REVISION OF DIEFFENBACHIA (ARACEAE) OF MEXICO, CENTRAL AMERICA, AND THE WEST INDIES¹

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Abstract

The genus Dieffenbachia Schott has approximately 135 species, most of them occurring in South America. Major centers of diversity for the genus include Colombia with 37 species, Ecuador (34), Peru (30), Brazil (27), Panama (20), and Costa Rica (13). There are 26 species in Central America, with 20 species (77%) new to science. These are D. burgeri Croat & Grayum, D. copensis Croat, D. crebripistillata Croat, D. davidsei Croat & Grayum, D. fortunensis Croat, D. fosteri Croat, D. galdamesiae Croat, D. horichii Croat & Grayum, D. isthmia Croat, D. killipii Croat, D. lutheri Croat, D. nitidipetiolata Croat, D. obscurinervia Croat, D. panamensis Croat, and D. standleyi Croat described herein and D. beachiana Croat & Grayum, D. concinna Croat & Grayum, D. grayumii Croat, D. hammelii Croat & Grayum, and D. tonduzii Croat & Grayum described elsewhere. Most species range from Nicaragua to Panama. Belize has only 1 species of Dieffenbachia; Mexico, El Salvador, and Guatemala have 2 species, followed by Honduras (3), Nicaragua (6), Costa Rica (13), and Panama (20). Only a few Central American species could be considered widespread. Among the most widespread are D. oerstedii Schott and D. wendlandii Schott, both of which range from Mexico to Panama, as well as D. nitidipetiolata and D. tonduzii, which range from Honduras to Ecuador. Species endemism is high, especially in Costa Rica (3) and Panama (9). A total of 9 species are shared between Panama and Costa Rica. Eight species, almost 31% of the total, range into South America. These are D. davidsei, D. isthmia, D. killipii, D. longispatha, D. nitidipetiolata, D. obscurinervia, D. seguine, and D. tonduzii. Most of these only extend to Colombia, but three species, D. killipii, D. nitidipetiolata, and D. tonduzii, range to Ecuador. Only D. killipii ranges to the eastern slope of the Andes. Dieffenbachia seguine ranges into Brazil and Bolivia, from the West Indies.

Key words: Araceae, Central America, Dieffenbachia, Mexico, South America, West Indies.

The family Araceae is worldwide in distribution, but most species occur in tropical areas. Its centers of distribution include both Asia and America (Croat, 1979), with 31 genera in the Americas and 28 found in Asia. There are 16 genera in Africa, Madagascar, and the Seychelles. A few genera are restricted to temperate regions of the Northern Hemisphere, including the Mediterranean region (*Calla L., Lysichiton Schott, Orontium L., Peltandra* Raf., *Symplocarpus* Salisb. ex Nutt.), including the Mediterranean region (*Arisarum Mill., Ambrosina* Bassi, *Arum L., Dracunculus Mill., Helicodiceros* Schott ex K. Krause). Important local centers of generic endemism in the family include Brazil, which has four endemic genera (*Bognera* Mayo & Nicolson, *Dracontioides* Engl., *Gearum* N. E. Br., *Zomicarpa* Schott), and the Indomalaysian region, with 14 endemic genera. At least 2550 species, representing four-fifths of the total, occur in the Neotropics. The Central American flora comprises 19 genera within the Araceae.

With an estimate of more than 2550 species in Latin America, the Araceae are one of the largest families of flowering plants in the region. Yet no

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other family is so poorly known taxonomically. Plants exhibit considerable morphological plasticity at all stages of development. Many of the genera, especially the hemiepiphytic genera *Rhodospatha* Poepp., *Monstera* Adans., and *Syngonium* Schott, exhibit complex patterns of heterophylly, with drastically different morphology at different stages of development (Croat, 1981 [1982]; Ray, 1981, 1987). Most members of the family have succulent parts, making them difficult to collect and preserve.

Dieffenbachia is one of several medium-sized genera in the Araceae, with an estimated 135 species. This revision is the first major review of Dieffenbachia for Central America since Adolf Engler's (1915) generic treatment in Das Pflanzenreich. Dieffenbachia is one of the most important genera of understory herbs in the family, and it is often a dominant component of humid to wet tropical forests, especially from sea level to 1500 m. It inhabits life zones ranging through Premontane moist forest (P-mf), Tropical moist forest (T-mf), Premontane wet forest (P-wf), Tropical wet forest (T-wf), and Premontane rain forest (P-rf) (Holdridge, 1967). While most species occur in virgin humid forests, the genus is known from freshwater swamps, stream banks, regrowth forest, among rock outcrops, and occasionally on road banks. It often constitutes the most conspicuous element of the understory vegetation because of its abundance, frequent colonial growth habit, and generally large, showy leaves. The genus provides a wide variety of choice ornamental plants for horticulture, including most of the species treated here.

The genus is distinct and not easily confused with any other aroid. It is closest to Bognera, which differs in lacking staminodia surrounding the pistillate flowers and in having higher-order venation reticulate. In contrast, Dieffenbachia has several staminodia surrounding the pistils and higher-order venation parallel-pinnate. However, the monotypic genus Bognera is endemic to Brazil, and it is not likely to be a problem with determination of most Dieffenbachia. Alternatively, Dieffenbachia is frequently confused with Philodendron Schott, particularly the terrestrial species of the latter with noncordate blades. Philodendron species are mostly hemiepiphytic, rarely terrestrial as is *Dieffenbachia*. Even when Philodendron species are terrestrial and have non-cordate blades, they can be distinguished by the remotely many-flowered pistils that are not surrounded by staminodia, as well as the lack of the acrid foul-smelling, irritating sap that is so closely associated with Dieffenbachia.

Species diversity of *Dieffenbachia* shows a general diminution from Mexico to Middle America with the lowest totals just north of the San Juan depression (Nicaragua), followed by a marked increase approaching the South American continent. (In this treatment, Central America is defined as all the area between Mexico and Colombia, whereas Middle America is all the area between Mexico and Panama.) Mexico has 2 species, Guatemala (2), Belize (1), Honduras (3), El Salvador (2), Nicaragua (6), Costa Rica (13), and Panama (20) (Table 1). Endemism is high, especially in Costa Rica with 3 endemic species and Panama with 9. A total of 7 species are shared between Panama and Costa Rica. Just under one-third (31%) of Central American species of Dieffenbachia range into South America, these being D. davidsei, D. isthmia, D. killipii, D. longispatha, D. nitidipetiolata, D. obscurinervia, D. seguine, and D. tonduzii.

MATERIALS AND METHODS

This revision is based on more than 29 years of field studies in Central and South America, between 1967 and 1996. All but one species were studied live in the field or under cultivation at the Missouri Botanical Garden. The descriptions have been prepared from both living and dried specimens. The exception is D. fosteri, where the description was based solely on the type specimen. The use of ("dried") preceding all or any part of the description is an indication that all that follows is based on herbarium material only. Morphological characters were coded directly into a computerized database to ensure parallel and sortable descriptions. The aroid descriptions database contains 784 character states applicable to the morphological diversity expressed in Dieffenbachia (Croat, 1997). Discussions and references to illustrations, as well as exsiccatae, are stored separately, but tied to a particular species description and to the nomenclatural information by a unique taxon number. Terminology and usage in the descriptions in this revision are largely defined by Croat and Bunting (1979) and elaborated in Croat (1997).

Ecological zones, though sometimes estimated from my own experience with Central American vegetation, are largely taken from Holdridge lifezone maps (Holdridge, 1967; Holdridge et al., 1971), where they exist for Central American countries, and for Mexico from the "Mapa de tipos de vegetación de la República de México" (Flores et al., 1971).

Herbarium material has been widely distributed and original field vouchers are cited for all herbaria whose material was seen (see Appendices 1, 2). Herbarium material may consist of one of three

X = species present; $E =$ endemic species.														
	Country													
Species	Mexi- co	Gua- te- mala	Belize	El Salva- dor	Hon- duras	Ni- cara- gua	Costa Rica	Panama	West Indies	Col- om- bia	Ecua- dor	Vene- zuela	Brazil	Boliv- ia
D. aurantiaca							Х	Х						
D. beachiana							Х	Х						
D. burgeri							Е							
D. concinna						Х	Х							
D. copensis								Е						
D. crebripistillata								Е						
D. davidsei							Х	Х		Х				
D. fortunensis								Е						
D. fosteri								Е						
D. galdamesiae								Е						
D. grayumiana							Х	Х						
D. hammelii							Е							
D. horichii							Е							
D. isthmia								Х		Х				
D. killipii							Х	Х		Х	Х			
D. longispatha								Х		Х				
D. lutheri								Е						
D. nitidipetiolata						Х	Х	Х		Х	Х			
D. obscurinervia								Х		Х				

Х

Х

Х

Х

6

Х

Х

Х

13

(23%)

Х

Е

Е

Х

Х

20

(40%)

Х

1

Х

Х

8

X

Х

4

X

1

Х

1

Х

1

Table 1. Distribution and endemism in *Dieffenbachia* species from Mexico, Central America and the West Indies. X = species present; E = endemic species.

kinds: (1) complete original sets (wild collected); (2) sterile original material with an inflorescence added from a cultivated plant of the same number; and (3) material collected entirely from the cultivated plant. Specimens based entirely or in part on cultivated material are clearly indicated on the herbarium label.

Х

Х

 $\mathbf{2}$

Х

Х

2

X

1

Х

Х

2

Х

Х

Х

3

Herbarium specimens were borrowed from most major herbaria including: A, AAU, B, BBS, BM, BR, CAS, CAY, CHOCO, CM, COL, CR, CUVC, DAV, DS, DUKE, EAP, ECON, ENCB, F, FLAS, FSU, FTG, G, GH, GOET, GUAY, HBG, HUA, INB, ISC, K, L, LA, LL, M, MEXU, MICH, MY, NY, P, PMA, PORT, QAP, QCA, QCNE, RSA, S, SCZ, SEL, STRI, TEFH, TEX, TULV, U, UC, UMO, US, USC, USJ, VEN, and WIS. Unless specifically designated as not seen, all specimens are to be presumed to have been examined personally.

Data on the living collection of *Dieffenbachia* are

computerized, and the entire collection, including many South American species that are being described separately, undergoes regular inventories to include events such as flowering time and attempted hybridizations. This allows electronic access to information on status, location, flowering dates, the number of vouchers prepared, and the status of the description. All specimens cited have been recorded in a computerized database for permanent referral. See www.mobot.org.

HISTORY OF THE GENUS DIEFFENBACHIA

HEINRICH WILHELM SCHOTT

The genus *Dieffenbachia* was described in 1829 by H. W. Schott (Schott, 1829). Schott based the genus on a single species, *Caladium seguinum* (Jacq.) Vent. (Ventenat, 1800), previously described as *Arum seguine* Jacq. (Jacquin, 1763) as well as

D. oerstedii

D. pittieri

D. seguine

D. standlevi

D. tonduzii

D. wendlandii

Total number of

species (percent of endemics)

D. panamensis

Species treated by H. W. Schott (1860)	Origin	Synonymizations as treated by Engler (1915)
1. D. cognata Schott	Suriname	= D. seguine var. lineata (Mart. ex Schott) Engl.
2. D. consobrina Schott	Brazil	= D. seguine var. viridis Engl.
3. D. costata H. Karst. ex Schott	Venezuela	
4. D. gollmeriana Schott	Venezuela	= D. seguine var. viridis Engl.
5. D. humilis Poepp.	Peru	
6. D. irrorata Mart. ex Schott	Brazil	= D. seguine var. lingulata (Mart.) Engl. subvar. irrorata (Mart.) Engl.
7. D. lineata K. Koch & Bouché	New Granada	= D. seguine var. lineata (K. Koch & Bouché) Engl.
8. D. lingulata Mart. ex Schott	Brazil	= D. seguine var. lingulata (Mart. ex Schott) Engl.
9. D. liturata Schott	Unknown	= D. seguine var. liturata (Schott) Engl.
10. D. macrophylla Poepp.	Peru	
11. D. neglecta Schott	Jamaica	= D. seguine var. viridis Engl.
12. D. obliqua Poepp.	Peru	
13. D. oerstedii Schott	Central America	
14. D. picta Schott	Unknown	
15. D. plumieri Schott	Martinique	= D. seguine var. viridis Engl.
16. D. poeppigii Schott	Peru	= D. seguine var. viridis Engl.
17. D. robusta Schott	Unknown	
18. D. seguine (Jacq.) Schott	Martinique	
19. D. spruceana Schott	Brazil	= D. humilis Poepp.
20. D. ventenatiana Schott	Suriname	= D. seguine var. ventenatiana (Schott) Engl.
21. D. wendlandii Schott	El Salvador	= D. seguine

Table 2. Treatment of Dieffenbachia species by H.W. Schott (1860).

by Linnaeus (1763). The next species described were three from Peru (Poeppig, 1845), *D. humilis* Poepp., *D. macrophylla* Poepp., and *D. obliqua* Poepp.

Between 1852 and 1864 an additional 18 species were described, all but 4 of them by H. W. Schott. Of these only 3 were recognized in Engler's (1915) revision, while the remainder were synonymized or recognized at the subspecific level, mostly under *Dieffenbachia seguine*. Those recognized at the specific level were *D. picta* Schott, *D. costata* H. Karst. ex Schott, and *D. oerstedii* Schott. Between 1866 and 1878, 12 species were described, with 6 more of these being recognized as distinct in Engler's revision (Table 3). The first major revision of the genus was that of Schott (1860) in his *Prodromus Systematis Aroidearum*, treating 21 species, of which Engler later (1915) recognized only 7 (see Table 2).

ADOLF ENGLER

The next revisionary effort made with *Dieffenbachia* was by Engler (1878) in the treatment of the Araceae in Martius's *Flora Brasiliensis*. In this treatment 3 species were included and 16 new combinations made (these within *D. seguine* and *D. picta*). A year later, in his treatment of *Dieffenbachia* in DeCandolle's *Monographiae Phaneroga*- *marum* (Engler, 1879), 6 species were treated and 2 more combinations were made. Between 1879 and 1899, 14 additional species were described, only 3 of which were recognized by Engler in 1915. These were *D. daguensis* Engl., *D. enderi* Engl., and *D. olbia* L. Linden & Rodigas.

In 1899, Engler produced another small work on *Dieffenbachia* in which he treated 19 species and made 24 new combinations, but provided no descriptions except for one new species, *Dieffenbachia aurantiaca* Engl. Only 9 species were described between this work (1899) and Engler's (1915) revision. Those taxa still recognized by Engler (1915) were *Dieffenbachia cordata* Engl., *D. weberbaueri* Engl., *D. gracilis* Huber, and *D. cannifolia* Engl. ex Ule.

The last revision of the genus *Dieffenbachia* was by Engler (1915) in *Das Pflanzenreich*. This revision contained both keys and descriptions for 27 species. A total of 11 new combinations were made and 6 new species described (see Table 3). The new species were *D. aglaonematifolia* Engl., *D. brittonii* Engl., *D. longispatha* Engl. & K. Krause, *D. parvifolia* Engl., and *D. pittieri* Engl. & K. Krause.

MODERN WORK

Very little work was done with *Dieffenbachia* after Engler (1915). Gleason (1929) described *D. pal*-

Table 3. Treatment of *Dieffenbachia* species by A. Engler (1915).

	Species treated by A. Engler (1915)	Origin	As treated in this manuscript
1.	D. aglaonematifolia Engl.	Paraguay	
2.	D. antioquensis Linden & André	Colombia	
3.	D. aurantiaca Engl.	Costa Rica	D. aurantiaca Engl.
4.	D. bowmannii Carr.	Colombia & Brazil	0
5.	D. brittonii Engl.	Colombia	
6.	D. cannifolia Engl.	Peru	
7.	D. cordata Engl.	Peru	
8.	D. costata Klotzsch	Colombia & Peru	
9.	D. daguensis Engl.	Colombia	
10.	D. enderi Engl.	Colombia	
11.	D. gracilis Huber	Peru	
12.	D. humilis Poepp.	Brazil & Peru	
13.	D. imperialis Linden & André	Peru	
14.	D. latimaculata Linden & André	Colombia	
15.	D. leopoldii Bull	Costa Rica	
16.	D. longispatha Engl. & K. Krause	Panama	D. longispatha Engl. & K. Krause
17.	D. macrophylla Poepp.	Peru	
18.	D. obliqua Poepp.	Peru	
19.	D. oerstedii Schott	Central America	D. oerstedii Schott
20.	D. olbia J. Linden & Rodigas	Peru	
21.	D. parlatorei Linden & André	Colombia	
22	D. parlatorei var. marmorea Linden & André	Unknown	
22.	D. parvifolia Engl.	Brazil	
23.	D. picta (Lodd.) Schott	Brazil?	D. seguine (Jacq.) Schott
	D. picta var. angustior Engl.	Unknown	D. seguine (Jacq.) Schott
	D. picta var. angustior subvar. angustifolia Engl.	Unknown	D. seguine (Jacq.) Schott
	D. picta var. angustior subvar. jenmanii (Veitch) Engl.	Unknown	D. seguine (Jacq.) Schott
	D. picta var. angustior subvar. lancifolia (Linden & André) Engl.	Unknown	D. seguine (Jacq.) Schott
	D. picta var. angustior subvar. schuttlesworthi- ana (Hort. Bull.) Engl.	Unknown	D. seguine (Jacq.) Schott
	D. picta var. barraquiniana (Verschaff. & Lem.) Engl.	Unknown	D. seguine (Jacq.) Schott
	D. picta var. latior Engl.	Unknown	D. seguine (Jacq.) Schott
	D. picta var. latior subvar. amoena Hort. Bull.	Unknown	D. seguine (Jacq.) Schott
	D. picta var. latior subvar. carderi Hort. Bull.	Unknown	D. seguine (Jacq.) Schott
	D. picta var. latior subvar. gigantea (Ver- schaff.) Engl.	Brazil	D. seguine (Jacq.) Schott
	D. picta var. latior subvar. magnifica (Linden & Rodigas) Engl.	Venezuela	D. seguine (Jacq.) Schott
	D. picta var. latior subvar. meleagris (Linden & Rodigas) Engl.	Ecuador	D. meleagris L. Linden & Rodigas
	D. picta var. memoria (Corsi Salviati) Engl.	Unknown	D. seguine (Jacq.) Schott
	D. picta var. latior subvar. mirabilis (Ver- schaff.) Engl.	Unknown	D. sequine (Jacq.) Schott
	D. picta var. latior subvar. picturata (Linden & Rodigas) Engl.	Venezuela	D. seguine (Jacq.) Schott
	D. picta var. typica Engl.	Unknown	D. seguine (Jacq.) Schott
24.	D. pittieri Engl. & K. Krause	Panama	D. pittieri Engl. & K. Krause
25.	D. seguine (L.) Schott	Martinique	D. seguine (Jacq.) Schott
	= D. seguine (Jacq.) Schott		
	D. seguine var. decora (Hort. Vershaff.) Engl.	Brazil?	D. seguine (Jacq.) Schott
	D. seguine var. lineata (K. Koch & Bouché) Engl.	Venezuela	D. seguine (Jacq.) Schott

Table 3. Continued.

	Species treated by A. Engler (1915)	Origin	As treated in this manuscript
	D. seguine var. lingulata (Martius) Engl.	Suriname & Brazil	D. seguine (Jacq.) Schott
	D. seguine var. lingulata subvar. irrorata	Brazil	D. seguine (Jacq.) Schott
	(Mart.) Engl.	_	
	D. seguine var. liturata (Schott) Engl.	Unknown	D. seguine (Jacq.) Schott
	D. seguine var. liturata subvar. wallisii (Lin- den) Engl.	Unknown	D. seguine (Jacq.) Schott
	D. seguine var. nobilis (Hort. Verschaff.) Engl.	Brazil	D. seguine (Jacq.) Schott
	D. seguine var. robusta (K. Koch) Engl.	Unknown	D. seguine (Jacq.) Schott
	D. seguine var. ventenatiana (Schott) Engl.	Suriname	D. seguine (Jacq.) Schott
	D. seguine var. viridis Engl.	Widespread in West Indies, Central and South America	D. seguine (Jacq.) Schott
96	D. waharhawari Engl	Down	
20. 2-	D. weberbauert Engl.	reiu	
27.	D. weirii Berkl.	Colombia	

udicola N. E. Br. ex Gleason from Guayana, and Jonker and Jonker (1966) described *D. elegans* A. M. E. Jonker & Jonker for Suriname. Three species were described from Venezuela, *D. bolivarana* G. S. Bunting (Bunting, 1963), *D. liesneri* Croat, and *D. longipistila* Croat (Croat & Lambert, 1987). Another Venezuelan species, *D. duidae* (Steyerm.) G. S. Bunting, was transferred (Bunting, 1988) from Spathicarpa duidae Steyerm., described in 1951.

Dieffenbachia has been so confusing that floristic accounts dealing with Central America have been of little value. Hemsley (1885) listed only a single species, D. oerstedii Schott, for his Biologia Centrali-Americana. Engler (1915) reported only five species for Central America, D. oerstedii, D. aurantiaca Engl., D. pittieri, D. longispatha, D. seguine, and D. leopoldii Bull. The first four were properly circumscribed, largely owing to the fact that he was dealing with little beyond the type specimens. Dieffenbachia leopoldii has proven to be a species known only from Colombia. The only plants Engler (1915) called D. seguine were from El Salvador, the type country of D. wendlandii, which he erroneously synonymized with D. seguine. Dieffenbachia wendlandii differs from D. seguine in having unilocular ovaries, and a long-tapered spadix that does not protrude forward at anthesis, as is the case with D. seguine.

Matuda (1954) reported only *D. seguine* for Mexico, whereas Bunting (1965) reported both *D. seguine* and *D. oerstedii* for Mexico, the latter being a new report. One of the species that Bunting was dealing with, which he named as *D. seguine*, is recognized herein as *D. wendlandii*.

These earlier floristic accounts for Central America, in addition to being inaccurate, also grossly undercounted the number of existing species. This inaccuracy was in part due to a poor understanding of the collections that existed at the time, but also to the fact that most collections of Araceae have been made in the last 25 years. Panama, for example, has shown vast increases in the number of species collected and identified since the treatment of Araceae in the *Flora of Panama*. Some genera have increased by nearly 544% since 1944 (Croat, 1985). *Dieffenbachia* now has 26 species recognized for Central America, with 77% of them new to science since work on the revision began. This represents a 400% increase from the number reported in Central America by previous workers (Engler, 1915; Standley, 1937, 1944; Standley & Steyermark, 1958; Matuda, 1954; Bunting, 1965).

Standley's treatment of the Araceae of the Lancetilla Valley (Standley, 1931) dealt with only 2 species, *D. oerstedii*, which was at least in part correctly determined, and *D. seguine*, probably *D. standleyi* Croat in the present treatment. However, in the case of the latter species he did not mention the almost fully sheathed petiole that is so distinctive on *D. standleyi*. Standley also confused *D. seguine* with other species, mentioning that it ranged to El Salvador (probably *D. wendlandii*) and to the West Indies (referring to the real *D. seguine*).

The treatment of the Araceae in the Flora of Guatemala (Standley & Steyermark, 1958) is especially confusing. In this treatment they dealt with four names, D. oerstedii, D. picta (Lodd.) Schott, a maculate species that I consider synonymous with D. seguine and not occurring in Central America, and D. pittieri, which I consider to be a narrow endemic in the Canal Zone of Panama. Since they did not cite specimens, it is difficult to interpret their treatment, but their description of D. pittieri with a petiole sheathed almost to the apex and

ranging from Guatemala to Honduras may be what I am currently calling *D. standleyi*. The plant they were calling *D. oerstedii* probably was, at least in part, the species named. The plant they called *D. seguine* was probably *D. wendlandii*. The mottled plants they referred to as *D. picta* may have been cultivated forms of *D. seguine*, the mottled forms of which are popular with horticulturists and have been known to persist in areas of abandoned dwellings.

The Flora of Costa Rica (Standley, 1937) treatment of Dieffenbachia was somewhat less confused, probably because it was adapted from Engler's (1911) treatment. Because several of the species types came from Costa Rica, fewer names were misapplied. Here Standley treated D. aurantiaca, an endemic to southwestern Costa Rica, D. leopoldii (a Colombian species not believed to be in Central America and perhaps confused with what I am calling D. killipii in the present treatment), D. pittieri, and D. seguine. Unfortunately, he cited no specimens nor gave any characters by which to recognize the species. Certainly, no material currently exists in Costa Rica of D. pittieri or D. seguine.

In the Flora of Panama, Standley (1944) did cite specimens for four species. Dieffenbachia pittieri is endemic to the Isthmus of Panama. Standley (1944) cited the type, Pittier 3766, but he also cited material from El Valle (Alston & Allen 1839) that represents D. crebripistillata. Dieffenbachia aurantiaca was even more confused, with only one of the cited collections, Woodson & Schery 861, being D. aurantiaca. Other collections cited assign to three different species, D. isthmia, D. killipii, and D. tonduzii. A total of five species were represented among the 12 collections cited as D. oerstedii, only one of which actually was that species (Pittier 2836 in western Panama). Other specimens cited under this name belong to D. isthmia, D. killipii, D. nitidipetiolata, and D. obscurinervia.

Collecting History of Dieffenbachia

Collecting Araceae has not been particularly popular, and this would be especially true for *Dieffenbachia*. Many collectors who have been careless when collecting *Dieffenbachia* found themselves badly burned with the often high concentrations of oxalic acid in the cut parts. Perhaps this has led to the generally low numbers of collections of *Dieffenbachia*. A survey of those who collected in Central America, based on the extensive TROPICOS database of collections, shows that aside from myself (338 Croat collections for Central America out of a total of 537 Croat collections in the Neotropics)

relatively few botanists made many collections of Araceae. Mike Grayum, also an aroid specialist, made 68 collections of Dieffenbachia in Central America, mostly Costa Rica, out of a total of 73 Dieffenbachia collections for that country. Barry Hammel, a close associate of Grayum and myself, made 57 collections of Dieffenbachia in Central America. Paul Standley, one of the most ambitious collectors in the Neotropics made 54 collections. Julian Stevermark, another giant in the field of collecting, made 46 collections, but only 13 of these were in Central America (Guatemala), whereas the balance were from Venezuela. Al Gentry also collected a lot of Dieffenbachia, 57 in all, but even fewer were from Central America (only 5 collections).

The earliest botanist to collect Central American species of Dieffenbachia was Friedrich Carl Lehmann over a century ago. These were D. killipii (Lehmann 5311) and D. tonduzii (Lehmann 8876), the latter as early as 1819. Herman Wendland collected D. wendlandii, in this case before 1858. Other collectors included Adolfe Tonduz (D. aurantiaca) and Henri Pittier, the first to collect D. longispatha (Pittier 2715), D. obscurinervia (Pittier 3766), D. pittieri (Pittier 3766), and D. killipii (Pittier 2600), all collected as early as 1911; Paul Standley, who was the first to collect D. concinna (Standley 36739), D. isthmia (Standley 29867), and D. beechiana (Standley 36840), all in 1924; Paul Allen initially collected D. crebripistillata (Allen 1839) in 1939; E. P. Killip, D. nitidipetiolata (Killip 35113) in 1939; and Louis O. Williams, D. horichii (Williams 28479) in 1965.

Other Central American species were collected only in the past few decades. *Dieffenbachia burgeri* dates to William Burger and Ronald Liesner (*Burger & Liesner 7254*) in 1970, and *D. davidsei* was not seen until Scott Mori made his collection in 1974 (*Mori et al. 4184*). Tom Croat encountered *Dieffenbachia fortunensis* in 1976 (*Croat 37268*), *D. galdamesiae* in 1979 (*Croat 49124*), and *D. panamensis* in 1974 (*Croat 27206*). *Dieffenbachia grayumiana* was first noticed by Burger and Matta in 1967 (*Burger & Matta 4181*), *D. fosteri* by Robin Foster in 1993 (*Foster et al. 14649*), and *D. hammelii* by David Neill in 1978 (*Neill & Vincelli 3484*).

SUPRAGENERIC CLASSIFICATION OF SUBFAMILY PHILODENDROIDEAE AND RELATIONSHIPS OF *DIEFFENBACHIA*

Engler (1915) placed *Dieffenbachia* in the subfamily Philodendroideae Engl. The same position is taken by Bogner and Nicolson (1991) in their modern revision. Grayum (1984, 1990) placed Dieffenbachia in its own tribe and does not disagree with Bogner and Nicolson about its relative placement or taxonomic status. However, Grayum substantially modified the Philodendroideae by including the genus Calla and thus mandated a change in the name of the subfamily to Calloideae Endl. on the basis of priority. This group, as defined by Grayum, is substantially larger than that of Bogner and Nicolson's, with 40 genera arranged in 17 tribes in five alliances. This contrasts with 18 genera in 7 tribes according to Bogner and Nicolson. The latter system closely mirrors Engler's Philodendroideae, except for the inclusion of new genera and the synonymizing of others since the time of Engler. The size of Grayum's Philodendroideae resulted from the inclusion of tribes from the subfamilies Aroideae Adans., Pothoideae Engl., and Lasioideae Engl. (Croat, 1990 [1992]).

In recent suprageneric classifications by Mayo et al. (1997, 1998) all the genera with unisexual flowers were grouped together in the subfamily Aroideae and further divided into non-ranked groups, the perigoniate Aroideae and aperigoniate Aroideae. Dieffenbachia, in the latter group, was placed in the Dieffenbachia alliance, one of four alliances (the others called Philodendron, Schismatoglottis, and Caladium alliances respectively). These alliances comprise 33 genera with an additional 37 genera being placed in a group labeled "No alliance." The classification by Mayo et al. was able to make use of the results of the recently completed chloroplast DNA studies and anatomical studies of French and colleagues (1995, 1997). Dieffenbachia, along with Bognera, was placed in the tribe Dieffenbachieae, a tribe characterized by having the pistillate flowers completely adnate to the spathe.

In the most recent suprageneric classification of the family by Keating (2002, 2003a) *Dieffenbachia* is included in subfamily Philodendroideae, tribe Spathicarpeae Schott, along with *Bognera*, *Spathantheum* Schott, *Gorgonidium* Schott, *Synandrospadix* Engl., *Gearum* N. E. Br., *Spathicarpa* Hook., *Asterostigma* Fisch. & C. A. Mey., *Mangonia* Schott, and *Taccarum* Brongn. ex Schott. Keating's revision makes use of a wealth of vegetative anatomical information he has accumulated on the family. All members of the Spathicarpeae share in common Type B collenchyma; vascular bundle type II (or occasionally types I or III); and either lack laticifers or have non-anastomosing type laticifers.

The Dieffenbachia alliance of Mayo et al. (1997) is distinguished by having simple laticifers and free synandria. It contains two tribes, the Dieffenbachieae with two genera (Dieffenbachia and Bognera) and the tribe Spathicarpeae with eight genera, Mangonia, Taccarum, Asterostigma, Gorgonidium, Synandrospadix, Gearum, Spathantheum, and Spathicarpa. Their tribe Spathicarpeae differs from the tribe Dieffenbachieae in having tuberous stems and leaves with reticulate higher-order venation. However, the latter character is also present in Bognera, one of the two genera in their tribe Dieffenbachieae. In the Dieffenbachia alliance Dieffenbachieae are distinguished from other tribes by having anatropous ovules; the primary lateral veins forming a single marginal vein but also lacking collective veins; and, perhaps most importantly, in having the pistillate portion of the spadix completely fused to the spathe. Tribe Dieffenbachieae sensu Mayo et al. (1997) is distinguished from other tribes of subfamily Philodendroideae by having stamens connate into synandria, and in having several free staminodia associated with the female flowers. Other useful distinguishing features include a constricted spathe partly adnate with the pistillate spadix, terrestrial caulescent habit, closely parallel primary and minor veins, and seeds with endosperm.

The Dieffenbachia alliance of Mayo et al. (1997) has been supported by molecular studies with chloroplast *trn*L-F genes (Barabé; Tam et al., 2004). This study shows close relationships between Spathicarpeae and Dieffenbachieae with *Dieffenbachia* being paired with *Spathicarpa* on one branch and with *Cercestis* Schott, *Rhektophyllum* N. E. Br., and *Culcasia* P. Beauv. forming another branch of the tree.

Although both Grayum (1984, 1990) and Bogner and Nicolson (1991) placed *Dieffenbachia* in its own tribe, the authors of both systems now agree that *Bognera*, another Neotropical genus, is very close to or within the tribe Dieffenbachieae, sensu Mayo et al. (1997). Keating (2002, 2003a) simply subsumed this tribe (or its genera) within his larger Spathicarpeae, still in essential agreement.

The subfamily Philodendroideae is worldwide in distribution and, sensu Grayum (pers. comm.), it is somewhat equally divided between the Old World and the New World, with 19 genera (17 of them endemic) and 761 species in the New World and 23 (21 endemic) genera and 354 species in the Old World. Grayum places the Dieffenbachieae in his Aglaonema alliance with Zantedeschieae Engl. (Zantedeschia Spreng.), Aglaonemateae Engl. (Aglaonema Schott, Aglaodorum Schott), Spathicarpeae (Mangonia, Asterostigma, Synandrospadix, Taccarum, Gorgonidium, Gearum, Spathanthemum, Spathicarpa), and Bognereae S. Mayo & D. Nicolson (*Bognera*). Anubiadeae Engl. (1876) (*Anubias* Schott) and Zantedeschieae are restricted to Africa, while the Spathicarpeae are restricted to southern South America.

MORPHOLOGY OF VEGETATIVE STRUCTURES

HABIT AND GROWTH PATTERNS

Dieffenbachia is always terrestrial and caulescent (Croat, 1988 [1990]). In terms of growth behavior and habit, Dieffenbachia is not as variable as Philodendron, a related genus, but sterile plants disassociated with notes about habit can be confused with those of Philodendron. Stems of Dieffenbachia are erect, at least on the younger portions, with older portions of the stem typically becoming decumbent. This creeping portion of the stem is sometimes even longer than the erect portion (Fig. 23A). The overall height of any species is usually determined by the thickness, strength, and rigidity of the stem. Typically, species such as D. burgeri, D. hammelii, and most plants of D. oerstedii, with small-diameter stems, do not get to more than 1 m tall nor do they usually have stems more than 2.5 cm in diameter. Alternatively, the taller species like D. horichii, D. longispatha, and D. standleyi have thick stems and reach heights of 2 to 3.5 m. Cultivated plants growing in a pot and unable to become reclined at the base can grow to indefinite height. A plant of D. standleyi cultivated in the greenhouse of the Missouri Botanical Garden grew up the side of a wall from a pot to the height of 8 m.

The portion of the stem that comes in contact with the ground becomes rooted at the nodes, but stems are rarely buried. Instead, the stems usually creep over the surface of the ground. The growth behavior often leads to vegetative reproduction, since on some species the creeping portion of the stem tends to produce active branch buds that form new growth. Another feature that tends to induce additional branching is the often fragile stem extending laterally over the ground, which may be broken by being walked on by animals. Broken stems invariably produce new branches. These results often cause Dieffenbachia to grow in large colonies, especially in open, better illuminated areas of the understory of a forest, along stream banks or in open swamps. Examples of colonial growth occur in D. crebripistillata, D. isthmia, D. killipii, and D. oerstedii. Some species, such as the taller D. longispatha (to 3.5 m), are usually less colonial. This is perhaps because it is a species with a large, stout stem that is less likely to be broken up by the elements. This species also has a thicker sap that is more foul-scented and caustic than many other species, and may in part account for less breakage by deterring animals from the plant.

In some cases *Dieffenbachia* may grow in standing water. In such cases the stems may be rather deeply buried in the mud. Some species, such as *D. grayumiana*, are frequent in wet habitats, but most species thrive in well-drained soils. The genus is seldom found on road embankments, a habitat that is very common for species of *Anthurium* and *Philodendron*. This is perhaps because the two latter, principally hemi-epiphytic genera can more easily become established on the excessively welldrained and poor clay soils of typical road embankments in the Neotropics.

Development in *Dieffenbachia* is never heteroblastic. Instead, changes in internode size and leaf size progress without any marked changes in blade shape. However, leaf blades of *Dieffenbachia* that ultimately become cordate at the base are at first simple and acute to obtuse at the base.

STEMS

Internodes are typically about as long as broad or even shorter than broad. Sometimes, as in the case of D. galdamesiae, petioles are affixed to the stem at an oblique angle and the internodes are not of equal width across the diameter of the stem. Instead, one side is as much as 1 cm wider than the other. Most commonly, internodes are glossy to semiglossy and smooth, though they may be minutely roughened, appearing with a somewhat weak velvety sheen, as in the case of D. oerstedii. Though for most species the internodes remain moderately glossy even in age, when fresh, the internodes may change promptly. In D. obscurinervia, the stem, though initially semiglossy, promptly becomes etched in a deep, areolate pattern to such an extent that the stem becomes matte and is conspicuously scurfy.

Cataphylls are never present on *Dieffenbachia*. Instead, the new growth on stems of *Dieffenbachia* is protected by the sheathing petiole of the preceding leaf.

Stem color varies considerably between species and even within populations of the same species. Species such as *D. longispatha*, which typically possess stems that are solid green, can sometimes be variegated with paler colors. Typically, stem color variegation is in the form of streaks rather than mottling. The stem may be relatively dark green with even darker streaks, in which case the mottling would not be too apparent, or, as is more frequently the case, it may be streaked with pale green or yellow-green. Dried stems are often highly diagnostic for key characters such as the degree to which they are contorted, usually ridged or cracked, or the color that they dry.

LEAVES

Leaves may be clustered near the apex of the stem such as in *Dieffenbachia panamensis* or sometimes they are rather well scattered along the stem as in *D. grayumiana*.

Dieffenbachia petioles are on average shorter than the blades, ranging from 0.23 to 1.08 as long as blades, and averaging 0.65 times as long as blades. Typically, the blades average about 1.5 times longer than the petioles. The petioles are typically sheathed for a significant portion of their length. The extent and nature of the leaf sheath constitutes one of the most important species-level characters. The sheath margins are virtually always persistent, but the degree to which the sheath is open, i.e., erect-spreading (Fig. 24D), erect, or inrolled, remains an important characteristic. The petiole sheaths of D. wendlandii are typically inrolled at the apex, whereas the sheath of D. oerstedii is erect. The petiole sheath is typically unequal at the apex with one side more acute than the other. Some species (D. davidsei, D. seguine) have the petiole sheath free-ending (Figs. 8D, 23D).

Petiole cross-sectional shape is given only for the free portion of the petiole (when present). While sometimes variable within the species, it often constitutes an important taxonomic difference between species. Petioles are most commonly subterete with the adaxial surface frequently somewhat flattened (as in D. longispatha, Fig. 16C) or sulcate (D. beachiana, Fig. 3D). When sulcate the petioles may be obtusely sulcate or sharply sulcate, as is usually the case in D. oerstedii (Fig. 20D). Though rare, the petiole cross-sectional shape may be triangular, as in D. aurantiaca where, in addition to being flattened adaxially, the lateral margins are bluntly winged and spreading (Fig. 2C, D). In D. panamensis the free portion of the petiole is also winged; the wing itself is usually thin, spreading, and markedly undulate. The free portion of the petiole may also have a prominently winged margin with the wing itself usually thin and undulating as in D. panamensis and D. standleyi (Fig. 24).

Dieffenbachia has leaf blades usually considerably longer than the petioles, ranging from 0.9 to 4.3 times longer than the petioles. Blades are typically conspicuously longer than wide, ranging from 1.1 to 4.3 times longer than wide. The blades are similar to those of many species of *Philodendron*, and sterile specimens for which habit is not mentioned are often difficult to separate from *Philodendron*. Most leaf blades are ovate to oblong-ovate, elliptic, oblanceolate or obovate, and are usually acuminate at the apex and acute to obtuse or rounded at the base (rarely subcordate at base as in *D. wendlandii* and *D. isthmia*). As is true of *Philodendron*, *Dieffenbachia* vernation is always supervolute (Cullen, 1978).

Venation patterns are similar to those in Philodendron (cf. Croat, 1997). The midrib is especially variable and diagnostic, especially on the adaxial surface, being usually prominently raised and varying from angular to broadly convex. The shape of the midrib is often taxonomically significant. In D. killipii the upper midrib is raised with square margins (Fig. 15B, C). In other cases the midrib may be broadly convex as in D. panamensis (Fig. 21D) or flat to sulcate as in D. standleyi. The midrib color is also important, since the midrib may be conspicuously paler than the lamina as sometimes in D. oerstedii (Fig. 20) or concolorous as in D. galdamesiae (Fig. 10B). In D. obscurinervia the midrib may be conspicuously speckled as is the petiole (Fig. 19C).

Primary lateral veins are usually well spaced with many, much finer minor veins between each pair of primary lateral veins. In all cases, the primary lateral veins extend to the margin and do not form a collective vein that extends all the way to the apex. Instead the primary lateral veins typically course along the margin of the blade, where they may form a weak collective vein that joins several primary lateral veins (especially near the middle of the blade) that eventually merge with the margin before reaching the apex. Primary lateral veins are usually somewhat sunken to weakly quilted-sunken above and raised on the lower surface (sometimes thicker than broad and sometimes weakly pleatedraised). Blades of D. davidsei may be rather conspicuously quilted-sunken (Fig. 8B). Leaf blades typically are glabrous, but the major veins may rarely be puberulent, as in D. beachiana, to granular-puberulent or conspicuously granular, as in D. fortunensis (Fig. 9C). Minor veins may arise only from the midrib, as appears to be the case in D. longispatha and D. nitidipetiolata, or they may arise from both the midrib and the primary lateral veins. The latter situation appears to be the most common in Dieffenbachia.

MORPHOLOGY OF FLOWERING STRUCTURES

INFLORESCENCES

Dieffenbachia inflorescences are far less diagnostic than those of *Philodendron*, since nearly all are solid green on both surfaces. There are considerable differences in the number of inflorescences per axil, ranging from solitary on a number of species at least part of the time or up to eight per axil as with *D. concinna*. In any population the number of inflorescences per axil may vary. Studies made with *D. oerstedii* in Costa Rica (Valerio, 1984) showed that this species produced primarily one or two inflorescences per axil.

SPATHE

Each spathe in a cluster of inflorescences in *Dieffenbachia* is subtended by linear-lanceolate bracteoles, each of which are unribbed. The bracteoles are typically about as long as the peduncles, but can sometimes be shorter or longer. They are somewhat marcescent.

Spathes of *Dieffenbachia* are uniformly green, though the inner surface tends to be somewhat paler than the outer surface and frequently much glossier. The outer spathe surface is typically semiglossy to weakly glossy. Sometimes the inner surface of the spathe is somewhat whitish on the inside near the tip.

The spathe of most *Dieffenbachia* is only weakly constricted above the spathe tube (Figs. 7A, 16D, 20F, 22E, 23E, 24F, 25F). When the entire spathe is fully flattened, the tube portion is considerably wider (Figs. 2B, 15H, 22F, 23F) and the spathe is gradually tapered from the lower ¼ to the usually acuminate apex (Fig. 23F). Sometimes there is a weak central constriction. The point of maximum constriction corresponds to the sterile section of the spadix between the fertile staminate flowers and the pistillate flowers.

At anthesis the spathe of *Dieffenbachia* is open to about the middle (Figs. 5B, 7A, 13E, 16D), or somewhat below the middle, but does not open as widely as that of *Philodendron*. At anthesis the spathe blade is wider than the tube. Typically only the staminate portion of the spadix is visible at anthesis but sometimes, as in *D. crebripistillata*, a portion of the pistillate spadix is also exposed. Closure of the spathe after anthesis is sometimes not complete, with the margins of the spathe meeting irregularly. At anthesis the blade of the spathe is usually arched somewhat forward, hooding the spadix slightly. For some species, such as *D. crebripistillata*, the spathe may be recurled at anthesis (Fig. 7C).

SPADIX

Flowers of *Dieffenbachia* are unisexual and naked, dispersed on the spadix in the typical manner with the staminate flowers at the apex and the pistillate flowers at the base. The spadix of Dieffenbachia is usually shorter than the spathe by 1-3cm (Fig. 2B). The spadix is contained within the spathe, and is more or less straight or weakly curved (Fig. 8F) at anthesis, rather than being prominently protruded forward. Some species have the spadix protruded forward at anthesis, such as D. burgeri (Fig. 4C), D. crebripistillata (Fig. 7C), D. horichii (Fig. 13E), D. wendlandii (Fig. 26C), and D. seguine (Fig. 23E). The last species, which ranges throughout the West Indies, has a spadix that notably protrudes and is cylindrical, rather than tapered to the apex as in the remaining Central American species (Fig. 23F). Dieffenbachia seguine also has a spadix (Fig. 23) that is caught in the protruded position when the spathe re-closes. In contrast to D. seguine, all of the Central American species have spathes that close normally with the spadix withdrawing inside of the spathe.

Like other members of the Philodendroideae, the spadix in *Dieffenbachia* is divided up into a fertile staminate section at the apex, a sterile section lying beneath the fertile staminate portion, and the pistillate portion (Figs. 2B, 7, 18, 25). The lowermost section, as with all Araceae with unisexual flowers, is the pistillate section. Typically the pistillate portion and the staminate portion are of roughly equal lengths, but the length of the sterile segment (when apparent) is highly variable both in terms of length and the degree to which staminodia and pistillodes are dispersed on it (Figs. 2B, 4C, 5D, 7, 15H, 18D, 23F, 25G). In most cases the pistillate region is slightly longer than the staminate.

The fertile staminate portion is somewhat cylindroid to spindle-shaped, broadest in the middle and weakly tapered toward both ends, being bluntly rounded at the apex. The fertile male flowers are compacted and sub-rounded or with angular margins (Figs. 2E, 5G). As the spadix approaches anthesis the synandria loosen and the anthers become visible between the synandria. Toward the base of the staminate portion of the spadix, the flowers are somewhat more irregular in size and shape, but do not become radically different as in the case of Philodendron and Xanthosoma, where the lowermost male flowers are sterile and swollen. In contrast, Dieffenbachia relies entirely on club-shaped staminodia surrounding the pistils (Figs. 5E, 14C). The lowermost staminate flowers are smaller or very irregular in shape, sometimes showing signs of two or more flowers fused together. Sometimes the uppermost pistils are reduced, apparently sterile, and surrounded by sterile male flowers (Fig. 15H). Apparently the lowermost staminate flowers are also

679

more attractive to beetle pollinators, since only the lowermost flowers are eaten (Fig. 1B).

ANDROECIUM

Staminate flowers consist of 4 stamens united into a 4- or 5-sulcate truncate synandrium (Figs. 2E, 5G, 23G, 26E). The apex of the synandrium often has a minute slit or an equidistant series of 3 minute slits connected at the center. Upon drying the apex of the synandrium may become wrinkled along the margin and may also have a concave surface. The anthers are contiguous or nearly so, affixed near the upper edge of the synandrium. The thecae are obovoid to cylindroid, opening by apical slits just below the upper edge of the synandrium. The pollen is dispersed in slender, subterete filaments and typically projects up to 1 cm above the surface of the synandrium. When the stamens are at anthesis, the shedding pollen can completely fill the now closing spathe (Fig. 5F).

POLLEN

Pollen of *Dieffenbachia* is released in monads that are inaperturate, subisopolar to virtually polar, boat-shaped-elliptic to oblong, or nearly spherical. They are bilaterally symmetrical or radiosymmetric (Grayum, 1992).

Dieffenbachia pollen is moderately large for Araceae, ranging from 54 to 99 μ m (as in *D. oerstedii*) and averaging 79 μ m. Exine sculpturing is psilate to obscurely verruculate (as in *D. oerstedii*) and/or sparingly punctate-foveate to densely foveate with scattered compound foveolae (as in *D. pittieri* and *D. seguine*). Grayum (1992) pointed out that the compound foveolae found on the pollen of *D. pittieri* and *D. seguine* resemble those of *Chlorospatha croatiana* Grayum.

STERILE SPADIX SECTION

Dieffenbachia typically has a nearly barren section of the spadix lying between the fertile staminate portion at the apex and the pistillate portion at the base (Figs. 5D, 23F). This section occurs in the area where the spadix first becomes free from the spathe. Only rarely is the transition between the fertile staminate and the sterile portion of the spadix clearly defined with the fertile flowers abruptly ending on a clear flowerless sterile portion. Instead, there is usually an assortment of sterile male flowers toward the apex of the sterile segment (Fig. 7E). Less frequently there are pistillodes in the lower half of the sterile segment. In *D. beachiana* and *D. killipii* (Fig. 15H) the sterile section is apparently absent, with the fertile staminate and fertile pistillate portions essentially contiguous. The length of the sterile portion of the spadix is here defined as that portion which lies between the lowermost functional androecium and the uppermost functional pistil regardless of the presence of pistillodes and staminodes along its length. However, the sterile portion of the spadix is usually quite obvious since a significant proportion of the sterile section is devoid of flowers. The axis of the sterile portion is typically convex as if the terete axis of the spadix (now fused) was half sunken into the leafy tissue of the spathe.

PISTILLATE SPADIX

The pistillate portion of the spadix is fused throughout its entire length to the spathe. What appears to be a stipe is readily apparent at the base. The pistillate flowers rarely extend very close to the base of the spathe (Fig. 4C). After the presence or absence of a sterile segment in the spadix, the number and disposition of the pistils is perhaps the most important taxonomic character in the inflorescence. Unlike many genera in the Philodendroideae that have the pistillate flowers closely aggregated on the spadix, the pistillate flowers of Dieffenbachia are moderately dispersed on the spadix. The degree of dispersal on the spadix is in itself different from species to species. There are generally only 2 or 3 pistils across the width of the spadix axis (regardless of whether they are lined up or not). Rarely, as in the case of D. killipii, there up to 6 pistils visible across the width of the spadix. At the opposite extreme, D. longispatha sometimes has a solitary row of pistils across the spadix axis. The arrangement of the pistils is generally quite irregular, lacking any obvious equidistant spacing or alignment in rows, but sometimes a series of pistils might be arranged in a loose row (as in D. killipii) or even in a broad arc across the width of the spadix.

Pistils are 2- or 3-carpellate, sometimes 1-carpellate, sessile, depressed-globose to depressedovoid, pale green, semiglossy, and smooth or 2- or 3-lobate. The stigma is a 2- or 3-lobate cushionlike layer that covers the entire apex of the pistil. The stigmatic papillae are orange or yellow. The papillae are close, dense, and moderately short, similar to those of *Philodendron*, but appear less interspersed with the gelatinous matrix that is so common on the stigmas of that genus. The stylar region is inconspicuous. With the stigma removed, the surface is truncate or broadly sulcate with a solitary medial or near-medial pore. Ovules are anatropous, one per locule. Each pistil is surrounded by 4 or 5 claviform, fleshy, white staminodia. The staminodia may be fused somewhat at the base, often forming a cupuliform structure around the base of the pistil. Individual staminodia are subcylindrical, commonly somewhat flattened toward the base and usually enlarged, sometimes almost subglobular at the apex. Staminodia typically are erect-spreading or erect, vary considerably in length, but are almost invariably longer than the pistils, usually 2–5 mm long, and held well above the pistils.

MORPHOLOGY OF FRUITING STRUCTURES

INFRUCTESCENCE AND FRUIT

While the inflorescences are always first erect, they quickly become reflexed after anthesis. This is probably important to successful development of the infructescence as it prevents the spathe from filling with rainwater and thus possible decay.

Fruits develop within the re-closed spathe, which often turns yellow, pale to bright orange, or red as fruits begin to mature. The spathe enlarges somewhat during the course of maturation, and finally begins to reflex along the middle, especially the portion that is fused to the spatia. In the process most of the margins of the spathe slough off, leaving just the fruiting spadix. The spadix remains arched backward with the bright red to orange-red berries held somewhat apart by the recurving process and displayed against the generally pale remains of the spathe (Figs. 1D, 4D).

