Croat 75574, 75402; G. Zhu 1494, 1511 (MO); Limón Cocha, cult. at MBG, from Selby 78-2038, G. Zhu 1448, 1486 (MO); Morona-Santiago, cult. by Betsy Feuerstein, vouchered as Croat 78393 (MO); Zamora-Chinchipe, Pachicutza, 900 m, coll. by Henk van der Werff, Mar. 1994, G. Zhu 1492 (MO); Pastaza, Mera, cult. at Selby Gardens (95-76-14), Plowman 4490 (SEL), Christenson 1102 (SEL), Cobb 45 (SEL), Madison 4176 (SEL not seen); Esmeraldas, 10 mi. N of Lita in July 1989, coll. by Morell, Hyndeman & Fisk, from J. Boos (West Palm Beach, Florida), cult. at Dewey Fisk's, Davie, Florida, G. Zhu 1443 (MO).

23. Dracontium ulei K. Krause, Notizbl. Bot. Gart. Berlin-Dahlem 6: 115. 1914. TYPE: Brazil. Acre: near São Francisco & Alto Xapury, Oct. 1911, E. Ule 9215 (holotype, B!; isotypes, B not seen, K!). Figure 27.

Tuber hemispherical or rarely rounded, 6–12 cm diam., 6–9 cm thick, flat above, rounded, white to brown below, 8–20 cm below ground level; tubercles few, rounded or cylindrically elongated, $0.5-1 \times 1-1.5$ cm, borne around the periphery of tuber; roots white, sometimes tinged pink above the tuber, to 2.5 mm diam.; *cataphylls* 1 (concealed from view soon after leaf development), 10–20 cm long, 1–2 cm wide, light brown, reaching or surpassing ground level. *Leaves* solitary; *petioles* 1–1.2 m long above ground, 2–4 cm diam. at midpoint, dark green tinged



Figure 27. A–D, *Dracontium ulei*. —A. Two separate inflorescences, one in face view, one cut into two halves (*Nee* 31734). —B. Two infructescences with base of petiole, the inflorescence on the right with the spathe still persistent, the one on the left with loosening berries. —C. Leaf showing the three divisions of the blade (*Croat* 85115). —D. Seeds in lateral view (*Ule* 9215).

brown, contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, usually smooth in upper half and with irregular protuberances in lower half; juvenile blade sagittate, or sagittately lobed; mature blades ascending to 45° to the petiole (often), 0.8-1 m diam., papyraceous, rarely fenestrate, never variegated, with abundant raphide cells and often dark markings, glossy and medium green above, glossy and dark green below; middle division twice trichotomously branched, 50- 60×50 -55 cm, with terminal subdivision consisting of 3 sections, with each basal subdivision consisting of many segments; lateral divisions twice dichotomously branched, 50–65 \times 55–60 cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections free; leaf segments often entire, broadly oblanceolate, more than 5 cm wide on each side of the major ribs, oblanceolate, mostly free from each other in each division, often with contrastingly smaller rounded or triangular segments alternating with larger segments; apices acuminate; ultimate segments 10-15 cm long, often free from penultimate segments; other segments 3-8 cm long; penultimate segments free from subterminal sections; medial segments free from basal subdivisions; basal segments present, free from each other; rachises patterned distinct from petiole, pale green, smooth; tertiary veins obscure above and weakly raised below; bracteoles 2 or 3, 8–20 \times 1–2 cm, pink, the longest one \pm as long as the peduncle, reaching the spathe. Inflorescence solitary, appearing before new leaf; peduncle 8-20 cm long above ground, 0.6-0.8 cm diam. at midpoint, often almost completely subterranean, scarcely mottled, whitish tinged pink, smooth; spathe 6-10 cm long, 3-4 cm wide, non-cymbiform, constricted at a certain point and differentiated into a proximal tube and a distal lamina (blade), cucullate, arching 45°-90°, apex acuminate; $4-6 \times 3-4$ cm at widest point; lamina shorter than the tube; inner surface covered with dense, translucent scales to 1 mm long, violet-purple, with translucent area obscure; outer surface maroon tinged brown, matte; margins entire, broadly overlapping in the lower two-thirds; veins obscure inside and outside, similar to the spathe in color; spadix hidden, stipitate, cylindric, brown-purple, 3-4 cm long, 1.2-1.4 cm diam. at anthesis, never with appendages at apex; stipe 0.4-0.5 cm long, 0.5 cm diam. at anthesis. Flower tepals 4 to 6, 2-3 mm long, 1-1.5 mm wide, light brown; stamens 4 to 6; filaments 1.5-4 mm long; anthers 0.8 mm long (elliptic), completely exserted; ovary incompletely 3- or 4-locular, white; stigma 3- or 4-lobed; style 1-1.5 mm long above tepals, brownish purple, persistent. Infructescence with spadix 6-7(-10) cm long, 1.5-2(-3) cm diam. in fruit; berries 2-seeded, young berries 0.4-0.5 cm diam., 0.5-0.7 cm thick, obliquely obovoid, apically subtruncate; young berries medium green; mature berries color unknown, with abundant raphide cells; seeds 0.4-0.5 cm diam., reniform, reddish brown, laterally raised, smooth; dorsal ridges obscure.