Although fruit develops with self pollination, fruit and seed size are greater when the plants are out-crossed (Young, 1986). Since Dieffenbachia flowers are naked, all protection of the flowers must be provided by the spathe. In the manner of many other genera in the Philodendroideae, the spathe re-closes over the female flowers after pollination. In most cases, protection of the developing fruits after pollination is provided by the thickness of the spathe, as is true of other aroid genera such as Philodendron, but in Dieffenbachia protection is also provided by toxins in the sap, which may burn the mouth of any animal eating it. However, the pericarp and mesocarp of the berry appear to have no injurious effects when eaten and apparently lack the same toxic effects found elsewhere.

Generally, most pistils of an inflorescence are pollinated and develop into fruits, but the number produced per plant is variable. Studies in Costa Rica on *D. oerstedii* (Valerio, 1984) showed that the fruits varied from 13 to 43 with an average of 26 per plant. Valerio also reported that some berries were sterile, varying from 1 to 17 per infructescence.

Germination of seeds is usually prompt if the mesocarp is first removed. Valerio (1984) found that naked seeds of cleaned berries of D. *oerstedii* began to germinate within four days in a germination chamber. The percentage of seeds germinating ranged from 77.3% to 100% for different infructescences (averaging 91.7%). However, berries left intact usually did not germinate, but remainded viable for up to 90 days.

Valerio (1984) also reported that although 82% of the 729 berries studied were green, the remainder were red or yellowish. All seeds produced only albino plants. Germination rates for both the green seeds and the abnormal seeds were the same, but the albino plants perished. His studies with seed germination of *D. oerstedii*, as well as observations of other plants in the field led him to conclude that plants of this species required between five and six years to reach reproductive age.

Fruit maturation is normally a slow process in Dieffenbachia, requiring up to nine months in the case of D. nitidipetiolata (Young, 1986) (reported as D. longispatha). Valerio (1984) reported that fruit maturation in D. oerstedii was approximately one year. Valerio (1984) suggested that the seeds of Dieffenbachia are bird-dispersed because the seeds will not germinate unless the fruit mesocarp is first removed. At maturity the mesocarp of Dieffenbachia berries is pasty and somewhat sweet. The fruits would appear to be most suitable to bird dispersal, being colorful and having only a thin layer of edible portion available. The seeds are soft and could easily be destroyed by chewing, so effective animal dispersers are probably just removing the pericarp and thin mesocarp. Fruits of Dieffenbachia have been observed being eaten by white-faced monkeys, Cebus capucinus (J. Oppenheimer, pers. comm.), but it is not known whether they are the primary dispersal agents, since cebus monkeys are known to be generalists in their eating behavior (J. Oppenheimer, pers. comm.).

FLOWERING BEHAVIOR AND POLLINATION

Dieffenbachia populations tend to be aggregated, perhaps due as much to the vegetative reproduction of the stems as by local germination of seeds. A single clone may have many stems, but relatively few stems flower in a given year, and the number of inflorescences open on a given day is few (Young, 1988b). Inflorescences borne on a single stem generally do not anthesally overlap, thus there is little potential for geitonogamy (Young, 1990). For D. ni*tidipetiolata* (reported as *D. longispatha* in Young, 1988b) a reproductive stem may have two to seven inflorescences during a single growing season, maturing at intervals of 3 to 12 days (Young, 1986). For *D. oerstedii* there may be between one and four inflorescences per axil. Valerio (1984) reported that plants which produced a solitary inflorescence (34 of the 83 plants studied produced inflorescences) did not develop fruit. Valerio was unable to ascertain whether this was due to a lack of pollinators or age of the plants.

The pollination biology of Dieffenbachia has been studied (Croat, 1978, 1983b; Valerio, 1984; Young, 1986, 1988a, 1990). It has long been known to aroid workers that Dieffenbachia and several other aroid genera, e.g., Philodendron, some Syngonium, and Xanthosoma, are visited regularly by large scarab beetles (Coleoptera). Young (1986, 1990) found that D. nitidipetiolata (reported as D. longispatha) is pollinated mostly by beetles of the genus Cyclocephala (Scarabaeideae, Dynastineae) or more infrequently by the genus Erioscelis, also a dynastine scarab. Other visitors, including Diptera, Hemiptera, Dermaptera, Thysanoptera, and nitidulid beetles (Coleoptera, Nitudulidae), proved not to carry pollen and were deemed by Young not to be pollinators (Young, 1990).

Other monoecious aroid genera, such as *Philodendron* and *Xanthosoma*, are known to be beetle pollinated and provide food by means of oil-rich sterile male flowers. In *Dieffenbachia* the food reward consists of the protein-rich club-shaped staminodia surrounding each female flower (Young, 1986, 1990), but the beetles have also been seen feeding on the lowermost portion of the fertile staminate portion of the spadix. An indication that the staminodial food source is important to the beetles and preferred over other floral parts, is that the beetles will leave an inflorescence.

The production of scents during flowering is facilitated by the thermogenic behavior of the spadix, which may increase as much as 4°C during anthesis (Young, 1990). Scent production coincides with the flight activity of the scarab beetle pollinators (Schatz, 1990). Active movement of pollinators is usually at dusk, seemingly in direct paths to an open inflorescence. Beetles arrive at the inflorescence by first landing on the spadix (Young, 1990), then entering the lower tube portion of the spathe where the pistillate portion of the spathe is at anthesis. Beetles typically remain in the inflorescence for 24 hr. after their arrival. While in the spathe the beetles mate and eat the nutritious staminodia (Young, 1986) surrounding the pistils. Beetles depart the following day as the inflorescence begins

to close and the staminate flowers are emitting pollen in long filaments (Fig. 5F). In order to leave the inflorescence the beetle must literally wade through pollen, ensuring that it will be covered with pollen before flying away to the next receptive inflorescence.

While some Dieffenbachia species, perhaps most, have spathes that remain open only 24 hr. (based on my observations in the field), the pollination event for D. nitidipetiolata (reported by Young as D. longispatha) involves three days (Young, 1990). Inflorescences of this species open in the evening of the first day, but the spadix is not initially receptive. On the evening of the second day the stigmas become receptive (about 17:30) and the spadix temperature increases to 4°C above ambient temperature (Young, 1990). It is at this time that beetle pollinators arrive, and they enter the spathe where they generally persist for another full day, departing on the evening of the third day. Young (1990) found that for most days there were fewer than four inflorescences open and in female phase at any one time in an area of 700,000 m². In her studies at La Selva in Costa Rica she found that beetles flew between 1 and 680 m (averaging 83 m) between consecutive visits to D. nitidipetiolata (reported as D. longispatha).

Beetle pollination of *Dieffenbachia* is not species-specific. Nine different scarab beetle species of *Cyclocephala* as well as *Erioscelis columbica* Endrodi were found to pollinate *D. nitidipetiolata* (reported by Young as *D. longispatha*) at the La Selva Reserve in Costa Rica (Young, 1986). Still, *Dieffenbachia* species produce different scents and differentially attract particular beetle species (G. Schatz, pers. comm.).

Because of the loose relationship between the pollinators and any one species of *Dieffenbachia*, hybridization does occasionally occur (Young, pers. comm.). It is known that seeds from hybrid plants do germinate and produce viable F1 plants. It has not yet been determined if this F1 generation is capable of reproducing sexually. Still, this phenomenon of hybridization might explain the many different, seemingly related, but distinct, populations of *D. nitidipetiolata* that occur in some regions, such as the Río Guanche region of Colón Province in Panama. Since asexual reproduction is so prevalent in *Dieffenbachia*, occasional hybridization followed by vegetative reproduction might explain these patterns of variation.

PHENOLOGY

Some species of *Dieffenbachia* are in flower all year-round. In general, more flowering takes place

during the rainy season even if the species flowers at other times of the year as well. This may be tied to the fact that the beetles pollinating *Dieffenbachia* are more frequent during wet periods. Although *D. beachiana* and *D. burgeri* flower primarily in the dry season in Costa Rica and Panama, they occur in wetter habitats where beetle pollinators are reliably available.

CYTOLOGY

Dieffenbachia has chromosome counts of 2n =34 and 68 (Petersen, 1989). Grayum argued that Dieffenbachia is closely related to Philodendron (Grayum, 1984). Petersen (1989) argued that Philodendron would not be considered so closely related if its chromosome base number were not 17 as assumed by Grayum. She also argued that the differences in the "size and constitution of the chromosomes (small metacentrics of Philodendron versus medium to large submetacentrics to subtelocentrics of Dieffenbachia) also indicate that no close relationship exists between the two genera" (Petersen, 1989: 128). Petersen considered the chromosome basic number in *Philodendron* to be x = 18 based on the fact that all members of Philodendron subg. Meconostigma (Schott) Engl. have 2n = 18 and subgenus Philodendron Schott also has 2n = 18 in part. Grayum (1984) suggested that Dieffenbachia was close to the tribe Spathicarpeae (subfam. Aroideae). Petersen (1989) considered this a reasonable suggestion since they share the same basic number of x = 17 and large chromosomes also with the centromere frequently located distally on the chromatids. Petersen (1989) believed that the Aglaonemateae may be the closest relatives of Dieffenbachieae based on the similarity in the constitution and size of the chromosomes, despite the fact that the former has a different chromosome base number (x = 20). Chromosome counts for Bognera recondita (Madison) Mayo & Nicolson, the only other member of Dieffenbachieae, are also 2n = 34. Bognera, a monotypic genus, also shares a karyotype of medium-sized metacentric to sub-telocentric chromosomes with Dieffenbachia (Petersen, 1989).

GEOGRAPHICAL DISTRIBUTION AND ENDEMISM

The genus *Dieffenbachia* has approximately 135 species, most of them in South America. It ranges from Mexico, throughout Central America, and to the West Indies, Trinidad, and most of South America as far south as Argentina, Paraguay, and Bolivia. Distribution of species is unequal, with major centers of diversity including Colombia with 37 species, Ecuador (34), Peru (30), Brazil (27), Panama (20), and Costa Rica (13), principally at lower to middle elevations in the Andes. The genus is also widespread in the Amazon basin as is evidenced by the large number of species at low elevations in Brazil with a total of 27 species. Only 8 species occur in the Guianas region in eastern South America and the Territorio Amapá of northeastern Brazil. The genus is exceptionally abundant in the western Amazon basin in the foothills of the eastern Andes, with 57 species. The wetter forests at middle elevations in the foothills of the Andes are particularly rich. For example, there are 5 species in the vicinity of the Jatún Sacha Reserve along the Upper Río Napo near Misahuallí in Ecuador.

As is true for many other genera of Araceae (Croat, 1992, 1983a, 1986a, 1986b), the northwestern part of South America, especially on the Pacific slope of Colombia and adjacent Ecuador, is rich in species of Dieffenbachia. About 14 species occur on the eastern slopes of the Andes in Ecuador and about 15 species are known from the Pacific slope in Colombia. Relatively few species occur in southern South America, with only Dieffenbachia aglaonematifolia Engl. occurring in southern Brazil, Paraguay (Croat & Mount, 1988), and Argentina. Collections of only 7 species, mostly new species, have been seen for Bolivia. Northcentral South America is also not particularly rich in species. Only 2 species occur in the Cordillera de Mérida in Venezuela, and only 1 of these occurs in the Cordillera de la Costa (Bunting, 1979; Croat & Lambert, 1987).

A preliminary key and preliminary descriptions have been produced for South American *Dieffenbachia* species, but many species remain poorly known. Thus the figures given for South America remain tentative.

Central American species constitute a group relatively isolated from South America, and only seven species range into South America, especially along the Pacific slope and in the Magdalena River Valley in Antioquia Department. The majority of Dieffenbachia in Central America occur from Nicaragua to Panama, and most are relatively widespread in this region. The most widespread species of Dieffenbachia, D. oerstedii, ranges from southern Mexico to western Panama (Fig. 29). Dieffenbachia wendlandii ranges from Mexico to Costa Rica (Fig. 28) and both D. nitidipetiolata and D. tonduzii range from southeastern Nicaragua to Ecuador (Figs. 30 & 29, respectively). In the latter country, D. nitidipetiolata crosses the Andes into the Amazon drainage in Napo. Remaining Dieffenbachia are all narrowly isolated. Nine species are shared between Costa Rica and Panama, but even these are not widespread in the two countries. Those shared are *D. aurantiaca, D. beachiana, D. davidsei, D. grayumiana, D. killipii, D. nitidipetiolata, D. oerstedii, D. tonduzii,* and *D. wendlandii. Dieffenbachia aurantiaca* occurs only in southwestern Costa Rica in the vicinity of the Osa Peninsula and in adjacent Panama in the Burica Peninsula area (Fig. 27). Both *Dieffenbachia beachiana* and *D. grayumiana* range from northern Costa Rica to western Panama (Bocas del Toro) (Figs. 28, 27), while *D. davidsei* ranges from northwestern Costa Rica to central Panama (San Blas) and Colombia (Fig. 27).

A total of 11 species (42% of the total) of *Dief-fenbachia* are endemic to either Costa Rica or Panama. Endemism is particularly high in Panama where 8 of the 26 species (31%) are endemic. In Panama endemic species are *D. copensis*, *D. crebripistillata*, *D. fosteri*, *D. fortunensis*, *D. galdamesiae*, *D. lutheri*, *D. panamensis*, and *D. pittieri* (Figs. 27–30). In Costa Rica 3 of 26 species (12%) are endemic. Costa Rican endemics are *D. burgeri*, *D. hammelii*, and *D. horichii* (Fig. 27). Neither Mexico nor Middle America have endemic species.

Dieffenbachia isthmia (Fig. 28), D. longispatha (Fig. 29), and D. obscurinervia (Fig. 29) range across the Isthmus of Panama from Veraguas Province to northern Colombia. Dieffenbachia aurantiaca, D. beachiana, and D. grayumiana (Figs. 27, 28) are the only species occurring in both Costa Rica and Panama. Some species are further isolated. Dieffenbachia aurantiaca and D. burgeri are restricted to the region of the Osa Peninsula in southwestern Costa Rica (or in the case of D. aurantiaca in Panama on the adjacent Burica Peninsula; Fig. 27) and D. horichii is restricted to a relatively small area on the Pacific slope of Costa Rica (Fig. 27). Several other species are also narrowly restricted or known only from the type specimen. Dieffenbachia fosteri is restricted to northeastern Panama (Fig. 27). Dieffenbachia fortunensis is restricted to the northern Chiriquí Province (Fig. 28). Dieffenbachia copensis is found only in the Coclé Province of Panama (Fig. 27), and D. galdamesiae in a small area south of the Panama Canal (Fig. 28).

Further collecting in Colombia, especially along the western slope of the Andes, may change the distribution of *Dieffenbachia*, but the current patterns most likely reflect the realities of life zone ecology and geologic history of the area rather than under-collecting. Since relatively few species of Araceae are known to occur at lower elevations on both the eastern and western side of the Andes, it can be presumed that the evolution of the respective Amazonian and Pacific coastal floras occurred independently after the Andes began to arise toward the end of the Cretaceous (Raven & Axelrod, 1974). The fact that there are no truly wide-ranging species, i.e., those ranging from Mexico to Brazil, attests to this isolation. The high rates of endemism in Costa Rica and Panama as well as Mexico perhaps reflects the isolation of these areas during periods when the oceans were at much higher levels than they are today, and when the area that is now central Panama and Costa Rica was subsequently disconnected from South America. At the close of the Tertiary period, 18,000 years ago, the sea level was about 100 m higher than today (Holmes, 1969). Much earlier the land mass of what is now Central America began to emerge as a series of islands during the Oligocene epoch with further uplifting during the Middle Miocene. It was not until the Upper Miocene and Pliocene epochs that the final portions of the isthmus of Panama emerged above sea level (Torre, 1965), and the final connection of Central and South America was about 5.7 million years ago. To put these geological events in relation to the modern aroid flora, it should be noted that even during this era precursors to the extant flora probably already existed. The angiosperm floras of the Oligocene were believed to have consisted almost entirely of extant genera and with existing species among Oligocene and Pliocene floras (Takhtajan, 1969).

Equally important as geology to the isolation of the Central American aroid flora are ecological factors for Central American species of Dieffenbachia. Much of eastern Panama consists of broad expanses of Tropical moist forest (T-mf) with other, generally smaller areas of Premontane wet (P-wf) and Tropical wet forest (T-mf) (Holdridge, 1967). In contrast to Panama, much of the Chocó area of northwestern Colombia consists of much wetter pluvial forest with annual precipitation exceeding 11,700 mm (Gentry, 1982). This broad band of pluvial forest with its own suite of unique endemic species no doubt acts as a dispersal barrier for species from regions with less rainfall. It may account for those Panamanian and Costa Rican species that skip the wettest areas of northwestern South America but reoccur in the relatively drier areas of mesic western Ecuador.

Middle America has low species diversity with Guatemala having only two species and Honduras three. Only Nicaragua, with six species, four of them restricted to the southeastern corner near Costa Rica, is moderately rich in species. All except *D. standleyi* and *D. wendlandii* appear to range into the country from Costa Rica. The low species diversity and very low aroid endemism in *Dieffen*-

bachia in Middle America is perhaps explained by its historic remoteness from existing large land masses to the north and to the south. The distribution of modern aroid species suggests that the northwestern part of Middle America may have been isolated from Costa Rica in the area of the San Juan Depression (Nicaragua). Many of the species that occur in Costa Rica or Panama enter into Nicaragua in only a small area in the southeastern part of the country. Though the existing flora of Guatemala does not reflect isolation from Mexico to the same degree, it is possible that the more elevated portions of Guatemala, Nicaragua, and Honduras were isolated from major portions of Mexico by the Isthmus of Tehuantepec. With no endemic Mexican species, the *Dieffenbachia* flora reveals less endemism than does Anthurium (Croat, 1983a) or Philodendron (Croat, 1997). Both Mexican Dieffenbachia are relatively widespread, with D. oerstedii ranging to Panama (Fig. 29) and D. wendlandii ranging to Panama (Fig. 28).

The remaining Costa Rican and Panamanian species not already discussed above appear not to have strong affinities with South American species and clearly do not have affinities with other Central American species. On the other hand, there are some, relatively few, Central American species, among them *D. killipii*, *D. nitidipetiolata*, and *D. tonduzii*, that are likely to be of South American origin since they are wide-ranging species in South America.

HORTICULTURAL SIGNIFICANCE

Dieffenbachia, like many other members of the Araceae, is one of the world's most important ornamental plants. Owing to the attractive leaves and hardiness under the difficult conditions found indoors, *Dieffenbachia* remains one of the most important ornamental plants in homes, offices, and professional displays. Ornamental aroids play a major role in the foliage-plant industry in the United States, making up about one-third of total foliage plant sales (Henny, 1988). *Dieffenbachia* is one of 5 aroid genera routinely among the top 10 foliage plants in annual sales volume (Henny, 1988).

The Araceae hold 7 of the top 13 positions in terms of overall sales in North America, including the first two (R. Henney, pers. comm.). An ornamental cultivar of *Dieffenbachia* is the second most important in sales, and the genus consistently has one or more taxa on the list of most popular ornamental plants in North America. *Dieffenbachia* breeding and culture plays a major economic role

in the United States in Florida, California, and Hawaii.

TAXONOMIC TREATMENT

- **Dieffenbachia** Schott, Wiener Z. Kunst 3: 820. 1829. TYPE: *Dieffenbachia seguine* (Jacq.) Schott.
- Seguinum Raf., Fl. Tellur. 3: 66. 1836 [1837]. TYPE: Seguinum maculatum Raf. [= Dieffenbachia seguine (Jacq.) Schott].
- Maguirea A. D. Hawkes, Bull. Torrey Bot. Club 75: 635. 1948. TYPE: Maguirea spathicarpoides A. D. Hawkes = [Dieffenbachia paludicola N. E. Br.].

Terrestrial; caudices thick, often elongate and prostrate, rooting at the lower nodes, the older portions of the stem trailing across the surface of the ground, often for considerable distances; sap often milky and frequently with varying concentrations of oxalic acid, with conspicuous annular leaf scars. Petioles elongate, amplexicaul, sheathed to the middle or sometimes to the apex; sheath unequal and often free-ending at apex; leaves clustered in a tight whorl at the stem apex; blades ovate to oblongovate, elliptic, oblanceolate, or obovate, acuminate at apex, acute to obtuse to rounded at base, typically subcoriaceous, sometimes variegated throughout or in areas along the midrib with paler colors; midrib raised on both surfaces; primary lateral veins pinnate, usually sunken above, raised below, much more prominent than the minor veins, all lateral veins extending to the margins without forming a single collective vein but with several primary lateral veins often forming a series of short, discontinuous collective veins; interprimary lateral veins sometimes present; minor veins distinct to obscure, usually not markedly raised, sometimes connected by transverse tertiary veins. INFLORESCENCES shorter than the leaves, 1 to several per axil; bracts short and usually inconspicuous; peduncle usually somewhat flattened and angular with one edge narrowed; spathe oblong, persistent, convolute at base, often somewhat constricted about midway, opening usually only above the middle, usually green on outside, somewhat paler within; spadix slightly shorter than the spathe, divided into pistillate and staminate portions, each with naked unisexual flowers; the pistillate portion basal, about as long as the staminate portion, fused to the spathe, remotely many-flowered (typically 20 to 80 rarely to 160); staminate portion clavate, white, free from the spathe, densely many-flowered, often separated from the pistillate portion by a naked interval. Staminate flowers consisting of 4 stamens united into a 4- to 5-sulcate, truncate synandrium; anthers lateral, contiguous, the common connective thick, fleshy; the thecae obovoid to oblong-elliptic, dehiscing by short, apical, pore-like slits; pollen extruded in strands, inaperturate, ellipsoid or oblong or nearly spherical, large, averaging more than 75 μ m, exine psilate to obscurely verruculate and/or sparingly punctate-foveolate to densely foveolate; pistillate flowers moderately dispersed but often in weak rows with 1 to 5(6) pistils per spiral, and surrounded by 4 or 5 claviform white staminodia, these longer than the ovary usually 2–5 mm, usually spreading, sometimes fused briefly at the base; ovaries 2- or 3-carpellate, sometimes 1-carpellate, sessile, depressed globose to depressed ovoid, 2- or 3-lobate; ovules 1 per locule, pale green, semiglossy, erect, anatropous; placenta axile to basal; stylar region inconspicuous; stigma large, hemispheric or 2- or 3-lobate, about as broad as the ovary, yellow to orange in color. INFRUCTESCENCE with fruiting spathe often turning yellow, orange, or red, breaking up longitudinally in fruit to expose the colorful berries; fruits baccate, globose or 2- or 3lobed, 1- or 2(3)-seeded; seeds globose or ovoid, the testa thick, smooth, green to blackish green; embryo large; endosperm lacking.

Chromosomes 2n = 34, 68.

KEY TO DIEFFENBACHIA OF MEXICO, CENTRAL AMERICA, AND THE WEST INDIES

- 1a. Petiole involute, extending to base of blade and frequently prolonged beyond the base of the blade.
- Larger leaves regularly to more than 45 cm long and 23 cm wide, cuneate at base, coriaceous, usually glossy above, not variegated, uniformly green.
 - 3a. Petiole sheath markedly undulate, at least near the base; Atlantic slope.
 - - - 5b. Primary lateral veins usually 15 or more.

 - 6b. Leaf blades with primary lateral veins usually more than 18 per side; usually cordulate at base, usually matte and subvelvety above, usually bullate, often variegated; petiole lacking a whitish band on the abaxial surface; Nicaragua to Colombia
- 1b. Petiole sheath erect to involute, ending short of blade base (except rarely on upper leaves).

7b. Petiole beyond sheath subterete, rounded abaxially, with margins rounded to acute (not winged).
 8a. Plants with petioles or major veins of lower blade surface minutely granular-puberulent to puberulent.

- 9b. Primary lateral veins usually less than 18 pairs (rarely to 22 in *D. grayumiana*) usually departing midrib 40°–60° at blade midpoint; midrib and primary lateral veins inconspicuously granular-puberulent.
 - 10a. Blades narrowly oblanceolate, 6.4 times longer than wide, less than 6 cm wide

 5. D. copensis Croat
 - 10b. Blades elliptic to obovate-elliptic, oblong-elliptic, to narrowly oblong-lanceolate (rarely narrowly oblanceolate in *D. fortunensis*), 1.7–5.2 times longer than wide, 6.7–39 cm wide.
 - 11a. Petioles with sheaths ending no more than 5 cm from base of blade ------
 - 24. D. standleyi Croat
 11b. Petioles with sheaths ending more than 13 cm from base of blade.
 12a. Primary lateral veins arising at 30°-40° angle; central Panama
 - 10. D. galdamesiae Croat 12b. Primary lateral veins arising at mostly 55°–70° (to 80° in D. grayumiana);
 - Costa Rica and western Panama. 13a. Plants usually stout, 1.5 m tall; blades narrowly ovate, (22) 30–54
 - cm long, 10–32 cm wide (averaging 36×18 cm), 1.5–2.6 times

8b. Plants with petioles or major veins of the lower blade surface glabrous.
14a. Petiole sheaths decurrent apically (lacking prominent protruding extensions); Atlantic low-lands.

15a. Blades drying blackened; Panama (Bocas del Toro), near sea level ----

9. D. fosteri Croat
 15b. Blades drying yellowish brown, greenish to yellowish brown.
 16a. Petioles very glossy, drying as if covered with shellac; Nicaragua to Ecuador ...

18. D. nitidipetiolata Croat 16b. Petioles not glossy, not drying as if covered with shellac.

- 17b. Stems usually more than 1 m tall; blades more than 10 cm wide.18a. Petioles matte; leaf blades usually subcordate at base, usually flecked
 - - base, usually plain green (rarely mottled with pale green).
 19a. Petioles terete; sheaths decurrent at apex, tightly inrolled with one side completely hidden by the other; Mexico to Panama but but primarily on Pacific slope (except in Oaxaca and Veracruz on Atlantic slope) ______ 26. D. wendlandii Schott

14b. Petiole sheaths (at least on one side) rounded to auriculate at apex.

20a. Blades with more than 18 primary lateral veins or with primary lateral veins obscure, barely more conspicuous than interprimary veins.

- 21a. West Indian and South American species; plants with both sharply sulcate petioles and a thickened, protruding spadix; fruits 2- to 3-lobed
- 23. D. seguine (Jacq.) Schott
 21b. Mainly Central American species (D. killipii, D. isthmia, and D. obscurinervia also in South America).
- 20b. Blades variously shaped, matte to glossy above, with 8 to 18 primary lateral veins per side.

 Spadix lacking medial sterile region, the male and female regions contiguous or nearly so.

- 24a. Petioles usually solid green, not densely and conspicuously pale-maculate. 25a. Blades with major veins on the lower surface granular-puberulent ...
 - 25b. Blades with major veins on the lower surface glabrous
- 24b. Petioles densely and conspicuously pale-maculate. 15. D. killipii Croat

 - 26b. Stems usually less than 1 cm thick; petioles distinctly pale-maculate; primary lateral veins usually departing midrib at 90° or more; Costa Rica, Sixaola region, Panama, and Colombia -------

23b. Spadix with an evident medial sterile region, pistillate and staminate portions

- separated by a distinct naked spadix axis.
 - 27a. Plants usually less than 0.5 m tall _____ 20. *D. oerstedii* Schott 27b. Plants to more than 0.5 m tall.

28a. Blades drying dark brown to blackened on upper surface.

29a. Blades usually with posterior lobes; lower blade surface drying

yellowish brown to yellowish gray-brown to dark yellow-brown or yellowish green; stems solid dark green, drying glossy and minutely wrinkled (the areoles interspersed with raphide cells); Panama, Veraguas Province and the Azuero Peninsula in the west (at 700–900 m in Herrera and Los Santos Provinces) to Darién Province in the east, and to Colombia 50–800(1000) m _______ 14. D. isthmia Croat

- 29b. Blades lacking posterior lobes; lower blade surface drying grayish black; stems mottled dark green, drying smooth with a dense layer of raphide cells (but not minutely wrinkled); Panama, Bocas del Toro, sea level _________9. D. fosteri Croat
- 28b. Blades drying yellowish green to dark gray-green, rarely brownish on upper surface.
 - 30a. Petioles usually white at base; blades usually less than 20 cm long ______ 20. D. oerstedii Schott
 - 30b. Perioles not whitish at base, frequently paler than stem but not markedly paler than the remainder of the petiole; blades usually more than 20 cm long.
 - Petioles usually sharply C-shaped, discolored and whitish at the base; blades matte ______ 20. D. oerstedii Schott
 - 31b. Petioles terete to obtusely C-shaped or obtusely D-shaped, not sharply sulcate, not discolored and whitish at base; blades glossy to semiglossy.
 - 32a. Species of mostly dry habitats in western Central America (Mexico to Panama); blades subcoriaceous, semiglossy on upper surface, (15)20–55(65) cm long (averaging 35 × 17 cm); 75 to 900 m in elevation ______ 26. D. wendlandii Schott
 - 32b. Species of wet habitats, southeastern Nicaragua and along the entire Atlantic slope and the Osa Peninsula of Costa Rica; blades moderately coriaceous, glossy on the upper surface, 16–36 cm long, (averaging 23 × 12 cm); sea level to 200 m, mostly at less than 100 m in elevation

..... 4. D. concinna Croat & Grayum

 Dieffenbachia aurantiaca Engl., Anales Inst. Fis.-Geogr. Nac. Costa Rica 9: 209. 1898. TYPE: Costa Rica. Puntarenas: "in silvis prope Santo Domingo ad sinum dulcem [Santo Domingo de Golfo Dulce], fructif. Mart. 1896," *A. Tonduz 9961* (holotype, B!; isotypes, CR!, US!). Figures 2, 27A.

Stout herb, 0.7-2.3 m tall; sap fetid and caustic; stems erect at apical part, to 2 m long, the older portion reclining and up to 2 m long; internodes 2.0-4(6) cm long, 5-7(10) cm diam., dark green to pale green, semiglossy to glossy, streaked with paler green; petioles 13-33(48) cm long (averaging 24 cm long), C-shaped at base in cross section, moderately spongy, medium green, semiglossy adaxially, matte and acutely 1-ribbed abaxially, the surface finely dark striate, sometimes variegated with paler green markings, sheathing 1/3 to nearly throughout (35%-97% their length and averaging 77%); sheath 6.5- $25.5(38)~\mathrm{cm}$ long (averaging $17.7~\mathrm{cm}),$ medium green, finely dark green striate, sometimes variegated with paler green markings, adaxially acute margins sometimes much paler, with margins incurled but usually not overlapping, the apex freeending and obliquely rounded to rounded-auriculate distally; unsheathed portion 0.5-2 cm long, angular to \pm triangular in cross section, flat to broadly sulcate adaxially (sometimes with a medial keel), adaxial margins thin and revolute, acutely keeled abaxially, abaxial margins thickly winged, sometimes with a medial keel, thin, revolute, sometimes medially keeled at margins; blades oblongelliptic to ovate-elliptic, slightly inequilateral, one side 1-1.5 cm wider than the other side, usually subcoriaceous, acuminate to abruptly acuminate at apex, slightly inequilateral and obtuse to rounded or subcordate (rarely attenuate on one side) at base, $(26)31-57 \times 11-27$ cm (averaging 39 × 19 cm), 1.7-2.6 times longer than wide (averaging 2 times), ranging from about as long as petioles to 2.8 times longer than petioles (averaging 1.7 times longer); margins weakly undulate; upper surface dark green, concolorous or sometimes variegated, drying dark olive-green to medium gray-green, weakly glossy to semiglossy; lower surface moderately paler, matte to weakly glossy, drying pale yellowish green; midrib flat to broadly concave above (broadly sulcate near base), 5-20 mm diam., sometimes



Figure 1. —A. Dieffenbachia longispatha, spathe blade showing open position at anthesis with thrips present on inner surface of spathe (Croat & Zhu 77042). —B. Dieffenbachia tonduzii, inflorescence at anthesis showing fully opened spathe with beetles in base of spathe tube and partially eaten sterile staminate flowers (Croat & Zhu 76653). —C. Dieffenbachia wendlandii, close-up of inflorescence showing intact unilocular pistils with mostly eaten staminodia (edge of spathe tube partially removed) (Croat 39749). —D. Dieffenbachia wendlandii, mature infructescence showing exfoliated spathe and berries splayed out for display (Croat & D. Hannon 65536).

whitish, faintly striate above, bluntly acute to Vshaped (a continuation of the triangular petiole) below, drying brown below, faintly striate; primary lateral veins (8)12 to 14 per side, departing midrib at a steep angle, spreading at a 50°-70° angle, gradually spreading in a broad curve, slightly to moderately paler than surface in the proximal one-half, weakly raised to convex in valleys, flat and darker than surface toward margins, drying mostly paler, sometimes darker than surface above, weakly convex and slightly paler than surface below, drying vellowish and paler than surface or brownish and darker than surface below; interprimary veins present or absent, usually with 1 between each pair of primary lateral veins in the lower ¹/₃ of the blade; minor veins darker than surface, visible but moderately obscure below. INFLORESCENCES to 3 per axil; peduncle (7)10-18 cm long, acutely angular on one side, drying striate, 3-6 mm diam.; spathe 17-25(38) cm long, 2-3.5 cm wide, flattening to 5.7-8 cm wide on tube, 2.5-6.5 cm wide at constriction, 3-4.3 cm longer than the spadix, gradually long-tapered toward apex from the middle, uniformly light green to medium green throughout; weakly glossy outside, glossy inside; spathe blade 2.5-7 cm wide when flattened; spadix 16-20(33) cm long; free portion to 15.5 cm long; pistillate portion 6.5-8.5(15.5) cm long, 1.5-2 cm diam. throughout (mostly drying 6-9 mm diam.); fertile staminate portion 7-12.5 cm long, white, tapered toward apex and weakly tapered slightly toward base; intermediate sterile segment 1.5-4 cm long, with a few scattered pistils in lower half and a few scattered staminodia in upper half; pistils 51 to 72, irregularly scattered, with 3 to 4(6 to 7) across the width of the spadix, separated from one another by ¹/₂ to 4.0 times their width, depressed-globose, to 2 mm long, 1.2-1.6(2.8) mm diam., pale green; stigmas cushion-shaped, to 2 mm high, 2.5-3 mm wide, white; staminodia 3 to 5 per pistil, 1.5-2(3.8) mm long, free or briefly united at base, held well above the stigmas sometimes united for much of their length; synandria 1-2(3.4) mm diam., margins irregularly angled with rounded, linear to 3-sided slit medially at apex. INFRUCTESCENCE 19-24 cm long; spathe orange outside; spadix 8-15 cm long; berries red-orange, B & K yellow-red 6/2.5 to B & K yellow-red 7/5 to red B & K red 6/10 (Berlin & Kay, 1969), subglobose, ovoid to ellipsoid, 7-10 mm long.

Distribution and habitat. Dieffenbachia aurantiaca is known only from southwestern Costa Rica and adjacent Panama, in the region of the Osa Peninsula in Costa Rica and the Burica Peninsula in Panama. It occurs in wet forests and swampy sites from near sea level to 780 m in *Tropical wet forest* (T-wf) and *Premontane wet forest* (P-wf) life zones (Holdridge, 1967).

Phenology. Dieffenbachia aurantiaca begins to flower in the early rainy season with flower buds having been seen as early as May and as late as August, and mature open inflorescences seen between May and December. Fruiting occurs between September and March.

Discussion. The species is characterized by its more or less elliptic, usually unvariegated, greendrying blades, obtuse to subcordate at base, but especially by the triangular and weakly sheathed petioles, decurrent at apex. It is probably most closely related to *D. horichii*, but differs from that species in having a longer free portion of the petiole, which is more or less triangular. Also vegetatively similar are *D. longispatha* and *D. nitidipetiolata*, but both differ primarily for the same reasons, i.e., that the free portion of the petiole is not triangular.

An unusual collection, *Croat 67700*, from a relatively dry area on the Pacific slope of Costa Rica (drier than the typical sites for this species), has a petiole that is described as terete though the collection otherwise matches *D. aurantiaca*. The collection looks vaguely like *D. nitidipetiolata*, which is otherwise found only on the Atlantic slope. A Tonduz collection at US originally labeled *Tonduz 9961*, was relabeled *7177* despite the fact that it was also collected in March 1896. It appears to be identical to two other specimens labeled *Tonduz 9961*, the type collection number.

Additional specimens examined. COSTA RICA. 18XX, Pittier & Durand s.n. (BR). Puntarenas: near Palmar Norte, Allen 5972 (UC); Playa Blanca, Golfo Dulce, Valerio 462 (CR, F); Golfo Dulce-Río Terraba, Skutch 5328 (US); Cantón de Osa, Buenos Aires, Fila Retinto, from Palmar Norte to Jalisco, Grayum & G. Herrera 9139 (CR, MO); Pan-Am Hwy. 287 (ca. 3 km NW of Chacarita & 30 km S of Palmar Sur), Grayum et al. 7549 (MO); near Pan-Am Hwy. vic. Piedras Blancas, Croat 32955 (HUA, INB, MO); W side of Fila Gamba, ca. 6 km from Golfito airport, Croat & Grayum 59906 (CR, MO); Cantón de Golfito, Par. Corcovado, vic. Estación Sirena, 14 Apr. 1995, Picado & Gamboa 138 (INB, MO); Piedras Blancas-Rincón (on Osa Peninsula), 3.7 mi. W of Pan-Am Hwy., Croat 67700 (MO): San Vito de Coto Brus to Ciudad Neily, NE slopes of Fila de Cal, Hammel & Grayum 14169 (MO); Palmar Norte-Panama border, 3 km N of turn-off to Rincón, Croat & Hannon 79193 (COL, INB, MEXU, MO, UB, WU); Osa: 2 km N of Chacarita, S of Palmar Norte, Maas et al. 7834 (INB, MO, U), San José: N of Palmar Norte, trail to Ialisco, Croat 35210 (F, MO); 5 km W of Palmar Norte on rd. to Puerto Cortes, Lent 161 (F, NY, US); San Isidro del General-Dominica, ca. 1 mi. beyond divide, Croat 35292 (INB, MO). PANAMA. Chiriquí: Puerto Armuelles, Woodson Jr. & Schery 861 (F, MO); Puerto Armuelles-San



Bartolo Limite, 7 mi. W of Puerto Armuelles, *Croat 35079* (MO); Burica Peninsula, 8 km W of Puerto Armuelles, *Croat 21961* (F, MO); Quebrada Manzanillo, 9 km S-SW of Puerto Armuelles, *Busey 743* (MO); Quebrada Quanabanito beyond La Represa, 2 mi. SW of Puerto Armuelles, *Liesner 114* (MO, US).

 Dieffenbachia beachiana Croat & Grayum, Novon 9: 492. 1999. TYPE: Panama. Bocas del Toro: Chiriquí Grande-Fortuna, 13.2 mi. W of Chiriquí Grande, 8°45'N, 82°10'W, 310 m, *T. B. Croat & M. H. Grayum 60130* (holotype, MO-323065!; isotypes B!, K!, PMA!, US!). Figures 3, 28B.

Slender herb, 40-100 cm tall; stems briefly creeping at base; internodes 2-6 cm long, 1.5-3.5 cm diam., medium green to olive-green, sometimes streaked with cream, semiglossy and obscurely roughened. LEAVES clustered near stem apex, erect-arching; petioles 17-46 cm long (averaging 26.5 cm long), sheathed 25%-83% of petiole (averaging 54%); sheath 10-22 cm long (averaging 14.2 cm), decurrent at apex; unsheathed portion (2.5)10-30 cm long, broadly C-shaped in cross section, dark green to brownish, flattened with acute, erect margins or sharply to bluntly sulcate adaxially, surface pale green-mottled, matte, usually minutely roughened and with scattered scales, whitish raphide cells visible, drying with scattered clusters of pustular raised areas with granular-puberulent protrusions; blades narrowly elliptic to lanceolate, rarely narrowly ovate, inequilateral, one side 1-2 cm wider than the other side, thinly coriaceous to subcoriaceous, drying papyraceous, weakly bicolorous, \pm equilaterally acuminate at apex (the acumen to 5 mm long), slightly inequilateral and acute, rounded or truncate (rarely subcordate in Panama) at base, 16-41 cm long, 6.5-15 cm wide (averaging 28×10.7 cm), 1.8–5.3 times longer than wide (averaging 2.6), 0.7-1.9 times longer than petioles (averaging 1.12 times longer than petioles); margins crisped-undulate; upper surface dark green (in Panama sometimes mottled with white or cream), semiglossy (rarely matte), lower surface semiglossy to weakly glossy or matte, slightly paler; midrib flatraised above, often striate, usually concolorous above, convex to thicker than broad below, puberulent with thick, whitish trichomes below; primary

lateral veins 23 to 30(36) per side, departing midrib at a 70°-110° (to 45° toward apex and sometimes at base) angle, arising acutely then straight to weakly curved to the margins (then sweeping prominently toward apex), usually guilted-sunken above, convex, puberulent with thick, whitish trichomes, sometimes with adjacent veins alternating ascending and descending below; interprimary veins usually present, scarcely less visible than primary lateral veins; minor veins moderately distinct and weakly raised below. INFLORESCENCES 1 to 3 per axil; peduncle 9–13 cm \times 5–7 mm, drying 3– 4 mm diam.; spathe 10-19 cm long, gradually constricted at middle, green throughout, gradually long-tapered to apex; spathe blade to 3 cm diam. when flattened; spathe tube 1-2 cm diam.; spadix 13-15 cm long; pistillate portion 4.5-6 cm long, drying 7 mm diam. throughout; fertile staminate portion 5-6.5 cm long, drying 4 mm diam. throughout; intermediate mostly sterile portion usually 2-3.5 cm long, 2 mm diam., sometimes with pistillate and staminate portions almost contiguous; pistils 46 to 66(100), 2 to 4 situated across the width of the spadix, ovary oblong-ellipsoid, $1.5-2 \times 1-1.6$ mm; stigmas subglobular, about as broad as the ovary; staminodia narrowly clavate, usually not at all fused at base, ca. twice as long as pistil; synandria 1.8-2.6 mm diam., margins irregularly subrounded, drying smooth and light brown at apex. INFRUC-TESCENCE with spathe (10)14-16 cm long, somewhat flattened, yellow-green mottled green and white with darker flecking, maturing to orange; spadix 6-10 cm long; berries orange, subglobose, 6-8 mm diam.

Distribution and habitat. Dieffenbachia beachiana ranges from northeastern Costa Rica to western Panama (Bocas del Toro, Chiriquí, and Veraguas) at elevations of 40 to 800 m. In Costa Rica it occurs on the Atlantic slope of the Central Cordillera and the Cordillera Talamanca, ranging from the Sarapiquí region to Tortuguero and Siquirres.

Phenology. Dieffenbachia beachiana initiates inflorescences in the late rainy season with plants reaching anthesis in the dry season (January through April). Immature fruits have been seen from April to September and mature fruits have been seen from April to December.

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Figure 2. Dieffenbachia aurantiaca (Croat 35292). —A. Habit, showing open inflorescence. —B. Close-up of spathe and spadix (spathe held in a fully splayed position). —C. Close-up of leaf showing fully sheathed petiole. —D. Leaf cluster with open spathe, showing side view. —E. Close-up of portion of spadix with pistils showing stigmas and the overtopping club-shaped staminodia. —F. Close-up of staminate portion of spadix showing strands of pollen emerging from between androecia.



Figure 3. *Dieffenbachia beachiana*. —A. A series of leaves showing adaxial surface (*Croat 44283*). —B. Close-up of leaf cluster showing variegated leaves and a cluster of inflorescences (*Sims 8*). —C. Adaxial surfaces of leaves and open inflorescences. —D. Close-up of inflorescence showing emergent portion of the spadix and adaxial surface of petiole. C, D. (*Croat 68444*).

Discussion. The species is characterized by its moderately thin, quilted blades with many broadly spreading primary lateral veins and crisped-undulate margins with the lower midrib and primary lateral veins puberulent. Dieffenbachia beachiana is similar to D. galdamesiae, a species from central Panama that also has somewhat puberulent midribs on the lower blade surfaces. That species differs in having the pubescence much shorter, merely granular-puberulent, and has fewer than 22 veins per side (vs. 23 to 36 for *D. beachiana*) that arise from the midrib at a 30° - 40° angle (vs. 70° - 110°). In addition, Panamanian populations of D. beachiana differ in having their blades usually white- to cream-mottled, whereas those of D. galdamesiae are always solid green in color. Dieffenbachia beachiana is also somewhat similar to D. grayumiana, but that species differs in having the veins merely minutely granular in slender rows on drying, and in having somewhat more ovate and wider blades.

A single collection (*Croat 66953*) from Veraguas Province in Panama differs in having the primary lateral veins curving more prominently toward the apex than material from elsewhere in western Panama and Costa Rica. In addition, the pubescence is merely granular-puberulent rather than puberulent. *Hammel 9660*, collected at La Selva in Heredia Province in Costa Rica, probably represents a hybrid between *D. beachiana* and *D. concinna*. The specimen has the slightly scabrous petioles and the impressed major veins of *D. beachiana*, but the blades are more or less elliptic and dry the color of *D. concinna*.

Additional specimens seen. COSTA RICA. Heredia: Río Peje-Río Sardinalito, Atl. slope of Volcán Barva, Grayum 6899 (MO); San José-Pto. Viejo, vic. of Chilamante, 11.6 mi. N of Cariblanco, Croat 68358 (B, CR, MO); Finca La Selva, near Río Puerto Viejo, Burger & Stolze 5754 (CR, F); Zona Protectora, N slopes of Volcán Barba, Río Peje-Río Guacimo, Gravum & Schatz 3220 (DUKE). Limón: Río Pacuare-Quebrada Diablo, ca. 2.5 km E of Siquirres, Grayum 7698 (MO); Par. Tortuguero, Est. Agua Fría, R. Robles 1234 (CR, MO); La Colombiana Farm, United Fruit Co., Standley 36840 (US). Puntarenas: Golfito, Par. Nac. Esquinas, Quebrada Gamba, Sanchez 539 (MO). San José: Vazquez de Coronado, Braulio Carrillo NP, along hwy. San José to Siquirres, trail to Río Sucio, Croat 78771 (INB, MO, WU). PANAMA. Bocas del Toro: Chiriquí Lagoon, Water Valley, von Wedel 1438 (MO); 10 km SW of Chiriquí Grande, Thompson 4937 (CM); Fortuna Dam-Chiriquí Grande, 7.3 mi. N of bridge over Fortuna Dam, 3.2 mi. N of Continental Divide, Croat & Grayum 60255 (MO); Chiriquí Grande-Fortuna, 7.7 mi. W of Chiriquí Grande, 1.5 mi. W of Punta Peña, Croat & Grayum 60094 (K, MO, SCZ); near hwy. to Chiriquí Grande, McPherson 11816 (MO). Veraguas: vic. of Santa Fe, 8 mi. N of Escuela Circlo Alto de Piedra, Croat 66953 (MO, PMA, SCZ, US).

Cultivated specimens. Costa Rica. *Henny 5* (MO). Heredia: Finca La Selva, O.T.S. Field Station, originally collected by Jim Beach, cultivated at Missouri Botanical Garden (MBG), vouchered as *Croat 59152* (MO).

 Dieffenbachia burgeri Croat & Grayum, sp. nov. TYPE: Costa Rica. Puntarenas: Palmar Norte-Panamanian border, 3 km N of turn-off to Rincón, 8°48'39"N, 83°16'18"W, 110 m, 10 Sep. 1996, *T. B. Croat & D. Hannon 79211* (holotype, MO-5170493!; isotypes, AAU!, B!, CAS!, CR!, COL!, DUKE!, EAP!, F!, GH!, HUA!, INB!, K!, M!, MEXU!, NY!, PMA!, RSA!, US!, VEN!, UB!, WU!). Figures 4, 27B.

Planta terrestris, 0.5–1 m; internodia 0.5–2.0 cm longa, 1.2–2.5(3.5) cm diam.; petiolus 13–48 cm longus, vaginatus ½–½ longitudinis; vagina 8.5–20 cm longa, inequilateralis acute ad apicem apex; pars libera 5.3–29.5 cm longa; lamina oblongo-lanceolata vel anguste elliptica, 25–40 cm longa, 5–16 cm lata, nervis primariis lateralibus (13)18–28 utroque; inflorescentia 1–7 in quoque axilla; pedunculus 7.5–12 cm longus; spatha 11.5–15(21) cm longa; spadix 9–15.6 cm longus; pistilla 21–37.

Herb, 0.5-1 m tall, sap milky, sharply foetid; internodes glossy to semiglossy, drying frequently matte and minutely warty, 0.5-2 cm long, 1.2-2.5(3.5) cm diam., dark green to blackish green, drying dark brown to black or yellow-brown or yellow-green. LEAVES scattered along stem with areas exposed except near apex; petioles 13-48 cm long (averaging 26 cm long), dark green, surface somewhat mottled, weakly pale-streaked near base, glossy to semiglossy, sheathing 1/3 to 2/3 the length of the petiole (0.5 their average length); sheath 8.5-20 cm long (averaging 12.6 cm), sometimes solid creamy white, with margins often drying thin and light brown, the tip inequilaterally acute; unsheathed portion 5.3-29.5 cm long (averaging 12.9 cm), variable in cross section, from subterete to Cshaped or U-shaped, sharply sulcate to somewhat flattened near apex adaxially, the margins obtuse to acute; blades oblong-lanceolate to narrowly elliptic, 25–40 cm long, 5–16 cm wide (averaging 30.5 \times 10.5 cm), 1.9-3.7 times longer than wide (averaging 2.8 times longer than wide), 0.83-1.6 times longer than petiole (averaging 1.21 times longer), slightly inequilateral, one side 0.4-1.4 cm wider than the other side, thinly coriaceous to subcoriaceous, slightly to moderately bicolorous, gradually long acuminate at apex, narrowly acute to rounded and equilateral or slightly inequilateral at base (one sometimes up to 6 mm higher on the midrib than the other); upper surface solid dark green, matte to weakly glossy (sometimes variegated with pale mottling), drying gray-green to dark olive-green; lower surface slightly paler, semiglossy to weakly glossy



Figure 4. *Dieffenbachia burgeri*. A, C, D. (*Croat & D. Hannon 79211*). —A. Side view of whole plant showing roots, stem, leaves, and inflorescences. —B. (*Croat & Grayum 59814*). Cultivated collection with open inflorescence. —C. Close-up of inflorescence with spathe cut open. —D. Mature infructescences, one open with berries exposed.

(sometimes matte or weakly glossy on both surfaces), drying medium yellow-green to yellow-brown; midrib above flat to sharply sulcate, sometimes flatraised, 3-5 mm wide, semiglossy, concolorous, drying slightly darker than surface; convex to thicker than broad below, convex toward apex, slightly paler than surface, drying dark brown to yellow-brown, often acutely 1-ribbed; primary lateral veins (13)18 to 28 per side, departing midrib at an acute angle, then spreading at $(40^{\circ})45^{\circ}-70^{\circ}$ angle, sweeping along margin, not forming collective veins, sunken to quilted above, convex beneath, drying darker or lighter than surface; the interprimary veins slightly less prominent than primary lateral veins; minor veins moderately close and darker than surface (drying weakly raised); surface minutely speckled on drying. INFLORESCENCES 1 to 7 per axil; peduncle 7.5–12 cm \times 4 \times 7 mm, medium green, moderately glossy (sap with a faint, unusual scent); spathe 11.5-15(21) cm long at anthesis, 1.1-1.9 cm longer than the spadix, glossy to semiglossy on both surfaces, flattening 2.7-3 cm diam. at constriction, dark green outside throughout, slightly paler inside; spathe blade < 2 cm diam. when furled; spathe tube to 10 cm long, 1.5-2.0 cm diam., flattening 3.7-7 cm wide; spathe blade 2.7-3.7 cm diam. at anthesis; spadix 9-15.6 cm long at anthesis; free portion 4-8.7 cm long; pistillate portion 5-6 cm long; the fertile staminate portion 4-6.5 cm long, 5-6 mm diam., directed slightly forward out of the spathe; sterile intermediate segment 1.5-3 cm long, 5 mm diam., with many staminodia near base and few just below fertile staminate portion; pistils 21 to 37, moderately closely spaced, almost contiguous, to 3 dispersed across spadix width, weakly constricted below middle, green to pale yellow; stigmas pale yellow, 1-1.5 mm on drying; staminodia about as long as or slightly longer than pistils, somewhat flattened and thickly swollen, subglobular and somewhat truncate at apex; synandria drying irregularly somewhat rounded, the margins usually irregularly turned upward, 1-1.4 mm diam. at apex, orange to yellow-orange, green, narrowly angled on one side. INFRUCTESCENCE with spathe usually orange; fruiting spadix 5-7 cm long, ca. 3 cm wide; berries orange-red to red-orange drying pale yellow-brown, ovoid, 7-8 mm long; seeds drying blackened, minutely warty.

Distribution and habitat. Dieffenbachia burgeri is endemic to southwestern Costa Rica on the Pacific slope from Dominical to the Osa Peninsula, sea level to 500 m, rarely 1000 m elevation, in *Tropical wet forest* (T-wf), *Premontane wet forest* (Pwf), and sometimes in *Premontane rain forest* (P-rf) life zones (Holdridge, 1967). It occurs in wet forests and swampy sites.

Phenology. Flowering in *D. burgeri* occurs in the late wet season to early dry season from November to March, and mature fruits have been seen from early April to early October.

Discussion. The species is characterized by the petiole sheathed $\frac{1}{2}-\frac{2}{3}$ of its length, with the sheath acute at the apex; and the usually matte, greenish-drying leaf blades with numerous primary lateral veins. The blades are quite variable, ranging from narrowly oblong-elliptic to ovate-elliptic, oblong-lanceolate or narrowly elliptic. *Dieffenbachia burgeri* is most easily confused with *D. oerstedii* and differs from that species in having the petiole sheath acute at the apex, rather than free-ending and rounded to auriculate as in *D. oerstedii*. In addition, *D. burgeri* has more primary lateral veins, numbering (13)18 to 28 per side (vs. (4)6 to 9(11) per side in *D. oerstedii*).

Burger & Liesner 7254 describes the spathe at anthesis as having a strong unpleasant aroma.

Etymology. The species is named in honor of William Burger of the Field Museum of Natural History, long-time expert on Costa Rican plants, who made the first collection of the species as well as most of the earliest collections during his expeditions to Costa Rica.

Paratypes. COSTA RICA. Puntarenas: Palmar, Sur-Chacarita km 287, ca. 3 km NW of Chacarita, Gravum et al. 7547 (INB, MO); Refugio Nac. Golfito, Fila Gamba, Río Cañaza drainage, Grayum & G. Herrera 9236 (CR, MO); Fila Barriganes, ca. 1 km S, 3 km W of Cañasas, Croat & Grayum 59814 (COL, CR, INB, MO, PMA, OCNE, SCZ, TEFH, US); Piedras Blancas Rincón 3.7 mi. W of Pan-Am Hwy., Croat 67692 (MO); Chacarita-Rincón de Osa, ca. 6 km W Chacarita, Croat & Gravum 59731 (CR, MO); Rincón de Osa, ridge betw. Quebrada Aparicio-Quebrada Aguabuena, Grayum et al. 4014 (CR, MO); W of Rincón de Osa, Croat & Grayum 59851 (MO); Par. Nac. Sector Esquinas, vic. of Fila Gamba hills behind Esquinas Rain Forest Lodge, along Quebrada Negra, at end of side rd. off of Villa Bricena to Golfito Rd., Croat & D. Hannon 79286 (CM, INB, MO); San José, along rd. to San Isidro del General, Burger et al. 10671 (F, MO); Golfito, Quebrada Negra, Marten 848 (F); Osa, ca. 5 km W of Rincón de Osa, Burger & Gentry Jr. 8898 (CR, F); near the airfield ca. 4 mi. W of Rincón de Osa, Burger & Stolze 5489 (F); W of airstrip, Utley & Utley 1100 (CR, F). San José: Pérez Zeledon Cantón, San Isidro General-Dominical, Fila Tinamastes, Croat & D. Hannon 79112 (INB, MO, QCNE, USM); San Isidro del General-Dominical, above Alfombra, Burger & Baker 10121 (F, MO).

4. Dieffenbachia concinna Croat & Grayum, Novon 9: 492. 1999. TYPE: Costa Rica. Puntarenas: Palmar Norte-Panamanian border, 3 km N of jct. to Rincón, 8°48′39″N, 83°16′18″W, 110 m, 10 Sep. 1996, *T. B. Croat & D. Hannon*

79191 (holotype, MO-5170498!; isotypes, AAU!, B!, CAS!, COL!, CR!, DUKE!, F!, GH!, HUA!, INB!, K!, M!, MEXU!, NY!, PMA!, US!). Figures 5, 28A.

Small, erect herb, 0.6-1.3 m tall, sap milky; internodes glossy, 1.5-4(7.5) cm long, 1-4 cm diam., medium green to dark green, obscurely marbled light to medium green. LEAVES erect-arching; petioles 7.5-25(35) cm long (averaging 17 cm long), terete and obtusely sulcate near apex or subterete to C-shaped or D-shaped in cross section, flat to shallowly sulcate adaxially (the margins obtuse to acute), rounded or sometimes acute abaxially, moderately erect, semiglossy or almost matte, dark green to olive-green, blotched striate or streaked white or silver-green, drving green to sometimes light yellow-brown, sheathing from lower % to nearly throughout (averaging 0.63 of length); sheath 6.7-13(20) cm long (averaging 9.5 cm), to 1.5 cm diam., margins erect to involute, the tip asymmetrically auriculate to rounded and free-ending, with one side obtuse to rounded, with the other side acute to obtuse: unsheathed portion 1–13 cm long. to 1.5 cm diam.; *blades* usually \pm elliptic, ovateelliptic, rarely ovate or broadly lanceolate, 16-36 cm long (averaging 23 cm long), (7.8)10-15.5(20.5) cm wide (averaging 12 cm wide), 1.5-2.9 times longer than wide, broadest usually at or near middle, 0.8-2.4 times longer than petiole, equilateral to slightly inequilateral, one side to 1 cm wider than the other side, equilaterally acuminate at apex, the acumen sometimes apiculate, broadly acute or usually rounded, slightly inequilateral at base, moderately coriaceous, weakly to moderately bicolorous; upper surface semiglossy to glossy, dark green or rarely white to cream or yellow-green splotched or flecked, drying dark olive-green, dark gray-green to vellowish brown; lower surface moderately paler, matte to weakly glossy, green, rarely dark graygreen, drying yellowish brown to green, rarely dark gray-green; midrib flat to broadly flat-convex and concolorous to paler than surface above (sometimes paler in distal ¹/₃ above), low-convex to convex or rounded-triangular, slightly paler than surface below, drying light brown to dark brown with medial portion usually drying darker; primary lateral veins 6 to 12(14) per side, spreading from midrib at a 45°-70° angle (sometimes arising at an acute angle), only rarely at different angles on opposite side of blade, weakly sunken above, convex to obscurely raised below; the interprimary veins sometimes visible, 1 between each pair of primary lateral veins; minor veins indistinct to visible and darker than surface below. INFLORESCENCES 2 to 8 per axil; peduncle (2.5)8-17.5 cm long (averaging 10.5 cm long), somewhat compressed dorsiventrally in cross section, 3-4 mm wide on drying; spathe 11-25.7 cm long, 1.5-2.0 cm wide when furled (as long as or up to 2 times longer than peduncle and averaging 1.6 times longer), constricted 4.5 cm above base, the constricted area 1.8-3 cm wide when flattened, medium to pale green outside, somewhat darker on tube except white on open face, uniformly paler within, drying dark brown to blackened throughout; spathe blade 3.3 cm wide when flattened; spathe tube 4.5-8.5 cm wide when flattened, paler inside; spadix protruding forward at anthesis, 12-14 cm long; free portion 6.5-9.5 cm long; pistillate portion tapered toward apex, $4.5-9 \text{ cm} \times 5-$ 12 mm, stipe and axis pale green; fertile staminate portion white, tapered slightly toward both ends, 8-9 cm long, 7-10 mm diam. midway; sterile staminate portion 2.5-4 cm long; mostly sterile intermediate segment 5-7 mm diam., mostly bare but with a scattering of staminodia on both ends (especially at base); pistils 42 to 65, closely spaced; ovary globose, 1-2.5 mm diam., pale green; stigma pale yellow; staminodia 1-5 mm long, up to 3 times longer than pistil, somewhat flattened toward base and free at base, tapering and somewhat globular, 1-2 mm diam. at apex; synandria with flowers irregularly rounded, 0.8-1.4 mm diam. INFRUC-TESCENCE with spathe yellow-orange to bright orange outside; spadix to 6-8 cm long; berries bright red to orange-red, oblong-ellipsoid, to 1 cm long, 8 mm diam.

Distribution and habitat. Dieffenbachia concinna ranges from southeastern Nicaragua along the entire Atlantic slope to the Osa Peninsula of Costa Rica, sea level to 200 m, mostly < 100 m, sometimes locally common in rocky sites along streams.

Phenology. Flowering in *D. concinna* occurs mostly during the middle of the rainy season, from July through November (rarely December), especially September and October. A cultivated collection at the Missouri Botanical Garden flowered repeatedly over a two-week period during late May and early June. Collections with immature fruits have been seen from December to March. Mature fruits occur primarily December through June, especially January to May but with one fruiting collection each seen in August and September.

Discussion. The species is recognized by the glossiness of all parts of the plant; its relatively small stature; moderately coriaceous, more or less elliptic, weakly inequilateral blades; and auriculate petiolar sheaths. It is most easily confused with *D. oerstedii*, but differs from that species in its larger



Figure 5. *Dieffenbachia concinna*. A–E, G. (*Croat 78318*). F. (*Croat 67594*). —A. Close-up of adaxial surface of blade. —B. Crown of plant with inflorescences, one open. —C. Close-up of stem and petiole bases showing variegations. —D. Close-up of opened inflorescence exposing entire spadix. —E. Close-up of inflorescence with portion of spadix showing elongated staminodia overtopping pistils. —F. Close-up of spathe showing emerging threads of pollen filling spathe. —G. Close-up of male portion of spadix showing androecia with anthers exposed.

size (to 1.3 m vs. 0.75–1 m in *D. oerstedii*), and more coriaceous blades typically broadest at the middle (vs. broadest below the middle in *D. oerstedii*) with more numerous primary lateral veins (6 to 12(14) vs. mostly 6 to 9 for *D. oerstedii*). In addition, the blades of *D. concinna* are glossy above and almost rounded at the base versus weakly glossy to matte and subcordate in *D. oerstedii*.

Grayum et al. 10588, from the headwaters of the Río Piedras Blancas in Puntarenas Province, is unusual not only in occurring much higher (to 900 m) than most collections of this species but in having a broader leaf (to 19 cm wide) with a longer petiole (to 30 cm). In other respects it agrees with other collections of D. concinna. Hammel 9660, collected at La Selva in Heredia Province in Costa Rica, probably represents a hybrid between D. beachiana and D. concinna. The specimen has the slightly scabrous petioles and the impressed major veins of D. beachiana, but the blades are more or less elliptic and dry more the color of D. concinna. Croat & Hannon 79199, collected south of Palmar Norte, appears to be a hybrid between D. aurantiaca and D. concinna. Its blade shape and maculations, and numerous inflorescences suggest D. concinna, while the broadly sulcate petiole favors D. aurantiaca.

Additional specimens examined. COSTA RICA. Heredia: near Puerto Viejo along rd. near Río Sucio, Croat 35688 (MO), Croat 35702 (MO); Finca La Selva, OTS Field Station on the Río Puerto Viejo just E of its junction with the Río Sarapiquí, Hammel 9688 (DUKE), Croat 78732 (INB, MO, W). Limón: La Colombiana Farm, United Fruit Co., Standley 36739 (US); headwaters of Quebrada Mata de Limón, Finca Anai (Sixaola region), Grayum et al. 4447 (MO); Cerro Tortuguero junto a la Barra de Tortuguero, R. Robles 2090 (CR, INB, MO), Barringer et al. 1973 (F); Par. Nac. Tortuguero, Gómez-Laurito 7856 (CR); Boca de las Lagunas de Tortuguero, Burger & Antonio 11249 (F, MO); Pococi, Refugio de Vida Silvestre Barra del Colorado, SE base of Cerro del Tortuguero, Grayum et al. 11139 (CM, CR, INB, MO, USJ); Río Chirripócito-Río Sardina, Refugio Nac. Barra del Colorado, Grayum 9777 (CR, MO); Río Reventazón, Finca Montecristo below Cairo, Standley & Valerio 48960 (US). Puntarenas: McAlpin 85-33 (SEL); 2 km NW of Chacarita, 30 km S of Palmar Sur, Gravum & Fleming 8119 (CR, INB, MO); ridge betw. Río Rivito (valley of Laguna Chocuaco) & Quebrada Banegas, S of Cerro Rancho Quemado, Grayum et al. 7567 (MO); Rincón de Osa Rancho Quemado, ca. 10 km W of main Rincón-Pto. Jimenez Rd., Croat & Grayum 59785 (CR, MO); Osa, 6 km W of Rincón, Grant & Rundell 92-01928 (CR, MO, US); near the airfield ca. 4 mi. W of Rincón de Osa, Burger & Stolze 5461 (CR, F); Osa Península, NW of airfield, ca. 5 km W of Rincón de Osa, Burger & Liesner 7196 (CR, F, MO, PMA); Osa Península, Nicolson 3393 (BM, US); Costena-Cruces, Río Piedras Blancas, Cerro Anguciana, Grayum et al. 10588 (INB, MO, CR); Río Sandalo, Dodge 10198 (F, MO), Dodge 10020 (F, MO); Palmar Norte de Osa, Allen 5669 (EAP, UC, US); Osa Península, 4 mi. W of Rincón de Osa,

Raven 21532 (F); Rincón de Osa, Quebrada Aparicio-Quebrada Aguabuena, Grayum et al. 3982 (CR, MO); vic. of Boscosa, at Quebrada Aguabuena, Croat & D. Hannon 79238 (COL, INB, MO, NY, PMA, TEFH, TEX, UB); Sector Esquinas, vic. of Fila Gamba hills behind Esquinas Rain Forest Lodge, along Quebrada Negra, at end of side rd. off of Villa Bricena to Golfito Rd., Croat & D. Hannon 79291 (CM, DUKE, INB, MO, P); Refugio Nac. Golfito, S tributary of Río Cañaza, Grayum et al. 9250 (MO); W side Fila Gamba, ca. 6 km from Golfito airport, Croat & Grayum 59930 (CM, K, MO); Río Claro, 2.5 mi. SE of Golfito, Croat 67594 (MO); Orotina-Jaco, valley of Río Grande Tárcoles, 1 km S of Quebrada Ganado, vic. Hotel Pink Paradise, Croat 79076 (INB, MO); Par. Nac. Corcovado, Monkey Woods, Kernan & Phillips 831 (CR, MO); Lower Lookout Trail, Kernan 748 (CR, MO); Est. Sirena, Quesada 51 (INB, MO, US, CR); Península de Osa, Estación Biológica Los Patos, 8°34'N, 83°31'W, 200 m, 2 Sep. 1993, R. Aguilar 2195 (CR, INB, MO); 0-1 km W of park headquarters at Sirena, Liesner 2871 (CR, MO); Pan-Am Hwy., Rincón, Croat & D. Hannon 79167 (MO); Rincón-Rancho Quemado, just S of Rincón near Río Rincón, Croat & D. Hannon 79170 (HUA, INB, MEXU, MO, QCA, RSA, WU); vic. Palmar Norte, Allen 5669A (F, UC); Punta Banco, M. Chavarría et al. 257 (CR); Coto Brus, Guaymí Reserve, river trail along Río Limóncito near jct. of Villa Palacios school trail, Koshear 59 (CR); Golfito, Refugio de Vida Silvestre, Marten 789 (CR); Carr. Interam.-Sinaí, Fila Huacas, ca. 4 km NE (by road) at Las Huacas ("Venecia"), Grayum & Evans 10156 (CR, MO); Palmar Norte-Jalisco, Quebrada Benjamin, Grayum et al. 9962 (CR, MO). San José: above Palmar Norte, Croat 35108 (MO). NICARAGUA. Río San Juan: Res. Indio-Maíz, Caño el Tambor, branch of Río San Juan, Rueda et al. 4070 (MO). PANAMA. Panamá: rd. to Puerto Jiménez, Osa, 40 km W of Panam. Hwy., rt. 2, L. Gómez 19531 (MO).

Cultivated collections. Costa Rica. Puntarenas: Esquinas, 25 km SE of Palmar Sur, along Pan-Am Hwy., originally collected by Bruce McAlpin (Selby 85-33), 25 m, 2 Jan. 1994, cultivated at MBG, vouchered as *Croat* 77281 (MO); 15 May 1996, *Croat* 78318 (MO).

 Dieffenbachia copensis Croat, sp. nov. TYPE: Panama. Coclé: El Copé, forest on Continental Divide above El Copé, 8°38'N, 80°38'W, 700– 900 m, 27–29 Apr. 1985, *B. Hammel 13636* (holotype, MO-3284876!). Figures 6, 27B.

Herba 45 cm alta; internodia 7 mm longa, 7 mm diam., petiolus (17)21–29.5 cm longus, vagina 8–12.5 cm longa; pars libera 10.5–15.5 cm longa; lamina anguste oblanceolata, 25.5–33.3 cm longa, 5.2 cm lata; nervis primariis lateralibus 9–12 utroque; inflorescentia 1 per axillam; pedunculus 5 cm longus; spatha 15.7 cm longa, 1.2 cm lata; spadix 12.3 cm longus.

Small herb, to 45 cm tall; *internodes* about as long as broad, 7 mm diam., drying matte, dark brown, finely and irregularly folded; *petioles* (17)21–29.5 cm long, sheathed 41%–56% their length; sheath 8–12.5 cm long, narrowly acute at apex, drying dark brown to medium yellow-brown; free portion 10.5–15.5 cm long, subterete, obtusely sulcate, drying medium yellow-brown to dark



Figure 6. Dieffenbachia copensis (Hammel 13636). Type specimen.

brown, minutely granular to somewhat scabridulous; blades narrowly oblanceolate, 25.5-33.3 cm long, 5.2 cm wide, 6.4 times longer than wide, narrowly long-acuminate at apex, narrowly attenuate at base, dark green and matte above, moderately paler and semiglossy below, drying dark gray-green and minutely granular above, light yellowish gray below; midrib concolorous and narrowly raised above, convex and granular-puberulent to hispidulous and slightly darker below; primary lateral veins 9 to 12 pairs, arising at an acute angle then spreading at 45°-50° angle, prominently curved upward along the margins and extending to above the origin of the next higher veins, paler and weakly sunken above, convex and slightly darker below, drying narrowly raised and granular; minor lateral veins weakly visible; cross-veins equally visible on lower surface; lower surface moderately granular. INFLO-RESCENCE solitary, longer than the petioles; peduncles 5 cm long, drying 2.5 mm diam., pale yellow-brown; spathe 15.7 cm long, 1.2 cm diam., pale green, drying medium yellow-brown, narrowly longacuminate at the apex (acumen 1.7 cm long); spadix 12.3 cm long; free portion 8.5 cm long; pistillate portion 5 cm long, 4-5 mm diam.; staminate portion 5.5 cm long, 4 mm diam., drying yellow-brown; mostly naked; intermediate sterile portion 1.1 cm long, 2.5 mm diam. on drying, with only a few staminodia scattered throughout its length; pistils 38, 2 to 3 situated across the width of the spadix; ovary 0.5-6.0 mm diam.; stigmas about as broad as the ovary; staminodia 2 to 4 per pistil, 1-1.4 mm long, slightly thickened toward the apex, not at all broadened toward the base; the sterile male flowers in 2 rows, somewhat separated from the fertile flowers; synandria 2.2-2.8 mm long, 1.6-2.0 mm wide, irregularly rounded to rhombic at apex. INFRUC-**TESCENCE** not seen.

Distribution and habitat. Dieffenbachia copensis is known only from the type specimen in the Coclé Province of Panama at 700 to 900 m in the Lower montane rain forest (LM-rf) life zone (Holdridge, 1967).

Discussion. The species is characterized by its narrowly oblanceolate, narrowly long-acuminate blades with densely granular primary lateral veins and a granular-hispidulous midrib on the lower surface. The species is somewhat similar to both *D.* galdamesiae and *D. fortunensis*, differing from both in having proportionately narrower blades that are broader well above the middle. In contrast, the blades of *D. fortunensis* are broadest well below the middle and have the pistillate and staminate portions of the spadix contiguous or nearly so (vs. a free section to 1.1 cm long in *D. copensis*). *Dieffenbachia galdamesiae* differs in having blades proportionately broader, 2.7–4.2 times longer than wide, versus 6.4 times longer than wide in *D. copensis*.

6. Dieffenbachia crebripistillata Croat, sp. nov. TYPE: Panama. Coclé: Alto Calvario, above El Copé, ca. 6 km N of El Copé, Atlantic slope along trail which leads down to Las Ricas, Limón & San Juan, 8°39'N, 80°36'W, 710–800 m, 22 June 1988, *T. B. Croat 68746* (holotype, MO-3610884!; isotypes, B!, CAS!, COL!, DUKE!, F!, GH!, HUA!, INB!, K!, M!, MEXU!, NY!, PMA!, US!). Figures 7, 27A.

Planta 30–100(120) cm alta; internodia 2.5–4 cm longa, 1.5–3(5) cm diam.; petiolus 7.5–24 cm longus; lamina ovata vel raro elliptica vel oblongo-elliptica, (22)27–46(55) cm longa, 10–25 cm lata, nervis primariis lateralibus (10)15–17 utroque; inflorescentia 1–2 per axillar; pedunculus (8.5)10–14 cm longus; spatha 13–28 cm longa, 2.0–3.2 cm lata; spatix 13–26.5 cm longus; parte pistillata 6–10(12) cm longa, 8–12 mm lata.

Short, thick-stemmed herb, 30-100(120) cm tall; sap foul-smelling, eventually turning white; internodes dark green, glossy, 2.5-4 cm long, 1.5-3(5) cm diam.; petioles 7.5-24 cm long (averaging 16 cm long), somewhat spongy, solid dark green or with a white band on the abaxial surface, conspicuously sheathed ranging from 0.7 to fully throughout the length (but rarely ending more than 1 cm below the blade and often extending beyond the base of the blade); sheath to 1.5 cm high, 7.5-19.5 cm long, inequilaterally rounded to auriculate at apex; unsheathed portion usually not apparent but when present 1-7 cm long (averaging 1.6 cm long), broadly sulcate, the margins sharp; blades ovate to rarely elliptic or oblong-elliptic, (22)27-46(55) cm long, 10–25 cm wide (averaging 37×18 cm), 1.5– 3.3 times longer than wide (averaging 1.9 times longer), 1.9-3.7 times longer than petioles (averaging 2.3 times longer than petiole), somewhat inequilateral, one side up to 0.5-2.7 cm wider, moderately coriaceous, abruptly acuminate and downturned at apex, obtuse to rounded at base, the basal portion of the blades held somewhat erect; upper surface glossy to moderately glossy, usually solid dark green sometimes mottled with pale green, slightly bicolorous; lower surface glossy, paler; midrib flat-raised to flat-rounded and paler especially near base, 12-20 mm wide, becoming obtusely convex toward apex and diminishing before reaching the apex above, broadly flat-rounded to narrowly rounded and pale green to white below (especially near the base); primary lateral veins



Figure 7. *Dieffenbachia crebripistillata (Croat 75172).* —A. Potted plant with open inflorescence (*Croat 75172*). — B. Close-up of crown of plant with open inflorescence. —C. Close-up of inflorescence with pollen emerging from androecia (*Croat 49243*). —D. Close-up of inflorescence with tube flared out and spathe blade recurved. —E. Close-up of inflorescence showing pistillate portion, intermediate sterile section, and lower section of staminate portion.

(10)15 to 17 per side, sunken to weakly sunken above, raised below; interprimary veins obscure above, obscurely visible below; minor veins moderately distinct on lower surface. INFLORES-CENCES 1 to 2 per axil; peduncle (8.5)10-14 cm long, flattened laterally, pale green; spathe 13-28 cm long, 1.3–1.5 times longer than peduncle, pale to medium green outside (sometimes white at anthesis), paler within, unmarked, \pm oblong, acuminate at apex, only weakly constricted midway (constricted area to 3.2 cm wide when flattened); spathe tube 1.5-3 cm wide when furled, 8-8.5 cm wide when flattened; spathe blade to 2.0-3.2 cm wide when furled; spadix 13-26.5 cm long (averaging 18 cm long), the free portion 8.5-11 cm long; pistillate portion 6-10(12) cm long, 8-12 mm wide; fertile staminate portion 5-9 cm long, 6-10 mm diam.; the mostly sterile intermediate portion (1)1.5-2.5 cm long, with some sterile male flowers in the upper ¹/₃; pistils (57)80 to 100, scattered, frequently adjacent, up to 5 in a row across the width of the spadix, never more than 5 mm apart; stigmas pale orange, densely pubescent; staminodia white, \pm oblong, ca. 2-3 mm long, rounded at apex; synandria irregularly rounded at apex, smooth or weakly dimpled medially, to 2.6-2.8 mm diam.; pollen exserted in slender cream-colored threads to 3 mm long. INFRUCTESCENCES with berries ovoid to subellipsoid, orange to bright red, 8-11 mm long.

Distribution and habitat. Dieffenbachia crebripistillata is endemic to central and eastern Panama at (100)250-800(975) m, in Tropical wet forest (Twf), Premontane wet forest (P-wf), and Premontane rain forest (P-rf) life zones (Holdridge, 1967) in Coclé, Colón, Panamá, and San Blas Provinces. While the species mostly occurs in a few areas of moderately high elevations (including Santa Rita Ridge, Cerro Bruja, Cerro Jefe, Cerro Campana, and La Mesa), it dips down to as little as 100 m along the Colón Province coast in the area of Río Guanche and Portobelo. Most of these collections differ in having petioles that dry less orange and have the petiole sheath ending somewhat below the blade, never overtopping the blades. As mentioned elsewhere under D. nitidipetiolata (and below) these collections may represent hybrids with either D. nitidipetiolata or D. longispatha.

Phenology. Dieffenbachia crebripistillata flowers principally at the end of the dry season (April) and in the early part of the rainy season from May to July, less commonly during the balance of the dry season (January–March) and in the latter part of the rainy season (August–October). Fruiting time is poorly known, but most fruiting collections have

been made during the late rainy season (August–December).

Discussion. This species is related to D. longispatha, which differs in being a much more robust and taller plant (to 3.5 m), having petioles that dry green and with a long unsheathed portion, and pistils that are much larger (to 7 mm diam.), many fewer in number (only to 26), and widely spaced. See that species for additional discussion of the differences. Though D. crebripistillata usually has solid green blades, some plants from Coclé (at La Mesa near El Valle de Antón and along the Continental Divide north of Llano Grande) have palemaculate leaves. Typically the petiole of Dieffenbachia crebripistillata is fully sheathed; however, some plants from the Cerro Jefe region (Croat 35915, Croat & Zhu 76644, and Dwyer 9497) or the Río Guanche region (D'Arcy 9678 and Croat 11420) rarely have a significant free portion of the petiole 3-5(7) cm long.

Collections from lowland Colón (*Croat 75172*, *D'Arcy 9678*) are somewhat intermediate between *D. longispatha* and the more typical *D. crebripistillata* from the highlands of Panama. The petioles are not as fully sheathed, with the free portion of the petiole ranging from 4 to 5 cm long in these specimens.

Most collections from El Copé in Coclé Province have fully sheathed petioles and leaf blades proportionately smaller and narrower, averaging only 25 cm long (vs. an average of 37 cm for all other populations of the species) and 2.5 times longer than wide (vs. an average of 1.9 times longer) with petioles averaging only 11.5 cm longer (vs. an average of 16 cm for other populations). These collections (Antonio 3039; Croat 44558, 44682, 49155, 67576; Croat & Zhu 76757; Folsom 1265, 3211, 6218; and Sytsma & Andersson 4573) differ in having smaller elliptic blades. The El Copé region is well known for having many endemics, and these plants may represent differences that may ultimately prove to be important, but for now are being considered as D. crebripistillata. One collection from El Copé in Coclé Province (Croat 74861) differs from the above only in having the petiole free above the sheath for a distance of 4.5 cm.

Etymology. The specific epithet is derived from "creber" (meaning crowded together) and "pistilla" (pistils) and refers to the very closely aggregated pistils on this species in contrast to the widely separated pistils of *D. longispatha* with which the species had long been confused.

Paratypes. PANAMA. Coclé: N of El Valle, Cerro Gaital, Knapp 5758 (MO); El Valle de Antón Region, at La Mesa, 3.2-6 mi. above El Valle, Luteyn & Kennedy 1612 (DUKE), FLORPAN, Guerra et al. 5252 (PMA), Lewis et al. 1753 (MO), Allen & Alston 1839 (MO); La Mesa, Finca Mandarinas, along rd. to Finca Furlong, Croat 67115 (AAU, B, CAS, JAUM, M, MO, P, PMA, TEFH, VEN); 1 km E of Finca Macarenita, Croat 7478 (MO); Divide SW of La Mesa, Stein & Hamilton 990 (MO); La Mesa, above El Valle de Antón, ca. 2 km W of Cerro Pilón, Croat 37361 (F, MO); above El Valle on rd. to Cerro Pilón, Croat 25352 (MO); 2 km W of Cerro Pilón, Sullivan 537 (MO); 3 km N of El Valle de Antón, Wilbur et al. 15664 (DUKE); above El Valle, Croat 13403 (MO); La Pintada-Coclecito, 5.3 mi. N of stream at Llano Grande, Atlantic slope, Croat 49243 (HUA, MEXU, MO, PMA, SEL, VEN); rd. to Coclesito, 12 mi. from Llano Grande, Churchill et al. 3993 (MO); past Llano Grande on rd. to Cascajal, Sytsma et al. 4398 (MO); Llano Grande-Cascajal, Hammel 7212 (MO); vic. Alto Calvario, 7 km N of El Copé, Folsom 3211 (MO), Folsom 6218 (MO), Folsom 1265 (MO), António 3039 (MO); above El Potroso sawmill, Cont. Divide, N of El Copé, Sytsma & Andersson 4573 (MO); 9.4 km above El Copé, Croat 44682 (MO), Croat 44558 (MO); Alto Calvario, ca. 4.6 mi. above El Copé, Croat 74861 (MO); Alto Calvario, 5.5 mi. N of El Copé, 3.5 mi. N of Escuela Barrigón, Croat 67576 (MO, PMA), Croat & Zhu 76757 (HUĂ, INB, K, MO, PMA, TEX), Croat 49155 (MO, RSA, SCZ); Río Indio, on rd. from Portobelo to Nombre de Dios, Croat 33568 (MO). Colón: ca. 5 mi. SW of Portobelo, Croat 14175 (MO, PMA); 2 mi. S of Portobelo, Croat 11420 (MO); S approach of Cerro Bruja from Río Escandaloso, Hammel 3140 (MO); 9-12 mi. E of Trans-Isthmian Hwy. on Santa Rita ridge, Thompson 4874 (CM, K, MO); Santa Rita Ridge, 26 km from Trans-Isthmian Hwy., Knapp et al. 1717 (MO); Río Gatun, Portobelo, Antonio 3820 (MO); Río Guanche, ca. 3-5 mi. above bridge inland, Croat 26193 (MO), D'Arcy 9678 (MO); ca. 3-5 km above bridge, Croat 36958 (MO); ca. 3-5 mi. inland, Croat 26239 (MO); Sabanitas-Portobelo, Río Piedras Lumber Rd, 6.7 mi. E of Sabanitas, 3.9 mi. up logging rd., Croat 75172 (MO). Panamá: Par. Nac. Altos de Campana, Buena Vista, Chame, FLORPAN, Espinosa et al. 4723 (MO, STRI), Espinosa & E. Martínez 3308 (PMA); Sendero del Tigre, Correa & Montenegro 10419 (PMA); trail to summit, Correa & Montenegro 10647 (PMA); Cerro Campana, ca. 1 mi. from Interamerican Hwy., Croat 35951 (F, MO, MY, PMA, QCA), Croat 14707 (MO); along trail to summit, Croat 17210 (MO, PMA, UB, VEN), Croat 12123 (MO), Croat 12086 (MO), Croat 14789 (MO), C. E. Smith Jr. & H. M. Smith 3389 (F), Luteyn & Kennedy 1837 (DUKE), Hammel 3781 (MO), Luteyn 3188 (DUKE), Croat 25213 (MO); Cerro Campana, 8.6 mi. SW of Capira, Luteyn 1010 (DUKE); 6.1 mi. above Pan-American Hwy., Croat 74760 (MO); 5-10 km NE of Altos de Pacora, Mori & Kallunki 6026 (MO); rd. past Altos de Pacora, 3-3.5 mi. NE of Altos de Pacora, 7.8-8.2 mi. above Pan-Am Hwy., Croat 68699 (MO); 0.8 mi. beyond turn-off to Altos de Pacora, Croat & Zhu 76644 (MO); 4.6 km beyond peak on rd. to Altos de Pacora, 26.3 km from Interamerican Hwy., Croat 35915 (MO); Cerro Jefe, Dwyer & Gentry 9479 (DUKE, MO).

 Dieffenbachia davidsei Croat & Grayum, sp. nov. TYPE: Costa Rica. Limón: headwaters of Quebrada Mata de Limón, central fork & hills betw. central & westernmost forks, Finca Anai (Sixaola region), 9°35′N, 82°39′W, 25–40 m, 19 Nov. 1984, *M. H. Grayum, G. Herrera, A. Matute & F. Chavarría* 4483 (holotype, MO-3229671!; isotype, INB!). Figures 8, 27B.

Herba 30–100 cm alta; internodia (1.0)1.5-5 cm longa, 1.5–1.9 cm diam.; petiolus 3–11.5 cm longus, 5–6 mm diam., vaginatus 0.4–0.97 longitudinis, pars libera subteres vel D-formata, (1.5)2-5.5 cm longa; lamina oblongo-elliptica, 9–26.8 cm longa, 2.3–9 cm lata, nervis primariis lateralibus (6)9–15 utroque; inflorescentia 3 per axillam; pedunculus 1.5–4 cm longus; spatha 8–16 cm longa; spadix (7.5)10–12.5 cm longus; baccae 8–11 diam.; semina 2–3.

Slender herb, 30-100 cm tall; sap clear; internodes (1.0)1.5-5 cm long, 1.5-1.9 cm diam., weakly glossy to semiglossy, minutely roughened, usually with an even mixture of medium yellow-green and black-green streaks with no obvious background color, sometimes medium yellow-green toward base with black-green streaks, reversing to dark black-green with yellow-green streaks toward the apex, drying obviously minutely wrinkled, striate and matte. LEAVES spreading-pendent to pendent; petioles 3-11.5 cm long (averaging 6.5 cm long), 5-6 mm diam., arched-spreading from stem, sheathed from 0.4 to 0.97 (averaging 0.73) the length of the petiole, paler than stem, white to yellowish green speckled, especially near the base, the base often white, tinged with pink and dark-striate; sheaths auriculate-prolonged at apex (often appearing \pm acute on dried specimens), the margins inrolled on both sides throughout their length, the opposite sides usually in contact and sometimes in part overlapping; unsheathed portion (1.5)2-5.5 cm long, subterete to D-shaped or broadly and obtusely sulcate, the margins moderately blunt; blades narrowly to broadly oblong-elliptic, 9-26.8 cm long, 2.3–9 cm wide (averaging 20.4×5.4 cm), broadest near the middle, (2)2.7-4.8 times longer than wide (averaging 36 times longer than wide), 1.9-6.2 times longer than petiole (averaging 3.1 times longer than petiole), slightly inequilateral, one side 3-9 mm wider than the other, sometimes weakly falcate, thinly coriaceous, gradually to abruptly longacuminate at apex (acumen down-turned and apiculate), acute to rounded or cordulate and nearly equilateral or markedly inequilateral at base (one side sometimes also ending lower on the midrib); margins sometimes undulate; upper surface plain dark green in Costa Rica, sometimes variegated with irregular light green blotches in Panama populations, glossy to semiglossy; lower surface slightly paler, matte to weakly glossy; drying dark brown to dark gray-brown above, yellow-brown to yellowgreen below; midrib flat at base, becoming weakly convex toward the apex, concolorous or paler


Figure 8. *Dieffenbachia davidsei.* —A. Potted plant showing habit with several inflorescences. —B. Blade adaxial surface with quilted primary lateral veins. —C. Close-up of stem showing mottled petiole and stems. —D. Crown of plant with cluster of inflorescences, and petiole showing free-ending sheath apex. —E. Abaxial surface of leaf blade and immature inflorescence. —F. Close-up of open inflorescence.

above, convex and paler than surface below, frequently pale-mottled; primary lateral veins (6)9 to 15 per side, flat to sunken, weakly quilted above, raised and darker than surface below, drying usually darker than surface below, sometimes paler than surface, usually departing midrib at 65°-90° angle throughout most of its length (rarely with the veins in the distal half of the blade arising at 30°- 50°), prominently curved toward the apex in the outer ¹/₃, those near the base to as much as 120° angle, sometimes forming a weak sigmoid curve, the primary lateral veins in the upper ²/₃ to ¹/₂ sometimes loop-connected for some distance, forming a weak collective vein 2-5 mm from margin, but this usually not extending all the way to the apex; interprimary veins almost as prominent as primary lateral veins, flat to sunken above, weakly raised and darker than surface below. INFLORESCEN-CES usually to 3 per axil, sometimes with more than one axil producing inflorescences; peduncles 1.5-4 cm long, 4-5 mm diam., ovoid to D-shaped in cross section; spathe 8-16 cm long, 3.1-4.8 times longer than peduncle, coriaceous, semiglossy on both surfaces, medium to light green outside, slightly paler within; tube oblong to somewhat ellipsoid, 6-7 cm long, oblong-lanceolate when opened, acute at apex (acumen apiculate for 2 mm); spadix (7.5)10-12.5 cm long, up to 1.7 cm shorter than the spathe; pistillate portion (4.0)5.5-6 cm long, (6)8-10 mm wide (the axis ca. 5 mm diam.), almost contiguous with the staminate portion (a wide sterile intermediate section lacking); the pistillate flowers more widely spaced near the apex, 4-6 mm apart; pistils 20-35, ovary globose, pale green; stigma bright yellow with long brushy papillae, 2-2.4 mm diam.; staminodia white, usually broadly united at base and forming an often nearly complete bowl around the pistil, somewhat flattened throughout, barely thickened at the apex, 3.4-5 mm long; staminate portion oblong, 4-6 cm long, creamy white, bluntly pointed at apex; synandria irregularly 4- to 6-lobed, drying 1.5-2.3 mm diam., deeply depressed with the margins turned up. IN-FRUCTESCENCES with spadix 5.5-7 cm long, berries orange, 8-11 mm diam., subglobose, 2- to 3-seeded.

Distribution and habitat. Dieffenbachia davidsei ranges from northeastern Costa Rica to Panama (Darién Province) and Colombia (Chocó) in Premontane wet forest (P-wf), Tropical wet forest (T-wf), and Premontane rain forest (P-rf) life zones (Holdridge, 1967). In Costa Rica it is known only from the Sixaola region at 20–40 m elevation. In Panama it ranges from 100 to 900 m in Panamá Province. The species frequently occurs in mature forest along streams.

Phenology. Dieffenbachia davidsei flowers in the rainy season sometime after May (one plant seen with both flower buds and seemingly mature inflorescences in late October). Mature fruits have been seen during the dry season, in the late rainy season, and early dry season from November through April. Immature fruits have been seen in late April indicating that flowering may begin even earlier than May.

Discussion. The species is distinguished by its slender, dark, semiglossy, mottled stems, mottled petioles with a prolonged, usually acute sheath apex, and more or less oblong blades with rather prominent primary lateral veins that spread at nearly 90°.

Dieffenbachia davidsei is probably most closely related to *D. obscurinervia*. That species differs in usually being a larger plant (to 1.5 m) with prominently scurfy brown internodes, petiole sheaths which are typically only rounded at the apex (not free-ending), and blades which have weakly developed primary lateral veins that arise at an angle, usually about 45° to the midrib.

Although the broadly spreading primary lateral veins are one of the most distinctive characteristics of D. davidsei (with the veins usually spreading from the midrib at a broad angle even to near the apex of the blade), a few collections from the El Llano-Cartí Road in Panama (especially the PMA sheet of Paredes 940) have primary lateral veins that spread at angles of up to 45°. The Paredes 940 collection also has more conspicuously punctate petioles than does the MO sheet of the same number. It is possible that Paredes 940 is a hybrid between D. davidsei and D. obscurinervia. Both species occur in the Nusigandí area along the El Llano-Cartí Road. Dieffenbachia obscurinervia also has conspicuously mottled petioles, but its veins arise at a much more acute angle. The stems of D. obscurinervia differ markedly in being matte and scurfy-brown rather than semiglossy, dark blackgreen with yellow-green mottling as in D. davidsei. Another unusual collection, possibly also a hybrid, is Croat & Zhu 76666 from La Mesa in Coclé Province near El Valle de Antón. It has the glossy internodes of D. davidsei but the veins of D. obscurinervia. It is perhaps just an unusual collection of D. obscurinervia.

Etymology. The species was first collected in Panama by Scott Mori in 1974 along the El Llano– Cartí road (*Mori et al. 4184*), and later in Costa Rica by Gerrit Davidse and C. H. Hamilton (*Davidse & Hamilton 23617*) in 1983. It is named in honor of Gerrit Davidse of the Missouri Botanical Garden, co-editor of the *Flora Mesoamericana* series.

COSTA RICA. Limón: Ouebrada Mata de Paratypes. Limón, Finca Anai (Sixaola region), Grayum et al. 4440 (CR, MO). PANAMA. Bocas del Toro: Fortuna Lake Area, Fortuna-Chiriquí Grande, 1.6 mi. N of Cont. Divide, Croat & Zhu 76533 (MO). Coclé: Caño Blanco del Norte-Caño Sucio, Davidse & Hamilton 23617 (MO, PMA); El Copé, Cont. Divide, Hammel 13685 (MO); El Copé, ca. 1/2 mi. N of Cont. Divide at Alto Calvario, Croat 75100 (MO); Atl. slope, Hammel 5607 (MO). Darién: Par. Nac. del Darién, of Río Pucuro, vic. Tacarcuna, ca. 18 km E of Pucuro, Hammel et al. 16397 (MO). Panamá: El Llano-Cartí Rd., 9.8 km from Interam. Hwy., Mori et al. 4184 (MO). San Blas: trail to Cerro Camucañala from Río Titamibe, de Nevers et al. 4709 (MO, PAN); Comarca de Kunayala, Nusigandí, El Llano-Cartí Rd., 10.1 mi. N of Interam. Hwy., Paseo Mariska, Croat & Zhu 77017 (INB, MO); El Llano-Cartí Rd., de Nevers & H. Herrera 3975 (MO); km 18, Galdames et al. 1330 (STRI); Nusigandí, El Llano-Cartí Rd., betw. Nusigandí and 1 mi. N of Nusigandí, Croat & Zhu 76597 (HUA, MO); Sede de Campo de PEMASKY, ca. 20 km on El Llano-Cartí Rd., Paredes et al. 940 (MO, STRI); Isla Narganá, tributary of Río Diablo, Galdames et al. 1570 (PMA, STRI). Veraguas: Cerro Tute, above Alto de Piedra, McPherson 10725 (MO). CO-LOMBIA. Chocó: Nuquí, Corr. Arusí, Est. Biol. El Amargal, along trail to Arusí, Croat & Mora 83685 (MO).

 Dieffenbachia fortunensis Croat, sp. nov. TYPE: Panama. Chiriquí: along road between Fortuna Lake and Chiriquí Grande, 4.5–5 km N of dam of Fortuna Lake, 8°43'N, 82°17'W, 1100–1135 m, 8 Mar. 1985, *T. B. Croat & M. H. Grayum 60002* (holotype, MO-349012!; isotype, PMA!). Figures 9, 28A.

Herba 40–100 cm alta; internodia 1–5 cm longa, 0.8– 2.0 cm diam.; petiolus 12–28 cm longus, vaginatus 0.37– 0.83 longitudinis; vagina 6.5–14.5 cm longa, decurrens ad apicem; lamina oblongo-lanceolata, raro interdum anguste ovata vel anguste oblanceolata, 15–33 cm longa, 4.5–9.5 cm lata, nervis primariis lateralibus 10–17 utroque; inflorescentia solitaria; pedunculus 4.7–7 cm longus; spatha 12–18 cm longa; spadix 9–11.5 cm longus.

Slender herb, 40–100 cm tall; sap lacking distinctly foul aroma; stem erect except at base, containing inconspicuous, white raphide cells; *internodes* 1–5 cm long, 0.8–2 cm diam., unmarked, semiglossy, dark green to medium green, sometimes minutely wrinkled and glistening, drying blackened, moderately smooth (but minutely granular on magnification). LEAVES erect-spreading, \pm clustered at/near stem apex; *petioles* 12–28 cm long (averaging 19.6 cm long), sheathing for 0.37–0.83 their length (averaging 0.58 their length); sheath 6.5–14.5 cm long (averaging 10.1 cm), with margins striate, decurrent distally, dark green, drying blackened to dark brown, surface matte, striate at

base, minutely granular-roughened throughout with white raphide cells; unsheathed portion 3-15.5 cm long, sharply C-shaped, flat-sulcate, with margins prominently raised; blades narrowly oblong-lanceolate, rarely sometimes narrowly ovate, or narrowly oblanceolate, 15-33 cm long, (3.5)4.5-9.5(13) cm wide (averaging 21×6.8 cm), 2–6.3 times longer than wide, 0.38-1.48 times longer than petiole (averaging 1.1 times longer), \pm equilateral or weakly inequilateral, one side 5-15 mm wider than the other side, thinly coriaceous to subcoriaceous, drying papyraceous, usually quilted, weakly bicolorous, \pm equilaterally or sometimes inequilaterally acuminate or sometimes acute at apex (acumen sometimes briefly apiculate), equilateral to slightly inequilateral and attenuate to acute, rarely rounded at base; margins usually conspicuously undulate, drying crisped; upper surface glossy to semiglossy or weakly glossy, medium to dark green, sometimes mottled white or cream; lower surface matte to weakly glossy, moderately paler; *midrib* flat or flatraised and concolorous above, thicker than broad to convex below, drying brownish matte and darker than surface to slightly paler than surface, granularpuberulent to conspicuously granular below; primary lateral veins 10 to 17 per side, departing midrib at an acute angle, then moderately curved toward the margin at 55°-90° (mostly 55° in the middle of the blade but at more acute angles toward the apex and more obtuse angles toward the base), turning upward along the margins and forming a series of fine collective veins along the margins, some of which extend to the apex, matte, prominently sunken to narrowly or weakly sunken and concolorous above, thicker than broad or convex and darker than surface, granular-puberulent to conspicuously granular below, drying darker than surface; interprimary veins usually about as conspicuous as primary lateral veins; minor veins moderately obscure to distinct; "cross-veins" loose-connected, weakly oblique, drying minutely dark-punctate. IN-FLORESCENCES 1 per axil; peduncle 4.5-7 cm long; spathe 12-18 cm long, 2-3.7 longer than spadix, 1-1.5 cm diam. on tube when furled, gradually contracted midway, gradually long-tapered to apex, uniformly pale green on both surfaces; spadix 9-11.5 cm long, drying 3-3.2 mm diam.; free portion 1.5-2 cm long, drying 2 mm diam.; pistillate portion 4.2-6 cm long, drying 7 mm diam. throughout; fertile staminate portion 5-6.5 cm long, drying 4 mm diam. throughout; mostly naked intermediate portion of spadix 1.5-2.0 cm long, drying 2 mm diam., with a few sterile pistillate flowers in the lower half; pistils 35 to 38, well-spaced, rarely more than 2 dispersed across spadix width, de-



Figure 9. *Dieffenbachia fortunensis*. A, B. (*Croat 60002*). —A. Habit of sterile plant. —B. Leaf blade adaxial surface. C–F. (*Croat 76340*). —C. Leaf blade abaxial surface. —D. Stem showing petiole bases and free-ending sheath. —E. Close-up of stem showing acutely and broadly sulcate petiole. —F. Stem showing internodes and petiole bases.

pressed-globose, to 1.6 mm long, 1 mm diam., pale green; stigma yellow, about as broad as the pistil; staminodia white, 1–1.4 mm long, conspicuously thickened, drying pale orange-brown; the synan-dium 2–2.6 mm long, 1.6–2.0 mm wide, white, drying yellow-brown, the margins irregularly angular-subrounded. INFRUCTESCENCE with spadix to 6 cm long; *berries* not seen.

Distribution and habitat. Dieffenbachia fortunensis is apparently endemic to Panama, known only from the Fortuna Dam region of Chiriquí Province (hence the epithet) at 900 to 1600 m in *Premontane rain forest* (P-rf) and *Lower montane rain forest* (LM-rf) life zones (Holdridge, 1967).

Phenology. Flowering occurs during the late dry season and early wet season from March to June with fruits maturing in the late rainy season after September.

Discussion. It is distinguished by its usually small stature, moderately thin, prominently veiny, undulate, narrowly oblong-lanceolate to narrowly ovate blades with a flat-raised midrib, and petioles with the sheath decurrent at its apex and with a long, free, sharply flattened-sulcate distal portion. Also characteristic are the granular to granular-puberulent major veins on the lower blade surface.

The species is closest to *D. beachiana*, the latter differing in having the major veins on the lower surface conspicuously whitish puberulent and blades with primary lateral veins more numerous and spreading consistently at broader angles (most to ca. 90° throughout most of the blade rather than only a few veins near the base of the blade). In terms of pubescence D. fortunensis is closer to D. galdamesiae, which also shares granular puberulence rather than the loose puberulence of D. beachiana, but D. galdamesiae differs from D. fortunensis in having the primary lateral veins 15 to 17 per side and arising at a 30°-40° angle (vs. 10 to 17 per side, and at a 55°-90° angle). Dieffenbachia galdamesiae is also restricted to areas east of the Panama Canal, while D. fortunensis is restricted to far western Panama.

The species has been confused with small plants of *D. lutheri*, a similar species from Cerro Colorado in Chiriquí Province. That species usually has wider leaf blades (to 15 cm) that are ovate and dry less blackened. In addition, that species has the pistillate and staminate portions of the spadix contiguous, and lacks the mostly sterile section between the pistillate and staminate portion as is present on *D. fortunensis*.

Paratypes. PANAMA. **Bocas del Toro:** along Cont. Divide rd. N off main Fortuna–Chiriquí Grande Hwy., on

mi. 1.1, Croat & Grayum 60346 (MO). Chiriquí: Gualaca-Chiriquí Grande, 1 km S of Cont. Divide & Bocas del Toro boundary, Croat 66866 (MO); 7.2 mi. beyond Los Planes de Hornito, Croat 67837 (MO); 8.3 mi. NW of Los Planes de Hornito, Croat 49971 (MO); rd. to Fortuna Dam site, N of Gualaca, 22.7 mi. beyond Río Estí bridge, Croat 48672 (MO, PMA); 4.8 mi. beyond IRHE facilities at dam, Croat 68012 (INB, MO, PMA), Croat & Zhu 76340 (MO), Thompson 4951 (CM, MO); Fortuna Dam area, Quebrada Los Chorros-Quebrada Hondo, to N of reservoir, Churchill & Churchill 6158 (MO), Churchill & Churchill 6159 (MO).