Phenology. Flowering in early September; young infructescences collected in October and mature fruits in October.

Distribution and habitat. Dracontium ulei ranges from Acre, Brazil, to Pando, Bolivia. It occurs in the *Tropical moist forest* (T-mf) life zone (Holdridge et al., 1971), at 125–230 m.

Local names. "Milho de cobra" (Lowrie et al. 592, NY).

Discussion. Dracontium ulei is characterized by its usually subterranean peduncle and inner surface of the spathe densely covered with translucent scales. It is easily confused with D. bogneri, which shares a cucullate spathe covered inside with translucent scales. However, D. bogneri has seeds laterally depressed with 3 obvious dorsal ridges (vs. laterally raised with obscure dorsal ridges for D. ulei). Dracontium ulei is also close to D. dubium and D. purdieanum, but can be distinguished by its spadix concealed at anthesis and deeply hooded spathe with small scales to 1 mm long on the inner surface. The latter two species differ by having the spadix exposed at anthesis and a spathe that is not hooded and lacks scales this small on the inner surface.

Additional specimens examined. BOLIVIA. Pando: Río Madre de Dios, Sena, Nee 31734 (MO, NY). BRAZIL. Acre: Rio Branco-Brasília, km 16, Nelson 752 (MG, MO, R); Rio Caete, 12 km above mouth, Prance et al. 7925 (NY, US); Rio Branco-Xapury, BR 317, km 16, Cid & Souza 2987 (MG, MO); Rio Branco-Sena Madureira, km 40, Cid & Souza 3022 (NY); Assis Brasil, basin of Rio Purus, upper Rio Acre, Daly et al. 9820 (NY).

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APPENDIX 1. List of species.

- 1. Dracontium amazonense G. Zhu & Croat
- 2. Dracontium angustispathum G. Zhu & Croat
- 3. Dracontium asperispathum G. Zhu & Croat
- 4. Dracontium asperum K. Koch
- 5. Dracontium bogneri G. Zhu & Croat
- 6. Dracontium croatii G. Zhu
- 7. Dracontium dubium Kunth
- 8. Dracontium gigas (Seem.) Engl.
- 9. Dracontium grandispathum G. Zhu & Croat
- 10. Dracontium grayumianum G. Zhu & Croat
- 11. Dracontium guianense G. Zhu & Croat
- 12. Dracontium longipes Engl.
- 13. Dracontium margaretae Bogner
- 14. Dracontium nivosum (Lem.) G. Zhu
- 15. Dracontium peruvianum G. Zhu & Croat

- 16. Dracontium pittieri Engl.
- 17. Dracontium plowmanii G. Zhu & Croat
- 18. Dracontium polyphyllum L.
- 19. Dracontium prancei G. Zhu & Croat
- 20. Dracontium purdieanum (Schott) Engl.
- 21. Dracontium soconuscum Matuda
- 22. Dracontium spruceanum (Schott) G. Zhu
- 23. Dracontium ulei K. Krause

APPENDIX 2. Index to exsiccatae. Type species in boldface.

R. Aguilar 1976 (16); R. Aguilar & V. Guzmán 2849 (16); Alarcon 62 (22); P. Alcorn & J. Mallet 8 (15); P. Allen 3427 (21), 5318 (16); Alson 971 (18), 1107 (18);
E. Ancuash 129 (22), 164 (22), 1415 (22); André 1025 (22); Anonymous s.n. in 1889 (8), s.n. (8), s.n. (8), s.n. (20); Archer 1729 (22); Aristeguieta 5381 (7), 12734 (7), s.n. (20); Asplund 19281 (22), 19588 (22); M. Aulestia 1823 (9); Aymard & Stergios 3807 (7).

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