9. Dieffenbachia fosteri Croat, sp. nov. TYPE: Panama. Bocas del Toro: Laguna de Chiriquí, Nuri, 15 km E of Punta Cricamola, Ensenada de Catavela to Quebrada Nuri, 8°55'N, 81°49'W, elevation near sea level, 20 Mar. 1993, R. Foster, A. Herre, E. Kalko & C. Handley 14649 (holotype, PMA!). Figure 27A.

Planta (0.4)1-2 m alta; internodia 1.5 cm longa, 1.5 cm diam. in sicco; petiolus 10–29 cm longus, vaginatus ½–½ longitudinis, pars libera subteres; lamina ovato-elliptica vel lanceolata vel anguste ovata, (14)17–28 cm longa, (6)7–14 cm lata, nervis primariis lateralibus 8–13 utroque; inflorescentia 1 per axillam; pedunculus 9.5 cm longus; spatha 20 cm longa, 2 cm diam.; spadix 18 cm longus; pars pistillata 6.5 cm longa (in fructu); baccae 6–7 mm diam in sicco, 1-loculares.

Slender herb, (0.4)1-2 m tall; sap smelling of oxalic acid; internodes medium green, dark greenmottled, 1.5 cm long, drying 1.5 cm diam. LEAVES clustered at/near stem apex; petioles 10-29 cm long, drying 2-3 mm diam., sheathing 1/3 to 1/2 their length; sheath margins drying ± hyaline and brown, sheath apex with one side obscure to rounded, with the other side acute; unsheathed portion of petiole subterete, oval in cross section, 12.5-18.5 cm from base of blade; blades ovate-elliptic to lanceolate or narrowly ovate, $(14)17-28 \times (6)7-14$ cm, 2-2.4 times longer than wide, somewhat inequilateral, one side 1–1.5 cm wider than the other side, acuminate at apex, the acumen apiculate, 1 mm long, inequilateral and obtuse or rounded at base; midrib convex to flat-raised and concolorous above, drying somewhat flattened and concolorous above, convex and densely hispidulous, darker than surface below, drying striate with white inclusions below; primary lateral veins 8 to 13 per side, weakly sunken above, raised beneath, departing midrib at an acute angle then spreading at 65°-80° in the lower ½ of the blade, spreading at 45°-55° toward apex, extending almost straight toward the margins then broadly sweeping toward the apex; upper surface dark green, matte, drying dark brown to somewhat blackened; lower surface slightly paler than above, weakly glossy, drying slightly less gravish black than upper surface, densely grayish-speckled

709

below. INFLORESCENCES 1 per axil; *peduncle* 9.5 cm long, 5 mm diam.; *spathe* 20 cm long, 2 cm diam., gradually long-tapered, green throughout, the tube flattening to 3.5 cm wide; *spadix* 18 cm long, with pistillate portion to 6.5 cm long in fruit; *berries* 6–7 mm diam., dried, 1-locular.

Distribution and habitat. Dieffenbachia fosteri is only known from the type in western Panama near sea level in Bocas del Toro Province in the *Tropical moist forest* (T-mf) life zone (Holdridge, 1967).

Phenology. Little is known about the phenology of this species, but the type collection was in early fruit in March. Flowering probably occurred sometime during the rainy season.

Discussion. Dieffenbachia fosteri is characterized by its slender, rather weakly sheathed petioles and especially by its ovate-elliptic, somewhat blackish-drying blades. It is apparently not closely related to any other Central American species, though in the shape of blades and the decurrent sheath apex it is most similar to D. killipii. That species differs in having semiglossy blades that dry more or less green. It could possibly be confused with D. grayumiana, a species ranging along the Caribbean coast of Costa Rica to western Panama and probably occurring in the area where D. fosteri was collected; however, the latter differs from D. fosteri in having narrowly ovate-subcordate blades that are typically conspicuously pale-maculate and also in drying olive-green to yellowish brown rather than blackened.

Etymology. The species is named in honor of one of its collectors, Robin Foster, from the Field Museum of Natural History in Chicago, an expert on Neotropical plant ecology and the vegetation of the Neotropics.

 Dieffenbachia galdamesiae Croat, sp. nov. TYPE: Panama. Comarca de San Blas: Pemasky, Sendero Nergan Igar, km 15 on El Llano-Cartí Road, 9°20'N, 78°58'W, 350 m, 2 July 1994, C. Galdames, T. B. Croat & M. Alba 1222 (holotype, MO-5548504!; isotypes, AAU!, B!, COL!, F!, GH!, INB!, K!, MEXU!, NY!, PMA!, RSA!, S!, SCZ!, UB!, US!, VEN!). Figures 10, 28A.

Planta 50–80 cm alta; internodia 6–20 mm longa, 0.5–2.0(3.0) mm diam.; petiolus 18–43 cm longus, C-formatus, vaginatus 0.25–0.66 longitudinis; lamina oblongo-elliptica, 27–60 cm longa, 6.7–18 cm lata, nervis primariis lateralibus 15–17 utroque; inflorescentia 3 per axillam; pedunculus 5.5–15 cm longus; spatha 14–25 cm longa, 2 cm diam.; spadix 15.7–18 cm longa; pars pistillata 7.3– 10 cm longa, 8 mm diam.

Small herb, to 50-80 cm tall; sap lacking foul odor but weakly caustic to skin; stem supported at base by adventitious roots; internodes $6-20 \times 0.5-$ 2.0(3.0) mm diam., dark green, weakly to moderately glossy; petiole scar oblique, one side 3-4 mm wider than the other; petioles 18-43 cm long (averaging 29 cm long), densely granular-puberulent, sheathed 0.25-0.66 their length (averaging 0.43 their length); sheath erect to involute, 6.5-20 cm long (averaging 12.3 cm long), inequilaterally rounded to acute at apex; unsheathed portion 10-25 cm long (averaging 16.5 cm long), sharply Cshaped, broadly concave adaxially; blades oblongelliptic, 27-60 cm long, 6.7-18 cm wide (averaging 40.8×11.7 cm), 2.7–4.2 times longer than wide (averaging 3.6 times longer), 1.1-1.8 times longer than petioles (averaging 1.2 times longer than petioles), acuminate at apex, acute at base, inequilateral, one side to 1.5 cm wider than the other, thinly coriaceous, drying moderately thin; upper surface dark green and semiglossy, drying dark brown to olive-green; lower surface slightly paler, almost matte, drying weakly glossy, gravish to yellowish brown; midrib broadly convex-flattened and concolorous above, narrowly rounded, matte, darker and sparsely granular-puberulent below, drying darker than surface, flattened to ridged with one or both margins narrowly raised; primary lateral veins 15 to 17 per side, arising at 30°-40° angle, sweeping prominently toward the apex with as many as 4 to 5 of them simultaneously coursing along the margin within 1 cm of the margin, sometimes forming weak collective veins, weakly quilted-sunken above, convex and sparsely granular-puberulent and somewhat scurfy below, drying darker than surface with the center collapsed and the margins often thin and upturned; minor veins obscurely to moderately visible and darker than surface above, drying moderately distinct; cross-veins sometimes drying moderately distinct below. INFLORES-CENCES to 3 per axil; peduncle 5.5-15 cm long, 5-8 mm diam., drying 2.5-5 mm diam.; spathe 14-25 cm long, 1.6-2.5 times longer than peduncle, 2 cm diam. at tube, green on both surfaces; spadix 15.7–18 cm long; free portion 9.5–12 cm long; pistillate portion of spadix 7.3-10 cm long, 8 mm diam.; staminate portion of spadix 7-8.5 cm long, 6 mm diam.; the mostly sterile intermediate portion 1.3-2.5 cm long with a few pistillodes extending in the lower 1/2; pistils 59 to 68, moderately closely spaced, 2 to 4 situated across the width of the pistils; ovaries 1.2-2.0 mm diam.; stigmas 1.6-2.2 diam., depressed-globose; staminodia club-shaped, 1.8-2.8 mm long, 0.4-1.0 mm wide, flattened, free to base, not expanded toward the base, thickened



Figure 10. Dieffenbachia galdamesiae (Croat 76560). —A. Habit. —B. Leaf blade adaxial surface. —C. Close-up of stem showing roots and petiole bases. —D. Petioles and clusters of inflorescences.

and somewhat granular-puberulent at apex; synandria 2.4–2.8 mm diam., irregularly rounded, broadly sulcate to truncate with slightly overlapping edges, the margins \pm crenulate. INFRUCTES-CENCES not seen.

Distribution and habitat. Dieffenbachia galdamesiae is endemic to Panama, known only from central Panama on both sides of the isthmus in the *Tropical wet forest* (T-wf) life zone (Holdridge, 1967) at 350 to 500 m elevation. It occurs in swampy conditions in creek beds in virgin forest in nearly full shade. *Phenology.* The species has been seen in flower in June as well as in October. Mature fruits have been seen in December.

Discussion. The species is characterized by its moderately small habit, only to 80 cm tall, the granular-puberulent petioles and major veins on the lower blade surface. It is most closely related to D. beachiana and D. fortunensis, differing from both in having the primary lateral veins ascending at less than a 50° angle. It may prove to be only subspecifically distinct from D. fortunensis.

Etymology. The species is named in honor of

Chilean botanist Carmen Galdames, a long-time resident of Panama, who has collected in Panama for the SCZ herbarium at the Smithsonian Tropical Research Institute. Carmen was the first to bring the species to my attention and also collected the type specimen.

Paratypes. PANAMA. Panamá: El Llano-Cartí Rd., 6.8 mi. from hwy., Croat 49124 (MO). San Blas: Comarca de Kunayala, Nusigandí, El Llano-Cartí Rd., 9 mi. N of main hwy., Nergan Igar (Nergan Trail), Croat & Zhu 76560 (MO, PMA). Veraguas: Dos Bocas del Río Caloveborita, 16–17 km NW of Santa Fe, Dressler 5316 (MO).

 Dieffenbachia grayumiana Croat, Novon 9: 494. 1999. TYPE: Costa Rica. Limón: Refugio Nacional Barra del Colorado, forests and pastures between Río Chirripócito and Río Sardina [Sardinal], 10°8'N, 83°5'W, 12 m, *M. H. Grayum 9773* (holotype, MO-4370212!; isotype, INB!). Figures 11, 27A.

Stout herb, 1-1.5 m tall; stems erect at apical part, the older portion reclining for up to 1.5 m; internodes 2.5-8.5 cm long, 2-3.5(-10) cm diam., dark green, glossy, variegated with cream-yellow or pale green (sometimes medium green with dark green lines as in Croat & Grayum 60149); petioles (24-)30-59 cm long (averaging 39 cm long), sheathed from 0.3 to 0.55 their length (averaging 0.42), matte, dark olive-green to deep brown, streaked or tinged with cream-white in lower half, especially near the base, subterete; sheath 19-29 cm long, usually decurrent at apex, sometimes weakly free-ending (as in *Croat & Grayum 60149*); unsheathed portion 13-28.5 cm long, weakly sulcate adaxially, weakly flattened toward the apex, sometimes slightly white adaxially and continuing white onto lower midrib; blades narrowly ovate to oblong-ovate, (22)30–54 \times 10–32 cm (averaging 36×18 cm), 1.5–2.6 times longer than wide (averaging 1.9), ranging from 0.6 as long as petioles to 1.4 times longer than petioles, but averaging about as long as petioles, slightly inequilateral, one side 1-1.5 cm wider than the other, acuminate to abruptly acuminate at apex, inequilaterally subcordate (sinus to 3.5 cm deep) or rarely inequilaterally rounded at base (sometimes one side weakly subcordate, the other side rounded), subcoriaceous, drying thin, slightly concolorous to slightly bicolorous; upper surface usually glossy to semiglossy, dark green, to weakly mottled cream, drying dark olive-green, plain (unvariegated) to usually conspicuously mottled yellow-cream; lower surface semiglossy to nearly matte, slightly paler, drying yellowish green; midrib flat to weakly flat-raised or broadly convex (sometimes broadly sunken at base,

broadly flat-raised and striate toward apex) slightly paler and dark green-spotted to concolorous above, convex to narrowly rounded and white or narrowly acute and paler below; primary lateral veins 13 to 18(to 22) per side, gradually arising at a steep angle from the midrib, then spreading in a broad curve at 55°–80° angle, (those near the apex to 25° angle, those near the base sometimes 90°-110° angle and sometimes forming a sigmoid curve), deeply sunken above, convex below, forming a series of weakly developed collective veins that eventually merge with the margin; at least the midrib and primary lateral veins sometimes minutely farinose-granular; minor veins moderately obscure below. INFLO-RESCENCE 1 to 3 per axil, sometimes subtended by a reduced leaf with a fully sheathed petiole (the sheath emarginate at apex) and a reduced leaf blade, 12–15 \times 3.5–6.5 cm; peduncle 8–12 cm long, drying 2-3 mm diam.; spathe 16.5-23.5 cm long, 3-4 cm longer than the spadix, 4.0-5.0 cm wide at base, to 2.5-3.5 cm wide at constriction, 2.5-3 cm wide on blade (to 7 cm wide when flattened), uniformly light green to medium green on both surfaces, weakly glossy throughout outside, somewhat glossier within; spadix 15-27 cm long; free portion 7-13 cm long; pistillate portion 8.0-9.3 cm long, drying 7-10 mm wide; staminate portion 5-6.5 cm long, white, tapered toward apex and tapered slightly toward the base; the staminate and pistillate portions separated by an almost sterile intermediate segment 2-2.5 cm long with a few scattered pistils in the lower half and a few scattered staminodia in upper half; pistils 115 to 160, densely aggregated, separated from one another by 0.5 to 2.5 times their width, irregularly scattered with roughly 4 to 5 covering the width of the spadix; ovaries pale lemon-yellow, depressed-globose, 1.8-2 mm wide; staminodia white, 3 to 5 per pistil, free or briefly united at base, 1.5-2.2 mm long; synandria 1.2-1.6 mm diam., irregularly angled with rounded margins. INFRUCTESCENCES to 27 cm long, with fruiting portion 10-14 cm long; berries red-orange, subglobose, ovoid to ellipsoid, 5-7 mm diam.

Distribution and habitat. Dieffenbachia grayumiana ranges along the Atlantic slope from northwestern Costa Rica to western Panama, mostly near sea level but ranging up to 1300 m in Costa Rica in Alajuela Province (vic. of Monteverde Reserve) and to 480 m in Heredia Province. Grayum (pers. comm.) reports the species to occur mostly in light gaps and disturbed areas in primary forest at the La Selva Reserve in Costa Rica.

Phenology. Flowering occurs in D. grayumiana



Figure 11. Dieffenbachia grayumiana. —A. Habit (Croat 60149). B–D. (Croat 74953). —B. Leaf blade adaxial surface. —C. Blade abaxial surface. —D. Apex of stem showing heavily sheathed petioles with sharply sulcate free portion, and speckled petiole bases.

from January to June, rarely as early as November. Fruiting collections have been seen only from May to September.

Discussion. The species is characterized by its narrowly ovate, typically subcordate, mottled blades; weakly sheathed, decurrent petioles; and variegated stems and petioles. Also characteristic are blades that are frequently glossy on the upper surface and matte or nearly so on the lower surface. The major veins are sometimes minutely farinose-granular on the lower surface. In this regard it is similar to *D. beachiana*, a species with puberulent major veins on the lower blade surface. Aside from pubescence type, *D. beachiana* also differs in having much narrower blades (1.8–5.3 times longer than wide) with more numerous pairs of primary lateral veins (23 to 36 pairs).

Dieffenbachia grayumiana is superficially similar to *D. seguine* from the West Indies in the shape and coloration of its dried blades but lacks the sharply sulcate petioles, the bicarpellate ovaries, and the protruding stubby spadix with a reflexed spathe blade seen in the latter.

A collection from Bocas del Toro Province in Panama (*Croat 74945*) differs in having larger concolorous blades (54×30 cm) that are only weakly glossy on the upper surface, with only weakly sunken primary lateral veins. Another collection from Bocas del Toro, *Croat & Grayum 60149*, had stems to ca. 10 cm diam., substantially larger than those of any other collection reported.

Additional specimens examined. COSTA RICA. Alajuela: Puntarenas-Guanacaste, Peñas Blancas, Dryer 1681 (F); Río Peñas Blancas, Burger et al. 10734 (CR, F); Upala, Río Zapote, 5 km S of Canalete, Burger & Baker 9968 (CR, F). Heredia: Río Sarapiquí, La Virgen, 1974, Horich s.n. (M); La Zona Protectora, Río Peje-Río Guacimo, Gravum & Schatz 3206 (DUKE); Secondino's woods, off Occidental, Kress 84-1632 (SEL); Río Peje-Río Sardinalito, Atl. slope of Volcán Barva, Gravum 6887 (MO); San José, Pto. Viejo, vic. of Chilamante, 11.6 mi. N of Cariblanco, Croat 68359 (B, CR, M, MO); La Selva, Croat 78733 (COL, INB, MO, NY, SEL); upstream on Río Puerto Viejo, Burger & Matta 4181 (CR, F); OTS Field Station along Río Puerto Viejo just E of jct. with Río Sarapiquí, Beach 1440 (DUKE), Beach 1441 (DUKE), Chacón 507 (DUKE), Croat 44321 (MO), Folsom 9724 (MO), Hammel 8167 (MO), Hammel 8873 (DUKE), Grayum 2288 (DUKE). Limón: Ref. Gandoca-Manzanillo, Río Gandocaca, Grayum et al. 8038 (CR, MO); 3.5 air km S of Islas Buena Vista in the Río Colorado. 16 km SW of Barra del Colorado, Davidse & Herrera 31213 (INB, MO); Cerro Coronel, E of Laguna Danto, Stevens 23642 (CR, MEXU, MO); Río Chirripócito-Río Sardina, Ref. Nac. Barra del Colorado, Río Chirripócito-Río Sardina, Grayum 9830 (MO); Guacimo-Guapiles Rd., Barringer 2432 (F); Pococi, Par. Nac. Tortuguero, Río Suerte betw. Río Palacio-Caño Penitencia, Grayum et al. 11116 (INB, MO); Lomas de Sierpe, S from Río Tortuguero, Grayum et al. 11163 (INB, MO). PANAMA. Bocas del Toro: Almirante-Bocas del Toro, near Milla 5, *Croat & Porter 16499* (MO); Chiriquí Grande-Fortuna, 3 mi. W of Chiriquí Grande, *Croat & Grayum 60149* (K, MO, PMA, US); Gualaca-Chiriquí Grande, 8.1 mi. S of Punta Peña, *Croat 74953* (MO, PMA). **Chiriquí:** Gualaca-Chiriquí Grande, 1.4 mi. S of Punta Peña, *Croat 74945* (MO), *M. Akers 78A* (MO).

 Dieffenbachia hammelii Croat & Grayum, Novon 9: 496. 1999. TYPE: Costa Rica. Heredia: Finca La Selva, O.T.S. Field Station on the Río Sarapiquí, 50–80 m, *M. H. Grayum* 7670 (holotype, MO-3491533!; isotypes, B!, CR!, K!). Figures 12, 27B.

Small herb, 25-40(70) cm tall; sap not foulsmelling; stem becoming decumbent and subrhizomatous at base; internodes 1-1.5(2.7) cm long, on lower portions, 3.5-7.5 cm long toward the apex, 0.5-2 cm diam., glossy, dark blackish green, drying yellowish brown to gray-green, weakly striate. LEAVES erect-arching; petioles 7-25(35) cm long (averaging 15 cm long), erect, green or mottled with dull yellow-green, drying greenish to sometimes vellowish brown, surface drying matte, sheathing for (0.3)0.4-0.8 the petiole length (averaging 0.63 their length), sheath 5.5-13 cm long (averaging 8 cm); unsheathed portion 1-9 cm long, rarely to 15 cm long, narrowly C-shaped to D-shaped in cross section, narrowly sulcate adaxially, with margins finely acute, the tip narrowly decurrent, sometimes difficult to discern where it ends; blades narrowly to broadly elliptic or oblanceolate, $9-28 \times 3.2-$ 13(15) cm (averaging 19.5 \times 7.5 cm), 1.7–3.4 times longer than wide (averaging 2.7 times longer than wide), 1.1-1.5 times longer than the petiole; equilateral to slightly inequilateral, one side 0.5-1 cm wider than the other (the narrower side usually plane, the wider side usually minutely undulate), weakly to semiglossy, acuminate, narrowly to broadly acute or attenuate at apex, and equilateral or slightly inequilateral, rarely obtuse at base, thinly coriaceous, slightly to moderately bicolorous; upper surface medium to dark green, weakly glossy to semiglossy, drying light yellow-green to dark brown; lower surface weakly glossy to matte, slightly to moderately paler, drying yellow-green, sometimes vellow-brown; midrib flat-raised, rarely convex (sometimes obscurely sulcate medially), 1-3 mm diam., slightly paler than surface above, convex to narrowly convex below, drying pale brown, matte, with short, white raphide cells; primary lateral veins 9 to 17 per side, departing midrib at a 40°-50° angle, weakly curved to the margins, weakly sunken or slightly raised in weak valleys, weakly guilted and concolorous above, convex and weakly pleatedraised, drying moderately inconspicuous, slightly



Figure 12. Dieffenbachia hammelii. A, E. (Croat 78758). —A. Habit of plant in the wild. —B. Potted flowering plant showing habit (Duke 81-157). —C. Potted plant with inflorescence at anthesis (Croat 78731). D, F. (Croat 78731). —D. Leaf bases and cluster of inflorescences, the one on the right at anthesis. —E. Crown of plant with an open inflorescence. —F. Crown of plant with a cluster of inflorescences (one cut away to expose full-sized berries).

darker than surface or slightly paler than surface below; the interprimary veins almost as conspicuous as primary lateral veins; minor veins darker than surface below, drying moderately faint; "crossveins" darker than surface below, drying moderately faint. INFLORESCENCES 1 to 3 per axil; peduncle 4.5-11 cm long, subterete in cross section; spathe (8)10-16 cm long, 1.3-2.7 times longer than peduncle, medium green throughout, and weakly glossy outside, medium green and glossy inside, cuspidate to acuminate at apex; spathe tube 6.5-12.5 cm long, 1.2-2.3 cm diam., free portion 3-6 cm wide when flattened; spadix 6.5-15.5 cm long; free portion 4.7-7.5 cm long; pistillate portion 5-8.5 cm long, 6-7 mm diam. throughout, fused with spathe for up to 4 cm; fertile staminate portion tapered to both ends, moderately acute at apex, (1.7)3-4.5 cm long, 6-7 mm diam. throughout; sterile intermediate segment (0.8)2-3 cm long, with a few scattered staminodia throughout; pistils 26 to 43, ovoid, sparse to moderately dense, loosely scattered in clusters of 2 to 4 with up to 3 across the width of spadix but often with spaces between the groups of pistils up to twice the width of the spadix, sometimes in a spiral with up to 5 to 6 pistils; ovaries 1-locular, 2.4 mm long, 2.4 mm diam.; stigmas 1.6-1.8 mm diam.; staminodia 2.8-3 mm long, up to twice as long as pistils, free from one another at base, thickened at both ends, white at apex, but often translucent midway and drying flattened and very thin; synandrium bluntly 4- to 5-sided, margins irregularly shaped toward the base, \pm rounded at apex, 2-2.5 mm diam. INFRUCTESCENCE with spathe pale orange outside; spadix 22 cm long; berries orange to bright red, obovoid-ellipsoid, 1 cm long, 8 mm diam.

Distribution and habitat. Dieffenbachia hammelii occurs in southeastern Nicaragua (Dpto. Río San Juan) and northern Costa Rica from sea level to 100 m in the *Tropical wet forest* (T-wf) life zone (Holdridge, 1967), in wet forests and swampy areas on the Atlantic slope.

Phenology. Flowering plants of *D. hammelii* have been seen from March through May and also July, while mature fruits have been seen in August and September. Cultivated plants at the Missouri Botanical Garden flowered in mid July and mid October.

Discussion. The species is characterized by its small stature, typically 25–40 cm; its glossy, decumbent, subrhizomatous stems; weakly sheathed, matte-drying petioles (sheath decurrent at apex); and moderately small, more or less oblong-elliptic, weakly inequilateral green leaf blades with moderately numerous primary lateral veins. One blade margin is usually plane and one margin usually minutely undulate.

In Costa Rica it is most easily confused with *D. oerstedii* or small plants of *D. grayumiana*, both of which can be distinguished in having the petiolar sheath auriculate at the apex rather than decurrent as in *D. hammelii*. At La Selva, where the species was first studied, *D. hammelii* is uncommon. One collection (*Hammel 8784*) reported that the sap was not foul smelling, as is the case with many species.

Additional specimens seen. COSTA RICA. Heredia: Finca La Selva, OTS Field Station on the Río Puerto Viejo, Grayum 2772 (DUKE, MO). Limón: Tortuguero, near Boca de las Lagunas de Tortuguero, Burger & Antonio 11224 (CR, F); Cerro Coronel, E of Río Zapote, 1 km from banks of Río Colorado, Stevens 24257 (CR, MO); 2 air km SSE of Islas Buena Vista in the Río Colorado, Davidse & Herrera 31077 (CR, MO); 3.5 air km S of Islas Buena Vista in the Río Colorado, Davidse & Herrera 31154 (MO); Ref. Barra del Colorado [Sardinal], Grayum et al. 9744 (CR, MO); Pococi, Tortuguero, N end of Lomas de Sierpe, S from Río Tortuguero, Grayum et al. 11169 (CR, INB, MO). San José: Vazquez de Coronado, Braulio Carrillo NP, along San José to Siquirres Hwy., along trail to Río Sucio, Old Carillo Station site, Croat 78758 (COL, GOET, INB, MEXU, MO, PMA, TEFH, UB, WU). NICARAGUA. Río San Juan: near Caño Chontaleno, 20 km NE of El Castillo, Neill & Vincelli 3484 (MO); "Marcelo" near Río Sabalos, Salick 8092 (MO).

 Dieffenbachia horichii Croat & Grayum, sp. nov. TYPE: Costa Rica. San José: Cantón Pérez Zeledon, along road betw. San Isidro General– Dominical, Fila Tinamastes, 9°18'24"N, 83°46'11"W, 900–1100 m, *T. B. Croat & D. Hannon 79115* (holotype, MO-05095465!; isotypes, AAU!, B!, CAS!, COL!, CR!, DUKE!, F!, GH!, HUA!, INB!, K!, MEXU!, NY!, P!, PMA!, QCNE!, RSA!, S!, SCZ!, TEFH!, TEX!, UB!, US!, VEN!, WU!). Figures 13, 27A.

Planta terrestris, 1.0–1.5(2) m; internodia 1–3 cm longa, 4–6 cm diam.; petiolus 8–33 cm longus, vaginatus fere omnino; vagina libera 1.5 cm longa; lamina elliptica vel ovato-elliptica, 26–60 cm longa, 9–30 cm lata, nervis primariis lateralibus 14–21 utroque; inflorescentia 3–6 in quoque axilla; pedunculus 8.5–19 cm longus; spatha 14.5–32.5 cm longa; spadix 13–17 cm longus; pistilla 43– 69.

Stout herb, 1–1.5(2) m tall; sap white, copious, foetid, caustic; stem erect on younger parts, to 1.2 m long and reclining on older parts, *internodes* 1– 3 cm long, 4–6 cm diam., semiglossy to glossy, dark green to medium green; *petioles* 8–33 cm long (averaging 18.7 cm long), weakly glossy, sheathing nearly or completely throughout; sheath medium green streaked with yellow-green, margins involute, the tip free-ending and inequilaterally rounded-au-



Figure 13. *Dieffenbachia horichii*. A, B. (*Croat & Hannon 79115*). —A. Habit of flowering plant. —B. Crown of plant with cluster of inflorescences. C, D, E. (*Croat 79073*). —C. Plant with inflorescence at anthesis. —D. Close-up of stem with petiole bases. —E. Close-up of lamina base and close-up of inflorescence.

riculate (auricle sometimes extending up to 1.5 cm beyond blade); unsheathed portion lacking or to 1.2 cm long (rarely to 6 cm long), obtusely somewhat flattened in cross section; *blades* narrowly to broadly elliptic to ovate-elliptic, $26-60 \times 9-30$ cm (averaging 45×19 cm), 1.9-3.4 times longer than wide (averaging 2.5 times longer), 1.7-4 times longer than petiole, slightly inequilateral, one side 0.5-1.2 cm wider than the other side, subcoriaceous to coriaceous, somewhat bicolorous, acumi-

nate at apex, \pm equilateral and obtuse to rounded (rarely acute or narrowly rounded) at base, margins weakly undulate; upper surface dark green, semiglossy to highly glossy, drying dark gray-green to dark yellow-brown; lower surface weakly glossy to matte, moderately paler, drying yellow-brown to yellowish green; *midrib* broadly and shallowly sunken to flat-sunken above, 5–20 mm diam., convex and bluntly low-triangular below, drying light brown to dark brown paler than surface below; *pri*- mary lateral veins 14 to 21 per side, departing midrib at a mostly 30°-40° angle above middle, often 70°-90°, often arising at an acute angle, spreading to the margins, broadly curved toward apex, eventually merging at margins, weakly sunken above, weakly convex below, drying brownish and darker than surface below; the interprimary veins usually darker than surface, 1 between each pair of primary lateral veins; minor veins visible, slightly darker than surface, drying moderately obscure on lower surface. INFLORESCENCES 3 to 6 per axil; peduncle 8.5-19 cm long (averaging 13.5 cm), 3-6 mm diam., drying striate; spathe 14.5-32.5 cm long, 4-5.5 cm diam. (averaging 20.8 cm long), 2.5-4 cm diam. at constriction, 0.9-2.3 times longer than the peduncle (averaging 1.5 times longer than the peduncle), gradually long-tapered toward apex from midway, light green to medium green throughout; spathe tube 3×2.3 cm diam. when furled (flattening 4.0-5.5 cm wide), the constricted area flattening 2.5-4.0 cm wide; spathe blade 2.5-4 cm wide at anthesis; spadix 13-27 cm long (averaging 17.4 cm long); free portion 10-13.5 cm long; pistillate portion to (6.5)8-10.8 cm long (averaging 8.3 cm long), 8-17 mm wide, drying 8 mm diam.; fertile staminate portion 8.3-12 cm long, cream-colored, moderately tapered toward apex and weakly tapered toward base, 7-12 mm diam. midway; mostly sterile intermediate segment 1.7-3.7 cm long, with a few scattered staminodia throughout; pistils 43 to 69, irregularly scattered, nearly contiguous, 3 to 4(6 to 7) dispersed across spadix width, separated from one another by up to 4 times their width; ovary depressed-globose, 2 mm long, yellow-green; stigma cushion-shaped, 2.8-3.4 mm diam., about twice as wide as thick and usually broader than the pistil at anthesis, yellowish; staminodia white, 3 to 5 per pistil, 3-4 mm long, free or briefly united at base; synandria 1.6-3.0 mm diam., subrounded, depressed medially at apex, drying orange-brown. INFRUCTESCENCE 19-24 cm long; spathe orange outside; spadix 8-15 cm long; berries red, subglobose, ovoid to ellipsoid, 7-10 mm long.

Distribution and habitat. Dieffenbachia horichii is known only from the Pacific slope of Costa Rica from the Carara reserve and Puriscal region to the San Isidro region and Dominical. It occurs in *Premontane rain forest* (P-rf) and transition forests between *Tropical wet forest* (T-wf) and *Premontane rain forest* (P-rf) life zones (Holdridge, 1967), from sea level to 900 m.

Phenology. Dieffenbachia horichii begins to flower in the early rainy season from May to July,

but flowering collections have also been seen in September. Immature inflorescences have been seen from November to May, and mature fruits have been seen from the late rainy season (November) to early rainy season (late June).

Discussion. The species is characterized by its fully sheathed petioles, involute petiolar sheath, and by its thick and more or less elliptic, semiglossy to glossy, mostly unvariegated blades that dry somewhat greenish to yellow-brown.

Dieffenbachia horichii is closely related to two other species with petioles fully sheathed or nearly so. These are *D. panamensis* and *D. standleyi*. In comparison with *D. horichii*, *D. panamensis* has similarly shaped blades and petioles fully sheathed, but that species differs in having the petiole sheath usually flaring and recurled rather than involute as in *D. horichii*. It also has leaf blades with the upper surface matte and subvelvety that dry blackened. Another difference is that *D. panamensis* occurs principally on the Atlantic slope of central Panama, whereas *D. horichii* occurs on the Pacific slope of Costa Rica.

Dieffenbachia horichii is likely to be confused with D. standleyi, another species with fully or mostly winged petioles. That species occurs on the Atlantic slope of Honduras and Nicaragua, and differs by having the petiole sheath erect and recurled outward along the margins and acute at the apex with the sheath margins markedly undulate (vs. the sheath margins involute and smooth). The petioles of D. standleyi are also longer on average, frequently more than 25 cm long, and average 30 cm long (vs. frequently less than 25 cm long, averaging less than 20 cm long for D. horichii). In addition, the upper midrib on the blades of D. standleyi is broadly concave, whereas on D. horichii the midrib is broadly convex with a medial sulcus but with the entire midrib sunken in a valley.

Most of the typical material of D. standleyi has been collected in the Lancetilla Valley and its vicinity in Honduras, and has blades considerably longer on average than those of D. horichii. Some collections in Nicaragua and in western Costa Rica are unusual. Stevens 7457 from Zelaya and Moreno 17142 from Matagalpa dry a darker yellow-brown. The only other species in Central America that has a fully sheathed petiole is D. tonduzii. Dieffenbachia tonduzii is distinguished by having smaller and thinner blades (rarely to 45 cm long and 20 cm wide) that are usually matte to weakly glossy above (vs. usually glossy in D. horichii) with more primary lateral veins (18 to 25 vs. usually fewer than 20 in D. horichii). Grayum 4757, from the Carara Reserve in Puntarenas Province, is perhaps a hybrid

between *D. horichii* (*Grayum* 4756) and *D. oerstedii* (*Grayum* 4765). It differs in having petioles that are narrower and less fully sheathed.

Etymology. The species is named in honor of horticulturist Clarence Horich, who made the first collection of the species.

Paratypes. COSTA RICA. Puntarenas: San José Province, Playa Dominical-San Isidro del General Baru, Tinamastes, Burger et al. 10669 (F, MO), Burger & Baker 10137 (CR, F); along Quebrada Bonita, Carara Res., Gravum et al. 5723 (INB, MO): Finca El Edén, km 183, R. 2, ca. 400 m E of Santa Marta, L. Gómez 22951 (B, CM, CR, MO); Quebrada Bonita, Carara Res., Grayum 4756 (CR, MO), Croat 79073 (EAP, INB, MO, PMA); hills at SW part of Montañas Jamaica, ca. 2.5 km NE of Bijagual de Turrubares, Carara Res., Grayum et al. 5467 (MO). San José: Par. Nac. Braulio Carrillo, Quebrada Sanguijuela, Chavarría & Umaña 157 (CR, MO); Zona Prot. La Cangreja, vic. Quebrada Grande, ca. 2 km NNE of Mastatal de Puriscal, Grayum 8638 (CR, MO); ZP La Cangreja, ca. 1.5 km E of Santa Rosa de Puriscal, Gravum et al. 8336 (CR, MO); San José rd. from Parrita to Santiago de Purriscal, Barringer 1790B (CR); Res. Biol. Carara-Est. Quebrada Bonita, Chacón 1406 (CR); Cordillera Talamanca, Río Hermoso, Finca El Quizarra, L. Williams et al. 28479 (F, NY, US); Acosta, along Río Parritilla, ca. 1 km E of Zoncuano, Grayum et al. 11174 (INB, MO); Pérez Zeledón, Fila Tinamaste, Valverde 741 (CR, MO); Puriscal, Fila Túfares, Salitrales de Puriscal, Gómez-Laurito 7792 (CR); Z.P. La Cangreja, Cerros de Puriscal, San Martín de Puriscal, La Fila Vara Blanca, J. Morales 2035 (CR, INB, MO)

Cultivated specimens. Costa Rica. 800–900 m, cultivated at Munich as 1203/74, *Horich s.n.* (M).

14. Dieffenbachia isthmia Croat, sp. nov. TYPE: Panama: along trail betw. Río Maje & Quebrada Brava, 60 m, 4 May 1976, *T. B. Croat 34656* (holotype, MO-240198!; isotypes, B!, K!, PMA!, US!). Figures 14, 28A.

Planta plerumque ad 1 m; internodia 0.5–3 cm longa, 2–3(4.5) cm diam., atroviridia; petiolus 11–34(40) cm longus, vaginatus 0.4–0.77 longitudinis, vagina 8.5–21 cm longa; lamina oblongo-ovata vel anguste ovata, (12)15–30(39) cm longa, (6)10–26 cm lata, plerumque subcordata, nervis primariis lateralibus 7–12(15) utroque; inflorescentia 3–5 per quoque axillam; pedunculus (2.5)4–12.5 cm longus; spatha 15–17.5(23) cm longa, spadix 10.5–15.8 cm longus; pars feminea 6.5–9.5 cm longa, 1.4 cm diam.; pars masculina 6–7.5 cm longa.

Medium-sized herb, usually to no more than 1 m tall (rarely to 1.5 m tall); sap watery, sometimes white; stem creeping over surface of ground at base, then erect; *internodes* weakly glossy, 0.5–3 cm long, 2–3(4.5) cm diam., dark green, drying dark yellow-brown, olive-brown to blackened. LEAVES scattered along stem, denser near apex; *petioles* 11–34(40) cm long, (averaging 26 cm long), moderately soft, sheathing to midway or slightly above, for 0.4–0.77 their length (averaging 0.55 their length);

sheath 8.5-21 cm long (averaging 14 cm), with margins drying thin, light brown and minutely undulate, the tip inequilaterally acute to emarginate and free-ending; unsheathed portion flattened or rounded and becoming weakly sulcate toward apex in cross section (never sharply sulcate), blunt to moderately acute, rarely broadly and bluntly sulcate; blades oblong-ovate to narrowly ovate, (12)15-30(39) cm long, (6)10-26 cm wide (averaging 26 \times 16 cm), 0.78–1.77 times longer than petiole (averaging 1.1 times longer), inequilateral, one side 0.5-2.6 cm wider than the other side, thinly coriaceous, abruptly to gradually acuminate at apex, acute to cordate at base, the sides often \pm unequal, usually subcordate with at least one side subcordate at base; upper surface matte to weakly glossy, dark green, drying dark gray-green to sometimes blackened; lower surface matte, paler, drying yellowish gray-brown to dark yellow-brown; midrib 5-8 mm diam., flat to broadly and obscurely sunken at base, weakly raised toward apex above, concolorous to slightly paler than surface, frequently much paler than surface or even white toward apex, often with a light green streak distally, drying paler than surface or darker than surface above, convex to bluntly round-raised, drying somewhat flattened with acute ribs below, drying darker than surface below; primary lateral veins 7 to 12(15) per side, departing midrib at a 45°-55° angle (to 30°-50° at apex, 50°-90° at base), arising acutely, then spreading weakly or not at all sunken, often greenish toward apex, sometimes raised near midrib, and diminishing toward margins above; minor veins obscure above, obscurely visible to not visible below. INFLORESCENCES straight to slightly curved, 3 to 5 per axil, bracteoles 9-20 cm long; peduncle (2.5)4-12.5 cm long, 6-10 mm diam., sometimes flattened on one side in cross section, green; spathe 15-17.5(23) cm long, medium green outside, slightly paler green inside throughout, except the apical portion white at anthesis, to 1.7 cm longer than the spadix, elongating somewhat after closing; spathe tube less than 2 cm diam. when furled, spathe blade 2.5-3 cm diam. at anthesis; spadix 10.5-15.8 cm long; free portion 7-13 cm long, 6-8 mm diam.; pistillate portion 6.5-9.5 cm long, to 1.4 cm diam. throughout; fertile staminate portion 6-7.5 cm long, 9-10 mm diam. throughout; sterile intermediate segment 2 cm long, with a few staminodia scattered throughout its length, drying ca. 3 mm wide; pistils 30 to 51, closely spaced except near apex, ovary 3-3.2 mm diam., medium green to dark yellow; stigma 2.4-2.7 mm diam.; staminodia white, 2.5-3.5 mm long, flattened near base, subglobular at apex; synandria 2.6-3.2 mm diam., drying irregu-



Figure 14. Dieffenbachia isthmia (Croat & Zhu 77115). —A. Leaf blade adaxial surface. —B. Close-up of petioles showing inflorescence. —C. Close-up of female portion of spadix showing pistils and staminodes. —D. Infructescences, one cut off to show the fruits.

larly somewhat rounded, margins often irregularly turned upward. INFRUCTESCENCE with spathe to 23.5 cm long, usually orange; spadix, 9–12 cm long, ca. 3 cm wide; *berries* orange to red or orangered, drying pale yellow-brown, ellipsoid, 7–8 mm long, 6 mm diam. (the stigmatic area ca. 2 mm wide); seeds drying dark brown, 6 mm long, 5 mm diam., to 3 mm thick, moderately smooth, caved outward on funicular side.

Distribution and habitat. Dieffenbachia isthmia ranges from Panama to Colombia (Antioquia and Chocó). The species is highly variable ecologically, occurring principally in *Tropical moist forest* (T-mf) and drier parts of *Premontane wet forest* (P-wf) life zones at 50–800(1000) m elevation, but also in *Premontane moist forest* (P-mf), *Premontane wet forest* (P-wf), and *Tropical wet forest* (T-wf) life zones (Holdridge, 1967) in Colombia. In Panama, the species ranges from Veraguas Province to the Azuero Peninsula in the west (700–900 m in Herrera and Los Santos Provinces).

Phenology. Flowering for *D. isthmia* occurs in the early rainy season from May to September (rarely in November), with fruits maturing during the dry season and early rainy season of the following year, mostly in April and May, but with many collections made in fruit from August to October.

Discussion. The species is characterized by its moderately small (usually less than 1 m tall and with stems usually less less than 2.5 cm diam.) habit and frequently subcordate blackish-drying blades which often have a white streak on the distil half of the flattened (not flat-raised) midrib. In Panama, it is probably most easily confused with *D. killipii*, which differs in having proportionately narrower (typically only to 16 cm), usually subcordate greenish-drying blades with the upper midrib weakly flat-raised rather than merely flattened above.

Though its range does not overlap with *D. isthmia*, *D. oerstedii* may be confused with this species. The latter, ranging from Mexico to central Panama, differs in having a usually sharply sulcate petiole and blades that dry greenish to yellowish green rather than blackened as is usually the case in *D. isthmia*.

Etymology. The species epithet "isthmia" refers to its dominance in the area of the Isthmus of Panama.

Paratypes. PANAMA. Canal Area: Barro Colorado Island, Aviles 24 (MO), Shattuck 397 (MO); Lutz Trail, Croat 5378 (F, MO, RSA, SCZ, STRI), Croat 10133 (MO), Croat 5317 (MO), Croat 5896 (MO), Croat 7712 (MO), Croat 11291 (F, NY, SCZ), Croat 5183 (MO), Croat 10982 (MO, SCZ), Croat 5709 (MO), Foster 865 (DUKE), Luteyn

& Croat 906 (DUKE), Croat 15173 (MO), Croat 5819 (MO), Croat 6308 (MO), Croat 6502 (MO, PMA), Croat 4576 (MO), Killip 39979 (US), Kenoyer 188 (US); 12 mi. S of Colón on Río Providencia, Tyson & Blum 3998 (PMA); Frijoles vic., Pittier 3754 (US), Bailey 335 (F); Gatun Lake, Standley 41107 (US), Standley 40960 (US), Maxon et al. 6812 (US), Maxon et al. 6820 (US), Standley 31266 (US); Río Paraiso, above East Paraiso, Standley 29867 (US). Colón: Río Guanche, ca. 5 km upstream from rd. to Portobelo, Hammel & Trainer 14767 (MO). Darién: PN Cerro Pirre, vic. Río Perisenico, Croat & Zhu 77115 (INB, MO); 112 mi. E of Bayano Dam Bridge, vic. Canglón, Antonio 4546 (MO, PMA); trail from Cana to Colombian border along Río Setgandí, Gentry et al. 28574 (COL, MO); El Real-Pinogana, Duke 5014 (MO); 3 mi. N of Santa Fe, Tyson et al. 4631 (SCZ), 4632 (MO, SCZ); 2 mi. E of Santa Fe, Tyson et al. 4834 (STRI); PN del Darién, between Río Topalisa & Río Pucuro, ca. 17 km E of Pucuro, La Laguna area, Hammel et al. 16262 (CAS, COL, MO, PMA); airstrip at Cana gold mine area, Croat 38010 (MO), 38057 (MO); S of El Real, Alturas de Nique, near Cana mine, rd. to Boca de Cupe, McPherson 11591 (MO); Cana region, ca. 1.5 km from Cana trail to Boca de Cupe, McPherson 15037 (MO). Herrera: W of Las Minas, near Chepo, on Montosa de Chepo, McPherson 10958 (MO); Dist. Las Minas, Chepo, loma El Montuoso, Galdames et al. 1626 (MO, PMA, US); Las Minas, base of El Higo, Galdames et al. 2486 (PMA, US). Los Santos: Loma Prieta, Cerro Grande, Lewis et al. 2195 (COL, DUKE, MO, UC). Panamá: Distrito Chepo, Puerto Coquira, Zambrano & Delgado 1336 (PMA); San José Island, I. Johnston 1165 (GH); vic. Bayano Lake dam near Canita, Gentry & Tyson 1653 (MO, PMA); Chimán, Lewis et al. 3251 (MO); 3.8 mi. E of Río Ipetí, lower slopes of Serranía de Majé, Huft & Jacobs 1997 (MO); Río Majo-Quebrada Brava, ca. 2 mi. upstream from waterfalls near edge of Bayano Lake, Croat 34745 (MO); Isla Bayano, Garibaldi 68 (MO); near Chiman, ca. 2 mi. up Río La Maestra, Kennedy 1193 (F). Veraguas: near proposed route of rd. from El Cortezo to Arenas, Hammel 5378 (MO); Azuero Peninsula, trail between Jobero and headwaters of Río Pedregal, Croat 34475 (COL, F, MO, PMA); 18 km W of Las Minas, Cerro Alto Higo, Hammel 4298 (MO); "Los Girasoles," Escuela Agrícola Alto Piedra, ca. 5 km NW of Santa Fé, Dressler 4716 (DUKE, F, MO, PMA); 18 km W of Las Minas, Cerro Alto Higo, Hammel 4298 (MO); Cerro Delgadito just NW of Cerro Tuté, S of Santa Fe, Luteyn 4043 (DUKE); Dist. Montijo, Isla Coiba, Cerro de La Torre, Galdames et al. 2286 (MO); Isla Coiba, Río Escondido vic., Galdames et al. 2252 (MO). COLOMBIA. Antioquia: Mutatá, Bajira-Nuevo Oriente Road, Brand & Ascanio 277 (COL). Chocó: Ríosucio, PN Natural Los Catios, Campamento de Tilupo, Forero et al. 1723 (COL, MO).

 Dieffenbachia killipii Croat, sp. nov. TYPE: Panama. Coclé: vic. of El Valle de Antón, La Mesa, forested flat area near Finca Macarenita, 8°36'N, 80°07'W, 800 m, 6 July 1994, *T. B. Croat & G. Zhu 76666* (holotype, MO-04612287!; isotypes, AAU!, B!, CAS!, COL!, CR!, DUKE!, F!, GH!, HUA!, INB!, K!, M!, MEXU!, NY!, PMA!, SCZ!, US!, VEN!, WU!). Figure 15, 28B.

Planta terrestris, 40-100 cm.; internodia 1.5-5.5 cm



Figure 15. Dieffenbachia killipii. —A. Habit showing plant with quilted primary lateral veins (Croat 56902). —B. Leaf blade adaxial surface (Croat 78247). —C. Close-up of adaxial surface of blade (Croat 74759). —D. Habit of flowering plant (Croat 76666). E, G. (Croat 75154). —E. Close-up of stems. —F. Habit of flowering plant (Croat 76666). —G. Close-up of two inflorescences, one at anthesis. —H. Close-up of pistillate and sterile staminate portions of spadix (Croat 76259).

longa, (0.8)1.5–3(4) cm diam; petiolus (4)6–20(24.5) cm longus, vaginatus 2/5 longitudinis vel fere omnino; lamina oblongo-elliptica vel oblongo-ovato, (13)19–30(33.5) cm longa, (4.5)7–16(21.3) cm lata, nervis primariis lateralibus 8–12 utroque; inflorescentia 1–4 in quoque axilla; pedunculus 4.5–9 cm longus; spatha 12–19 cm longa; spadix 12–15 cm longus; pistilla 20–37.

Medium-sized herb, 40-100 cm tall, stem creeping over surface of ground at base, then erect; sap milky, unscented; internodes initially weakly glossy, often faintly dark green and medium yellowish green-marbled at lower nodes, becoming glossier in age, 1.5-5.5 cm long, (0.8)1.5-3(4) cm diam., medium to dark green or olive-green or black-green, drying dark yellow-brown to orange-brown, rarely dark brown, epidermis sometimes fissured in a cracked network so as to appear corky in some areas. LEAVES scattered along stem, denser near apex; petioles (4)6-20(24.5) cm long (averaging 12.2 cm long), firm to spongy, slightly paler or darker than stem, medium green to dark green, matte to weakly glossy, faintly striate toward the base, drying greenish to grayish yellow to brown, sheathing for $\frac{2}{5}$ to fully throughout (0.4–1 the petiole length and averaging 0.69); sheath 3-18 cm long, (averaging 8 cm), with the sheath margins not drying markedly different than the remainder of sheath; sheath apex with the tip free-ending and inequilaterally acute to emarginate, sometimes drying acute: unsheathed portion C-shaped and sharply sulcate to narrowly and sharply sulcate to subterete and weakly sulcate or obtusely and narrowly sulcate in cross section; blades oblong-elliptic to oblong-ovate, rarely narrowly ovate, (13)19- $30(33.5) \times (4.5)7 - 16(21.3)$ cm (averaging 25×11 cm), 1.5-4.2 times longer than wide, as long as or up to 4.8 times longer than petiole (averaging 2.3 times longer than petiole), inequilateral, one side 0.5-1.5 cm wider than the other side, sometimes falcate, subcoriaceous to weakly coriaceous, moderately bicolorous, acuminate to gradually acuminate at apex inequilateral, sometimes inequilaterally rounded to subcordate, rarely acute at base; margins moderately straight on one side, frequently markedly undulate on other side: upper surface semiglossy, dark green, frequently white, pale green or yellowish green-spotted or white-streaked, drying dark brown to olive-brown or gray-green; lower surface paler, matte to weakly glossy, drying yellowbrown; sinus less than 1 cm deep, rarely to 2.5 cm deep; midrib flat-raised, 3-5 mm wide, sometimes sulcate toward base, usually in moderately deep valleys, usually concolorous, sometimes paler than surface above, sometimes weakly 3- to 4-grooved on upper surface, drying flat-raised to broadly con-

vex, slightly paler to concolorous above, thicker than broad and narrowly rounded to almost roundraised, matte, paler than surface to almost concolorous below, drying brown with ridges, darker than surface below; primary lateral veins 8 to 12 per side, arising at an acute angle, then spreading at mostly (40°)45°-70° angle (rarely to 30°, sometimes to 80° toward base, rarely to 110° at base), frequently forming collective veins that merge with the margin higher up on the blade, narrowly sunken to weakly guilted-sunken above, thicker than broad to convex and weakly pleated-raised, darker than surface to almost concolorous below, usually drying darker than surface; minor veins few, obscure above, obscurely visible and darker than surface to moderately distinct below. INFLORESCENCES 1 to 4 per axil; bracts 9-20 cm long; peduncle 4.5-9 cm long, 6-7 mm diam., medium green, white at base; spathe 12-19 cm long at anthesis, 1-2 cm longer than the spadix, medium green throughout, sometimes faintly dark green-lineate on faded areas outside, slightly paler and glossy inside; spathe tube 2-3 cm diam. when closed, 5.5-7.5 cm wide when flattened, 1.5-2 cm diam. at constriction (flattening 3.5-4 cm wide); spathe blade 2.5-3 cm diam.; spadix bluntly pointed, weakly protruding forward at anthesis, 12-15 cm long; free portion 5.5-6 cm long (sometimes with a few pistillate flowers in the basal portion); pistillate portion 5-8.5 cm long, 10 mm diam. throughout; fertile staminate portion 4.5-6.8 cm long, 7-8 mm diam. midway, sometimes bluntly pointed (frequently with the withered portion weakly protruding out of the front of the spathe after anthesis); sterile intermediate segment to ca. 5 mm diam., but usually absent with the pistillate and staminate portions almost contiguous; pistils 20 to 37, well-spaced, sometimes aggregated into weak rows, frequently irregularly gapped, 2 or 3(6) dispersed across spadix width, widely spaced at base and at apex, pale yellowgreen, 2.4 mm diam., 1.4 mm high; stigma 1.8-2.2 mm diam.; staminodia very thickened and mostly joined at base, tapered gradually toward apex and not markedly thickened, sometimes broadened laterally and apparently consisting of a union of 2 staminodia, sometimes with 2 pistils contiguous and apparently sharing staminodia; synandria 1.2-1.4 mm diam., ca. 4 per spiral, irregularly rounded to 4- to 6-sided, drying widely spaced, the margins of apex markedly turned upward. INFRUCTES-CENCE to 23 cm long; spathe orange outside; spadix 9-10.5 cm long, 2.5 cm wide; berries red to reddish orange or orange-red, drying pale orangebrown, ellipsoid, 2- to 3-lobed, 7-8 mm long, 6-10 mm diam.; seeds 1 to 2 per berry, drying dark brown, flattened on funicular side, to 4.9 mm long, 4.4 mm diam., drying smooth, 3 mm thick.

Distribution and habitat. Dieffenbachia killipii ranges from southwestern Costa Rica (Puntarenas) to Panama and the western slopes of the Andes in Colombia (Antioquia, Chocó, Tolima, and Valle) and Ecuador (Esmeraldas, Guayas, El Oro, Pichincha, Los Ríos, and Manabí on the Pacific slope and in Napo on the Atlantic slope) at 0 to 900 m elevation. In Panama it occurs in *Tropical wet forest* (T-wf) and *Premontane wet forest* (P-wf) life zones (Holdridge, 1967) and ranges from Coclé Province to Darién Province in the east. In Colombia it is known from *Tropical wet forest* (T-wf) and *Tropical rain forest* transition to *Premontane wet forest* (T-rf/ P-wf) life zones.

Phenology. Flowering occurs in *D. killipii* throughout the year, with most flowering specimens having been made in the late rainy season from September to November. Fruiting collections were made mostly during the late dry season and early rainy season of the following year from May to July. Few fruiting collections were seen between August and May.

Discussion. The species is characterized by its medium stature (to 1 m), slender sulcate petioles with the sheath inequilaterally auriculate at apex (and usually ending well below the base of the blade), and especially by the frequently subcordate blades (which dry yellowish green) with a flat-raised midrib. Also unusual for the species is the near absence of a sterile portion between the pistillate and staminate spadices.

Dieffenbachia killipii is similar to D. leopoldii, which was described from a cultivated plant of unknown specific origin, believed to have been obtained in Colombia. Engler saw living material of this species and illustrated it in his 1915 revision. While it has very similar leaves, D. leopoldii differs from D. killipii in having the pistillate and staminate portion of the spadix separated by a sparsely flowered, almost sterile section. In addition, while the upper surface of D. killipii is semiglossy, D. leopoldii is described as having a blade "velvety green" on the upper surface in the notes of N. E. Brown (on specimen of Lehmann 1052), at least suggesting that the upper surface was matte. Finally, the midrib of D. leopoldii is described as white, whereas this is not the case with D. killipii.

Collections from the eastern slopes of the Andes in Napo Province, Ecuador, appear also to be this species but more studies are needed to confirm this, as they would be the only collections of *D. killipii* in the Amazon basin. The collections include *Croat* 50480 and Plowman & Davis 4094, both collected along the Baeza to Tena Road, at 1410 and ca. 1743 m, respectively, and *Croat* 72573 south of Coca at 300 m. An unvouchered collection made by Tan, Halton, and Besse at the Auca Oil Field at 240 m is also the same species. It has been vouchered from the Marie Selby Botanical Gardens' living collection (SEL 79-0090) by *Plowman* 14121 and *Ingram* 1124.

Gentry et al. 65306, from Quindío Department, Colombia, at 1400 m, may also be this species, but it is from higher elevation than other Colombian collections. A collection made in Venezuela at Maiquetía at 30 m near the Caribbean (André 457A) appears to also be D. killipii. However, this may be questioned because Andre 457 was labeled as having been collected in Colombia at Angostura de Honda (Tolima). Both collections were dated December 1875.

In South America the species may be confused with D. enderi, described from the valley of the Río Cauca in Colombia. That species is similar in having the petiole sheath auriculate and free-ending at the apex, and in having the staminate and pistillate spadices contiguous. It differs in having a thicker stem (to 8-9 cm diam.), longer blades (to 50 cm long) with acute bases and more numerous primary lateral veins (ca. 24 per side, spaced 1.5-2 cm apart). In contrast, D. killipii has blades that are rounded or subcordate at the base, and fewer than 15 primary lateral veins. It is also similar to D. daguensis from the valley of the Río Dagua in Valle Department, which similarly has staminate and pistillate zones contiguous on the spadix. That species differs in having larger blades (to 40 cm long) with many close primary lateral veins (up to 25), and a petiole only 5 cm long.

Dieffenbachia killipii is probably most easily confused in Central America with D. isthmia, which differs in having stems that dry usually blackened; somewhat more ovate, blackened blades; and a spadix with a more or less sterile portion between the staminate and pistillate portions. The species may also be confused with D. oerstedii from Costa Rica and western Panama. That species shares leaves of similar shape and size, but it has blades that are matte, rather than semiglossy, on the upper surface and dry greenish or yellowish green. In addition, D. oerstedii has petioles that are typically more sharply sulcate than those of D. killipii. The petiole base is green in D. killipii and whitish in D. oerstedii. Furthermore, the spadix has staminate and pistillate portions nearly contiguous in D. killipii, but separated by a distinct sterile portion in D. oerstedii.

In Panama the ranges of *D. oerstedii* and *D. killipii* do not actually overlap, but come close in Chiriquí on the western slopes of the country. All known collections there occur in the mountains at 900 to 1300 m. *Dieffenbachia oerstedii* occurs in Panama in western Chiriquí Province at highland sites and with an outlying population at El Copé in Coclé Province, while *D. killipii* ranges in general no further west than the Azuero Peninsula and Veraguas Province in Panama. There is an unusual outlying population of *D. killipii* in the area of the Osa Peninsula in Costa Rica (*Kennedy 1594*). A collection from Cerro Colorado (*Croat 48437*) in Chiriquí Province has blades slightly larger than most specimens of the species.

Croat 74789 from La Mesa in Coclé Province, Panama, is unusual in having a series of rather prominent collective veins and in having the minor veins distinct when fresh (typically they are rather obscure). It was, in fact, so unusual that it was initially mistaken for a *Xanthosoma*. It is, however, within the degree of variation for *D. killipii*.

Kress 77-830 and 77-831 from the vicinity of Santa Fe in Veraguas, Panama, are unusual collections in having the staminate and pistillate portions of the spadix separated by as much as 1 cm. In this regard they are similar to *D. lutheri*, but differ from that species in lacking the granular puberulent major veins on the lower blade surface.

Some collections of the species from Darién Province, Panama (e.g., Antonio & Hahn 4405, Duke 15591, Polanco 1485, and Schmalzel 1212), are unusual in having petioles more fully sheathed, sometimes to less than 1 cm from the base of the blade or even with the petiole sheathed throughout.

The Costa Rican population of *D. killipii* is noteworthy in that the single collection made there in the Osa Peninsula is quite disjunct from the nearest population in Panama, where the species has not been collected west of Coclé Province. The species is to be expected at other sites in Veraguas and in Chiriquí Province, Panama.

Etymology. The species is named in honor of the late E. P. Killip, botanist at the U.S. National Herbarium and one of the more prodigious plant collectors in the Neotropics, who was one of the earliest collectors of this new species.

Paratypes. COSTA RICA. Puntarenas: Osa Peninsula, 2.5 mi. SW of Rincón, Kennedy 1594 (MO). PAN-AMA. Bocas del Toro: Cerro de Bocatorito, Peterson & Annable 6768 (MO). Canal Area: 12 mi. S of Colón, Tyson et al. 4486 (SCZ); 12 mi. S of Colón, near Río Providencia, Tyson & Blum 3997 (MO, SCZ); Pipeline Rd. 10 mi. from Gamboa gate, Croat 15082 (DUKE, MO); ca. 7– 8 km N of Gamboa, Knapp 2275 (MO); Pipeline Rd. near Gamboa, Clewell & Tyson 3306 (MO, SCZ); Pipeline Rd.

at Río Agua Salud, Croat 12353 (MO); Río Frijol on Pipeline Rd., 6 m N of Gamboa, Tyson 1443 (FSU, MO, SCZ); Frijoles-Monte Lirio, Killip 12154 (US); N of Frijoles, Standley 27413 (US); W of the Canal, near Gatún, Standley 27224 US); rd. S-10 N of Escobal near junction with Rd. S-1, Croat 12489 (MO); 1.5 mi. N of Escobal, Croat 12491 (MO, SCZ); near Limbo Gun Club camp, 10 mi. W of Gamboa on Pipeline Rd., Lazor & Tyson 3492 (FSU); lake shore along Gatun River valley, Pittier 6845 (US); vic. Gamboa, Pittier 2600 (US); Pipeline Rd. N of Gamboa, Kennedy 455 (F). Chiriquí: 8.8 km past Gualaca on rd. to Chiriquí Grande, Hoover 1324 (MO); Gualaca-Fortuna Dam site, 2.8 mi. beyond Los Planes, Croat 48816 (MO); Cerro Colorado, 15.6 mi. above Río San Felix, Croat 48437 (MO). Coclé: El Limón, Mendieta 1-10 (PMA), Mendieta 1-101 (PMA), Mendieta 1-121 (PMA); vic. of El Copé, PN El Copé, 5-6 mi. N of El Copé, below Old Rivera saw works area, Croat & Zhu 76746 (CAS, DUKE, MO); 5 hours' walk N from Alto Calvario to Río Blanco, Sytsma et al. 2414 (MO); La Mesa, above El Valle de Antón, Croat 14388 (MO), Croat 14309 (MO); trail beyond La Mesa towards Los Llanos and the border between Coclé and Panamá Provinces, N of El Valle de Antón, Luteyn 3175 (DUKE), Croat 37383 (MO); La Mesa above El Valle, Gentry 7423 (MO, NY); 5 mi. N of El Valle de Antón, Luteyn 1203 (DUKE); La Mesa trail towards Cerro Caracoral, NE of El Valle de Antón, Lutevn 3180 (DUKE); vic. El Valle, Bartlett & Lasser 16678 (MEXU, MO); Penonomé-Coclecito, 5.6 mi. N of Llano Grande, along Río Cascajál 5.6 mi. N of Llano Grande, 1.4 mi. N of Cont. Divide, Croat 67480 (MO, SCZ); at La Mesa, 3.2 mi. above El Valle, 0.1 km E of Finca Macarenita, Croat 74789 (MO), Croat 74792 (INB, MO, PMA); ca. 1 km W of rd. betw. Finca Mandarinas and Finca Furlong, Croat 67197 (MO); area between Caño Blanco del Norte, Caño Sucio and Chorro del Río Tife, Davidse & Hamilton 23599 (MO); rd. to Coclesito, logging camp 12 mi. from Llano Grande, Churchill et al. 4032 (MO), Churchill et al. 4125 (MO); 7 km N of El Copé, near Rivera Sawmill, Folsom & Collins 6436 (MO); La Mesa, above El Valle de Antón, ca. 2 km W of Cerro Pilón, Croat 37479 (MO, PMA, WU); base of Cerro Pilón above El Valle, Gentry & Dwyer 3643 (DUKE, F, MO). Colón: PN Chagres, Sección Boquerón, Río San Juan de Pequení, Espinosa et al. 3611 (PMA), Espinosa & Guerra 3762 (PMA), Espinosa et al. 4478 (PMA); Dist. Donoso, Campamento Botija, J. Polanco et al. 1905 (PMA); Río Providencia, 12 mi. S of Colón, Tyson & Blum 3954 (FSU, SCZ); Río Guanche, between Puerto Pilón and Portobelo, ca. 1.5 mi. S of rd., Croat & Zhu 76253 (MO. PMA), Croat & Zhu 76259 (MO, SEL, SCZ); lower Río Guanche, Dressler 4688 (PMA); N of Río Guanche, Davidse & D'Arcy 10098 (MO); Río Guanche, 3-5 km above bridge on Colón-Portobelo Rd., Croat 79329 (MO), Croat 79359 (MO), Sytsma 1658 (MO); near Peluca, km 25.6 from Transisthmian Hwy. on rd. to Nombre de Dios, Kennedy 2661 (MO); ca. 8 km E of Piña, Thompson 4816 (CM, MO); Portobelo-Nombre de Dios, 1.2 mi. beyond the jct. of rd. to Isla Grande, Croat 49805 (INB, MO); Nuevo Tonosi-Río Indio, Portobelo-Nombre de Dios, Croat 33551 (AAU, MO, QCNE); Achiote, McPherson 9176 (MO); Santa Rita ridge rd., ca. 22 km from transisthmian hwy., Hammel et al. 14472 (MO). Darién: Quebrada Biboto (Peccary) off Río Areti, Duke 13601 (MO); 1-3 mi. N of Paya, Duke & Kirkbride 14019 (MO); Río Cocalito, Whitefoord & Eddy 136 (BM, MEXU, MO); PN Cerro Pirre, vic. headquarters on Río Perisenico, Croat & Zhu 77102 (COL, HUA, INB, L, MO, NY, QCA, SCZ, TEFH, US, VEN); Paya-Pucro, Stern et al. 433 (GH, MO, US); Punta Guayabo Grando to Río Jagué, Antonio & Hahn 4405 (MO); 5 mi. W of Yaviza, Schmalzel 1212 (MO), Schmalzel & Alverson 1199 (MO, PMA); vic. of gold mine at Cana, Croat 37605 (HUA, INB, K, MO); S of El Real, headwaters of Río Pirre at fork known as Dos Bocas, Kennedy & Foster 395 (DUKE); Pinogana-Yaviza, Duke 5169 (MO); 10 mi. S of El Real on Río Pirre, Duke 5437 (MO); trail from Río Pucro to Quebrada Maskia, Duke 13082 (MO); Río Tucutí upstream ca. 2 hrs. (piragua) vic. Tucutí, Duke 5260 (MO); Punta Guayabo Grando-Río Jaqué, Antonio & Hahn 4406 (MO); Cerro Campamento, S of Cerro Pirre, Duke 15591 (US); Rancho Frio, halfway up slope of Cerro Pirre from Piji Vasal, Folsom 6247 (MO); gold mine at Cana, Sullivan 745 (MO); Bajo Lepe, 7 km al SE of Boca de Cupe, Polanco 1485 (PMA); base camp Cerro Pirre NP, Croat 68961 (COL, MO, PMA); PN del Darién, RENARE station, McDonagh et al. 433 (BM), 439 (BM, MO); Est. Biol. Rancho Frío at N base of Cerro Pirre, ca. 9 km S of El Real, Quebrada Perisenico, de Nevers et al. 8267 (CAS, MO); Río Coasi, Cana-Coasi trail, R. Hartman 12488 (K, MO, PMA); Río Pavarando, 10 km NE of Jaqué, D'Arcy & Sytsma 14498 (MO); Río Pirre, 2.5 mi. above El Real, Duke 5099 (MO); Río Torti, 38.6 mi. E of Bayano Dam Bridge, near Torti, Antonio 4638 (MO); Río Tuquesa, Clezio 221 (MO), 226 (MO); Río Chico, from Yaviza at junction with Río Chucunaque to ca. 1 hr. by outboard from jct., Burch et al. 1123 (DAV, MO, NY); ca. 10 km upstream from Nazareth, Hahn 142 (F, MO); Río Jaqué Valley, Knapp & Mallet 3089 (MO); Río Balsas, Kursar & Coley 4 (SCZ), 15 (SCZ). Panamá: Piria-Cañasas trail near Piria, Duke 14346 (MO); El Valle de Madroño-La Saena, 2.5 mi. N of El Valle de Madroño, 3.5 mi. N of turnoff to San José, 11.6 mi. N of Las Margaritas, vic. Chepo, valley of Río Mamoní, Croat & Zhu 77048 (CAS, LPB, MEXU, MO, PMA, NY, SEL, TEX, US); N of Canita, Croat 14504 (MO); Cerro Campana, 45 km SW of Panama City on Inter-am. Hwy., Mori & Bolten 7698 (MO); ca. 10 km SW of Capira, Mori & Kallunki 3591 (MO), Croat 14706 (MO); above Su Lin Motel, Porter et al. 4282 (MO); 6.1 mi. above Pan-Am. Hwy., 3.2 mi. beyond park entrance & Guarda Bosque Station, Croat 74759 (MEXU, MO, PMA, SCZ), Witherspoon & Witherspoon 8401 (MO), Carrasquilla & Rincón 304 (MO), Miller et al. 753 (B, MO, PMA); PN Altos de Campana, Buena Vista, Bejuco, Chame, Espinosa et al. 3138 (PMA); natural bridge along Madden Lake, Croat 12401 (DUKE, MO), Thompson 4593 (CM); Cerro Azul, Dwyer 2077 (MO), Croat 17311 (MO); 1 mi. N of Cerro Azul, Tyson & Blum 4099 (SCZ); 1-2 mi. beyond Goofy Lake, Gentry et al. 3406 (NY), Dwyer 4565 (MO), Sullivan 59 (MO, PMA); rd. past Altos de Pacora, 3-3.5 mi. NE of Altos de Pacora, 7.8-8.2 mi. above Pan Am. Hwy., Croat 68679 (MO); El Llano-Cartí rd, 6.9 km N of Pan-am. Hwy., Folsom 1444 (MO); 4-5 hrs. walk upriver from Torti Arriba, Folsom et al. 6852 (MO), Folsom et al. 6848 (MO); near Bayano Dam, D'Arcy 9420 (MO); Serranía de Majé Trail, Charco Rico-headwater of the Río Ipetí Grande, Churchill & de Nevers 4333 (MO); Piria-Canasas trail near Piria, Duke 14346 (US); Cerro Jefe Region, vic. Finca Vega, 2.3 mi. above Lago Cerro Azul, 4.1 mi. above old Pan-Am. Hwy., Croat 75154 (MO), Croat 11570 (F, MO, SCZ); Río Maje, above first waterfall, Croat 34442 (F, MO, PMA); Río Torti, S of Panam. Hwy. near village of Upper Torti, Folsom & Mauseth 7844 (MO). San Blas: SW of Puerto Obaldía, Croat 16803 (MO); Ailigandí, Hammel & D'Arcy 5018 (MO), A. Jones & Tejada 275 (PMA); Kuna Yala Nusigandí FS, NW

of El Llano-Cartí Rd., Schatz 1079 (B, K, MO, US). Veraguas: rd. beyond Escuela Agrícola Alto Piedra, NW of Santa Fé, Pac. slope, 0.6 mi. beyond fork in rd., Croat 49056 (MO); Escuela Agricultura above Santa Fe, Kress 77-830 (DUKE), 77-831 (DUKE). COLOMBIA. Antioquia: Río Anorí valley, Quebrada La Tirana-Providencia, 28 km SW of Zaragoza, Alverson et al. 376 (WIS). Chocó: Quibdó-Istmina, 6.6 km S of Quibdó, Croat & Cogollo 52174 (COL, MO); ca. 10-15 km S of Quibdó, and 8-10 km E, Grayum et al. 7657 (MO); Sautatá, PN de Los Katios, Rentería 10680 (HUA); Río Atrato, Tagachi, Forero et al. 9007 (COL); Bahía Solano, Corr. El Valle, Quebrada Tundó, tributary of Río Valle, Espina et al. 2902 (MO); San José del Palmar, Río Torito, Finca "Los Guaduales," Forero et al. 6272 (COL), 6489 (COL). Tolima: Angostura de Hondo (Magdalena), Lehmann s.n. (K). Valle: Bajo Calima Region, Buenaventura-Málaga, km 11, Croat 69343 (CUVC, MO); Pulpapel Headquarters, Bay 278 (MO); 5 km N of main Cali-Buenaventura Hwy., Croat & Bay 75707 (MO); Cali, Vereda Pico de Aguila, Gamboa et al. 71 (MO); Río Dagua, Buenaventura, Lehmann 5311 (K). ECUADOR. Cotopaxi: Guayacan-Montenegro, N of Pucayacu, Croat 73792 (QCNE). Guayas: Cordillera Chongón-Colonche, Cerro La Torre, Cornejo & Bonifaz 3107 (GUAY). El Oro: ca. 11 km W of Piñas on rd. to Arenillas, Thompson 160 (MO); 7.6 km from Tahuin on rd. to Piedras, Thompson 128 (MO); Machala-Loja, 25 km SE of junction in rd. to Piñas, Croat 50725 (MO, QCNE). Esmeraldas: Cerro Mutiles, Cornejo & Bonifaz 5191 (GUAY); Santo Domingo de los Colorados-Esmeraldas, 90 km NW of Santo Domingo, 8.8 km NW of Quininde, Croat 55549 (MO); 6 km beyond bridge over Río Esmeraldas (near San Mateo, rd. to Esmeraldas airport), ca. 6.6 km beyond Univ. Techn. Luis Vargas Torres-Est. Exp. Mutile, Río Mutile, Croat 55629 (HUA, MO, QCA, US); Ibarra-San Lorenzo rd., Madison et al. 5008 (F, SEL); Hacienda Guavas, ca. 20 km S of Esmeraldas, Sparre 15499 (S); Río Verde, Businga, Juncosa 797 (MO, QCA); Res. Forestal de Jardin Tropical, Univ. Tecnica Luis Vargas Torres, Gentry & Lajones 73108 (GUAY, MO); Bilsa, Quinindé-Bilsa, 6.4 km W of Sto. Domingo-Esmeraldas Hwy., departing ca. 15 km N of Quinindé, Croat et al. 83804 (DUKE, F, MO); Río Lita, Lita, Croat 38947 (F, MO, QCA); Eloy Alfaro, Res. Ecol. Cotacachi-Cayapas, Río Bravo Grande, ¹/₂ km from Centro Chachi de Corriente Grande, A. Alvarez & P. Herrera 699 (MO, QCNE); Charco Vicente, Río San Miguel, tributary of Río Cayapas, Palacios & Tirado 11327 (MO, QCNE); Esmeraldas-Quininde rd., 40-50 km SE of Esmeraldas, Harling & Andersson 16727 (GB); Esmeraldas-Borbón, 2.5 km W of Borbón, Croat 71119 (QCNE). Guayas: Naranjal-Machala, 13 km S of Naranjal, Harling & Andersson 19371 (GB); Cañar-Chimborazo, vic. Bucay, Camp E-3653 (MO, NY, SEL); Cord. Chongón-Colonche, Bosque Protector Loma Alta, Cornejo & Bonifaz 4195 (GUAY, MO); Loma Alta, Cornejo & Bonifaz 5210 (GUAY, MO); Capeira, km 12 Guayaquil to Daule, Dodson & Dodson 11130 (MO, SEL); La Libertad, Camp E-3599 (MO, NY). Los Ríos: El Centinela, Montañas de Ila, Patricia Pilar-24 de Mayo, Dodson et al. 8415 (MO); Río Blanco, Santo Domingo-Esmeraldas hwy., 3 km S of km 24, Croat 50684 (MO); Santo Domingo de Los Colorados, Rancho Brahman, ca. 10 km NW of Santo Domingo, Sparre 14122 (S); Hacienda Zaracay, Sparre 15182 (S), Acosta Solís 10896 (F, S); Tsachila Chiguilpe, Cerón et al. 29159 (QAP); Santo Domingo-Quevedo, km 11.5, Est. Gustavo Orcés, Quishpe & Dávila 82 (QAP, QCNE); km 41, Zak et al. 5726 (QCA); vic. of Montalvo, 40 km E of Babahoyo, Holm-Nielsen et al. 2769 (AAU, NY, QCNE, S); Hacienda Monica, 12 km E of San Carlos, Sparre 19397 (S); Hacienda Clementina, Harling 313 (S); Babahoyo-Montalve, Sparre 14556 (S), Cornejo & Bonifaz 4828 (GUAY, MO); Centro Cientifico Río Palenque, Croat 38669 (MO, QCNE), Dodson & Tan 5338 (SEL), Croat 73826 (MO, QCNE), Croat 50655 (MO), Fallen & Ray 860 (SEL); Quevedo, Asplund 15574 (S), Dodson 6188 (RPSC, SEL); Vinces, Mocachi-Palenque, Jauneche forest, km 70 Quevedo-Palenque, via Mocachi, Dodson et al. 10594 (GUAY, MO, SEL). Manabí: Portoviejo-Pichincha rd., ca. 20 km E of San Plácido, Harling & Andersson 24778 (GB, MO); Cerro Montecristo, S of Manta, Sparre 19488 (S); Machalilla NP, zona de San Sebastian, Gentry et al. 72496 (MO, OCNE); Chone-Santo Domingo Rd., ca. 20 km NNE of Flavio Alfaro, Montañas de Convento, Harling & Andersson 18898 (GB); Hacienda Don Juan, 10 km NE of Jama, N of Río Don Juan, Neill et al. 11683 (QCNE); 28 km S of Pedernales, 3.5 km SW of Camarones, Delinks 452 (AAU, NY, MO). Napo: Auca, Plowman 14121 (F). Pastaza: Coca-Río Tiguino, 85.8 km S of Coca, Croat 72573 (MO). Pichincha: vic. Hotel Tinalandia, 9.6 km E of Santo Domingo de los Colorados, Croat 55666 (GUAY, MO, QCA); Machachi-Santo Domingo, 19.3 km E of Alluriquín, Thompson & Rawlins 1104 (MO); Centinela, Montañas de Ila, 12 km E of Patricia Pilar, Løjtnant & Molau 15839 (AAU): Santo Domingo-Ouevedo, Patricia Pilar. Dodson et al. 14638 (MO, QCNE), Gentry et al. 26709 (MO); vic. of Santo Domingo de Los Colorados, Peripa, SW of Santo Domingo, Croat & Nuñez 82064 (MO, QCNE); Nanegalito-Pto. Quito Rd., km 113, ENDESA, 5 km W of San Vincente Andoas, Croat 82829 (MO), Croat et al. 83795 (MO); Río Silanche, Quito-Pto. Quito, km 113, Rodríguez 262 (NY, OCA); Santo Domingo-Quininde rd., km 41, Zak et al. 5414 (QCA); vic. Maquipuquna Res., rd. to Maquipucuna Lodge, Leimbeck R. 306 (AAU). Sucumbios: Lago Agrio-Baeza, ca. km 107, Croat 50480 (MO). VENEZUELA. Maiquetia, Andre 457 (K).

Cultivated specimens. Ecuador. Napo: Auca Oil Field, 23 Sep. 1991, Ingram 1124 (MO).

 Dieffenbachia longispatha Engl. & K. Krause, Pflanzenr. IV, 23 Dc(Heft 64): 44. 1915. TYPE: Panama. Colón: Fato (Nombre de Dios), July 1911, *H. F. Pittier 3838* (holotype, US!; isotypes, B!, F!, MO!). Figures 16, 29B.

Terrestrial, (1)1.5-3.5 m tall; sap very foul and pungent; stem prostrate at base, then erect; internodes 4-12 cm diam., with leaf scars prominent, dark green, semiglossy, drying dark brown to orange-brown; petioles thick and succulent, semiglossy, usually solid dark green, rarely streaked with pale green, 23-55 cm long (averaging 36 cm long), sheathed to about middle (0.58-0.85 their length, averaging 0.72); sheath 25-41 cm long (averaging 25 cm long), inequilaterally rounded at apex, sometimes weakly free-ending; unsheathed portion 4.0-30.5 cm long (averaging about 11 cm), C-shaped and obtusely sulcate or \pm terete with a faint flat rib adaxially; *blades* oblong-elliptic, $41-72 \times 17-$ 38 cm (averaging 53 \times 24 cm), 1.7–2.9 times longer than wide (averaging 2.3 times longer than

wide), 1-2 times longer than petioles, coriaceous to subcoriaceous, semiglossy, bicolorous, weakly inequilateral, one side 0.6-3.5 cm wider than the other, usually short-acuminate at apex, sometimes acute to rounded with a short acumen, acute to rounded at base, with the edges turned up near the base; upper surface dark green, drying gray-green to dark olive-green, rarely yellowish brown; lower surface slightly paler, drying yellowish green, rarely vellowish brown; midrib flat, 1-2 cm wide at base, concolorous or slightly paler than surface above, drying slightly paler than surface and weakly raised above, concave to prominently raised on lower surface, drying brownish; primary lateral veins 15 to 26 pairs, sunken above, convex below, arising at an acute angle to the midrib then spreading at an angle of $45^{\circ}-60^{\circ}(70^{\circ})$, sometimes to 90° near the base of the blade, sometimes drying moderately wrinkled; interprimary veins lacking or 1 between each pair of primary lateral veins, sometimes almost as prominent as the primary lateral veins; minor veins indistinct. Juvenile blades with acute base and solid green midrib. INFLORESCENCES 1 to 3 per axil; peduncles (5.5)7–25 \times 1.5–2 cm; spathe medium to dark green, broadly curved, long-acuminate, 27-48 cm long, 2.5-8.2 times longer than peduncle, to 4 cm wide at anthesis, tube flattening 5-12.5 cm wide, constricted area 2.5-3 cm diam., flattening 3.2-5 cm wide, spathe blade 3-6 cm wide at anthesis, flattening to 6-12 cm wide midway, the distal inner surface sometimes white when open; spadix (21)35-38 cm long; free portion 12-19 cm long; pistillate portion of spadix (except sometimes the uppermost part) fused to spathe, 13-15 cm long; fertile staminate portion (8)11-14 cm \times (9)12–14 mm (drying 6–9 mm diam.); mostly sterile intermediate portion (2)3-4.3 cm long with a few scattered staminodia in the upper half (sometimes to throughout its length); pistillate flowers 10 to 26, round or barely bilobed, widely spaced, 5-10(20) mm apart, forming in a single irregular row or scattered but usually no more than 2 flowers across the width of the spadix (rarely 3); ovaries pale green, 4-7 mm diam.; stigmas 4-6 mm diam., vellow to orange, somewhat broadly bowl-shaped, 5-7 mm thick on the edge, medially with 1 to 2 somewhat elongate lobes, the lobes 1-1.5 mm diam., somewhat longer than broad; staminodia 5 to 6 per pistil, white, irregular, $2-6 \times 2-3$ mm, much flattened at base, less so toward the apex, often somewhat puckered at the apex; synandria in spirals of 4 to 7 each, 3-4 mm wide, subrounded, drying light yellow-brown and concave at apex. IN-FRUCTESCENCES 17-24 cm long; berries 1.5-2 cm diam., often deeply emarginate at both ends and



Figure 16. *Dieffenbachia longispatha*. —A. Habit with open inflorescence. —B. Plant habit with cluster of inflorescences. —C. Crown of plant with close-up of leaf base with open inflorescence. —D. Inflorescence at anthesis with staminate spadix exposed. A, C. (*Croat & Zhu 76257*); B, D. (*Croat & Zhu 76203*).

appearing to be a double fruit, bright yellow to orange; mesocarp ca. 2 mm thick, soft, sweet and tasty at maturity; seeds oblong, 7–8 mm diam., brown to black, smooth.

Distribution and habitat. Dieffenbachia longispatha ranges from central Panama to northern Colombia, mostly from sea level to 180 m, but perhaps to 250 m (owing to a collection at Río Tuquesa with no elevation reported), occurring in *Tropical moist* (T-mf), *Premontane wet* (P-wf), and *Tropical wet forest* (T-wf) life zones (Holdridge, 1967). In Panama it occurs on both coasts, but it is relatively rare on the Pacific slope.

Phenology. While collections of *D. longispatha* have been made in both flower and fruit year-round, flowering occurs principally during the first half of the rainy season between June and August, while fruits mature throughout much of the dry season and the first half of the rainy season, especially from February to September.

Discussion. Dieffenbachia longispatha grows most frequently along streams, in deposits of sediment along lakes, in standing water, but also in deep soil in the forest understory. Frequently it is found solitary or in small clusters. While the species may colonize, it is typically much less colonial than other species in Panama and Colombia, such as *D. isthmia*, *D. oerstedii*, or *D. killipii*.

The species is characterized by its usually tall ((1)1.5-3.5 m high) and robust stem (usually 6-12) cm diam.), and by the petiole being inconspicuously sheathed and decurrent at the apex with a long subterete free portion beneath the blade, this drying characteristically olive-green or dark brown. Perhaps most characteristic of D. longispatha are the widely scattered, moderately sparse and very large pistils and the usually long spathe. Dieffenbachia longispatha is typically one of the tallest species (to 3.5 m) with the thickest stems (to 12 cm diam.) in Central America. Only some plants of D. panamensis and D. aurantiaca often develop plants of comparable stature, but one collection of D. standleyi (Madison 705), with stems to 2.2 m tall and 9-11 cm diam., is reported.

The species has long been confused with *D. ni-tidipetiolata*, which ranges from Nicaragua to Ecuador. That species differs in having a typically somewhat smaller stature (usually 1–1.5 m tall), petioles that are in general very glossy, and pistils that are moderately small (to 3 mm) and closely aggregated. *Dieffenbachia nitidipetiolata* also has a different beetle pollinator scent at time of flowering according to observations made at La Selva in Heredia Province, Costa Rica, by D. Beath (pers.

comm.). Dieffenbachia longispatha and D. nitidipetiolata do not occur together in Costa Rica since D. longispatha barely crosses west of the Panama Canal. In eastern Panama D. longispatha is found principally in areas of Tropical moist forest (T-mf) near El Real.

Smaller plants of *D. longispatha* may also be confused with *D. crebripistillata*. In addition to being a plant of smaller stature (rarely to 1.3 m tall), it has more fully sheathed petioles (often to the base of the blade and sometimes overlapping the blade) that usually have a whitish band abaxially and dry conspicuously yellow or orange-brown (vs. green for *D. longispatha*). In addition, *D. crebripistillata* differs in having smaller spathes (to 28 cm) with the pistils closely aggregated on the spadix, with (57)80 to 100 pistils versus 10 to 26 for *D. longispatha*. Finally, though there may be a certain overlap in their ranges in areas along the Atlantic coast in Colón Province, *D. crebripistillata* generally occurs at higher elevations, mostly 250 to 975 m.

Additional specimens examined. PANAMA. Bocas del Toro: 1.5 km N of La Gruta, Peterson 6405 (US). Canal Area: Barro Colorado Island, Armour Trail 2000, Croat 11321 (F, MO, US); Barbour Trail 225, Croat 6471 (MO); Barbour Trail 200, Croat 7136 (MO); Drayton Trail, near end, Croat 5767 (MO); Drayton Trail 1610, Croat 5761 (MO); Lake Trail, Croat 6276 (MO, SCZ); Oppenheimer 67-1-3-1244 (MO); Miller Trail 300, Croat 4095 (MO); Miller trail 1400, Croat 17394A (MO); Miller Trail 1375, Croat 7455 (MO); Pearson Trail 400, Croat 4134 (MO); Snyder-Molino Trail, Croat 6192 (MO); Van Tyne Trail, Stimson 5277 (DUKE, STRI); Wheeler Trail 300, Croat 4125 (MO); Zetek Trail 500, Fuertes Cove, Croat 5259 (MO), Croat 6409 (MO); 0.6 mi. N of Gamboa near Río Frijol, Tyson 1438 (MO); vic. Curundu Housing area of Albrook Air Force base, Parque Metropolitano, Croat & Zhu 76203 (AAU, CR, MO, US); Gatun Locks-Fort Sherman, 1 mi. E of Fort Sherman, Croat & Zhu 76266 (MO, US); Río Grande-Pedro Vidal, rd. to Arraijan, Pittier 2715 (US); near Fort Randolph, Standley 28732 (US); Madden Forest ca. 3 mi. from Madden Wye, Croat 33018 (MO, P, PMA); N of Summit Garden, Croat 12319 (MO, US); Río Casaya headwaters, 6 km E of Gamboa, Nee 9023 (F, MO). Colón: Río Guanche, Puerto Pilón-Portobelo, 6 km S of Portobelo, ca. 1.5 mi. S of rd., Croat & Zhu 76256 (COL, MO, PMA, RSA), 76257 (COL, HUA, MO, PMA); Río Guanche, 1 km upstream, Croat 75195 (MO), Croat 11411 (MO). Darién: PN Cerro Pirre, vic. of station along Río Perisenico, Croat & Zhu 77101 (CM, STRI, US); tributary of Río Tuira, upstream from El Real, McDade s.n. (MO); PN Darién, Cerro Pirre base camp, Río Paracida, Croat 68971 (MO); 3 mi. E of Santa Fe, Tyson et al. 4701 (US); Río Tuquesa headwaters, ca. 2 km air distance from Cont. Divide, Kittridge gold mining camp, Croat 27196 (MO); Upper Río Tuquesa, LeClezio 135a (MO). Panamá: 5 mi. above Interam. Hwy., rd. to Cerro Azul, Croat 11514 (MO, SCZ); El Valle de Madroño-La Saena, 2.5 mi. N of El Valle de Madroño, Croat & Zhu 77042 (L, MEXU, MO); 5 mi. W of Chepo, Tyson 6700 (MO); Río Majo-Quebrada Brava, Croat 34654 (MO); El Llano-Cartí Rd., near border with San Blas Province, Croat 67399A (MO); Río Tapia, Standley 26156 (US), Standley 28238 (US). San Blas: E of Puerto Obaldía, Croat 16923 (MO). COLOMBIA. Antioquia: San Luis, Guillermo & Cardenas L. 863 (HUA, JAUM). Chocó: Acandí, Río Cuti, Corr. Unguia, Romero-Castaneda 6436 (COL); Nuquí, Corr. Arusí, vic. Arusí, Río Arusí, Croat & M. Mora 83777 (= Mora 394) (MO). Meta: PN Natural Tinigua, Serranía Chamusa, Centro de Investigaciones Primatológicas La Macarena, Camp Colombia, Stevenson 379 (COL).

17. Dieffenbachia lutheri Croat, sp. nov. TYPE: Panama. Chiriquí: along border of Bocas del Toro Province, Cerro Colorado, above mine, 1600 m, originally collected by Luther et al., cultivated at Marie Selby Botanical Gardens (acc. #86-0873), 4 Oct. 1991, S. W. Ingram 1146 (holotype, MO-4224350!; isotypes, B!, COL!, K!, MEXU!, PMA!, SEL-065912!, US!). Figures 17, 27B.

Planta 0.6–1.5 m alta; internodia brevia, 2.0–2.4 cm diam.; petiolus 23 cm longus, vaginatus 0.7 longitudinis; lamina anguste ovata, (24)27–34 cm longa, 14–15 cm lata, nervis primariis lateralibus 14–16 utroque; inflorescentia 1 per axillam; pedunculus 4–6 cm longus, 1 cm diam.; spatha pallide viridis, 16.5–20.5 cm longa.

Herb, 0.6-1.5 m tall; sap not smelling of oxalic acid; internodes short, to 2 cm long, 2.0-2.4 cm diam., dark green and semiglossy, drying matte and blackened; petioles ca. 23 cm long, dark green and weakly glossy, smooth or with fine, obscure lines on fresh material, sheathed 0.7 their length, drying dark olive-gray toward base, somewhat yellowish brown toward apex; sheath acute on one side at apex, the other side narrowly rounded at apex, with both sides confluent, the sheath margins drying thin, pale brown, the inner surface of the sheath pale yellow-green and very glossy, drying light yellow-brown, much paler than the outer surface; free portion of the petiole oval to sharply C-shaped in cross section, 7 cm long, sharply sulcate to flattened with sharply ridged margins; blades narrowly ovate, $(24)27-34 \times 14-15$ cm, 1.9-2.2(2.7) times longer than wide, slightly inequilateral, one side 0.9-1.7 cm wider than the other, weakly to narrowly acuminate to acute and apiculate at apex, rounded and usually inequilateral, sometimes acute and decurrent on the petiole at base, moderately undulate along the margins, moderately coriaceous to subcoriaceous, very dark green and semiglossy to weakly glossy above, sometimes mottled in a band along the midrib (especially heavy on one side below the middle) with yellow-green to cream above, drying dark gray-brown to dark brown and matte to weakly glossy above, slightly to moderately paler and weakly glossy to matte below, drying yellowgreen, weakly glossy; midrib slightly flat-raised, concolorous and 4-5 mm wide, weakly ribbed and medially sulcate above, narrowly rounded and slightly paler below, drying flat-raised and slightly darker yellow-brown above; primary lateral veins 14 to 16 per side, arising at an acute angle, then spreading at 25°-70° angle (25°-45° angle toward the apex, 65°-70° toward the base), weakly quiltedsunken to narrowly sunken and concolorous, sometimes in weak valleys above, darker and convex to round-raised, minutely granular-puberulent to scabridulous below, drying weakly and narrowly raised, concolorous above, irregularly angular and yellow-brown below; minor veins on upper surface in part weakly etched, concolorous, those on the lower surface moderately obscure to easily visible, darker than surface; lower surface densely palespotted, the spots regularly rounded and evenly spaced. INFLORESCENCE 1 per axil; peduncle 4-6 cm long, 1 cm diam., drying dark yellow-brown, 3.5-8 mm wide; spathe pale green on both surfaces, white near tip, acuminate at apex, 16.5-20.5 cm long, flattened to 3.5 cm wide on tube, drying yellowish brown; spadix 14-20 cm long (including 1-1.5 cm long stipe); pistillate portion of spadix 7.0- $7.3 \text{ cm} \times 8-9 \text{ mm}$, completely contiguous with staminate portion or nearly so; staminate portion of spadix 5.3–8 cm \times 5–9 mm on drying, with the remnants of thickened thecae visible along upper margins; pistils 55 to 66, 2 to 4 of them in a spiral across the width of the spadix, sometimes moderately sparsely spaced, drying sometimes prominently convex and the pistils thus visible from both top and side views; pistils 1.4-2.3 mm wide; stigmas pale yellow, 1.3-1.7 mm diam., drying with short, mostly acute, mostly erect strigose trichomes; staminodia 2-3 mm long, 1.0-1.6 mm wide, markedly thickened at the apex, sometimes broader than long, white, drying yellow-brown; synandria creamy white, drying irregularly rounded to angular, 0.5-3.0 mm wide, yellow-brown, the apex sunken on drying, medium yellow-brown with pale, rounded, cellular inclusions. Berries not seen.

Distribution and habitat. Dieffenbachia lutheri is apparently endemic to the region of Cerro Colorado in Chiriquí and Bocas del Toro Provinces at 1390 to 1600 m in the *Lower montane rain forest* (LM-rf) life zone (Holdridge, 1967).

Phenology. A flowering collection was made in Panama, and the species has flowered in cultivation in October at the Marie Selby Botanical Gardens.

Discussion. The species is most similar to *D. longispatha* in having a considerable portion of the petiole unsheathed and obtusely sulcate; the sheath



Figure 17. *Dieffenbachia lutheri*. —A. Habit of potted plant. —B. Plant habit with inflorescence. —C. Close-up of stem showing petiole sheath and sulcate petioles. —D. Close-up of inflorescence.

acute at the apex; and a blade of generally similar shape and dried color. It differs from *D. longispatha* in occurring at a much higher elevation (1390–1600 m vs. 180 m), in having the staminate and pistillate portions of the spadix contiguous (separated by a conspicuous, mostly sterile portion in *D. longispatha*), and in having a spathe that is much shorter (to 20.5 cm vs. 27–48 cm).

Dieffenbachia lutheri is also similar to *D. killipii* and even shares with that species the contiguous pistillate and staminate portions of the spadix. It differs from *D. killipii*, however, in having the major veins on the lower surface granular-puberulent rather than glabrous.

Dieffenbachia lutheri might be confused with another high-elevation species, *D. crebripistillata*, but that species occurs only up to 950 m, lower than *D. lutheri*, and differs in having a fully sheathed petiole that dries yellow-brown. *Dieffenbachia lutheri* has a petiole that dries dark gray and is unsheathed for more than 5 cm at apex.

Etymology. The species is named in honor of botanist Harry Luther from the Marie Selby Botanical Gardens, Sarasota, Florida, who collected living material of the type species.

Paratypes. PANAMA. **Bocas del Toro:** Cerro Colorado, 9.2 mi. W of Chamé, *Croat 69070* (MO). **Chiriquí:** Cerro Colorado, 18.6 mi. N of Río San Felix, 6.6 mi. beyond Chame, *Croat 75007* MO); 34.1 km of Río San Felix, *Croat 37268* (MO).

Dieffenbachia nitidipetiolata Croat & Grayum, sp. nov. TYPE: Panama. Bocas del Toro: Valle del Silencio, along Río Changuinola, ca. 1 km above mouth of Río Teribe, vic. Teribe Indian population, disturbed forest among cocoa plantations, 9°21'40"N, 82°31'40"W, 100 m, 25 June 1994, *T. B. Croat & G. Zhu 76449* (holotype, MO-04614032–33!; isotypes, AAU!, B!, CAS!, COL!, CR!, F!, GH!, INB!, K!, MEXU!, NY!, PMA!, US!). Figures 18, 30A.

Planta 50–75(120) cm alta; internodia 0.7–1.5 cm longa, 1.5–2.5(4.0) cm diam.; petiolus 13–44 cm longus, vaginatus 0.3–0.76 longitudinis; vagina 14–34 cm longa, acuta ad apicem; pars libera 5–22 cm longa; lamina oblongo-elliptica vel oblongo-lanceolata vel ovato-elliptica, 19–59 cm longa, 7–27.5 cm lata, nervis primariis lateralibus (10)12–20(22) utroque; inflorescentia 1–5 in quoque axilla; pedunculus 11–18(24) cm longus; spatha 15–36 cm longa; spadix 13–29 cm longus; pistilla 48– 60(79).

Herb, 50–75(120) cm tall; sap moderately foulsmelling; stems erect or partially reclining; *internodes* 0.7–1.5 cm long, 1.5–2.5(4.0) cm diam., glossy to semiglossy, dark green to medium green, smooth, drying dark brown to light yellow-brown, matte, moderately smooth; petiole scars 4-5 mm thick. LEAVES erect-spreading, clustered at apex of stem; petioles 13–44 cm long (averaging 28.4 cm long), 1-1.5 cm diam. midway, sheathed 0.3-0.76 their length (averaging 0.48), very glossy as if varnished, rarely only semiglossy, dark green, drying orange-brown to blackened; sheath 14-34 cm long (averaging 14.3 cm long), erect to involute, acute and decurrent (but sometimes weakly elevated) at apex; the unsheathed portion 5-22 cm long (averaging 13.4 cm long), usually terete to C-shaped, sometimes obtusely and narrowly to broadly sulcate or V-sulcate, rarely D-shaped; blades oblong-elliptic to oblong-lanceolate, or ovate-elliptic, gradually acuminate to acute, equilateral to inequilateral at apex, usually only weakly inequilateral with one side 0.3-1.5 cm wider (but can be up to 3.5 cm wider) than the other, acute to obtuse or rounded at base, usually equilateral, sometimes inequilateral with one side acute and the other rounded, 19- $59 \times 7-27.5$ cm (averaging 38×12.6 cm), 2.1– 4.8 times longer than wide, broadest usually at middle, 0.7-2.4 times longer than petiole (averaging 1.38 times longer than petiole), subcoriaceous to thinly coriaceous, moderately to weakly bicolorous; margin sometimes weakly undulate; upper surface dark green and glossy to semiglossy, plain green or rarely weakly variegated with pale green in some areas or throughout much of the blade, sometimes plain green with just the midrib whitened, drying gray-green; lower surface moderately paler, matte to weakly glossy, drying yellow-green; *midrib* \pm flattened (slightly sunken toward base), concolorous or slightly paler, sometimes white above, convex or bluntly acute below, drying pale vellow-brown often with a medial ridge on drying; primary lateral veins (10)12 to 20(22) per side, departing midrib at 20°-40°(55°) angle on narrower leaves (especially in Panama), often to 70°-85° angle on broader blades (mostly in Costa Rica), weakly arcuate-ascending, weakly sunken above, weakly convex and slightly paler below; minor veins visible, not prominent below. INFLORESCENCES mostly 1 to 5 per axil; bracts 2-ribbed throughout; peduncles 11-18(24) cm long, 0.9-1.3 cm diam., somewhat flattened, medium green, semiglossy; spathe 15-36 cm long, 1.3-2 times longer than peduncle, uniformly pale green to greenish white or greenish cream, becoming pale yellow post-anthesis, semiglossy to matte outside, slightly paler and glossy within, spathe tube 2-2.9 cm diam., flattening to 8-9 cm wide, weakly constricted above the tube to 1.7 cm diam., the constricted area to 5 cm wide when flattened, narrowly acuminate at apex; spathe blade 2.5-3.5 cm wide at anthesis, flatten-



Figure 18. *Dieffenbachia nitidipetiolata*. —A. Habit. —B. Close-up of leaves, adaxial surface. —C. Close-up of crown of plant showing newly opened leaf and inflorescence. —D. Opened inflorescence exposing spadix. A, B. (*Grayum 3218*); C, D. (*Croat 76942*).

ing to (3.7)4.5-5.7 cm wide midway; spadix 13-29 cm long, ca. 1-9 cm shorter than the spathe; the free portion 11-16 cm long; fertile staminate portion 5.7–10.5 cm \times 6–11 mm, slightly broader at middle, gradually tapering toward both ends, bluntly rounded at apex; male flowers 4 to 6 per spiral, subrounded to hexagonal, sometimes depressed medially, the margins irregularly and smoothly indented; pistillate portion 5.5-14 cm long, 11-15 mm diam., extending down to the very base of the spathe; pistils 48 to 60(79) globose, green, to 2.5-3 mm diam., moderately closely spaced except sometimes in uppermost 1 cm (the distance between them generally equaling or up to twice their width), usually to 3 per spiral or 4 to 6 in an arch across the width of the spadix; stigma yellow, depressed-globose, simple; staminodia 3 to 5 per flower, clavate, white, 2-6 mm long, up to 2 times longer than pistil, somewhat flattened and mostly contiguous at base (sometimes united in pairs), sometimes slightly thickened and somewhat puckered at apex, drying orange; staminate portion interrupted from pistillate portion by a \pm naked portion, 2.5–4.5 cm \times 5–9 mm with a few sterile staminate flowers scattered at both ends or sparsely in the lower half. INFRUCTESCENCES with spathe orange, to 23 cm long; berries globose, bright red, 4-6 mm diam.

Distribution and habitat. Dieffenbachia nitidipetiolata ranges from Nicaragua to Costa Rica (Heredia, Limón) to Panama (Bocas del Toro, Colón, San Blas), Colombia (Antioquia, Chocó), and Ecuador (Esmeraldas and Morona-Santiago), from near sea level to 1200 m in wetter parts of Tropical moist forest (T-mf), Premontane wet forest (P-wf), Tropical wet forest (T-wf), and Premontane rain forest (P-rf) life zones (Holdridge, 1967).

Phenology. Dieffenbachia nitidipetiolata flowers principally at the beginning of the rainy season (June–September), but also as early as March and as late as October, with the heaviest flowering apparently in August. Fruiting collections have been made from May through January.

Discussion. The species is characterized by its long, glossy petioles with the unsheathed portion being moderately elongate, 0.7–0.24 cm of their length, and which dry glossy as though varnished, and by the moderately closely spaced pistils. It is most easily confused with *D. longispatha*, differing from that species in having the pistils much smaller and aggregated and from *D. crebripistillata* in having the petiole almost unsheathed (vs. sheathed mostly to the apex in *D. crebripistillata*). The species may be confused with *D. hammelii*. That species differs in having a minutely granular upper surface, a matte-drying lower midrib with prominent raphide cells (vs. drying glossy without raphide cells), and matte-drying petioles (vs. drying glossy).

In the Río Guanche area of Colón Province, Panama, the species may be hybridizing with D. crebripistillata since both species occur along the Río Guanche and in the Santa Rita area further inland and at higher elevations. Some plants have the free portion of the petiole over half its length on average, which is characteristic of D. nitidipetiolata (but not of D. crebripistillata), yet the free portion is not notably glossy as is usually the case for D. nitidipetiolata. Examples of these collections are McPherson & Merello 8235 from Santa Rita Ridge and Thompson 4874 from Río Guanche. The Mc-Pherson and Merello collection also describes the petiole as having a white streak on the abaxial surface, a feature otherwise known only in D. crebripistillata.

Paratypes. COSTA RICA. Alajuela: 34 km beyond San Ramón beyond Los Angeles, Luteyn 3385 (DUKE); 3.5 km W of Fortuna, 2.5 km NW of New Volcán Arenal, Taylor & Taylor 11660 (MO); Naranjo-Aguas Zarcas, along Hwy. 15, 8 km NE of Quesada, Croat 46947 (MEXU, MO); N side of Volcán Arenal, Lent et al. 3374 (F); Cordillera de Tilarán, San Ramón-Bajo Rodríguez, 36-37 km NW of San Ramón, Croat 68195 (CM, K, MO); 15 km WNW of Quesada by air 1 km W of Jabillos, Liesner et al. 15144 (B, CR, MO, WIS); Río San Lorenzo, San Lorenzo-Los Angeles de San Ramón, Burger & Antonio 11198 (F, MO); Río San Rafael, W of La Marina, Burger & Stolze 5024 (F, US). Cartago: Turrialba-Limón, Hwy. 32, ca. 9 mi. NE of Turrialba, Croat 43368 (MO); Guacimo-Guapiles Rd., Barringer 2416 (F), Heredia: La Selva at Sarapiquí, Jimenez 103 (MO); La Zona Protectora, Río Guacimo, Grayum & Schatz 3218 (DUKE); La Selva, OTS Field Station on the Río Puerto Viejo, E of its jct. with the Río Sarapiquí, Croat 44254 (MO), Hammel 8123 (DUKE, F, MO), Burger & Stolze 5753 (F, GH), Folsom 9200 (DUKE), Hammel 10082 (DUKE), Beach 1436 (DUKE), Beach 1439 (DUKE, MO), MacDougal 1027 (DUKE), Jiménez 103 (MO); Río Sarapiquí, 2 km S of San Miguel, Lent 37 (F); Sarapiquí, Croat 44307 (MO), Grayum 2225 (DUKE, MO); San José and Pto. Viejo, vic. of Chilamante, 11.6 mi. N of Cariblanco, Croat 68379 (MO). Limón: Hitoy Cerere reserve, SW of Valle La Estrella, along Río Cerere to ca. 1 km upstream from Quebrada Barrera, Grayum & Hammel 5785 (MO); Res. Biol. Hitoy Cerere, Valle de la Estrella, trail to Cerro Bobócara, G. Herrera 4116 (CR, MO); N of Quebrada El Molinete, Río Chirripó-Río Corinto, Grayum & Jacobs 3524 (MO); Ref. Nac. Barra del Colorado, Río Chirripócito-Río Sardina, Grayum 9844 (CR, MO); Río Catarata, Burger et al. 10323 (F, MO, SEL); BriBri-Río Sixaola, Río Catarata, Burger & Antonio 10905 (F, MO, PMA); BriBri-Caribbean coast, Croat 43217 (MO). Puntarenas: E of Monteverde on the Pacific watershed, Burger et al. 10699 (MO); Palmar Norte-Panamerican border, 3 km N of turn-off to Rincón, Croat & D. Hannon 79199 (INB, MO, US). San José:

Vazquez de Coronado, Braulio Carrillo NP, along Hwy. San José to Siquirres, trail to Río Sucio, site of the Old Carillo Station, Croat 78788 (IBE, INB, MO, WU). NICARA-GUA. Zelaya: Caño Montecristo, E of Campamento Germán Pomares, P. Moreno & J. Sandino 15160 (MO); Río Punta Gorda, Atlanta, "La Richard," 200 m SE, Moreno & Sandino 12976 (MO). PANAMA. Bocas del Toro: Río San Pedro, Gordon 55C (MO); Santa Catalina, 4 Dec. 1967, Blackwell et al. 2704 (COL, MO, UC); Chiriquí Lagoon area, Cocoa Cay, von Wedel 2892 (COL, F, MO, UC); above RR stop at Milla 7.5, Croat & Porter 16303 (MO), Croat & Porter 16412 (MO), Croat 38120 (HUA, INB, MO, UB, VEN), Croat & Porter 16375 (MO); Chiriquí Grande-Fortuna, 7.7 mi. S of Chiriquí Grande, 1.5 m W of Punta Peña, Croat & Grayum 60116 (MO), Akers 78 (MO); IRHE vic., Carrasquilla & Mendoza 1239 (MO, PMA); Almirante-Ojo de Agua, 3-6 km W of Almirante, Croat 38229 (F, MO, PMA); about 10 mi. W of Veraguas border, McPherson 11401 (CM, MO); Valle del Silencio, along Río Changuinola, ca. 1 km above mouth of Río Teribe, vic. Teribe Indian population, Croat & Zhu 76422 (INB, MO, WU); Cocoa Cay, vic. of Chiriquí Lagoon, von Wedel 2892 (F); Río Teribe, vic. Teribe II, IRHE, Carrasquilla 2005 (PMA); Changuinola-Tuibe Rivers, Zigla Rd., Lazor et al. 2578 (MO); limit trail of Par. Intl. La Amistad, from Quebrada Boca Chica to Quebrada Bonyic, Polanco 1591 (PMA). Chiriquí: Fortuna Lake Area, 3.4 km N of Quebrada Chorro, 1.6 mi. N of center of bridge over lake, Croat 74958 (MO); vic. Fortuna Dam, McPherson 9829 (MO); Quebrada Los Chorros-Quebrada Hondo, N of Fortuna Lake, Churchill & Churchill 6105 (MO); Fortuna-Chiriquí Grande, 0.7 mi. NW of center of dam, Croat & Zhu 76482 (INB, MO, PMA); trail from rd. near Forestry Nursery to Río Hornito, Thompson 5028 (CM). Coclé: Cont. Divide, N of Penonome on rd. to Coclesito, Hammel 4049 (MO). Colón: Santa Rita Ridge rd., ca. 8 mi. E of Transisthmian Hwy., McPherson & Merello 8235 (MO); Santa Rita Ridge Rd., ca. 1 hr. walk from end of rd., Antonio 4488 (MO); Santa Rita Ridge Rd., 6.5 mi. E of Boyd-Roosevelt Hwy., Croat & Zhu 76942 (CR, GOET, GUAT, HUA, INPA, ISC, LE, MO, PMA TEFH, UB, WISC); Puerto Pilón-Portobelo, Río Guanche, ca. 1.5 mi. S of rd., Croat & Zhu 76254 (MO, PMA); Río Guanche, 3-5 km above bridge, Croat 79348 (B, INB, MEXU, MO, US), Sytsma 1695 (MO); 3-7 km above bridge, Hammel et al. 4882 (MO); ca. 3 km above bridge, Croat 49761 (MO); Santa Rita-Serra Llorona, Galdames et al. 1138 (STRI); Río Iguanita, Croat 49768 (MO). Darién: W side of Cerro Pirre, Croat 68854 (MO); Río Tuquesa, ca. 2 km air distance from Cont. Divide, near upper gold mining camp of Tyler Kittredge, Croat 27161 (MO); Serranía de Pirre, Río Cana-Río Escucha Ruido, above Cana Gold Mine, Croat 37746 (MO). Panamá: El Llano-Cartí Rd., near border with Province of San Blas, Croat 67379A (MO). San Blas: Comarca de Kunayala, Nusigandí, El Llano-Cartí Rd., 10.1 mi. N of Inter-am. Hwy., then ca. 0.5 mi. N Paseo Mariska, Croat & Zhu 77023 (MO); SE of Puerto Obaldía, Croat 16769A (MO); trail from dock to airport to village of Cangandí, de Nevers et al. 7407 (MO, PMA); El Llano-Cartí Rd. km 16.7, trail W to waterfall 5 km from rd., de Nevers & S. Charnley 5898 (MO, PMA); Canagangí, de Nevers et al. 5727 (MO). Veraguas: Boca de Concepción, in Golfo de los Mosquitos, McPherson 11381 (MO). COLOMBIA. Antioquia: Mutatá, Corr. Longani, Callejas et al. 5661 (HUA). Chocó: trail from Río Mecana to Alto de Mecana, Gentry & Juncosa 41037 (MO); Serranía de Baudo, Las Animas-Pato, Río Pato, 10

km SW of Pato, Croat 56070 (CHOCO, MO); Río Condoto-Río San Juan, Killip 35113 (COL, US); Alto de Buey, Gentry & Forero 7342 (COL, MO); Bahia Solano, Puerto Mutis, Gentry & Forero 7217 (COL, MO); Bahia Solano, Croat 57462 (CHOCO, COL, MO); N of Bahia Solano, Cerro Mecana, Juncosa 1795 (MO); Mecana, Quebrada Resaquita, Juncosa 1898 (MO), 1912 (MO); Río San Juan, Noanama, Forero et al. 4571 (COL); Río Bicordo, tributary of Río San Juan, Noanama, Forero et al. 4659 (COL); Acandí, Quebrada Sardí, El Páramo, Roldan et al. 1199 (HUA, MO); Corr. San Francisco, Vereda Coquital, sitio El Páramo, Quebrada Zardí, Betancur et al. 1177 (HUA); Vereda Coquital, Fonnegra et al. 2899 (HUA, NY), 2907 (HUA, NY); Nuquí, Corregimiento Arusí, vic. of Arusí, Est. Biol. El Amargal, Croat & Mora 83652 (= Mora 270) (MO); Corr. Arusí, Est. Biol.. El Amargal, Mora 170 (COL). ECUADOR. Esmeraldas: Zapallo Grande, Río Cayapa, Barfod et al. 48348 (AAU); Lita-San Lorenzo Rd., 0.9 km E of El Durango, 19.8 km W of Alto Tambo, Croat et al. 82520 (MO); Playa de Oro, 1 km from Río Santiago, Cerón & J. Corozo 33858 (QAP), 33947 (QAP), Cerón & J. Corozo 34097 (QAP); San Lorenzo-Mataje, departing main Lita-San Lorenzo Hwy., 11.6 km N of Gasolinera San Lorenzo, 2.9 km W of main Lita-San Lorenzo Hwy., Croat et al. 84041 (AAU, B, CAS, COL, DUKE, G, K, M, MO, NY, P, UB, US, WU); Cotacachi Cayapas, San Miguel, Río Cavapas, Sector Loma Linda, Tipaz et al. 2280 (MO, QCNE); Río Cayapa, Zapallo Grande, Barfod et al. 48154 (AAU, MO); Zapallo Grande, Kvist et al. 48348 (AAU, QCA); Río Cayapa, Zapallo Grande, Kvist & Asanza 40756 (AAU); Río Grande, at Zapallo Grande, Barfod & Skov 60101 (AAU); Río San Miguel, upstream from Pueblo Cayapas, Holm-Nielsen et al. 25355 (AAU); San Lorenzo, Sparre 18326 (S). Morona-Santiago: Santiago-Morona, Río Morona, 23.4 km E of Santiago, Croat 87448 (MO, QCNE).

 Dieffenbachia obscurinervia Croat, sp. nov. TYPE: Panama. San Blas: trail from dock to airport to village of Cangandí, 9°24'N, 79°24'W, 3–30 m, 26 Mar. 1986, *G. de Nevers*, *H. Herrera & S. Charnley 7409* (holotype, MO-3475792!; isotypes, B!, US!). Figures 19, 29A.

Planta 0.8–1.5 m; internodia brevia, (1)3–4(5) cm longa, 1.5–2.5(3) cm diam.; petiolus 8–12 cm longus, vaginatus ad medium vel ad apicem; lamina anguste elliptica, 20–30 cm longa, 5–8 cm lata; inflorescentia 1–3 per axillam; pedunculus (1.7)3–5 cm longus; spatha 11.5–20 cm longa; spadix 10–18 cm longa, cum parte pistillata 5–5.5 cm longa.

Slender herb, 0.8–1.5 m tall, stem decumbent on older parts, weakly rooted, leaf scars inconspicuous; *internodes* glossy, (1)3–4(5) cm long, 1.5– 2.5(3) cm diam., dark green, epidermis fissured minutely into a netlike reticulum becoming uniformly fissured and brown-scurfy with age; *petioles* 8–12 cm long, averaging 10.6 cm long, sheathing ½ to throughout (average 0.8 their length), light green or yellow-green with the surface dark green-splotched or dark green with white or yellow spots (sometimes with spots forming a repeated series of irregular



Figure 19. *Dieffenbachia obscurinervia*. A, B. (*Croat 12660*). —A. Cluster of several potted plants with plant on left with open inflorescence. —B. Close-up of crown of plant showing adaxial and abaxial surfaces and inflorescence at anthesis. —C. Close-up of stem showing mottled epidermis and speckled petioles (*Croat 61234*). —D. Close-up of inflorescence showing both pistillate and staminate portions of spadix (*Croat 13849*).

bands); sheath 6.7-10 cm long, the tip usually rounded to inequilaterally emarginate, rarely decurrent, frequently with one side emarginate and with the other side acute; unsheathed portion lacking or to 5.2 cm long, sharply to bluntly sulcate; blades narrowly elliptic, 20-30 cm long (averaging 24 cm long), 5-8 cm wide (averaging 7.5 cm wide), 2.4-5.2 times longer than wide, 1.6-3.1 times longer than petiole, slightly inequilateral, one side 0.7-1 cm wider than the other side, subcoriaceous, weakly bicolorous, gradually acuminate, briefly apiculate at apex, frequently somewhat falcate, cuneate to obtuse or rounded, often weakly inequilateral, rarely weakly subcordate at base; upper surface dark green, semiglossy, drying dark yellow-green to dark olive-green; lower surface slightly to moderately paler, drying yellow-green; midrib slightly raised to flat above, concolorous, drying concolorous above, convex to narrowly rounded below, dark green, densely pale yellowish green-spotted, drying paler than surface or darker than surface below; primary lateral veins 10 to 13 per side, weakly etched above, weakly raised or not at all raised below; the interprimary veins almost as conspicuous as primary lateral veins; minor veins moderately distinct below. IN-FLORESCENCES 1 to 3 per axil; peduncle (1.7)3-5 cm long, somewhat flattened in cross section; spathe 11.5-20 cm long, 3.2-9.5 times longer than peduncle, dark green or pale green throughout, caudate-acuminate, sometimes sharply reflexed below apex; spadix 10-18 cm long; free portion 5-9 cm long; pistillate portion 5-5.5 cm long; sterile segment less than 1 cm long, 6 mm diam., with scattered staminodia throughout; pistils 20 to 40, moderately closely spaced, scattered, 2-2.6 mm diam.; stigma depressed-globose, 2 mm diam.; staminodia white, usually 3 per pistil, 1.5-2(3.4) mm long, flattened, oblong to clavate, grooved medially, drying flattened, thickened at apex; synandria irregularly rounded with margins undulate, minutely warty, widely sunken at apex, 1.8-2.6 mm diam., dark yellow-brown, matte on drying. INFRUC-TESCENCE broadly arching; spathe mostly deciduous; spadix to 8 cm long; berries red, broadly ellipsoid, to 1.5 cm long, less than 1 cm diam.

Common name. Abior (Kuna) (de Nevers et al. 7409).

Distribution and habitat. Dieffenbachia obscurinervia ranges from central Panama (as far west as Coclé) to northern Colombia (Antioquia and Chocó) from 30 to 800 m in *Tropical moist forest* (T-mf) and *Tropical wet forest* (T-wf) life zones (Holdridge, 1967).

Phenology. The species has been seen in flower from May to December and fruiting collections have been reported from from September to May.

Discussion. Dieffenbachia obscurinervia is characterized by its scurfy brown internodes, conspicuously splotched petioles, and narrow blades with weakly developed primary lateral veins. It is not easily confused with any other species but was incorrectly called *D. pittieri*, a species considered restricted to the Isthmus of Panama, for many years. See that species for a discussion of the differences.

Paratypes. PANAMA. Canal Area: Pipeline Rd., mi. 1-3, N of Gamboa, S. Knapp 1042 (MO); Pipeline Rd. at Río Agua Salud, Croat 12352A (MO); Barro Colorado Island, Armour Trail 1280, Croat 8623 (MO); Drayton Trail 1000, Croat 12660 (MO); Drayton 1910, Croat 6775 (MO, STRI); Drayton 1490, Croat 5759 (MO). Coclé: vic. El Valle de Antón, La Mesa, Finca Macarenita, Croat & Zhu 76666A (MO, PMA). Colón: Santa Rita Ridge, Croat 13849 (MO); Nombre de Dios, Croat 67329 (MO); Coclé del Norte, Hammel 4484 (MO); Portobelo-Nombre de Dios, 1.2 mi. beyond jct. of rd. to Isla Grande, Croat 49791 (MO, PMA); Río Guanche, ca. 5 km upstream from rd. to Portobelo, Hammel & Trainer 14786 (MO); Loma de la Gloria, near Fato (Nombre de Dios), Pittier 3847 (US). Panamá: Balboa West, Zapata et al. 289 (PMA); along trail off Llano-Cartí Rd., 4.6 mi. from jct. with Pan-Am. Hwy., McPherson & Merello 8143 (MO). San Blas: Río Cangandí, Cangandí, H. Herrera 245 (MO, PMA); Nusigandí, along El Llano–Cartí Rd., 0.7 km beyond Cuna headquarters, 11.6 km from Pan-Am. Hwy., Croat 75149 (K, MO). COLOMBIA. Antioquia: Río Anorí valley, near Planta Providencia, Shepherd 438 (MO, WIS); Anorí, Corr. Prov., Soejarto & Renteria 3556 (HUA); Zaragoza, Río Anorí, Quebrada La Tirana-Río Anorí, 2 km N of Quebrada La Tirana, 3 km upriver from Planta Providencia, Alverson et al. 283 (COL); Carepa, Tulenapa Reserva (ICA), Turbo-Mutatá, 40 km S of Turbo, Callejas et al. 4873 (MO, NY). Chocó: Nuquí, Quebrada Chaquí, Galeano et al. 4825 (MO); Quibdó, La Concepción, 15 km E of Quibdó, Archer 2215 (US); Cordoba, Tierralta, Río Esmeraldas-Río Simí, 2 km above confluence, Bernal et al. 1158 (COL).

20. Dieffenbachia oerstedii Schott, Oesterr. Bot. Z. 8: 179. 1858. TYPE: Guatemala. Aguacate, A. S. Oersted s.n. (holotype, C!). Figures 20, 29A.

Herb, 30–75(100) cm tall (usually less than 50 cm); stem erect or partially reclining, often conspicuously clustered with numerous plants; sap

Figure 20. *Dieffenbachia oerstedii*. —A. Potted plant with inflorescences and leaves with mottled blades (*Croat 68449*). —B. Potted flowering plant with pale midribs (*Croat & Zhu 76794*). —C. Leaves and post-anthesis inflorescence showing ovate-lanceolate blades with scarcely sunken primary lateral veins (*Croat 63208A*). —D. Close-up of



Figure 20. (Continued) stems showing the free-ending petiole sheath (*Croat 36297*). E, F. (*Croat 68449*). —E. Flowering plant with open inflorescences. —F. Close-up of flowering plant showing open spathe blade and exposed staminate portion of inflorescences.

moderately foul; leaf scars conspicuous, transverse or oblique (when oblique, up to $2 \times$ as wide on one side as the other), forming a T or forming a W on open side of sheath; internodes semiglossy to glossy, weakly warty on magnification, 1-5.7 cm long, 0.8-2(3) cm diam., dark olive-green to blackish green, medium green or dark green, sometimes variegated with streaks of paler green, drying dark brown to dark yellow-brown, glossy, smooth; petioles 10-20(30) cm long, (averaging 13.7 cm long), 3-4 mm diam., sheathing ¹/₃ to ³/₄ (rarely nearly throughout) their length (averaging 0.7 their length), medium green, matte, sometimes finely streaked throughout with darker green, usually weakly glossy and white near base; sheath 2.5-21.5 cm long (averaging 9.3 cm long), pale green to white on lowermost clasping portion (contrasting sharply with much darker stem), with margins involute, the tip with one side erect, free-ending and rounded to auriculate, with the other side rounded to acute (sometimes not freeending in Coclé Province, Panama); unsheathed portion 5-13 cm long, C-shaped to U-shaped in cross section, convex adaxially, acute to bluntly angled on margins; blades ovate to narrowly ovate or ovate-lanceolate or rarely oblanceolate, (5.5)14-22(35) \times (1.7)4–14(21.5) cm, (averaging 20.1 \times 8.5 cm), 1.4–5.9 times longer than wide (averaging 2.5 times longer than wide), 0.8-2.7 times longer than petiole (averaging 1.5), often inequilateral, somewhat thinly coriaceous to subcoriaceous, moderately bicolorous, gradually acuminate and apiculate at apex (the acumen 5 mm long), acute and weakly decurrent to obtuse or more often rounded, sometimes subcordate at base; upper surface matte and subvelvety to weakly glossy, dark green, frequently splotched light or medium green or with white areas especially near midrib (all variations frequently found in a single population), drying dark brown to gray-green, concolorous, sometimes faintly dark-striate; lower surface matte to weakly glossy (epidermal cells raised and sometimes translucent), drying yellow-green to yellow-brown, sometimes faintly dark-striate, slightly paler; midrib flatraised to obtusely flat-raised above, concolorous or sometimes white above (sometimes mottled on plants with mottled leaves, sometimes faintly darkstriate on both surfaces), slightly paler and convex to broadly convex to bluntly acute below; primary lateral veins (4)6 to 9(11) per side, departing midrib at a $40^{\circ}\!-\!\!45^{\circ}$ angle, broadly arcuate-ascending, sunken to quilted-sunken above, slightly darker than surface, weakly convex-pleated below; interprimary veins weak or as conspicuous as primary lateral veins; minor veins indistinct above, moderately distinct to moderately obscure below; "cross-

veins" sometimes visible. INFLORESCENCES 1 to 2 sometimes 3, rarely 4 per axil; peduncle (2.2)3.5-12(22) cm long (average 7.6 cm long), $\frac{1}{10}$ as long as spathe to fully as long as the spathe, averaging 0.43 as long, 6-13 mm diam., 2-4 mm diam. on drying, somewhat flattened in cross section; spathe (7.5)10-17(25.5) cm long, weakly constricted above tube, medium green on both surfaces, sometimes tinged whitish on back throughout (the median rib green), weakly glossy to semiglossy outside, glossy on inside, narrowly acuminate at apex; tube to 2-2.8 cm wide, 1.5-2.3 cm thick when furled, to 8 cm wide when flattened; spathe blade to 2.5 cm diam. when furled, 3.0-8 cm wide at anthesis; spa*dix* (7)10–17(21) cm long (averaging 14.6 cm), 1– 5 cm shorter than spathe; pistillate portion 4.3-7.5(10) cm long (averaging 6.4 cm long), 5-10 mm diam.; fertile staminate portion 3-8.5 cm long (averaging 5.3 cm long), 5-7 mm diam., broadest at middle, tapering toward both ends, especially at bluntly pointed apex; mostly sterile intermediate segment (1)2-3.2 cm long, to 2.5 mm diam. (dried), with a few widely scattered sterile staminate flowers in upper ³/₄ and a few pistillate flowers in lower ¹/₄, sometimes with only sterile staminate flowers scattered throughout, rarely almost bare; pistils (26)33-46(54), moderately closely spaced except in the lower 1.5 cm and the upper 1 cm (the distance between them generally equaling or twice their width), up to 4 in a row across the width of the spadix, subglobose, 1.5×1.4 –2.6 mm; stigma depressed-globose, yellow, 1 mm wide, puberulent; style caviform with a weak central dome; staminodia clavate, white, drying orange, 2-3(4.5) mm long, 1-2 mm wide at apex, 2-3 times longer than pistil, usually weakly fused at base, sometimes well separated, weakly flattened, thickened toward apex; synandria 3 to 5 per spiral, 1.4-2.0 mm diam., the margins smooth to irregularly and smoothly indented, smooth and subrounded at apex. INFRUC-TESCENCE to 22 cm long; spathe orange outside; berries bright red, globose, with 13 to 43 per spadix, 4-6 mm diam.

Distribution and habitat. Dieffenbachia oerstedii ranges from Mexico (Veracruz, Oaxaca, Chiapas, and Tabasco) mostly along the Caribbean slope in Central America in Guatemala, Honduras, Nicaragua, and Costa Rica (where it occurs on both slopes) and west-central Panama. The species also occurs on the Pacific slope of El Salvador (Department of Ahuachapán). The species ranges from sea level to 1260 m in Tropical dry (T-df), Tropical moist (T-mf), Tropical wet (T-wf), Premontane wet (P-wf), and *Premontane rain forest* (P-rf) life zones (Hold-ridge, 1967).

Phenology. Flowering of *D. oerstedii* occurs throughout the year, but with the heaviest flowering at the end of the dry season and the first part of the rainy season, April to September. Fruit maturation is more regularly scattered throughout the year.

Discussion. This species is characterized by its small stature (generally less than 1 m tall); frequently clustered stems; and sharply C-shaped petioles that are whitish at the base and sheathed mostly $\frac{1}{2}-\frac{3}{4}$ their length, with the sheath obscurely free-ending and inequilateral with at least one side usually merely rounded or acute rather than auriculate. Also characteristic are the moderately thin, usually small, \pm ovate-lanceolate blades, which are generally acute to rounded or truncate basally and matte or only weakly glossy adaxially.

Dieffenbachia oerstedii is the most widespread and ecologically variable species in Central America. It is extremely malleable in terms of leaf size, leaf blade shape, and markings, with different blade coloration types (cf. Fig. 20A, B) all found within the same population. For example, in populations at Río Grande de Taracoles at Carara in Costa Rica (0-200 m), the plants of this species are robust. The populations of D. oerstedii at 1400 m in Braulio Carillo National Park (also Costa Rica) have small and delicate leaves. In Costa Rica, the leaf blades tend to be matte or only weakly glossy on the upper surface. However, elsewhere in Central America the blades are often more glossy. A collection from El Salvador (Selby 77-3078) has blades that are initially rather glossy on the upper surface and weakly glossy on the lower surface (albeit soon turning only weakly glossy above). Plants in Panama and Costa Rica have blades 2-11 cm wide and acute to rounded at the base, whereas in other parts of Central America from Nicaragua to Mexico the blades are often 14-18 cm wide with subcordate leaf bases.

Standley (1937) considered *Dieffenbachia leopoldii* (Bull. Catal. 1878) similar to or synonymous with *D. oerstedii*, but the type specimen indicates that it was actually collected in Colombia, where *D. oerstedii* does not range. The species is actually closer to *D. killipii* (see discussion under *D. killipii*).

Collections from Mexico and Belize are larger on average than those in Panama, Costa Rica, and Nicaragua, with blades 16.5-35 cm long and 6-16.5 cm wide (averaging 23×11 cm). Petioles for the same area range from 8.5 to 30 cm long, about as long as the blades to 1.7 times longer than the blade with the sheath from 7.5 to 21.5 cm long, averaging 14 cm long (sheathed 0.48–0.9 the petiole length). In contrast, plants from Heredia Province in Costa Rica are smaller than average with blades averaging 13.9 cm long and 5 cm wide (2.9 times longer than wide).

The distribution of *Dieffenbachia oerstedii* in Panama is apparently disjunct with some collections known from far western Panama, but the species also occurs in the vicinity of El Copé and La Mesa in Coclé Province. The populations in El Copé have somewhat smaller leaves (9.5–15 cm long), but differ only slightly from those in Costa Rica. The El Copé material is otherwise morphologically identical to populations of *D. oerstedii* such as those found at La Selva in northern Costa Rica.

The petiole sheath of the Coclé populations is merely rounded on one side and acute on the other (vs. auriculate on one side and rounded on the other side for typical material of D. oerstedii). In addition, the midrib is not faintly striate on both surfaces as is usually the case with typical *D. oerstedii*. The petiole scars are much more oblique than usual with the internodes longer on one side of the stem than on the other (vs. more nearly perpendicular to the stem with the internodes of equal width on both sides of the stem for typical D. oerstedii). Despite the strong morphological similarities, plants from Coclé Province, Panama, differ markedly in their ecological requirements. Cultivated plants, for example, will survive well only in an area of nearly 100% humidity. Alternatively, the Costa Rican material from Heredia does very well in the drier parts of the greenhouse.

In Mexico, Dieffenbachia oerstedii may be confused with D. wendlandii since they have similar leaf blades. Living material of the latter is easily separated in having petioles with the free portion terete or obtusely and weakly sulcate (vs. sharply C-shaped and sulcate in *D. oerstedii*), the base solid green, and in having the sheath decurrent at the apex with one margin overlapping the other (vs. rolled in from both sides in D. oerstedii, with both sides visible and often protruded at apex and the sides inequilaterally rounded to auriculate). Compared with D. oerstedii, D. wendlandii is typically a larger plant with longer stems, thicker internodes, and larger leaves up to 33 cm long and 9.5-15 cm wide, and with the midrib 1.2-1.4 cm wide (vs. 5-6 mm wide for D. oerstedii). In addition, D. wendlandii has the stigma bowl-shaped at anthesis with a protruded central dome. In contrast, the stigma of D. oerstedii is cushion-shaped.

Dieffenbachia oerstedii is similar to D. killipii in general blade shape and size as well as in often having the "flat-raised" upper midrib, but D. killipii
often differs in having petioles not at all whitish at the base, blades which are typically semiglossy (vs. matte and subvelvety to weakly glossy in *D. oerstedii*), and especially in having the spadix with the pistillate and staminate portions nearly contiguous rather than well separated.

Herbarium material of Dieffenbachia oerstedii may be confused with D. seguine from the West Indies. Both species sometimes have blades of similar shape, and both have petioles that are comparably sheathed and sharply C-shaped on the free portion. The two species differ in stature, with D. oerstedii being much smaller and with blades matte, often subvelvety, whereas those of D. seguine are at a minimum weakly glossy on the upper surface. The auricles on the free-ending sheath of *D. seguine* are both rounded at the apex, whereas in D. oerstedii one of the sides of the sheath is almost rounded at apex and the other is usually acute at apex. However, the sheaths that subtend inflorescences in D. oerstedii may have the apex auriculate on both sides.

The type locality of *Dieffenbachia oerstedii* collected by Oersted remains in doubt but it may be from Guatemala. The type specimen contains only the name "Sanguinillo" on the label. Also penciled on the label is the name "Aguacato," perhaps added at a later date. Engler (1915: 15) cited a collection made by Oersted from "Schottige Berwälder des Berges Aguacate" (perhaps Cerro Aguacate in Sierra de las Minas). He also listed "sanquinello" (Engler, 1915: 15) as a common name for *D. oerstedii* (note the difference in spelling from that original label).

It is possible that Dieffenbachia oerstedii occurs in the Lesser Antilles and in French Guiana. Howard 11744, purportedly collected along the road between Rousseau and Sulfur Spring on Dominica, appears to be this species. Another specimen collected in French Guiana (Croat 74319) along the Cayenne-Regina highway, as well as cultivated material going by the name "D. oerstedii variegata" (Lyon 67-1086), appears to also represent this species. The same taxon is in cultivation in Port-au-Prince, Martinique (perhaps originating from French Guiana). Since the species is not apparently widespread in the areas mentioned, the field-collected plants may in fact be plants escaped from cultivation. Living specimens studied of the material from French Guiana and the cultivated material from the Lyon Arboretum are characterized by having the midrib creamy white from the lower 1/4 to the upper ¹/₄ of the blade. A similar feature is found in some populations of D. oerstedii in Costa Rica.

Additional specimens seen. BELIZE. El Dorado, Schipp 386 (F, GH, K, MO, NY); Caves Branch, halfway up St. Herman's Hill, Whitefoord 1176 (BM, MO); Cayo, Stann Creek Districts, Hummingbird Hwy., betw. mi. 25-34, Dwyer & Dieckman 13008 (MO); Vaca Plateau, Vaca Falls, Balick et al. 2080 (MO); Stann Creek, Cockscomb Basin, Jaguar Pres., 10 km W of Maya Center, off S Hwy., Balick et al. 2716 (MO); Toledo, vic. of trail to Esperanza beginning 1 mi. N of Columbia Forest Station, Vanderveen 590 (MO); Columbia For. Stat., Dwyer 9920 (MO); San José trail to Esperanza 1 mi. N of Columbia Forest Station, Croat 24250 (MO); San José, 6.7 mi. N of Columbia Forest Station, Dwyer 11184 (F); Bladen, Richardson Creek, affluent of Bladen Branch, lower part of Maya Mountains, Davidse & Brant 31879 (MO); along Bladen Branch from Richardson Creek to Quebrada de Oro, Davidse & Brant 32366 (MEXU, MO); Bladen, Solomon Camp, vic. of the jct. of Richardson Creek and Bladen Branch, foothills of the Maya Mountains, Davidse & Brant 32410 (MEXU, MO); Bladen, Bladen Nature Reserve, ca. 2 air km N of upper Bladen Branch, Davidse 35802 (BRH, MO, SEL); Bladen Res., Ek Xux archaeological site, Davidse & Holst 36041 (MO, MY); upper Bladen Branch basin, along main Bladen Canyon, Davidse & Holland 36505 (BRH, MO); Columbia Res. near Crique Negro, Whitefoord 3284 (BR, MO). COSTA RICA. Alajuela: Laguna Hule, NE of Cerro Congo, Luteyn 3342 (DUKE), Schubert & Rogerson 619 (A); canyon of Río Cariblanco and W slope and summit of ridge between Río Cariblanco and Quebrada Quicuyal, SW of Cariblanco, Grayum et al. 6194 (MO); 3 km N of La Luisa and 15 km N of Grecia, Murphy & Jacobs 1289 (DUKE, MO); San Carlos, Haber & Hammel 1799 (MO); Cordillera de Tilarán, San Ramón-Bajo Rodríguez, vic. La Balsa, 8.9 mi. NW of center of San Ramón, Croat 68069 (CR, K, MO); 10 km N of Bijagua, Croat 36473 (DUKE, F, INB, MO); Upala, Brasilia 1.5 km S of town, Finca de Mario Jirón, Herrera 1636 (INB, MO); 22 km NE of Quesada by air, 4 km W of Muelle San Carlos, Liesner 14102 (MO); 22 km NE of Quesada by air, 4 km W of Muelle San Carlos, Liesner 14155 (B, K, MO); 2 km N of Santa Rosa, Liesner et al 15035 (B, MEXU, MO); Cantón de Upala, Colonia Blanca, Finca Río Negro, Rivera 1560 (INB, MO); rd. to Los Angeles, NW of church in San Ramón, Stone 3317 (DUKE); San Ramón-Bajo Rodríguez, 12 km NW of Los Angelos, 16 km NW of San Ramón, Croat 78830 (MO); vic. km markers 11-12, ca. 7 km NW of Los Angelos, 11-12 km NW of San Ramón, Croat 78859 (INB, MO); Río Grande de Tárcoles, vic. Capulin, Standley 40223 (US); Río Segundo, ca. 1 km N of Intl. Airport, Croat 36855 (MO); Río Zapote, E slopes of Volcán Miravalles, W of Bijagua, Burger et al. 11695 (F, MEXU, MO): San Carlos (Pital), 1 km N de La Legua, Hammel 20231 (INB); Río Samen hacia Upala, Aguilar 5204 (INB, MO); San Ramón, ca. 13 km NW of San Ramón, Luteyn 3263 (DUKE); along rd. from San Ramón, N of Balsa, ca. 13.8 km N of bridge over Quebrada Volio, Stevens 13761 (MO); 3.5-4 mi. W of San Ramón, Croat 46785 (INB, MO); Río Grande, San Isidro, Carvajal 273 (K, MO); Upala, 13.8 km N of Bijagua, Croat 36444 (MO); Upala Cantón, Est. Biol. San Ramón, Dos Rios, Chinchilla 137 (INB, MO); Upala, Río Zapote, 4 km NNE of Bijagua, Croat 36297 (MO); 3.5 km W of Fortuna, 2.5 km NW of New Volcán Arenal, Taylor & Taylor 11660 (MO). Cartago: slopes of Miravalles above Bijagua, L. Gómez 19038 (MO); Cantón de Turrialba, 6 km W of La Suiza on the rd. to Pacavitas, Kennedy & Solomon 4629 (F, INB, MO). Guanacaste: SW slopes of Volcán Rincón de la Vieja and Volcán Santa María, Burger & Pohl 7825 (F); La Tejona, N of Tilarán, Standley & Valerío 46000 (US); PN Guanacaste Est. Mengo, Volcán Cacao, INBio 186 (INB, MO); Tilarán, San Pedro de Río Chiquito, Monteverde, Haber & Bello 7191 (CR, MO); La Cruz-Santa Cecilia, Finca La Pazmompa, Ríos et al 109 (CR); PN Rincón, Rivera 623 (K, MO); Las Nubes de Río Chiquito 1 km NW of village on Cont. Divide, Haber & Atwood 9163 (INB, MO); PN Guanacaste, Est. Cacao, Carballo et al. 47 (MO); Cord. de Guanacaste, Rincón de la Vieja, near refugee camp, along rd. NW of Quebrada Grande, Barringer et al. 4061 (F, MO); PN Guanacaste, Est. Mengo, Volcán Cacao, INBio I 186 (CR); Liberia, siguiendo el camino entre Nueva Zelandia (Quebrada Grande) y Dos Ríos, Upala, San Gabriel, G. Herrera et al. 2928 (MO); Liberia, PN Rincón de la Vieja, Cordillera de Guanacaste, sendero al Volcán, Taylor 216 (CAS, CR, INB, MO); Nandavure, Península de Nicova, Bejuco, finca de Abel Rodríguez, A. Rodríguez & Estrada 142 (CR, INB, MO); Tilarán, Standley & Valerio 45008 (US); Z.P. Tenorio, Cordillera de Tilarán, Tierras Morenas, Río San Lorenzo, G. Rodríguez 32 (CR, INB). Heredia: Finca La Selva, OTS Field Station on Río Puerto Viejo just E of its jct. with Río Sarapiquí, Jacobs 2159 (DUKE), Wilbur 37337 (DUKE), Wilbur 37243 (DUKE), Wilbur & Jacobs 34962 (DUKE), Folsom 8712 (DUKE), Hammel 8415 (DUKE), MacDougal 1090 (DUKE), Wilbur 28249 (DUKE); area between Río Peje and Río Sardinalito, Atl. slope of Volcán Barva, Grayum 6918 (MO); betw. Río Peje and Río Sardinalito, Atl. slope of Volcán Barva, Grayum 6925 (MO); PN Braulio Carrillo, betw. Río Peje and headwaters of Río Sardinal, Atl. slope of Volcán Barva, Grayum & G. Herrera 7829 (CR, MO); 8 km E of San Ramón, Loiselle 119 (MO); La Selva or Zona Protectora, Croat 77283 (F, HUA, K, MEXU, MICH, MO, R), Opler 246 (F); Tirimbina, Proctor 32251 (LL); San Isidro, Valle Central, below bridge over Rio Tibás, Valerio 246 (CR). Puntarenas: Palmar Norte-Panam border, 3 km N of turnoff to Rincón, Croat & D. Hannon 79199 (INB, MO, US); ca. 17 km N of San Vito on rd. to Potrero Grande, Davidson 7164 (MO, RSA); betw. guard station & Quebrada Bonita, Carara Res., Grayum & Warner 5710 (MO); Ref. Nac. Golfito, along S tributary of Río Cañaza, upstream from crossing of Golfito-Villa Briceño rd., Grayum 9251 (MO); Jardín Botánico Wilson, W of Río Jaba, 1.5-2 km SW of Las Cruces de Coto Brus, Grayum 9277 (CR, MO); Finca Loma Linda 1 mi. SW of Cañas Gordas, Croat 22252 (MO); Quebrada Bonita, to ca. 1 km E of Costanera hwy., Carara Res., Grayum 4765 (MO); along short rd. to Golfito from Villa Briceño on Inter-am. Hwy., W side of Fila Gamba, ca. 6 km from Golfito airport, Croat & Grayum 59929 (CR, MO, US); 9 km W of Monteverde on rd. to Inter-Am. Hwy., Haber & Zuchowski 9251 (F, INB, MO); PN Corcovado Sirena, Monkey Wood, Kernan 381 (CR, MO); Monteverde, Río San Luis river valley below community on Pac. slope, Haber et al. 4979 (MO); San Luis, Monteverde Finca de Chepe Rojas, Bello et al. 42 (CR, G, MBM, MO); 8 km N of Baranca, 1 km N of MiraMar turnoff, W side of km 123 on the Inter-Am. Hwy., Ouebrada Negros, Liesner et al. 15122 (CR, MO); foothills of the Cordillera de Talamanca, vic. of Helechales, along the Río Guineal, Davidse & Herrera 26262 (CR, MO); Pan-Am. Hwy. km 122, Hammel et al. 13962 (CR, MO, US); Cantón de Osa, Rancho Quemado, Quesada 175 (CR, MO, R, UB, VEN); hills N of Palmar Norte, along trail to Jalisco, Croat 35206 (MO); Est. Quebrada Bonita, Res. Carara, Croat 79072 (CAS, INB, MO); Orotina-Jaco, in valley of Río Grande Tárcoles, 1 km S of Quebrada Ganado, woods behind Hotel Pink Paradise, near sea level, 5 km S of bridge over Río Agujas on rd. to Jaco, Croat 79075 (INB, MO); Sector Esquinas, vic. Fila Gamba hills behind Esquinas Rain Forest Lodge, along Quebrada Negra, at end of side rd. off of Villa Bricena to Golfito Rd., Croat & D. Hannon 79284 (CAS, CM, COL, F, MEXU, MO, NY, SEL, TEX, VEN, WU); Nicoya Peninsula, Curú, Sanders et al. 19322 (MO); Cantón de Buenos Aires, Ujarrás, headwaters of Río Kuiyé, trail to Olán, Chacón 364 (F, MO); Coto Brus, Osa Peninsula, Sabanillas de Limoncito, L. Gómez 22016 (CR. MO); Golfito, Albergue Cerro de Oro, en el Sendero La Tarde, Moraga 173 (CR, INB, MO); PN Corcovado, Est. Sirena, Sendero Ollas, Picado & Gamboa 134 (INB, MO); Quebrada Negra, Marten 831 (F), Aguilar 2412 (CR, INB, MO, NY); Fila Costeña, Fila Cruces, headwaters of Río Piedras Blancas, Cerro Anguciana, Grayum et al. 10578 (CR, INB, MO); Est. San Pedrillo, Aguilar 2380 (INB, MO); Río Sandalo, Dodge & Goerger 10157 (F); Cordillera de Tilarán, Finca Buen Amigo (Arco Iris), Monteverde, Fuentes 367 (CR, INB, MO); Finca el Gaucho, Ocampo 3411 (CR); Península de Nicoya, Est. San Miguel, ca. 2 km S de Malpais, Hammel et al. 20114 (MO); Granadilla Curridabat, Valerio s.n. (ENCB). San José: Río Chirripó del Pacífico, General Valley, Burger & Liesner 7111 (F, MO, PMA); Río Hondura, Lent 2789 (F); Montañas Jamaica, ca. 3 km NE of Bijagual de Turrubares, Carara Res., Grayum et al. 5862 (MO); Zona Protectora La Cangreja Forests along Río Negro, ca. 1.5 km E of Santa Rosa de Puriscal, Grayum et al. 8345 (MO); Quebrada Micos, ca. 8.5 km W of Ciudad Colón, Grayum & Sleeper 6100 (MO); San José, Valerio 1355 (F); Bijagua, L. Gómez 20562A (MO); Río María Aguilar, Standley 38942 (US); Mora, Colón, Finca El Rodeo, Nilsson & Manfredi 505 (F, K); Puriscal, Z. P. La Cangreja, Cerros de Puriscal, Falda W Cerro Cangreja, Santa Gertrudis, Cabeceras Río Negro, Morales et al. 5413 (INB, MO); Vazquez de Coronado, Braulio Carrillo NP, along Hwy. San José to Siquirres, Croat 78784 (INB, MO, NY, WU). EL SALVADOR. Ahuachapán: Villacorta et al. 408 (CM, MO); 1-3 mi. above intersection with rd. to Río Cara Sucia, Croat 42133 (CHIP, MEXU, MO); Finca Colima, Sierra de Apaneca, Standley 20085 (US); El Imposible, San Benito al N of del Nacimiento del Río Aguachapio, Sandoval & Chinchilla 352 (MO); La Libertad, Villacorta et al. 314 (LAGU, MO, US); Finca Los Naranjos, SW of Santa Tecla, Carlson 153 (F); San Vicente, vic. Ixtepeque, Standley 21414 (US). GUATEMALA. Alta Verapaz: Sierra de las Minas, Quebrada Mercedes, Finca Mercedes, Telemán, Panzós, E. Martínez et al. 22713 (MEXU, MO); Finca Mercedes, Teleman, Panzós, E. Martínez et al. 23474 (MO); Río Icvolay, N & NW of Finca Cubilguitz to Quebrada Diablo, Steyermark 44754 (F); Chimaltenango, Volcán Fuego, above Finca Montevideo, along Barranco Espinazo and tributary of Río Pantaleón, Stevermark 52070 (F, MO). Chiquimula: Municipio Olopa, vic. Olopa, J. Kufer 394 (M). Escuintla: Torolá, J. D. Smith 2239 (GH, K, NY, US); La Trinidad, Standley 65041 (F); between Río Jute and Río Pantaleón, Standley 63529 (F), Standley 63620 (F); Torolá, D. Smith 7813 (MO). Guatemala: Finca la Aurora, Aguilar 256 (F). Huehuetenango: Sierra de los Cuchumatanes, Stevermark 49321 (F). Izabal: above Selempim along rd. to Bocancha and base of Sierra de Las Minas, Förther 10213 (M); Montaña del Mico, Stevermark 38775 (F); near Quiriguá, Standley 72447 (F); ca. 1 mi. E of Santo Tomas, Croat 41855 (GUAT, MO); Selempim-Bocancha, base of Sierra de Las Minas, Förther et al. 10213 {232} (MO, MSB); Montana del Mico, Stevermark

38647 (F). Jutiapa: vic. Jutiapa, Standley 75669 (F); between Mita and Asunción Mita, Stevermark 31763 (F). Petén: between Finca Yalpemech on Río San Diego and San Diego on Río Cancuen, Stevermark 45410 (F). Quezaltenango: Retalhuleu, near Chivolandia along rd. to San Felipe, Standley 87180 (F). Retalhuleu: Pueblo Nuevo, Stricker 342 (US); Río Samalá, vic. San Felipe, Stevermark 34555 (F). Sacatepéquez: below Barranco Hondo, Standley 88988 (F). San Marcos: 3 km SW of San Rafael Pie de Cuesta, Harmon & Fuentes 4740 (MO); Río Chopal, Finca El Porvenir, S-facing slopes of Volcán Tajumulco, Stevermark 37456 (F); Volcán Tajumulco, Stevermark 37153 (F); near El Molino, Standley 78523 (F); Río de los Esclavos valley, near El Molina, Standley 60715 (F); Volcán Tecuamburro, Heyde & Lux 4654 (GH, K, NY, US). Sololá: S-facing slopes of Volcán Atitlán, above Finca Mocá, Stevermark 47908 (F). Suchitepéquez: near Pueblo Nuevo, Standley 66844 (F); near Las Lajas, Standley 58291 (F). HONDURAS. Coyol, Carleton 508 (US), Standley 26305 (F, GH, US). Atlántida: along rd. for municipal water supply of Tela, Lancetilla Botanical Gardens, on rd. ca. 2 mi. WSW of Tela and S of main hwy., Croat & D. Hannon 64622 (MO, TEFH, US); Campamento Quebrada Grande ca. 10 km SW of La Ceiba, base of N slope of Pico Bonito, Liesner & Mejía 26236 (MO); Lancetilla, 4 km S of Tela, Mena 190 (TEFH); sendero a la Pica, El Dorado, Cruz 354 (TEFH); ca. 3 mi. S of Tela, Webster et al. 12624 (US), Webster et al. 12625 (F, MO, US); Tela, valley above Exp. Stat., MacDougal et al. 3193 (ENCB, F, MO, NY), MacDougal et al. 3299 (MO); near Tela, Pfeifer 2163 (US), Standley 52702 (F, US); 10 mi. SE of Tela along Río Lancetilla, Croat 42645 (INB, MEXU, MO, PMA, TEFH); Río San Alejo, S of San Alejo, Standley 7700 (F), La Ceiba area, 35 km S of La Ceiba on rd. to Olanchito, Madison 712 (GH); La Ceiba, Mt. Cangrejal, Mt. Cangrejal, La Ceiba area, Yuncker et al. 8395 (F, GH, K, MO, US). Comayagua: ca. 2 km S of Lake Yojoa, Balick et al. 1738 (MO). Copán: 24 km E of Santa Rita, Harmon & Dwyer 4035 (MO, MEXU); Nueva Arcadia, 6 mi. S, Harmon & Fuentes 6419 (MO). Gracias a Dios: Ahuas Bila, 200 km SW of Puerto Lempira, Nelson & Cruz 9215 (MO, TEFH, UMO). Yoro: Cordillera Nombre de Dios, hills S of San Jose de Texiguat, Davidse et al. 34478 (MO). MEXICO. Campeche: El Maculisal, 40 km al sur de la carretera, Escarciga, Chetumal, Bravo s.n. (MEXU 30199) (MEXU). Chiapas: Chiapas, Cabrera et al. 1937 (MO); Izabal, Mpio. Livingston, E. Martínez et al. 23175 (MEXU); 2 mi. S of Chiapas border along Hwy. 195, 8 mi. N of Pichucalco, Croat 40087 (MO), Croat 40089 (MO); 60 mi. SE of Palenque, Croat 40163 (CHIP, MO); near ruins at Palenque, Spellman et al. 164 (F, MO, NY); 2.5 mi. N of Isthuatan, Croat 47868 (MO); Bochil-Pichucalco, 17.1 km SW of Pichucalco, Croat 78678 (MO); 20 km S of Palenque on rd. to Ocosingo, Mayo & Madison 301 (K); Mpio. Ixhuatán, Clarke 60 (DS); Ococingo, 19 km NW of Crucero Corozal, E. Martínez 13445 (MEXU, MO); Tenejapa, along Río Tanate at Habenal, paraje of Mahbenchauk, Breedlove 12752 (F); Palenque Archaeological Site, 3 mi. S of Palenque, Thorne & Lathrop 40559 (RSA); Río Cuxtepeques, near Finca Gadow, Breedlove 40155 (DS); Las Margaritas, Breedlove & McClintock 34192 (DS); Mapastepec, Río Testecapa, 10 km SE of Mapastepec, Breedlove & Thorne 30681 (DS); Ocosingo, 5 km SW of Santo Domingo, 120 km SE of Palengue on rd. to Bonampak, Davidse et al. 20440 (CM, MEXU, MO); Ocosingo, 3 km NW of Vertice del Chixoy camino a Boca Lacantum, E. Martínez S. 13630 (MEXU); Río Usumacinta, at ruins

of Yaxchilán, Breedlove 33839 (DS); vic. Palenque archaeological site, Davidse et al. 20326 (MEXU, MO); 6-12 km S of Palenque on rd. to Ocosingo, Breedlove 34977 (DS); Pichucalco, cerca Campo Aviacion, F. Miranda 7546 (MEXU); Solusuchiapa, 2-4 km below Ixhuatan along road to Pichucalco, Breedlove 24166 (DS). Oaxaca: Choapan, Mpio., San Juan Lalana, trail Jalahui-Arroyo San Pedro, Noriega & H. Vasquez G. 1353a (MEXU). Tabasco: Cerro las Campanas, 3 km E of Teapa, ca. 50 km S of Villahermosa, Conrad et al. 2863 (MO); vic. of Teapa, Teapa-Tacotalpa, 3.1 m E of Teapa, Croat & D. Hannon 65370 (MEXU, MO); 3 km E of Teapa along rd. to Jalapa, Croat 40107 (MO); Grutas de Ocona near Teapa, Davidse et al. 29516 (MEXU, MO); Tacotalpa, 3 km È of Lázaro Cárdenas, Cowan 2063 (MEXU, MO); Teapa, Cerro las Campanas, 3 km E of Teapa, ca. 50 km S of Villahermosa, Conrad & Conrad 2882 (MO). Veracruz: Cordova, Bourgeau s.n. (P); Las Palmas-Catemaco, km 18, Leija & Garza 3341 (MEXU); Las Palmas-Catemaco, km 18, C-12-A, González 3341 (MEXU); Las Cruces, Las Choapas, Gómez-Pompa 1505 (F); Ebiotrolotu, Anaya 1 (MEXU); 6.5 km from Santiago Tuxtla and 3.6 km on trail to Cerro del Vigía, González 5597 (MEXU); Catemaco, 10 km N of Sontecomapan, vic. Hotel Playa Escondida, Nee 23733 (B, F, GH, MEXU, MO, NY); E side of entrance of Laguna de Sontecomapan into the Gulf of Mexico, 7 km NE of Sontecomapan, Nee 22595 (F, MO); Cerro Cochinitos, near Catemaco, R. Hernández 542 (F, MEXU, US); Playa Escondida, 12 mi. airline NNW of Sontecomapan, Holstein & Armbruster 20425 (UC); ca. 8 mi. S of Catemaco near Zapoapan on rd. to Acayucan, Moore Jr. & Bunting 8928 (BH); 5.7-6 mi. from Catemaco on rd. to Santecomapan, Moore Jr. & Bunting 8933 (BH); Catemaco-Montepio, 12.1 km beyond end of asphalt hwy. portion, 22.2 km N of Catemaco, along border trail to the Los Tuxtlas Res., Croat 78687 (MO); along rd. between Catemaco and Montepio, 2.6 km S of Los Tuxtlas Field Station, Croat 78695 (MO, WU); 3 mi. SW of Sontecomapan, Los Tuxtlas, Barlow s.n. (US); Chinameca, Pajapan, Tellez et al. 4466 (MEXU); Coatzacoalcos, 6 mi. E of Coatzacoalcos, Hwy. 180, Croat 40062 (CM, MO, QCA, TEFH); Hidalgotitlan, 3 km SW of Campamento La Laguna, Nee 29993 (F, M, NY, XAL); Hidalgotitlan, 1 km SE of Agustín Melgar, Nee 29752 (MO); Río Soloxuchil, entre Hnos. Cedillo y la Escuadra, M. Vasquez et al. V-907 (XALU); Las Choapas, Las Cruces, Nevling & Gómez-Pampa 1505 (F); Misantla, 8 km S of Misantla on rd. to Xalapa, Madison 589 (GH, SEL); San Andres Tuxtla, Est. de Biol. Tropical Los Tuxtlas, N of San Andrés Tuxtla between Sontecomapan and Montepio, Croat & D. Hannon 63129 (MEXU, MO), 19 Aug. 1972, Madison 627 (GH); San Andres Tuxtla, N and E sides of Laguna Encanatada, 3 km NE of San Andres, Nee et al. 24759 (F, K, MO, NY, SP, XAL), Ibarra 455 (MEXU), Ibarra & Cedillo 1804 (MEX, MO, NY), Ibarra 645 (MEXU, MO), Dillon et al. 1837 (F, MO, NY), Cedillo T. 3645 (MEXU, MO), Calzada 338 (F, MEXU), Chazaro 416 (F, MEXU); Monte Pío, 15 km al W de Catemaco, L. González 1473 (ENCB, MEXU); Santiago Tuxtla, 6.5 km de Santiago Tuxtla y 3.6 km camino al cerro del vigia, Leija & Garza 5597 (MEXU); Santiago Tuxtla, cerca Madero, Ramamoorthy et al. 3763 (MEXU); Tezonapa, 5 km SW of Motzorongo, vic. Felipe E. Martínez, R. Robles G. 815 (MEXU, XAL); Tlapacoyan, along Río Tablazos, upstream from Puente de Tomata, 6 km SSW of Tlapacoyan, Nee et al. 26103 (F, NY, XAL). PANAMA. Chiriquí: vic. David, Pittier 2836 (MO); 13-20 km W of Río Chiriquí Viejo, D'Arcy 10766 (MO); rd. to Río Serrano, Folsom et al. 2111



Figure 21. Dieffenbachia panamensis. —A. Habit of flowering plant (*Croat 67526*). —B. Potted plant showing ovate blades (*Cirino s.n.*). —C. Habit showing ovate-elliptic blades and inflorescences (*Croat 74856*). —D. Crown of plant with blade showing quilted blades and close-up of open inflorescence (*Croat 67526*).

(MO); W of Tolé, Río Cuvibora, Hammel 6264 (MO); Burica Peninsula, vic. of Puerto Armuelles, San Bartolo Limite, 10–12 km W of Puerto Armuelles, Croat 22173 (MO).
Coclé: 4–6 km N of El Copé, Montenegro & Chung 1462 (PMA, STRI), Aranda et al. 2860 (PMA); La Mesa, N of El Valle de Antón, 2 km W of Cerro Pilón, Croat 37351 (MO).
Veraguas: vic. Santa Fé, 1.7 km past Escuela Alto Piedra, Croat & Zhu 76859 (MO); 6–7 km past school, Nee 99121 (MO), Luteyn & Wilbur 4569 (DUKE).

Cultivated plants. Mexico. Veracruz: Catemaco, cultivated, *Bunting 1692*, Lankester Gardens, Cultivated, *Kew 70-76-494* (K); Finca La Selva, originally collected by Helen Young, 17 June 1971, *Croat 68449* (CM, CR, MO).

21. Dieffenbachia panamensis Croat, sp. nov. TYPE: Panama. Coclé: vic. of El Copé, 4.1 mi. N of village, along old logging road which leads down to the lowlands, 8°39′N, 80°36′W, 680–770 m, 25 Mar. 1993, *T. B. Croat* 74856 (holotype, MO-4342614!; isotypes, B!, CAS!, COL!, DUKE!, F!, GH!, INB!, L!, K!, MEXU!, NY!, PMA!, UB!, US!, VEN!). Figures 21, 30A.

Planta 0.75–2.5 m; internodia brevia, 3–4 cm diam.; petiolus 10–14 cm longus, vaginatus ad apicem; vagina effusa; lamina ovata ad elliptica, (26)45–75 cm longa, (13.5)17–40 cm lata; inflorescentia 3 per axillam; pedunculus 10–18 cm longus; spatha 13–20 cm longa; spadix 12–18 cm longa, cum parte pistillata 5–9 cm longa.

Stout erect herb, 0.75–2.5 m tall; *internodes* short, typically more than twice as broad as long, 1–3 cm long (typically somewhat longer on one side than on the other), 3–4(5) cm diam., dark green,

moderately glossy. LEAVES rosulate, erect-spreading to spreading; petioles (6)10-14 cm long (averaging 10.6 cm long), moderately erect, dark green (white at base), sheathed throughout, the margins flaring to recurled, sometimes incurled, markedly crisped-undulate nearly throughout; blades ovate to elliptic, (26)45-75 cm long, (13.5)17-40 cm wide (averaging 45.9×24.4 cm), 1–2.4 times longer than wide (averaging 1.6 times longer than wide), markedly inequilateral (one side 2.5-5 cm wider than the other), obtuse to rounded at apex (the tip inequilateral and weakly acute to acuminate), acute to rounded at base, moderately coriaceous, moderately bicolorous, dark green, matte and somewhat velvety to glisteningly velvety above, weakly quilted and minutely wrinkled on upper surface, much paler to moderately paler and slightly glossy to matte below, drying dark blackish brown to dark yellowish brown above, yellowish brown to gravish brown below; midrib broadly convex or sometimes flattened, 1.5-2 cm wide, slightly paler above, somewhat more convex and slightly paler below; primary lateral veins moderately quilted, (7)10 to 20 per side, arising at an acute angle, then spreading at 45°-60° angle, often at a somewhat wider angle on one side, obtusely sunken above, convex to obscurely raised and darker below; interprimary veins usually 1 per pair of primary lateral veins, about equal to primaries; minor veins not visible. INFLORESCENCES 3 per axil; peduncles 10-18 cm long (averaging 12.5 cm long), somewhat flattened, medium green, matte, weakly striate drying, to 6-10 mm diam.; spathe 13-20 cm long (averaging 18.4 cm long), medium to pale green, weakly and finely striate on back surface, with darker, oblique lines extending out to the margins, inner surface slightly paler; spadix 12-18 cm long; free part 8.5 cm long; pistillate portion $5-9 \times 1.8-2.2$ cm, narrowed slightly toward the apex; sterile staminate portion $3-4.2 \times 1-1.2$ cm; mostly sterile intermediate section 1.2 cm long, with a few scattered staminodia in the lower half; fertile staminate portion 5-7 cm long, the flowers irregularly 5-sided, 2.5-3 mm diam.; pistils 3.5-4 mm diam., irregularly rounded at apex, closely packed, almost contiguous; staminodia club-shaped, 4-5 mm long, generally extending above the pistils, broadest at base and apex, the tips 1.5-2 mm diam. Fruits orange.

Distribution and habitat. Dieffenbachia panamensis ranges principally along the Atlantic coast of Panama from 50 to 850 m, on both slopes along the Continental Divide east of the Canal Area.

Phenology. There are not enough collections of

this species to be certain of its flowering and fruiting phenology. However, flowering collections have been made in January, March, July, and September, and fruiting collections during September and November.

Discussion. The species is recognized by its fully sheathed petioles that are usually flaring to recurled, by the moderately coriaceous, somewhat velvety, weakly quilted blades, and usually broadly convex midribs. It has up to three large inflorescences (mostly more than 30 cm long) per axil.

The species may be most closely related to *D.* standleyi, which ranges from Nicaragua to Honduras along the Atlantic slope. Both share petioles mostly fully sheathed, and have the sheath margins rolled outward, but *D. panamensis* differs in having blades more coriaceous, matte, and somewhat velvety to glisteningly velvety above, weakly quilted and minutely wrinkled on the upper surface.

Though the species does not occur in the same area, it could be confused with *D. horichii*, a species with a similarly fully sheathed petiole, but the margins of which are incurled rather than flaring. The blades of *D. horichii* dry mostly greenish rather than somewhat blackened. *Dieffenbachia horichii* is restricted to the Pacific slope of Costa Rica, ranging from sea level to 900 m, while *D. panamensis* is primarily known from the Atlantic slope of Panama (also known from the Pacific slope at higher elevations).

Paratypes. PANAMA. Coclé: Alto Calvario, 7 km N of Copé, Folsom et al. 8264 (MO); Alto Calvario, old lumber trail to Las Ricas, Limón & San Juan, Croat 68820 (MO); Alto Calvario Region, 4.5 mi. N of El Copé, 2.5 mi. N of Escuela Barrigón, Croat 67526 (MO); 8 km above El Copé, Hammel 778 (MO), Folsom & Collins 6486 (MO). Darién: Río Tuquesa, ca. 2 air km from Cont. Div., vic. of Kittredge gold mine, Croat 27206 (MO). Panamá: above El Copé, 28 km NW of Penonomé, Read & Watson 84-75 (US).

22. Dieffenbachia pittieri Engl. & K. Krause, Pflanzenr. IV. 23 Dc(Heft 64): 42. 1915. TYPE: Panama. Canal Area [Colón]: Gamboa-Las Cruces [currently Madden Forest Reserve], 50–80 m, 2 July 1911, *H. F. Pittier* 3766 (holotype, US!; isotype, B not seen). Figures 22, 29B.

Herb, to probably less than 1 m tall; internodes 1–1.5 cm long, 1.5–2 cm diam., smooth, drying dark yellow-brown with conspicuous pale petiole scars; *petioles* 10–11 cm long, fully sheathed, free-ending and weakly auriculate on both sides at apex; *blades* obliquely oblong, 17.8–20.5 cm long, 6–8.0 cm wide, 2.9–3.1 times longer than wide, 1.8 times



Figure 22. Dieffenbachia pittieri. Herbarium type specimen.

longer than petioles, shortly acute and markedly inequilateral above, acute to obtuse at base; *primary lateral veins* 6 to 7 per side, concentrating mostly in lower half of the blade, extending parallel to the midrib, then spreading at 25°–30° angle, nearly straight to weakly curved to the margin and sweeping up along the margin, drying moderately obscure above, convex and darker than surface below; minor veins parallel with obscure and irregular cross-veining on drying; surface drying matte, moderately dark yellow-brown above, light brown and finely pale-speckled below. INFLORESCENCES 2 per axil; *peduncles* 3.5–5 cm long, drying light

brown, 2 mm diam.; *spathe* 17 cm long, to 3.5 cm wide when flattened; spadix 14.5 cm long; pistillate portion of spadix to 8.5 cm long, 4 mm wide; staminate portion of spadix 5 cm long; mostly sterile segment 2.2 cm long, drying 2 mm diam., with a few scattered cup-like pistillodes throughout its length; pistils 59, borne in a cup-like disk; staminodia mostly missing.

Distribution and habitat. Dieffenbachia pittieri is known only from the type in the Isthmus of Panama in an area of Tropical moist forest (T-mf) life zone (Holdridge, 1967) at less than 200 m elevation. It is most unusual to encounter an endemic species in this life zone, but the species is distinct from other species in *Dieffenbachia*. There is a possibility that this could be a hybrid between D. killipii and D. isthmia because hybridization does occur in the wild in Dieffenbachia. Its greatest resemblance is with D. killipii, which also occurs in this area and dries a similar color. Dieffenbachia pittieri differs from D. killipii in having a dark brown, smooth-drying stem (light yellow-brown, usually conspicuously ridged stems for D. killipii), fully sheathed petioles (usually with the petiole sheath ending well below the base of the blade for D. killipii), blades with the midrib flat on the upper surface ("square-raised" for D. killipii), and a spadix with the pistillate and staminate portions widely separated by a long, mostly sterile portion (vs. with the pistillate and staminate portions more or less contiguous in D. killipii).

Dieffenbachia pittieri has been confused with D. obscurinervia (Standley, 1944; Croat, 1978), but it proved to share little in common with that species once the type specimen was examined. It differs from that species in having smooth, not scurfy stems, unspotted, fully sheathed petioles, blades with distinct primary lateral veins and with a midrib flat, not "square-raised" above, and a spadix with pistillate and staminate portions separated by a broad sterile segment rather than having them contiguous or nearly so.

- Dieffenbachia seguine (Jacq.) Schott, Wiener Z. Kunst 1829(3): 803. 1829. Arum seguine Jacq., Enum. Syst. Pl. 30. 1760. Arum seguinum, orth. var. Caladium seguinum (Jacq.) Vent., Mag. Encycl. 30. 1801. Dieffenbachia plumieri Schott, Oesterr. Bot. Wochenbl. 69. 1852. TYPE: Plumier, Descr. Pl. Amer. tab. 61 (lectotype, designated here). Figures 23, 30B.
- Caladium maculatum Lodd., Bot. Cab. tab. 608. 1822. Dieffenbachia maculata (Lodd.) G. Don, in Sweet, Hort. Brit. ed. 3, 632. 1839. Dieffenbachia maculata (Lodd.) Bunting, Baileya 10: 145. 1963, nom. superfl. TYPE: Lodd., Bot. Cab. tab. 608. 1822 (lectotype, designated here).
- Dieffenbachia literata Schott, Oesterr. Bot. Wochenbl. 68.
 1852. Dieffenbachia seguine fo. liturata (Schott) Engl., Fl. Bras. 3(2): 175. 1878. Dieffenbachia seguine subvar. liturata (Schott) Engl., Bot. Jahrb. Syst. 26: 568. 1899. Dieffenbachia seguine var. liturata (Schott) Engl., Pflanzenr. IV, 23 Dc(Heft 64): 47. 1915. TYPE: based on a cultivated collection fide Schott (not seen). Schott painting 1874 serves as the type [microfiche 64. c 7] (lectotype, designated here).
- Dieffenbachia lineata K. Koch & Bouché, Index Sem. (Berlin) 14. 1853. Dieffenbachia seguine fo. lineata (K. Koch & Bouché) Engl., Fl. Bras. 3(2): 175. 1878. Dieffenbachia seguine subvar. lineata (Schott) Engl., Bot. Jahrb. Syst. 26: 569. 1899. Dieffenbachia seguine var. liturata (Schott) Engl., Pflanzenr. IV, 23 Dc(Heft 64): 47. 1915. TYPE: New Granada, based on a cultivated collection at the Berlin Botanical Garden, not seen. Schott illustration 1867 serves as the type [microfiche 64 d 7] (lectotype, designated here).
- Dieffenbachia robusta Schott, Oesterr. Bot. Wochenbl. 65. 1854. Dieffenbachia seguine var. robusta (K. Koch) Engl., Bot. Jahrb. Syst. 26: 568. 1899. TYPE: Locality unknown, cultivated collection of unknown origin at Berlin Botanical Garden. Schott illustrations 1907–1908 serve as the type [microfiche 66 b2, b3] (lectotype, designated here).
- Dieffenbachia consobrina Schott, Syn. Aroid. 131. 1856. TYPE: Brazil. Rio Negro, Martius s.n. (holotype, M!).
- Dieffenbachia poeppigii Schott, Syn. Aroid. 130. 1856. TYPE: Peru. Without locality, Poeppig s.n. (holotype, W destroyed during World War II); Schott illustration 1903 serves as the type (microfiche 64. b 6) (lectotype, designated here).
- Dieffenbachia cognata Schott, Syn. Aroid. 130. 1856. TYPE: Suriname. Paramaibo, Martius s.n. (holotype, M). [See also Schott paintings 1845 & 1846.]
- Dieffenbachia gollmeriana Schott, Oesterr. Bot. Z. 8: 387. 1858. TYPE: Venezuela. Without locality, Gollmer s.n. (holotype, B apparently lost); Schott drawing 1857 (microfiche 64 b. 7) serves as the type (lectotype, designated here).
- Dieffenbachia neglecta Schott, Bonplandia 7: 30. 1859. TYPE: Jamaica. Without locality, Distin (holotype, K!).



Figure 23. Dieffenbachia seguine. —A. Habit of plant showing the long creeping caudex and erect portion of stem apex (Croat 60613). —B. Potted plant showing habit and leaves with variegated blades and inflorescences at anthesis (Croat 69695). —C. Close-up of crown of plant with abaxial surfaces of blades and side view of the spathe (Croat 53921). —D. Petiole showing slightly free-ending, inequilateral sheath and acutely sulcate free portion above sheath (Croat 68494). —E. Crown of plant showing speckled petioles and inflorescence at anthesis (Croat 77298). —F. Spathe at anthesis, cut open to show inner surface of tube. —G. Close-up of inflorescence showing apical half with spathe blade somewhat spreading and staminate portion of spadix protruding somewhat forward. —H. Portion of spadix showing bicarpellate pistils. F, G, H. (Croat 71828).

- Dieffenbachia ventenatiana Schott, Bonplandia 7: 30. 1859. Dieffenbachia seguine subvar. ventenatiana (Schott) Engl., Bot. Jahrb. Syst. 26: 568. 1899. Dieffenbachia seguine var. ventenatiana (Schott) Engl. Pflanzenr. IV, 23 Dc(Heft 64): 48. 1915. TYPE: Suriname. Without locality, Hostmann s.n. (holotype, K!).
- Dieffenbachia lingulata Mart. ex Schott, Prod. Syst. Aroid. 334. 1860. Dieffenbachia seguine var. lingulata (Mart. ex Schott) Engl., Fl. Bras. 3(2): 175. 1878. Dieffenbachia seguine subvar. lingulata (Schott) Engl., Bot. Jahrb. Syst. 26: 568. 1899. TYPE: Brazil. Pará: C. Martius 3307 (holotype, M!).
- Dieffenbachia irrorata Schott, Prod. Syst. Aroid. 335. 1860. Dieffenbachia seguine fo. irrorata (Schott) Engl., Fl. Bras. 3(2): 175. 1878. Deffenbachia seguine subvar. irrorata (Schott) Engl., Bot. Jahrb. Syst. 26: 568. 1899. Dieffenbachia seguine subvar. irrorata (Schott) Engl., Pflanzenr. IV, 23 Dc(Heft 64): 48. 1915. TYPE: Brazil. Pará: C. Martius 2640 (holotype, M!).
- Dieffenbachia conspurcata Schott, J. Bot. 2: 52. 1864.
 Dieffenbachia seguine fo. conspurcata (Schott) Engl.,
 Fl. Bras. 3(2): 175. 1878. TYPE: Brazil. Pará: Schott
 paintings 1849 & 1850 (microfiche 65 b5 & b6)
 serve as the type (lectotype, designated here).
- Dieffenbachia barraquiniana Verschaff. & Lem., Ill. Hort.
 11: t. 387. 1864. Dieffenbachia seguine fo. barraquiniana (Verschaff. & Lem.) Engl., Fl. Bras. 3(2):
 174. 1878. Dieffenbachia seguine subvar. barraquiniana (Verschaff. & Lem.) Engl., Bot. Jahrb. Syst.
 26: 568. 1899. Dieffenbachia picta var. barraquiniana (Verschaff. & Lem.) Engl., Pflanzenr. IV, 23 Dc(Heft 64): 50. 1915. TYPE: not designated; the illustration in Ill. Hort. 11: t. 387. 1864, serves as the type (lectotype, designated here).
- Dieffenbachia gigantea Verschaff., Ill. Hort. 13: t. 470, 471. 1866. Dieffenbachia picta subvar. gigantea (Verschaff.) Engl., Bot. Jahrb. 26. 569. 1899. TYPE: not designated; the illustration in Ill. Hort. 13: 470– 471. 1866, serves as the type (lectotype, designated here).
- Dieffenbachia wallisii Linden, Ill. Hort. 17: t. 11. 1870. Dieffenbachia seguine subvar. wallisii (Linden) Engl., Pflanzenr. IV 23 Dc(Heft 64): 47. 1915. TYPE: Brazil. Rio Negro, 1866, Wallis s.n. (holotype, K!).
- Dieffenbachia brasiliensis Veitch, Cat. 12. 1875. Dieffenbachia picta fo. brasiliensis (Veitch) Engl., Fl. Bras. 3(2): 176. 1878. TYPE: Brazil. Not designated; drawing on p. 12 of Veitch Cat. serves as the type (lectotype, designated here).
- Dieffenbachia picturata L. Linden & Rodigas, Ill. Hort. 39: 101. t. 163. [CLXII] 1892. Dieffenbachia picta Schott subvar. picturata Engl., Bot. Jahrb. Syst. 26: 570. 1899. TYPE: Venezuela. Illustration in Ill. Hort. vol. 39: t. 163. 1892, serves as the type (lectotype, designated here).
- Dieffenbachia seguine (Jacq.) Schott subvar. ventenatiana (Schott) Engl., Bot. Jahrb. Syst. 26: 568. 1899. Dieffenbachia seguine (Jacq.) Schott, var. ventenatiana (Schott) Engl., Pflanzenr. IV. 23 Dc(Heft 64): 48. 1915. Dieffenbachia ventenatiana Schott, Bonplandia 7: 30. 1859. TYPE: Suriname. Hostman (K!).

Herb, to 1.5 m tall; stems reclining at base then erect; *internodes* $1.7-5 \times 1.5-4.0$ cm, medium

green and glossy soon becoming dark green, semiglossy to almost matte, smooth. LEAVES arching; petioles 10-34.5 cm long, averaging 29.7 cm long, medium green and weakly glossy, rarely white, sometimes densely pale green maculate, sheathed $\frac{2}{3}-\frac{4}{5}$ or more their length, free part of petiole 5-7 cm long, acutely sulcate; sheath 20-28 long, pale green and matte on inside, usually acute on one side, rounded on the other side, sometimes inequilaterally acute on both sides, curved inward along the margins but the sides not contacting, faintly striate throughout but especially noticeable toward the base, the basal portion of the sheath often persisting after much of the petiole falls free; blades ovate-lanceolate, 17-38.5 cm long, 10-20 cm wide (averaging 32.1×17.3 cm), 2.7–3.3 times longer than wide, 1.2–1.6 times longer than petioles, inequilateral, one side 1.5 cm broader, inequilaterally rounded at base or with one side acute the other rounded, subcoriaceous, semiglossy, medium-dark green, sometimes mottled with pale green or white, especially along midrib, moderately paler below; midrib flattened-convex and slightly paler, ca. 6 mm wide above, narrowly rounded and slightly paler below, sometimes darker green-maculate in lower half; primary lateral veins 13 to 15(19) per side, arising at 40°-50° angle, quilted-sunken and concolorous above, concolorous and concave below; interprimary veins usually present and nearly as conspicuous as primary lateral veins; minor veins moderately indistinct, arising from the midrib and paralleling the primary lateral veins. INFLORES-CENCES 1 to 4 per axil, usually solid green but sometimes pale greenish yellow maculate throughout (maculations sometimes appearing in irregular transverse rows on spathe); peduncles 2.5-14 cm long, $7-8 \times 8-12$ mm diam., medium green, weakly glossy, faintly dark green-striate; spathe 11-24 cm long, abruptly acuminate at apex, gradually constricted above tube, in the upper 2/3, mediumdark green and semiglossy to matte outside, slightly paler and glossy within; spathe blade at anthesis stiffly erect then recurving near apex; spathe tube 7-10 cm long, 1.2-1.8 × 2.0-2.5 cm diam.; spadix 10–19 cm long; the naked portion at base 1.5–2.5 cm long; pistillate portion of spadix 4-8.5 cm long; pistils 20 to 25, closely aggregated except in upper 10-12 mm, with up to 3 of them in a loose spiral across the spadix but usually with 1 or 2 at any level on the spadix; ovary bicarpellate, markedly bilobate, rarely 3- or 4-locular (and 3- to 4-lobate, respectively), pale green, semiglossy, $3.2-3.6 \times$ 2.1-2.4 mm; stigmas pale orange, doubled (one for each locule) but usually fused along the adjoining margins, $2.3-4.3 \times 2.0-2.4$ mm diam.; staminodia 4 per pistil, 2.8-3.1 mm long, 0.8-1.0 mm wide at apex, slightly thickened toward apex, flattened and free at base, the base equally as wide or up to twice as wide as the apex; fertile staminate portion of spadix 5-7.5 cm long, 5-15 mm diam., slightly broader midway, tapering slightly toward both ends, bluntly acute to rounded at apex, at anthesis protruding forward out of spathe and usually being trapped there by the closing spathe; staminate flowers 5 to 6(8?) per spiral, (1.6)2.2-3.5(4) mm diam., squarely rounded to rounded, sometimes broadest perpendicular to the axis, smoothly rounded at apex, sometimes with a transverse linear slit medially; anthers 5 to 6 per synandrium, shedding their pollen well below the rim of the synandrium; the mostly naked portion of spadix 2.0-4.0 cm long, 6-8 mm diam., medium green with 1 pistil in lower 1/3 and with 2 to 3 staminodes in upper 1/2, sometimes with only a few staminodia scattered in upper 34. Berries bright red or orange.

Distribution and habitat. Dieffenbachia seguine ranges throughout much of the West Indies from Cuba (Ileana Arias, Havana, pers. comm.), Jamaica, Hispaniola, and Puerto Rico, through the Lesser Antilles to Trinidad and South America, there ranging throughout much of Venezuela (Amazonas, Aragua, Apure, Bolívar, Carabobo, Delta Amacuro, Distrito Federal, Falcón, Lara, Miranda, Monagas, Nueva Esparta, Portuguesa, Sucre, Táchira, Trujillo, Yaracuy, Zulia), especially in the Cordillera de la Costa, to Guyana and Suriname (Boggen et al., 1992), French Guiana, eastern Brazil (Amapá, Amazonas, Goiás, Maranhão, Pará, Rondônia, São Paulo), and west to the lowlands of Colombia (Meta, Vaupes, Vichada), eastern Ecuador (Napo), and Bolivia (Pando, Santa Cruz).

Dieffenbachia seguine flowers and develops mature fruit to some extent all year-round, but with more flowering occurring in the late dry season and throughout the early part of the dry season between March and September.

The species is characterized by having petioles that are shorter than the blade and sharply sulcate on the free portion, with the sheath margins acute to rounded at the apex and with ovate-lanceolate blades. The best character for separation of the species, however, is the unusual inflorescence with large, bicarpellate ovaries and a spathe that is somewhat spread backward while the staminate portion of the spadix protrudes prominently forward and persists after the spathe has closed.

The species was long considered to be a common species in Central America but that material proved to be mostly *D. oerstedii*, and in some cases, *D.*

wendlandii. The latter species was even erroneously synonymized with *D. seguine* by Engler (1915). Both species sometimes have blades of similar shape, and both have petioles that are comparably sheathed and sometimes sharply C-shaped on the free portion. However, *D. wendlandii* differs in having pistils with a single ovule. The staminate spadix of *D. wendlandii* is also more or less tapered toward the apex and not protruding strongly forward at anthesis, whereas in *D. seguine* the spadix is stubbyellipsoid.

I agree with Bunting (1979), who synonymized both D. picta Schott and D. maculata (Lodd.) G. Don under D. seguine. This species has been the most confusing of all Araceae in the number of epithets (subspecies, varieties, subvarieties, and forms) recognized, over 60 in all. Some are varieties of D. picta, others varieties of D. seguine or combinations between the same two taxa. It is not clear why this should be so. Throughout its range it is no more variable than any other species of Dieffenbachia, but it is quite widespread and this brings it into contact with more workers. Most of the epithets were based on Schott names, but Engler treated most of these as varieties or subvarieties of D. seguine or D. picta. All of the taxa involved share a suite of characters that make it unique, namely the sharply sulcate petioles, the protruding and thickened staminate portion of the spadix, and bicarpellate ovaries.

A cultivated collection from Grenada (*Croat* 77298) had sap that was celery-scented, not at all smelling of oxalic acid, typical of so many *Dieffenbachia* species. *Croat* 78323, from Venezuela, also has a sweet- rather than a foul-scented sap.

Engler (1915) placed *Dieffenbachia lancifolia* Linden & André into synonymy with *D. picta*, but the former is a distinct species from Antioquia Department, Colombia. Also excluded are combinations of the name, *Dieffenbachia picta* Schott forma *lancifolia* (Linden & André) Engl. and *D. picta* Schott subvar. *lancifolia* (Lind. & André) Engl.

Also erroneously placed in synonymy with *D. picta* was *Dieffenbachia meleagris* Linden & Rodigas and the combination subvariety *meleagris* Engl. That species is from Ecuador (see illustration 159 in Ill. Hort.) and looks like it might be synonymous with *D. spruceana* Schott.

Dieffenbachia shuttleworthiana Engl. was synonymized with *D. picta* but should be excluded along with the following combinations: *D. picta* forma schuttleworthiana (Regel) Engl. and *D. shuttle*worthiana Hort. Bull. This Colombian species is not closely related to *D. seguine*.

Additional specimens examined. André 1202 (K), Cadet 6030 (K). BOLIVIA. Pando: Nicolas Suárez, a few km N of Cobija, Beck 17103 (LPB, MO). Santa Cruz: Velasco, 10 km SE of buildings of Est. Flor de Oro, Nee 41364 (MO, NY). BRAZIL. Engler 226 (K, P), Engler 227 (K, US). Mato Grosso Sul: Catharino et al. 1909 (SP). Pará: Mpio. Capanema, Río Quatipuru, near Miraselvas, ca. 30 km by rd. W of Bragança, Davidse et al. 18102 (MO); Río Anajás, Anajás-Vista Alegre, Cuanta do Anajás, Beck et al. 295 (NY); Río Anajás, Ilha do Marajó, Prance et al. 30247 (MO). Rondônia: Alta Floresta do Oeste, Rodovia P-50, Goncalves et al. 224 (MO). São Paulo: São Paulo, Instituto de Botanica de São Paulo, Secão de Fitoecologia, Lotto s.n. (K, MO). COLOMBIA. Vaupes: Río Kuduyari, tributary of Río Vaupes, Schultes & Cabrera 17890 (NY). Vichada: Río Meta, Manati, Cuatrecasas 4225 (US). ECUADOR. Napo: Auca Oil Field, Ingram 1169 (MO, SEL). FRENCH GUIANA. Vic. of Saül, route to Béllizon, 100-300 m past Eaux Claires, Croat 74137 (MO, US, VEN); Piste de Bélizon, pk 21.8, Billiet et al. 6257 (MO); Crique Gabaret, bassin de l'Oyapock, Cremers 9896 (CAY, K). Cayenne: Colline de Montravel, Ile de Cayenne, Le Goff A. 95 (CAY, MO); Piste de Saint-Elie, 15.7 km S of ORSTOM camp, Prevost 3258 (CAY, MO), Prevost 3580 (CAY, MO); Centre ORSTOM de Cayenne, Prévost 3382 (CAY, MO); Saint-Laurent-du-Maroni, Saül, trail to Mont Galbao, Mori & Gracie 18717 (MO, NY). PERU. Loreto: Alto Amazonas, Dtto. Manseriche, Pongo de Manseriche, R. Rojas et al. 607 (B, MO, US, WU). VENEZUELA. Amazonas: Río Guainia, S of Maroa, Maguire et al. 36461 (NY); Cãno Mosquito, Cãno Marieta, Lister & Colchester 272 (K); Tencua, Colchester 2108 (K); Dpto. Atabapo, Río Cunucunuma, Raudal Picure, J. Pérez & M. Sosa 671 (MO); Cãno Majagua, E. & S. Zent 2189 (MO); Casiquiare, Río Guainia, Bunting et al. 4108 (NY); Dtto. Atures, Río Cataniapo, 45 km SE of Puerto Ayacucho, Stevermark et al. 122412 (MO). Apure: Dtto. San Fernando, Río Arauca, 5 km SW of El Faro, Davidse & González 13410 (MO). Aragua: betw. Maracay and Ocumare de la Costa, Henry Pittier NP, 1.6 km N of summit, Croat 60567 (CM, F, MO); Pittier Park, Paraiso trail to Pico Periquito, Croat 21412 (MO); Ocumare-Portachuelo, Stevermark & Rogers 119364 (MO, USS); Portachuelo-Paraiso Trail, near Rancho Grande, Bunting et al. 1937A (NY); Rancho Grande to the Toma, Bunting et al. 1949A (NY); 12 km NW of Rancho Grande, Bunting 2035 (NY), Bunting 2036 (NY), Bunting 2622 (NY); Maracay, campos de la Facultad de Agronomía y Centro de Investigaciones Agrícolas, Univ. Central de Venezuela, near Pozo del Diablo, Bunting 2026A (NY); vic. Maracay, Bunting 2027 (NY); Río Tuy, NE of Maya, 7 km SE of Colonia Tovar, Steyermark & Liesner 121834 (MO). Bolívar: La Gran Sabana, El Dorado-Santa Elena, km 202, S of Salto Kamá, Davidse et al. 4844 (MO); base of Altiplanicie de Nuria, Bunting & Holmquist 4319 (NY); W of Hato de Nuria, Stevermark 88864 (NY, US); Río Karuai, base of Sororopan-tepui, W of La Laja, Stevermark 60796 (NY); near El Paito, 5 km S of Caño Paso Ancho, Bunting & Trujillo 2236 (NY); Kamarata, Bogner 965 (M). Carabobo: PN San Esteban, Río San Esteban, Benítez de Rojas et al. 4661 (MO, MY); Río San Gian, 5-6 km S of Borburata, Stevermark 94331 (MO, US). Delta Amacuro: Río Amacuro between "vuelta larga" and Cerro Wuausa, Dept. Antonio, Trujillo et al. 17397 (MY). Distrito Federal: Fila Las Delicias above Naiguatá, Bunting & Manara 2124V (NY), Drake 7 (P, US); Cerro Naiguatá, 6 km SW de los tanques de la Electricidad de Caracas (Cocuizal), Steyer-

mark 91896 (NY, US); Los Caracas-Higuerote Rd., between km 5 and Osma, Bunting & Fernandez 3295 (NY); Pico Naiguatá, Fila Las Delicias Naiguatá, vic. Las Delicias, Bunting & Manara 2126 (NY), Bunting & Manara 2119 (NY); Río San Julián, just above Caraballeda, Bunting 2044 (NY). Falcón: PN Quebrada de la Cueva El Toro, Liesner et al. 7681 (MO). Lara: Dtto. Jiménez, PN Yacambú, Quebrada Negra, Davidse & González 21012 (MO). Miranda: Cerros del Bachiller, 5.5 km S of village Santa Cruz on Hwy. 9 between Guatire and Cupira, Croat 53956 (MO); Cerros del Bachiller, near E end, 10 air km W of Cúpira, Stevermark & Davidse 116647 (MO); PN Guatopo, Fila la Guzmanera, Santa Teresa-Altagracia de Orituco, ca. 8 km S of jct. of rd. to Caucagua, Bunting et al. 2072 (NY), 2074 (NY); Sta. Teresa-Altagracia de Orituco, Aristeguieta 1764 (NY), Croat 21741 (MO); Caucagua, 600 m, Bunting et al. 2073 (NY). Monagas: Morichal Las Tetas, tributary of Río Tonoro, near Aguasay, Montes s.n. (MO); Caripe-Santa Ines Rd., ca. 3 km E of Teresen, Colorado-Los Cigarrones, Río Colorado, Bunting 2729 (NY); Jusepín-Barcelona Rd., 6 km SW of Jusepín, Bunting 2738 (NY); Caripe-Maturín Rd., Bunting 2678 (NY); Morichal El Esfrerzo, Jusepín, M. Heredia 60 (MO). Nueva Esparta: Margarita Island, Juan Griego trail, J. R. Johnston 305 (NY, US). Portuguesa: Quebrada Algarrobo, tributary of Río Morador, 7 km NE of Boca de Monte, 22 km NE of Río Suruguapo, Steyermark et al. 127204 (MO); Guanare-Biscucuy Rd., El Puente, 21 km above jct. of Guanare-Barinas rd., Bunting 3321 (NY); Dtto. Araure, Río Auro (La Lucia), NW of Sta. Lucia, Aymard & Ortega 3090 (MO); Dtto. Guanare, Guanare-Barinas, Mpio. Mesa de Cavacas, Stergios et al. 7940 (MO, PORT). Sucre: El Pilar-Guariquén, El Pilar and Guariquén, 4-10 km S of El Pilar, Croat 54380 (MO). Táchira: 8 km S of El Pinãl, Steyermark et al. 102036 (MO, MY); San Cristóbal-Chorro del Indio, Caño Secto-La Florida, km 14-20 al E de San Cristóbal, Bunting 11687 (MO); vic. Las Minas, N of La Laguna, 16 km SE of Santa Ana, Stevermark & Liesner 118891 (MO). Trujillo: Sabana-Mendoza, ca. 5 km below Betijoque, Bunting 2829 (NY). Yaracuy: Las Trincheras-El Cambur, N of Salom (NE of Nirgua, W of Valencia) on rd. to Candelaria, Croat 54649 (CM, MO); Marín and Aroa, Sierra de Aroa, Dtto. Felipe between Albarico and Tesorero, 9.8 km N of jct. of hwy. 1 at Marín, Croat 60613 (MO); Sierra de Aroa, PN Yurubí, 0-2 km N of San Felipe, Río Yurubí, Liesner & A. González 10126 (MO, NY); Sierra de Aroa, vic. Aracal, 7 km above San Felipe, Bunting et al. 1997 (NY); Cerro La Chapa, N of Nirgua, Stevermark & Bunting 97728 (NY); Dtto. Nirgua-Dtto. San Felipe, Cerro La Chapa, 7 km N of Nirgua, Davidse et al. 20914 (MO); Cerro La Chapa, Stevermark et al. 100213 (NY, US); Cerro La Chapa, Stevermark et al. 100318 (US), Stevermark et al. 100239 (US); Dtto. Nirgua, Salom-La Candelaria Rd., Cumbre Gamelotal, Meier et al. 5164 (MO, VEN); Dtto. Bruzual, Montaña de María Lionza, W of Sorte, Steyermark et al. 124955 (MO); Dtto. San Felipe, PN Yurubí, Aymard et al. 2714 (MO); Dtto. Urachiche, Quebrada Higueronal, W of Urachiche, vic. Sabana de Méndez, Steyermark et al. 124629 (MO); Río Guayabito, 15 km N of Marín, Steyermark & Bunting 105293 (MO). GREATER ANTILLES: HAITI. Nash 611 (NY); massif de la Lelle, Port au Prince, Mantflurry, Ekman 1983 (K). HISPAÑIOLA. SANTO DO-MINGO. San Cristóbal: Cordillera Central, San Cristóbal, Hato Damas-Mano Matuey, Croat 68582 (MO). Barahona: Fuertes 564 (GH); Santo Domingo, Zanoni et al. 27170 (GH, MO, NY); El Aguacate, La Leonor, Moncion,

Liogier 13307 (GH, NY); Carib Territory, Bataka, J. Higgins 119 (MO, NY); Sierra de Baoruco, Arroyo La Travesia near the La Travesia sugar mill, Zanoni et al. 25159 (MO, NY). El Seibo: El Guaraguao-Los Hurados, Miches-Higuev, km 15, Mejia & Ramirez 9929 (MO, NY). Monseñor Nouel (Peravia): Cordillera Central, Río Yuboa, Zanoni et al. 23113 (MO, NY); Cordillera Oriental, Arroyo de Agua, 11.7 km W of El Valle, Croat 68494 (MO); 9.2 km SE of Miches, along Río Yeguada, Arroyo Santiago, Croat 68547A (JBSD, K, MO). Samana: 2.3 km S of Playa El Valle, Mejia & Zanoni 6614 (MO, NY); Sanchez, Las Canitas Mts., N. Taylor 48 (NY); Sanchez Ramirez, Rose et al. 4375 (NY); Río Cevicos, W of Cevicos, 22 km E of Cotuí, Zanoni & Pimentel 23420 (MO, NY). San Cristóbal: San Cristóbal, a Jina (de Yamasa), 16 km del Parque Central de Yamasa, Zanoni & Pimentel 23456 (MO, NY); near Río Nigua, Lavastre 1845 (NY); near Nigua River, La Toma, Augo 1693 (NY); El Dajao, Bayaguana, Liogier & Liogier 20185 (NY). JAMAICA. Port António: Hitchcock s.n. (MO); Fury River, Harris 8361 (NY); John Crow Mts., Britton 4126 (NY). Portland: foothills of John Crow Mts., W of Ecclesdown, Gravum et al. 9973 (K, MO). St. Elizabeth: Frenchman, Proctor 38601 (NY). PUERTO RICO. Without exact locality: Engler 2793 (K), Sintenis P. 2793 (K), Britton & Britton 9664 (NY), Britton & Britton 7897 (NY); Maricao, Sargent 643 (MO); San Sebastian, Sargent 340 (MO); Laguna Tortuguero, Howard & Nevling 16978 (A); Quebrada Prieta, El Verde Field Station in Luquillo Experimental Forest, W side of Luquillo Mts., Whitehill 8 (MO); Luquillo Mts., Palmer-Florida, km 28.1, R. Wagner 558 (A); Río Abajo State Forest, Hwy. 621, Croat 60867 (MO, NY, PMA, RSA); km 21.5 on Rte. 2, W of Candelaria, Solomon 5761 (MO); Mayaguez vic., Cowell 550 (NY), Britton & Shafer 1625 (NY), Britton & Britton 10082 (NY); Mpio. Maricao, Bo Indiera Fria, Rt. 425, 0.3 km S of Rt. 105, Atha & Zanoni 770 (MO); Coamo, Woodbury et al. s.n. (MO); Caribbean Nat. For., ca. 1 km N of Río Sonadara, Hwy. 186, Thompson 3238 (MO); Mpio. Lugillo, Route 988, 1 mi. E of intersection with rt. 983, Miller & Taylor 5937 (MO); Río Piedras, Cowgill 532 (NY). LESSER ANTILLES: VIRGIN ISLANDS. St. John: N Bordeaux Mountain, Coral Bay Quarter, 100 m from communications tower, Acevedo-Rodríguez 4705 (MO, NY). Tortola: Carrot Bay, D'Arcy 769 (MO), Fishlock 326 (K). ST. KITTS. Britton 447 (NY). LEEWARD ISLANDS: DOMINICA. Roseau-Sulfur Springs, Howard 11744 (A); N of Calibishie, Hodge & Hodge 3174 (GH); Milton Estate, Hodge 2929 (GH); Castle Bruce Valley, Beard 656 (GH); St. Patrick Parish, Cote d'Or, Nicolson 2060 (GH), Lloyd 237 (NY); St. Mark Parish, Sulphur Springs area, S. Hill 24812 (NY). GRENADA. Near Mt. Horn, towards Birch Grove, Simmonds s.n. (K). GUADELOUPE. Guadeloupe: Duss 3790 (NY, US); Admdiv. Basse Terre, Piste vers 3e chute de Carbet, F. Billiet & B. Jadin 7359 (BR, MO); Basse Terre, Grande Etang (Près des chutes du Carbet), Billiet & Jadin 7357 (MO), Billiet & Jadin 7358 (BR, MO); Basse Terre, Crique Lézarde, Billiet & Jadin 7346 (BR, MO), Billiet & Jadin 7347 (MO). Marie Galante: ravine of Riviere de St. Louis, Grand Bassin-Les Balisiers, Proctor 20987 (A, US). WINDWARD ISLANDS: MARTINIQUE. M. Hahn 945 (GH, K, P, US), P. Duss 21496 (NY). ST. LUCIA. Sturrock 352 (A); Anse Louvet near nursery, Slane 634 (A), Howard 11564 (A). ST. VIN-CENT. H. H. Smith & G. W. Smith 1411 (K, NY). TRIN-IDAD. Arima-Blanchisseuse rd., at mi. 4, Croat 53921 (HUA, K, MO, NY, TRIN, VEN); Arima-Blanchisseuse Rd., near milepost 7 3/4, Philcox 8231 (K).

Cultivated specimens. Society Islands. Leeward. Raiatea Island, cultivated in Uturoa, 17 Dec. 1926, J. W. Moore 451 (MO). U.S.A. Hawaii: Honolulu, Kalihi Valley, 15 Mar. 1956, Harris & Neal s.n. (BISH); Foster Gardens, 3 Mar. 1962, Miyashiro s.n. (BISH); Lyon Arboretum, 10 Sep. 1975, D. Herbst & S. Ishikawa 5459 (BISH); Oahu, 5 May 1954, Won s.n. (BISH); Honolulu, Kaimuki, 5 May 1954, R. Won s.n. (BISH); Kapalama Heights, Kamehameha Girls School, 6 June 1932, Judd et al. s.n. (BISH). Missouri: Missouri Botanical Garden, originally obtained from J. Henny, Apopka, Henny 7 (MO), Croat 78287 (MO); 13 Sep. 1990, Miller & Schmidt 5551 (MO). Puerto Rico. Río Abajo (originally collected by Thompson 3238), 19 June 1997, Croat 78345 (MO). Hispañiola. Border of PN Los Haitises, 27 Apr. 2000, Luther s.n. (Holst 6237) (MO). Grenada. Originally collected by John Criswick, Grenville, Grenada, 1993, Croat 77298 (MO, VEN). Belize. Cavo: Nabatunich, near Sukkotz, 17°06'N, 89°W, 24 Jan. 1990, Balick et al. 2359 (MO). Venezuela. Carabobo: originally collected by Bunting from a Garden in Valencia, 300-500 m, (Bunting 13515) Croat 78323 (MO, VEN); Jardín Botánico, Caracas, 19 Aug. 1976, Croat 38344 (MO).

24. Dieffenbachia standleyi Croat, sp. nov. TYPE: Honduras. Lancetilla Botanical Gardens, ca. 2 mi. WSW of Tela and S of main hwy., 15°44'N, 87°27'W, 70–90 m, 9 Feb. 1987, *T. B. Croat & D. Hannon 64638* (holotype, MO-3442883!; isotypes, B!, CAS!, COL!, EAP!, F!, GH!, INB!, K!, MEXU!, PMA!, NY!, TEFH!, US!, USCG!). Figures 24, 28B.

Planta 0.6–1.5(3.0) m alta; internodia 3–6(10) cm longa, 6–11 cm diam.; petiolus 12.5–52 cm longus; lamina elliptica vel obovato-elliptica, 31–84(103) cm longa, 12.5–39 cm lata, nervis primariis lateralibus 12–24 utroque; inflorescentia 2–4 per axillam; pedunculus ad (7.5)15–29 cm longus; spatha 20–50 cm longa.

Terrestrial herb, frequently in streams or on stream banks, 0.6-1.5(3.0) m tall; sap foul-smelling, caustic and irritating; internodes 3-6(10) cm long, 6-11 cm diam., dark green, semiglossy; petioles 12.5-52 cm long (averaging 26 cm long), matte, light green, paler than stem, finely and densely striate throughout, sheathing nearly always to the base of the blade, the margin usually markedly undulate and thin, sometimes with the apical portion curled outward, otherwise erect, often drying undulate, free unsheathed portion 1-5 cm long (averaging 2 cm long); blades elliptic to obovateelliptic, 31-84(103) cm long, 12.5-39 cm wide (averaging 54 \times 23 cm), 1.7–3.1 times longer than wide (averaging 2.5), 2.1-4.6 times longer than petiole (averaging 3.2), inequilateral, one side 3-4 cm wider, abruptly acuminate at apex, somewhat inequilateral and acute to weakly attenuate or rounded to obtuse at base, coriaceous, dark green and semiglossy to glossy above, paler green and matte below, drying medium gray to dark brownish gray above, paler and yellowish gray to pale yellow-



Figure 24. *Dieffenbachia standleyi* (*Croat 42676*). —A. Habit of cultivated plant. —B. Stem and base of leaves. —C. Upper part of stem showing abaxial surface of leaf blade and cluster of inflorescences. —D. Close-up of petiole bases showing the markedly undulate petiole sheaths.

brown below; midrib slightly paler and flat to sulcate and finely paler striped above (especially near the base), sometimes white in distal ²/₃, convex to narrowly rounded, thicker than broad and paler to slightly paler below, drying 8-12 mm wide, medium yellow-brown, finely ribbed with the ribs minutely and obscurely scabridulous on magnification; primary lateral veins 12 to 24 per side, arising at an acute angle, then spreading at $40^{\circ}-65^{\circ}(70^{\circ})$ angle, obtusely sunken and weakly quilted, paler toward midrib above, bluntly angular and \pm concolorous below, drying pale yellow-brown; lower surface with minor veins moderately obscure, arising mostly from the midrib but also from the primary lateral veins. INFLORESCENCES 2 to 4 per axil; peduncle to (7.5)15-29 cm long (averaging 16 cm long), somewhat flattened; spathe matte, 20-50 cm long (averaging 28.3 cm long), 1.2-3.1 times longer than the peduncle (averaging 1.6 times longer), 2.5-3.0 cm diam.; spadix 20-30 cm long (averaging 25 cm long); pistillate portion of spadix 12-13 cm long; staminate portion 15-16 cm long. Fruits to 1 cm long, closely packed, reddish orange to scarlet at maturity with the spathe light yellow.

Distribution and habitat. Dieffenbachia standleyi ranges from Honduras (Atlántida, Comayagua, Cortes, El Paraíso, Gracias a Dios, Olancho, Yoro) to Nicaragua (Matagalpa and Zelaya) at 30–1000 m elevation. Most collections in Honduras were made in the Lancetilla Valley.

Phenology. Flowering specimens of *D. standle-yi* have been seen from May through September, although a few flowering collections were also made as early as February and March. Fruits start to develop in February and reach full size during March or April (in Nicaraguan collections) or July–August (in Honduras).

Discussion. The species is characterized by its stout stem, fully winged petioles, yellow-brown-drying ovate-elliptic blades with 12 to 24 pairs of primary lateral veins, and a long spathe (20–50 cm). It is most easily confused with *D. horichii* and may ultimately prove to be inseparable from that species. *Dieffenbachia horichii* differs in having shorter petioles with the sheath involute and moderately smooth, in contrast to the petiole sheaths erect and even curled outward as well as being undulate along the margins in *D. standleyi*.

A collection by *Stevens et al. 20998* from Matagalpa is unusual in being described as 3 m tall with a trunk 10 cm in diameter. Another Stevens collection (7457) from Zelaya Department is noteworthy in drying darker yellow-brown than other collections. Specimens from Nicaragua differ somewhat from those in Honduras, having leaf blades smaller on average, ranging from 37 to 69 cm long and 13 to 31 cm wide (averaging 51 \times 22.3 cm), but the petioles in both areas average 30 cm long. The Honduran populations have petioles consistently fully sheathed, whereas plants in Nicaragua often have a free portion of the petiole above the sheath ranging from 1 to 9 cm (averaging 4.4 cm long) with the petioles only rarely fully sheathed.

Blade shape is quite variable. Blades can be from 1.9 to 2.8 times longer than wide on the same plant (e.g., *Croat & Hannon 64638*). Plants from the Lancetilla Valley in Honduras have proportionately longer blades, with some plants having blades up to 3.2 times longer than wide (*Croat 42676*). Specimens collected at Lancetilla and its surroundings have blades that range from 1.9 to 3.5 times longer than wide (averaging 2.5 times longer than wide). Specimens from areas other than Lancetilla, and outside Honduras, have blades 1.6 to 2.7 times longer than wide (averaging 2.1 times longer than wide).

A collection from Zulia, Venezuela, between La Fría and San Juan de Colón (*Croat 78289*) differs in having the petiole less fully sheathed and in having narrower blades up to 2.6 times longer than broad and drying somewhat less blackened. It may prove to be the same species. If so, it would be the only Central American species (with the possible exception of *D. killipii*) that ranges from Central America to Venezuela.

Etymology. Dieffenbachia standleyi was first collected in 1928 by Paul Standley at Lancetilla, Honduras. Standley was not only the author of most of the aroid treatments for most existing Central American floras, but he also described a number of new species of Araceae, as well as collecting several paratypes of *D. standleyi*. The species is named in his honor.

Paratypes. HONDURAS. Atlántida: 5 km S of La Ceiba, Madison 705 (GH); near Lancetilla, Yuncker 4961 (F, MO, NY); Lancetilla valley, near Tela, Pfeifer 2124 (US); near Puente Alto stop on S.F. Co. R.R., E of Ceiba, Yuncker et al. 8551 (F, GH, MO, NY, US); ca. 3 mi. S of Tela, Webster et al. 12581 (DAV); vic. Tela, near Río Lancetilla, above Exp. St., MacDougal et al. 3303 (MO, NY, US); Tela, ca. 10 mi. SE of Tela along Río Lancetilla, Croat 42625 (MO), Croat 42676 (MO), Standley 53146 (F, US). Comayagua: Siguatepeque, Standley & Chacón 6701 (F). Cortes: 2-3 mi. SW of Omoa on rd. from Puerto Cortes to Guatemalan border, Croat 42556 (MO); El Paraíso, Yuscarán, Río de los Aguacates, Standley 25700 (EAP). Gracias a Dios: Ahuas Bila, 200 km SW of Puerto Lempira, Nelson & Cruz 9291 (TEFH, UNAH, US). Olancho: Catacamas, Standley 18786 (EAP); along Río Olancho, W of main Tegucigalpa-Catacamas Hwy., ca. 1

km upstream from and NW of Puente Boquerón, 8.6 mi. SW of Catacamas, 6 mi. SW of Sta. María del Real, Croat & D. Hannon 64109 (INB, MEXU, MO, TEFH, US); along Río Olancho, on rd. Gualaco-San Esteban at Río San Martín, 19.3 mi. E from Gualaco, 8.7 mi. SW of San Esteban, Croat & D. Hannon 64317 (B, MO, US); Río Olancho, San Esteban-Bonito Oriental, 19 mi. NE of San Esteban, Croat & D. Hannon 64476 (MO); Refugio de Vida Silvestre "La Muralla," Nelson & Andino 16247 (TEFH); Mpio. Jano, 16 mi. NE of La Unión along the rd. to Olanchito, Davidse et al. 35484 (MO). Yoro: near Puente Grande, on a tributary of the Río Agua (Río Puente Grande), Blackmore & Chorley 4073 (MO). NICARAGUA. Matagalpa: El Toma Rd., Neill 1571 (MO); ridge along rd. betw. La Danta and La Luna, E of Esquipulas, Stevens 11786 (CAS, MO, TEX); Macizos de Peñas Blancas, SE side, drainage of Quebrada El Quebradon, Hda. San Martín, border with Departmento de Jinotega, Stevens et al. 20998 (MO); Matagalpa-Siuna, 1.5 km al NE de Los Angeles, Moreno 17142 (MO); El Trébol, 7 km S of Peñas Blancas, rd. to El Tuma, Moreno & Robleto 20526 (MO). Zelaya: Finca Waylawas, Pipoly 4479 (MO, US); Siuna-Matagalpa, ca. 31.4 km beyond Río Ulí (near Waní), ca. 8.9 km beyond Rosa Grande La Balsama, Stevens 7457 (MEXU, MO); Cerro Livico, 7 km NE of Siuna, Neill 3629 (MO); Río Sucio, E of Bonanza, Stevens 12311 (MO), Stevens 8044 (MO); Res. Bosawas, Bonanza, Cerro Cola Blanca, vic. Cacerio de Vitinia, Rueda & Coronado 6557 (MO).

25. Dieffenbachia tonduzii Croat & Grayum, Novon 9: 497. 1999. TYPE: Panama: Bocas del Toro: Valle del Silencio, along Río Changuinola, ca. 1 km above mouth of Río Teribe, vic. Teribe Indian population, disturbed forest among cocoa plantations, 9°21'40"N, 82°31'40"W, less than 100 m, 25 June 1994, *T. B. Croat & G. Zhu 76452* (holotype, MO-04611212!; isotypes, AAU!, B!, BM!, BR!, CAS!, CM!, COL!, CR!, DUKE!, F!, GH!, HUA!, INB!, ITIC!, JAUM!, K!, L!, LE!, M!, MEXU!, NY!, P!, PMA!, QCA!, QCNE!, R!, RSA!, S!, SCZ!, SEL!, TEX!, UB!, US!, VEN!, WU!). Figures 25, 29B.

Terrestrial herb, 0.5-1.5 m tall, usually to less than 1 m tall; internodes 1.5-4.5(-6) cm long, 1.5-3(-4.5) cm diam., usually solid dark to medium green, sometimes faintly marbled with gray-green or yellowish gray throughout (on plants that also have streaked petioles), initially weakly glossy, becoming semiglossy to glossy, often with a subvelvety sheen; petiole scars manila to white, curved downward on the opposite side of the stem and ending unevenly; petioles 10-24 cm long (averaging 17.6 cm long), held \pm erect, medium green (except sometimes white to pale green at base), almost matte to weakly glossy, weakly striate (especially near the base), narrowly rounded to obtusely angular on abaxial surface and often white medially, sometimes streaked in a variegated pattern

throughout (this white coloration continuing onto the midrib), sheathed virtually throughout; sheath erect to involute (rolled inward throughout in age), free-ending and unequally rounded at apex, prolonged to 2 cm beyond the base of blade; unsheathed part obsolete or rarely to 1 cm long (when evident obtusely flattened); blades ovate to ovateelliptic or oblanceolate-elliptic, (15-)25-48(-63) cm long, (8–)15–32 cm wide (averaging 34×16 cm), broadest near the middle, sometimes below, frequently above the middle, 1.4-2.5(-3.5) times longer than wide (averaging 2.1 times longer than wide), 1.9-3 times longer than petioles, spreading to erect-spreading, inequilateral, one side 1-3 cm wider than the other, gradually to abruptly acuminate, sometimes acute at apex, inequilaterally cordulate at base, one side sometimes broadly rounded to obtuse, the other side cordulate, sometimes inequilaterally acute, subcoriaceous, often conspicuously quilted, moderately bicolorous; upper surface usually solid dark to medium green, sometimes conspicuously to sparsely variegated with pale green or pale yellow throughout much of the surface, the mottling large or small, but somewhat restricted to the area midway between the midrib and margin, matte to weakly glossy, sometimes appearing weakly velvety, drying gray-green to olive-green or dark brown; lower surface much paler and matte to weakly glossy, silvery-green, drying yellowish green to yellow-brown below; midrib flat to broadly rounded and moderately to strongly paler, pale green or sometimes creamy white above (sometimes only toward the apex), bluntly acute to obtusely angular and paler, sometimes white or creamy white below, (0.6-)1-1.7 cm wide; primary lateral veins (14 to)18 to 25(to 30) per side, arising at an acute angle and spreading at 45°-90°, sometimes reflexed toward the base, prominently to weakly and obtusely sunken above, convex to weakly raised and darker than surface or concolorous below, some of the lowermost with a weak fold near the base (Croat & Grayum 60112), sometimes convex-pleated below; interprimary veins almost as conspicuous as the primaries; minor veins moderately to distinctly visible, darker than surface below. INFLORES-CENCES 1 to 2(to 4) per axil, often with two oriented in opposite directions; peduncle (3-)6-17 cm long (averaging 10.3 cm long), 7-8 mm diam., weakly glossy, dark to medium green, sometimes with pale yellow-green streaks; spathe (12-)15-28 cm long (averaging 20 cm long), 2-4 times as long as peduncle, acuminate at apex, convolute to about the middle in lower part, matte to weakly glossy outside, glossy within, solid medium green on both surfaces, gradually and weakly constricted some-



Figure 25. *Dieffenbachia tonduzii.* —A. Close-up of stem, showing both creeping and erect portions. —B. Habit with inflorescences and variegated blades. —C. Crown of plant with open inflorescence. —D. Close-up of stem showing petioles streaked with creamy white. —E. Close-up of stem showing solid green petioles. —F. Close-up of spathe with the blade portion open (*Croat & Zhu 76452*, type plant). —G. Inflorescence open to show upper male flowers and lower portion of spadix with pistils and staminodia (*Croat 66533*). A, B, C. (*Croat & Zhu 76452*, type plant); D, E. (*Croat 76450*).

what above the middle; spathe tube 1.5–3 cm diam. when closed, 6.8-9 cm wide when flattened; constricted area 4.3-4.5 cm wide flattened; spadix (9-)16.5-25.5 cm long, about as long as or up to 3.0 cm shorter than the spathe; free portion 7.8-8.5 cm long; pistillate portion (4.8–)6–11.5 cm long; mostly sterile portion sparsely flowered to naked (rarely lacking, as in Croat 70768), 1.8-4.0(-8.5) cm long with 0.6–1.5 cm totally bare, the uppermost portion with a few staminodia, sometimes with a few scattered staminodia throughout, the lower half sometimes with an occasional pistil and much reduced staminodia, rarely with the female flowers \pm equidistant and nearly contiguous with staminate part (Croat 70768); fertile staminate portion (4–)5.5–10 cm long, 7-10 mm diam., slightly broader midway, weakly tapering to apex and base, bluntly pointed at apex; staminate flowers 5 to 6 per spiral, \pm rounded in outline, crenulate along margins, truncate at apex; sterile male flowers irregularly shaped, 1.8-2.5 mm diam.; pistillate portion of spadix to 11 cm long, 9-10 mm diam.; female flowers (15 to)48 to 62, closely aggregated except in the upper 1.5 cm of spadix, 4 to 5 across the width of the spadix (uppermost pistil borne on an almost bare segment of the spadix); pistils pale cream-yellow to pale yellow-green, smooth, 2.3-3.5 mm diam.; style (after stigma has fallen) sharply cupuliform, 1.5-1.7 mm diam. with a single central pore; stigmas yellow; staminodia clavate, white, 2-3 mm long, mostly contiguous and sometimes fused at base. INFRUCTESCENCES with spathe pale yellow; berries red to red-orange, 5-8 mm diam.

Distribution and habitat. Dieffenbachia tonduzii ranges from southeast Nicaragua throughout Central America to the Pacific slope of Colombia (Antioquia, Chocó, Cauca, Valle) and Ecuador (Esmeraldas, Loja, and Los Ríos), from sea level to 1400 m, in *Tropical wet forest* (T-wf) and *Premontane rain forest* (P-rf) in Central America and in *Tropical wet forest* (T-wf) and *Premontane wet forest* (P-wf) and *Tropical wet forest* transition to *Premontane* (T-wf/P) in Colombia.

Phenology. Flowering in *D. tonduzii* occurs throughout most of the year with flowering collections seen from February through November. Most collections have been made from April through August. According to the collections, fruits mature throughout the year but with the greatest concentration from October to January.

The species is characterized by its fully sheathed petioles, usually matte to weakly glossy, sometimes weakly velvety blades with cordulate bases and numerous, broadly spreading primary lateral veins. Because of the fully sheathed petioles it can be confused only with *D. horichii* and *D. crebripistillata*. Both of the latter typically have much larger leaves that are not at all cordulate at the base (though they are rarely broadly and weakly subcordate). *Dieffenbachia tonduzii* is polymorphic with regard to leaf markings in the same way as *D. oerstedii*, and is quite variable in all respects. It appears, in Panama, to hybridize with *D. oerstedii*. *Croat & Zhu 76857C* from the vicinity of Santa Fé in Veraguas Province is apparently a hybrid with characteristics intermediate between *D. tonduzii* and *D. oerstedii*.

The species is similar to *D. daguensis*, a Colombian species described from less than 200 m elevation on the Río Dagua in Valle Department. That species also has many rather close primary lateral veins and a fully sheathed petiole but differs in having the staminate and pistillate sections of the spadix contiguous or nearly so. In addition, it differs in having much shorter petioles (described as being up to 5 cm long).

A South American species, *D. parlatorei* Linden & André, also sometimes has petioles fully sheathed, but differs from *D. tonduzii* in having leaf blades usually broadest above the middle, semiglossy on the lower surface, and the midrib often broadly rounded and spongy. It also has the primary lateral veins arising at a 40° - 60° angle from the midrib (often at more than 60° and sometimes up to 90° in *D. tonduzii*).

Croat 70900, from 250 m in Chocó Department of Colombia, appears to be *D. tonduzii* but differs in several ways. It has leaves with the midrib flatraised above with the margins undercut. It also has stems that appear scurfy (though weakly glossy if rubbed clean). Another difference is that the petiole sheath is more prominently free-ending and subacute at the apex. In addition, the free portion of the petiole is broadly and sharply sulcate.

Additional specimens examined. COSTA RICA. Alajuela: rd. to Colonia Virgen del Socorro, Río Sarapiquí, Stevens 13564 (MO), Croat 68336 (CR, MEXU, MO, TEFH); Cantón de Alajuela, Gravum & Murakami 9939 (CR, MO); Finca Los Ensavos, ca. 11 mi. NW of Zarcero, Croat 43629 (CM, MO); Cañas-Upala, 10 km N of Bijagua, Croat 36472 (MO); Río Zapote, Cañas-Upala, Río Zapote, 4 km NNE of Bijagua, Croat 36260 (MO); Cordillera de Tilarán, San Ramón-Bajo Rodríguez, Río Cataratitas, Croat 68097 (INB, MO); Cordillera de Tilarán, San Ramón-Bajo Rodríguez, vic. of km 19.5 NW of San Ramón, Croat 78838 (MO); 17-20 km NNW of San Ramón by rd. on way to San Lorenzo, 4-7 km N of Balsa, Liesner & Judziewicz 14797 (CR, MO); San Ramón-Bajo Rodríguez, 36-37 km NW of San Ramón, Croat 68196 (CM, MO, W); Naranjo-Aguas Zarcas, along Hwy. 15, 8 km NE of Quesada, Croat 46945 (K, MO, PMA); Arenal Volcano, Funk et al. 10626 (CR, US), Funk et al.

10718 (CR); San Ramón-Fortuna, ca. km 25, D. Smith et al. 1059 (DUKE, MO); Cordillera de Guanacaste, Monteverde, San Gerardo Biol. Sta., 1.5 km NE of Station, D. Penneys 633 (CR, INB, MO); Cordillera de Tilarán, Bosque Eterno De Los Niños, Río Peñas Blancas, Laguna Poco Sol, Haber & Zuchowski 11175 (CR, MO). Cartago: Tucurrique, Tonduz 12874 (G, US); Río Naranjo, Finca El Cedral, Orosí, Lent 4042 (F, MO, NY, SEL); La Vuelta, Tucurrique, Tonduz 503 (US); 1.5 mi. E of Cachi, 10.2 mi. NE of jct. at Paraíso, Croat 47088 (MO); along Camino Raiz de Hule, SE of Platanillo, Croat 36727 (MO), Croat 36747 (MO), Croat 36821 (MO); Cantón de Turrialba, Río Reventazón, CATIE, Turrialba, Grayum et al. 9469 (CR, MO, NY); 3 km E of Turrialba "Los Espaveles" nature trail, Río Reventazón, Liesner et al. 15330 (MO); Turrialba, Instituto Interam., Lent 639 (F), Lent 694 (F); 12 km S of Turrialba by air, 4 km SE of Pejibaye along Río Gato, Liesner 14394 (MO); Tres Equis, 1.5 km E of Turrialba-Limón Hwy., Liesner et al. 15365 (MO); PN Tapantí, Oropendola trail, Nilsson et al. 632 (CR); Oropendola trail, Nilsson et al. 377 (CR); Monumento Nacional Guayabo, Pérez 1 (CR); Monumento Nacional Guayabo, Santa Teresita, Rivera 1718 (CR, K). Guanacaste: El Arenal, Standley & Valerio 45262 (US); El Real, Standley & Valerio 45206 (US); Cordillera de Guanacaste, Rincón de la Vieja, near refugee camp, along rd. NW of Quebrada Grande, Barringer et al. 4039 (F). Heredia: E of San Ramón, Loiselle 106 (MO); Porto Viejo-Río Sucio, Croat 35753 (F, MO, PMA); La Selva, Puerto Viejo de Sarapiquí, Croat 44317 (MO); La Selva, OTS Field Station on the Río Puerto Viejo just E of its jct. with the Río Sarapiquí, Hammel 8874 (DUKE, F, MO), Grayum 2780 (DUKE, F, MO); La Selva, 6 km by rd. from Río Peje crossing, 5 km SSE of Masasay, Schatz & Grayum 706 (DUKE); Puerto Viejo just E of jct. with Río Sarapiquí, Folsom 10116 (DUKE); Occidental trail, Kress 84-1630 (SEL); Río Sucio, near Porto Viejo, Croat 35682 (MO); Zona Protectora, N slopes of Volcán Barba, betw. Río Peje and Río Guacimo, Grayum & Schatz 3174 (DUKE). Limón: along hwy. 32 from Turrialba to Limón, ca. 11 mi. S of Siquirres, Croat 43333 (ISC, MO, PMA, WISC); Guapiles, Leon 720 (F); Guapiles, Toro Aurarillo, Leon 26573 (CR); Finca Anai, at headwaters of Quebrada Mata de Limón, W of Mata de Limón (Sixaola region), Grayum & Schatz 5279 (CR, MO); Finca Castilla, Dodge & Goerger 9489 (MO); 7 km SW of BriBri, L. Gómez et al. 20405 (B, MO); drainage of Río Parismina and Río Reventazón, Shank & Molina 4288 (DUKE); 10 mi. S of Punta Cahuita, ca. 3 mi. S of turnoff to BriBri, Croat 43201 (MO); Ref. Barra del Colorado, Río Chirripócito-Río Sardina, Grayum 9804 (CR, MO); Par. Tortuguero, Est. Biol. Agua Fría, Sendero Las Lomas, 5 km from station, Robles 1142 (CR, MO); Sendero Los Raudales, 8 km SE from station, Robles 1158 (CR, MO); PN Tortuguero, Lomas de Sierpe, 4 km NE of station along Río Sierpe, Robles et al. 2050 (CR, G, MO); Tortuguero Cantón, BriBri-Suretka, Barringer 3525 (CR, F); Res. Indígena Talamanca, Sukut, mouth of Río Sukut at Río Uren, Hammel et al. 17548 (CR, MO); Río Reventazón, Finca Montecristo below Cairo, Standley & Valerio 48997 (US); Río Segundo, Asunción, L. Gómez & Herrera 23477 (MO); Río Sixaola, BriBri-Caribbean coast, Baker & Burger 90 (F, MO); Limón-Shiroles, Río Sixaola, 0.9 mi. SW of Bambu, 6.5 mi. SW of BriBri, Croat 43298 (MO); Río Sixaola, ca. 0.5 mi. SW of Bambu, ca. 3 mi. NE of Bratsi, Croat 43266 (CR, MO); Tortuguero Cantón, BriBri-Sixaola, NW of Paraiso, Barringer et al. 3479 (CR, F); Cordillera de Talamanca, headwaters of Quebrada Kakebeta below divide between Río Xikiari and Río Boyei, Grayum 10858 (CR, INB, MO). Puntarenas: Cordillera de Tilarán, Bosque Eterno De Los Niños, Laguna Poco Sol, 18 km ENE of Monteverde, Haber et al. 10824 (CR, INB). San José: Cañón del Río Grande de Orosi, Chacón et al. 1488 (CR, MO); La Hondura, Standley 36314 (US); Vázquez de Coronado, Braulio Carrillo NP, along Hwy. San José to Siquirres, along trail to Río Sucio, site of the Old Carillo Station, Croat 78787 (MO). NICARAGUA. Río San Juan: "Los Filos" near Loma Los Filos, Río Santa Cruz, Salick 8153 (MO). Zelaya: ca. 6.3 km S of bridge at Colonia Yolaina and ca. 0.8 km S of ridge of Serranías de Yolaina on rd. to Colonia Manantiales, Colonia Somoza, Stevens 6420 (MO); Río Punta Gorda, Atlanta, mouth of Caño el Guineo, Moreno & Sandino 12855 (MO), Moreno & Sandino 12891 (MO); Río Punta Gorda, Atlanta, Caño Negro mouth of Río Chiquito, Moreno & Sandino 12917 (MO); Río Punta Gorda, Atlanta, mouth of Caño del Oro at Río Chiquito, Moreno & Sandino 12955 (MO); Río Punta Gorda, Caño El Guineo, Tellez et al. 4875 (MEXU, MO). PANAMA. Bocas del Toro: Limit trail, Parque Intl. La Amistad, from Quebrada Boca Chica to Quebrada Bonyic, Polanco 1615 (PMA); 7.7 mi. W of Chiriquí Grande, 1.5 mi. W of Punta Peña, Croat & Gravum 60112 (CR, MEXU, MO, PMA); Chiriquí Grande-Fortuna, 13.2 mi. W of Chiriquí Grande, Croat & Grayum 60139 (B, MO, PMA); Fortuna-Chiriquí Grande Hwy. near Cont. Div., 1.1 mi. from main hwy., Croat & Grayum 60355 (MO); Chiriquí Grande-Fortuna, above waterfall, 1.6 mi. N of Cont. Div., Croat & Zhu 76450 (CR, MO, PMA, SCZ, US); Changuinola, near Luzon, Kennedy 3253 (MO); Changuinola-Almirante, Mile 7.5, Croat & Porter 16249 (MO); Gualaca-Chiriquí Grande, 6.6 mi. N of bridge over Fortuna Lake, Croat 66732 (MO); Gualaca-Chiriquí Grande, 1.6 mi. N of Cont. Div., Croat 74930 (MO); Gualaca-Chiriquí Grande, 8.1 mi. S of Punta Peña, Croat 74952 (MO); N of Fortuna Dam, McPherson 11129 (MO); rd. to Chiriquí Grande, McPherson 7371 (MO); 5.3 mi. N of Fortuna Dam, then 1.4 mi. W along gravel rd. to Cont. Div. trail, Croat & Zhu 76328 (MO, PMA); along Cont. Div. trail, McPherson 9865 (MO); Fortuna Dam-Chiriquí Grande, 1 mi. from Cont. Div., Churchill & Churchill 6252 (MO); Río Cricamola, Finca St. Louis-Konkintoë, Woodson Jr. et al. 1909 (F, MO). Chiriquí: Gualaca-Fortuna Dam, 10 mi. NW of Los Planes de Hornito, Croat 50049 (CR, MO); vic. Fortuna Dam of Río Chiriquí, Croat 66533 (B, CM, ENCB, DUKE, KYO, L, MO, NY, OOMOTO, QCA, SAR, TEX, US); 4.5-5 km N of Fortuna Lake, Croat & Grayum 60070 (INB, MO); 7.9 mi. beyond (NW of) Los Planes de Hornito, Croat 49932 (MO); Gualaca-Bocas del Toro border, km 111, Gordon 339 (PMA); Fortuna Dam site N of Gualaca, 7.7 mi. beyond Los Planes de Hornito, Croat 48778 (MO). Coclé: vic. El Valle de Antón, La Mesa, Finca Macarenita, Croat & Zhu 76653 (BM, C, FSU, GOET, INPA, ITIC, L, LE, MO, QCA, PMA, R, TEFH, UB). Darién: Mamey, Whitefoord & Eddy 372 (BM, MO, PMA). San Blas: Río Armila, 10 km WSW of Puerto Obaldía, Mori et al. 6814 (MO). Veraguas: valley of Río Dos Bocas, 11 km from Escuela Agrícola Alto Piedra (above Santa Fe) on rd. to Calovebora, *Croat 27490* (MO); NW of Santa Fe, 11 km from Escuela Agrícola Alto de Piedra, in valley of Río Dos Bocas, Mori et al. 3817 (F, MO); 0.6 mi. beyond Escuela Agricola Alto Piedra, Croat & Folsom 33989 (MO); 1.7 mi. past Alto Piedra School, Croat & Zhu 76858 (MO, PMA); beyond Escuela Agrícola Alto Piedra, Croat 49070 (MO); 3-5 mi. N of Santa Fe, Gentry 3035 (MO); vic. Escuela Agricultura Alto Piedra near, Antonio 2994 (MO); 0.6 mi. beyond Escuela Agrícola Alto Piedra, Croat & Folsom 34042 (MO); Cerro Tute reserve, along ridge to summit, Croat 66993 (HUA, MO,

PMA); trail to top of Cerro Tute, Croat 48903 (MO, PMA); Cerro Tute, Sytsma & Antonio 3006 (MO). COLOMBIA. Antioquia: Murrí, La Blanquita, Río Murrí, Transect 7, Gentry et al. 75903 (MO); Villa Arteaga, Gutierrez, G. & Barkley 17115 (COL); PN Natural "Las Orquideas," Venados arriba, Río Venados, A. Cogollo et al. 3462 (JAUM, MO); Mutatá, Río Chontadural, Hacienda El Darién, Fonnegra 1344 (HUA); Carepa, Est. Exp. de Tulenapa (CA), Callejas et al. 9704 (NY). Chocó: Serranía de Baudo, Las Animas-Pato, Río Pato, ca. 4 km SW of Pato, Croat 56112 (CHOCO, JAUM, K, MO); Medellín-Quibdó, km 208.5, 9 km W of Tutunedo, ca. 9 km E of Quibdó, Croat 56205 (CHOCO, COL, CUVC, HUA, MO); Quibdó-Medellín, km 185, 14 km E of Tutunendo, Croat 56282 (CHOCO, COL, JAUM, MO, PMA); San José del Palmar-Novita, vic. Santa Rosa, Croat 56625 (COL, HUA, MO); Quibdó-Medellín, 25 mi. E of Quibdó, Croat 52300 (F, MO, PMA); ca. 2 km E of Playa de Oro, Croat 57427 (CHOCO, MO); Pueblo Rico (Risaralda)-Istmina (Chocó), Quebrada Antón, 15 km W of Santa Cecilia, 6 km W of Chocó-Risaralda border, Croat 70900 (MO); Medellín-Quibdó, 85 km W of Bolívar, Croat 49310 (MO); Acandí-Serranía del Darién, Juncosa 619 (MO); Pueblo Rico (Risaralda)-Istmina (Chocó), 1 km W of Guarato and Río Guarato at Risaralda and Chocó border, Croat 70868 (CM, MO); Nuquí, Quebrada Chaquí, Galeano 4600 (MO); Arusí, El Amargal, trail to Arusí, Mora 51 (COL), Croat & Mora 83696 (MO); Quibdó, Tutunendo-Alto del Viente Rd., 25 km N of Quibdó, Callejas & Jangoux 2692 (HUA). Nariño: Río Timbiquí, Lehmann 8876 (K); valley of Río Imbi, Pasto-Tumaco, vic. "Palmar" 3 km NW of Ricaurte, ca. 1 km E of Texas Gulf Pipeline Maintenance Station, Río Imbi, Croat 71461 (MO). Risaralda: Pueblo Rico, Santa Cecilia, Quebrada La Calera, Betancur et al. 3054 (MO). Valle del Cauca: Cali-Buenaventura, Loboguerrero-Cisneros, Quebrada la Guinea at 1.2 km E of Cisneros, Croat 62831 (COL, HUA, MO, UB); vic. Queremal, Río Cava, Croat & Gaskin 80391 (CUVC, MO); Cordillera Occidental, Río Digua, Cuatrecasas 15053 (US); Bajo Calima, Buenaventura-Malaga, km 51.3, Croat 71017 (MO); Buenaventura-Málaga, Pulpapel facilities at km 9, Croat 70099 (MO). ECUADOR. Esmeraldas: San Lorenzo, Río Palavi, vic. AWA encampment, Hoover et al. 3161 (MO); Awá camp to Río Palaví, Hoover et al. 3968 (MO); Lita-San Lorenzo rd., 14.2 km W of Río Lita Bridge (below Lita), Croat et al. 82305 (MO); 17.3 km E of Río Tululbí, Croat 83126 (MO, WU); 33.0 km E of Gasolinera San Lorenzo, Río San José, 1.1 km N Lita-San Lorenzo rd, Croat 83889 (AAU, F, GB, MO, NY, QCA, S); Lita-San Lorenzo Rd., 1.2 km W of El Durango, 21.1 km W of Alto Tambo, Croat et al. 82441 (MO, QCNE); Lita-Carondelet Rd., km 16, Schwerdtfeger 21422 (MO); Bilsa Biol. Res., Montañas de Mache, 35 km W of Quinindé, 5 km W of Santa Isabela, Pitman & Bass 995 (MO, OCNE); Fila de Bilsa, 7 km E of San José de Bilsa, ca. 80 km due SW of Esmeraldas, 12 km SE of El Salto on Atacames-Muisne Rd., Gentry et al. 72955 (MO); Eloy Alfaro, comuna de Corriente Grande (Río Chimbagal, tributary del Cayapas), Yanez et al. 1387 (MO); Res. Ecol. Cotacachi-Cayapas, Charco Vicente, Río San Miguel, Palacios & Tirado 11287 (MO, QCNE); Quininde, Herrera-Los Monos, headwaters of Río Aguacatal, Palacios 13626 (CM, MO, QCNE, US); NE of Las Golondrinas, Sitio La Bella Jungla, Cooperativa Unidos Venceremos, Palacios 11452 (MO, QCNE). Loja: Río Pichimá, Forero 719 (COL, MO). Pichincha: Río Palenque Science Center, halfway between Quevedo and Santo Dominga de los Colorados, Gentry et al. 24700 (MO); rd. E of Santo Domingo-Quevedo rd. (beginning 10.5 km N of Patricia Pilar), Caserío Palmar

de Bimbe, *Croat* 57000 (CM, MO); Centinela, 12 km E of Patricia Pilar on border with Los Ríos, *Gentry* 26705 (MO); Centinela, Montañas de Ila, 13 km E of Patricia Pilar, ca. 54 km S of Santo Domingo, *Hammel & Trainer* 15836 (MO).

26. Dieffenbachia wendlandii Schott, Oesterr. Bot. Z. 8: 179. 1858. TYPE: El Salvador. Santa Ana, *H. Wendland s.n.* (holotype, GOET!). Figures 26, 28B.

Stout herb, to (0.8)1.2-2(3) m tall; sap strong and foul-scented (only weakly foul-scented in some Atlantic slope populations); stems erect, decumbent at base; internodes dark green to blackish green or medium green, glossy to semiglossy, 1-5 cm long, 2-5.2 cm diam.; petioles (11.5)16-32(65) cm long (averaging 25 cm long), matte, medium dark green, sometimes finely darker green-striped throughout (or at least near the base), often weakly glossy toward the apex, moderately spongy, obtusely and shallowly sulcate (sometimes more acutely sulcate near the apex) to D-shaped, sometimes with a slender erect margin or often terete in populations in eastern Mexico, sheathed (0.3)0.5-0.9 their length; sheath (6)12-30(45) cm long (averaging 18 cm long); sheath sometimes markedly undulate on that portion clasping stem, incurled throughout its length with the margins incurled to erect and touching or well-spaced, initially decurrent or nearly so at the apex and with one side completely hiding the other from above the middle, sometimes with the margins somewhat erect and eventually \pm emarginate with one side rounded, the other side rounded and somewhat free-ending, rarely with the apex broadly rounded and free-ending; unsheathed portion of petiole (1)3.5-12(24) cm long (averaging 8 cm long), terete or thicker than broad, 12-14 mm diam., 13-15 mm thick, usually obtusely sulcate except terete in some areas on the Atlantic slope of Mexico (the sulcus sometimes broader toward the apex); blades narrowly ovate to ovate-elliptic, (15)20-55(65) cm long, (9)10-22(28) cm wide (averaging 35×17 cm), 1.3–2.4 times longer than broad (averaging 2 times longer than broad), subcoriaceous to moderately coriaceous, acute and apiculate to abruptly or gradually acuminate at apex (sometimes rounded and apiculate), acute to obtuse or rounded and attenuate at base, sometimes rounded to subcordate, slightly inequilateral, one side 0.8-3.0(4.5) cm narrower than the other; upper surface dark green, semiglossy to weakly glossy, drying gray-green to yellow-brown; lower surface paler, matte or nearly so, drying yellow-green to yellow-brown (both surfaces dark yellow-brown on very old specimens); midrib flat to broadly sunken



Figure 26. *Dieffenbachia wendlandii.* —A. Habit, plant with open inflorescence. —B. Adaxial blade surface. —C. Potted flowering plant with open inflorescence (*Croat 39749*). —D. Open inflorescence at anthesis (*Croat 47219*). — E. Staminate portion of spadix and spathe blade. —F. Close-up of spathe showing part of pistillate portion, the mostly sterile portion and the base of the staminate portion. A, B. (*Croat 47219*); D, E, F. (*Croat 47219*).





Figure 27. Distribution map. —A. Dieffenbachia aurantiaca, D. crebripistillata, D. fosteri, D. grayumiana, and D. horichii. —B. Dieffenbachia burgeri, D. copensis, D. davidsei, D. hammelii, and D. lutheri.





Figure 28. Distribution map. —A. Dieffenbachia concinna, D. fortunensis, D. galdamesiae, and D. isthmia. —B. Dieffenbachia beachiana, D. killipii, D. standleyi, and D. wendlandii.

to flattened and concolorous to weakly paler above with fine, close, slightly paler striations, convex to round-raised or narrowly rounded and slightly to moderately paler beneath, usually faintly striate, drying somewhat orange-tinged and paler than the surface, 5–10(18) mm wide; *primary lateral veins* (6)7 to 11(13) per side, weakly and obtusely quilted-sunken above, convex, weakly pleated-raised beneath, arising at an acute angle then spreading at $(40^{\circ})55^{\circ}$ -70° angle, slightly paler than surface



Figure 29. Distribution map. —A. Dieffenbachia obscurinervia and D. oerstedii. —B. Dieffenbachia longispatha, D. pittieri, and D. tonduzii.

when fresh, usually drying darker than surface, sometimes lighter than surface, moderately straight or weakly curved to near the margin then gradually curved upward along the margin to form a series of closely parallel marginal veins that do not form a collective; minor veins on lower surface moderately obscure on fresh material, more prominent and darker than surface on drying. INFLORESCENCE





Figure 30. Distribution map. - A. Dieffenbachia nitidipetiolata and D. panamensis. - B. Dieffenbachia seguine.

1 to 4 per axil; bracteoles to 25 cm long; *peduncle* (7)12–22 cm long, 1–1.5 cm \times 0.8–1.3 cm diam., subterete, pale medium green, weakly glossy, faintly and finely striate-streaked; *spathe* (16)25–32 cm long, narrowly acuminate to cuspidate-acuminate at apex (the tip turned back), medium-green, weakly glossy to semiglossy outside, equally colored and glossy within with weak, darker, short oblique lines running between the parallel vertical veins throughout the length of the spathe; the spathe tube

8–12 cm long, (2.7)3.5–4.5 cm diam. when furled, 6.5–12.5 cm wide when flattened, with dense minute depressions scattered throughout the tube; constricted portion of spathe (2)3.3–4.0 cm wide, 3.5–8 cm wide when flattened; spathe blade 3.7– 4.5 cm wide, flattening to 3.3–6.3 cm wide; *spadix* (12)18–29.3 cm long, 2.0–4.7 cm shorter than the spathe, scarcely protruded forward, its stipe 1–2 cm long, 1.3 cm diam.; the free portion of the spadix 9–11 cm long; pistillate portion (5.5)8.5–10 cm long, 1.2-1.7 cm diam., 0.9-1.1 cm on drying (rachis 0.9-1.2 cm diam.), the upper 1 cm sometimes with as few as two apparently fertile flowers; staminate portion of spadix (7)9-16 cm long, the fertile staminate portion (4.5)7-12.5 cm long, gradually tapered toward both ends, (0.7)1-1.3 cm diam. midway, 7 mm diam. 1 cm below the apex; mostly sterile intermediate portion of spadix 2.0-4.0 cm long, 7-9 mm diam., with a few aborted pistillate flowers in the lower half and a few sterile male flowers in the apical half, often with a totally barren segment of up to 1-2.8 cm long; pistils (33)45 to 55, depressed-globose, weakly pale yellow-green, moderately glossy, (2)3 to 5 across the width of the spadix, 3.0-3.7 mm diam., 1.5-1.7 mm high; stigma yellow to pale orange, 0.6-1 mm high, 2.0-2.7 mm diam., sometimes broadly sunken medially, sometimes with a prominent, protruding dome held slightly above the outer ring; staminodia 3 to 4, free to the base, broadened toward the base, 0.8-1.2 mm wide at base and sometimes partly fused, usually slightly thicker near apex, (2.5)3.5-5 mm long, white, slightly flattened, 1.5-3.5 mm wide, about as long as the pistils; synandria 4 to 7 visible per spiral, 3.5-4.0 mm diam., widely spaced at base, truncate and smooth at apex, irregularly rounded, pale tan, becoming bowl-shaped and brown except for white, erect margins, margins sometimes crenate, with thecae 6 to 8 per synandrium, these subglobose, ca. 1 mm long, held just below the apex of the synandrium. INFRUCTESCENCE with spathe green at maturity; berries red to bright orange, 6-8 mm diam.

Distribution and habitat. Dieffenbachia wendlandii occurs principally in seasonally dry habitats on the Pacific slope of Central America, ranging from central Mexico (Oaxaca and Chiapas) to Guatemala (Escuintla, Huehuetenango, San Marcos, Suchitepéquez), El Salvador, Honduras (Morazán), Nicaragua (Estelí, Granada, Matagalpa, Nueva Segovia, Zelaya), Costa Rica (Puntarenas Province), and Panama (Veraguas) at elevations of 75 to 900 m. In Mexico the species occurs on the Atlantic slope only in the State of Oaxaca in the Serranía de Juárez at 250-705 m and in Veracruz in or near the Estación Biológica de Los Tuxtlas near the Caribbean coast at 5-165 m elevation. The only collection of the species in Panama, from Bahía Honda in Veraguas Province, is unusual in having blades more ovate and in drying pale green. It may prove to be a new species.

Phenology. Dieffenbachia wendlandii flowers principally in the rainy season, beginning in May and especially in June and July, but continuing until August or rarely September. What appears to be a secondary flowering period may occur in the early dry season because flowering collections have been seen in December and February. Most fruiting specimens have been made in the dry season and early wet season from January to May.

Discussion. The species is characterized by its robust, but moderately short stature, dark green, semiglossy stems; narrowly ovate to ovate-elliptic yellowish brown, to yellow-green-drying leaf blades; but especially by the partially sheathed petioles with the sheath margins decurrent or ending abruptly and rounded at apex with a free, unsheathed sulcate portion 1–9 cm long at the apex. In addition, the species has an unusually large spathe for the size of its leaves, frequently exceeding 30 cm long.

Populations of *D. wendlandii* on the Atlantic slope have petioles completely terete, rather than sulcate adaxially, but this varies even on the same individual. In addition, these populations are more likely to have the petiole sheath even more decidedly decurrent at the apex. At least the populations of plants in Oaxaca at middle elevation above Valle Nacional have sap that is only mildly odorous, whereas elsewhere the sap is malodorous, smelling somewhat like skunk or peccary.

Dieffenbachia wendlandii is easily confused with D. oerstedii on the eastern slopes of Chiapas and Veracruz, but D. wendlandii is much more robust than plants of D. oerstedii, which are usually less than 1 m tall and have internodes usually less than 2.5 cm in diameter. In contrast, the stems of D. wendlandii are rarely less than 2.5 cm in diameter and are usually 4-5 cm in diameter. Other differences in D. oerstedii are the sharply sulcate (rather than terete to obtusely sulcate) petioles that are white (rather than green) at the base, and the sheath apex of which at least one margin is rounded and prominently free-ending. In contrast, D. wendlandii on the Atlantic slope is more than 1.5 m tall at maturity, has internodes more than 3 cm in diameter, and petiole sheath margins acute to only weakly protruded at apex with the free portion of the petiole at most obtusely sulcate. Another way D. wendlandii differs from D. oerstedii is by its typically larger spathe, over 25 cm long versus less than 20 cm long for D. oerstedii.

Previously most material of *D. wendlandii* from Mexico and Guatemala has been mistakenly called *D. oerstedii*, and indeed herbarium material without good field notes is difficult to separate. Several of the collections of *D. oerstedii* made in lowland Veracruz (*Holstein & Armbruster 20425*; *Nee 23773*, 29752, and 29993) appear to have the petiole sheath somewhat decurrent without a conspicuous free-ending apex. They are described as plants no more than 1 m tall. It is possible that these represent hybrid plants since both *D. wendlandii* and *D. oerstedii* occur in lowland Veracruz.

Dieffenbachia wendlandii has been confused with D. standleyi in eastern Nicaragua. However, that species occurs only on the Atlantic slope and has petioles sheathed completely to the apex and a proportionately longer blade, ranging from 1.9 to 3.5 times longer than wide, and averaging 2.5 times longer than wide. In contrast, D. wendlandii has blades ranging from 1.3 to 2.4 times longer than wide and averages only 2 times longer than wide. Throughout its range in western Mexico and Central America, D. wendlandii is variable in the blade shape with the proportionately broader blades occurring in Mexico and Guatemala, where they average 1.8 times longer than wide. The collections from El Salvador and Nicaragua, on the other hand, have leaf blades averaging 2.3 times longer than wide. The populations in Mexico and Guatemala have shorter petioles (averaging 19.8 cm long and 22.6 cm long, respectively) than those in El Salvador and Nicaragua (averaging almost 30 cm long).

The single Costa Rican collection made in Puntarenas Province, along the dry road approaching the Monteverde reserve, is noteworthy in being so far out of the range of the species. *Dieffenbachia wendlandii* may have been more widespread in Costa Rica, but much of the drier forests in the country have been eliminated between the Monteverde site and the Nicaraguan border.

Stevens 6027 from Matagalpa Department, Nicaragua, at 510 m is unusual in having the apex of the petiole sheath broad and conspicuously rounded and somewhat free-ending. It may ultimately prove to be a different species.

While many specimens of *D. wendlandii* in Mexico and Guatemala have blades that are subcordate at the base, most collections in El Salvador and Nicaragua have leaf bases attenuate at the base.

Engler (1915), in his revision of Philodendroideae–Dieffenbachieae, considered *D. wendlandii* a synonym of *Dieffenbachia seguine* var. *viridis* Engl., one of many varieties of what he considered a polymorphic species ranging throughout Central America, the West Indies, and South America. In my opinion, Engler misinterpreted the Central American material, much the same as later botanists, including myself, did for years. However, after actually seeing the live plants in the field in both Central America and in the West Indies, there is no doubt that *D. seguine* does not occur in Central America. The material previously determined as *D. seguine* in Central America has proven to be either *D. oerstedii* with blades larger than normal, or *D. wendlandii.*

Additional specimens examined. COSTA RICA. Alajuela: Río Cacao, near Atenas, L. Gómez 19572 (MO). Puntarenas: rd. to Monteverde, Wilbur et al. 15861 (DUKE). EL SALVADOR. Wendland 410 (GOET); San Salvador, Calderon 914 (US), Renson 266 (NY, US). GUA-TEMALA. Escuintla: Engler 2389 (GH); Escuintla-Alotenango, mi. 6, Croat 42050 (DUKE, MO); Cucunya at San André Osuna, Seler 2389 (G), Seler 2398 (GH). Huehuetenango: Cerro Victoria, Finca San Rafael, Sierra de los Cuchumatanes, Steyermark 49637 (F). San Marcos: Finca Armenia near La Trinidad above San Rafael, Croat 40790 (ENCB, MO); Río Ixpal, below Rodeo, Standley 68724 (F); Santa Rosa, Chiquimulilla-El Ahumado, N of Los Cerritos, Standley 79561 (F); E of Cuilapa, Standley 78161 (F). Suchitepéquez: Mazatenango, Morales 1047 (F, CR); vic. Tiquisate, Steyermark 47684 (F, MO). HON-DURAS. Francisco Morazán: San António de Oriente, above El Jicarito, Standley 21077 (F). MEXICO. Chiapas: Escuintla-Monte Ovando, 2.8 km NW of Turquiz, Croat 47510 (MO); Escuintla-El Triunfo, ca. 1 mi. N of Escuintla, Croat 43813 (MO); Tapachula-Nueva Aleman, mi. 4, Croat 43791 (CHIP, CM, MO); Mapastepec, Sierra de Soconusco, Croat & D. Hannon 63340 (MO); Tapachula-Union Juarez, at km 13.5, 1.3 mi. N of Trinidad, Croat 47219 (CHIP, MEXU, MO); Acacoyagua, Ejida Las Golandrinas, Cerro Mt. Ovando Trail, Croat 78480 (MO); Acapetagua, R. Hernández 473 (MEXU, MO, NY); Escuintla, Esperanza, Matuda 16765 (F, MEXU); Esperanza, Matuda 16369 (MEXU). Oaxaca: Tuxtepec, 6 mi. W of Valle Nac. on Hwy. 175, Croat 39749 (AAU, MEXU, MO, RSA, SEL, TEX, UB, US, VEN), Croat 43931 (MEXU, MO), Croat & D. Hannon 65536 (MEXU, MO), Croat 78711 (MO), Croat 78720 (MO); Sta. Maria Chimalpa, Hernández 1318 (MO); Arroyo Sangre, ca. 1-2 km al E de Sta. Maria, Hernández 2586 (MO). Queretaro: Huimilpan, Mpio. Comaltepec, Puerto Eligio, Lopez Garcia & Martin 122 (MO, CR). Veracruz: 9.3 mi. from Tabasco/ Veracruz border on Hwy. 180 to Coatzacoacos, Thompson 441(MO); San Andres Tuxtla, Catemaco-Montepio, 22.2 km N of Catemaco, vic. Est. Biol. Los Tuxtlas, Croat & M. Pérez 78686 (MEXU, MO), G. E. Martínez 2287 (F, MEXU, NY); Catemaco, Sontecomapan, arroyo Basuras, R. Hernández 645 (F, MEXU, NY, US). NICARAGUA. Estelí: Estelí-La Concordia, km 14, Río Isiquií, Moreno 15290 (MO). Granada: Volcán Mombacho, Finca Cutirre, Atwood A212 (MO); Sardela Hacienda Cutirre, Moreno 16421 (MO); 2 km al SE de la Hacienda Cutirre, Moreno 16464 (MO), Sandino 1248 (MO); 1 km SE of Cutirre, Moreno & Henrich 8427 (MO). Managua: Garnier 772 (US). Matagalpa: Hwy. 5 ca. 38.7 km from Hwy. 3 intersection, ca. 5.5 km N of Río Tuma bridge, Stevens 6027 (DUKE, MEXU, MO). Nueva Segovia: ca. 1.6 km W of Murra-El Jícaro, km 1, Quebrada El Carmen, Stevens et al. 17591 (MO); Río Solonli, Quebrada Tastasli, 3 km S of Jalapa, 6 Apr. 1977, Neill 1657 (MO). PANAMA. Veraguas: Soná, Bahía Honda, 7°58', 81°17'W, Ibáñez et al. 1829 (PMA).

EXCLUDED SPECIES

Dieffenbachia lancifolia Linden & André, placed in synonymy of D. seguine by Engler (1915); however, this is a distinct species from Antioquia Department, Colombia.

Dieffenbachia picta Schott forma lancifolia (Linden & André) Engl. and Dieffenbachia picta Schott subvar. lancifolia (Linden & André) Engl. are combinations of Dieffenbachia lancifolia Linden & André that also must be excluded from consideration in this revision of Central American Dieffenbachia.

Dieffenbachia meleagris Linden & Rodigas, placed in synonymy of *D. seguine* by Engler (1915); however, this is a distinct species from Ecuador, possibly one synonymous with *D. spruceana* Schott. The recombined *Dieffenbachia meleagris* Linden & Rodigas subvar. *meleagris* is also to be excluded.

Dieffenbachia shuttleworthiana Engl. was synonymized with D. picta by Engler (1915), but it must be excluded along with the combination D. picta Schott forma schuttleworthiana (Regel) Engl. and D. shuttleworthiana Hort. Bull. This Colombian species is not closely related to D. seguine.

Species Incertae Sedis

The following species names are believed to be synonyms of *Dieffenbachia seguine* based on the revision of *Dieffenbachia* by Engler (1915); however, owing to the destruction of many herbarium specimens during World War II, lectotypification was impossible. The specimens were no doubt available during Engler's time, and it is assumed that he saw the material.

- *Dieffenbachia picta* fo. *mirabilis* Engl., Fl. Bras. 3(2): 176. 1878. TYPE: based on a plant of unknown origin cultivated by Verschaffelt, not designated. No type listed by Engler.
- Dieffenbachia seguine fo. decora Engl., Fl. Bras. 3(2): 175. 1878. Dieffenbachia seguine subvar. decora (Engl.) Engl., Bot. Jahrb. Syst. 26: 568. 1899. Dieffenbachia seguine var. decora (Engl.) Engl., Pflanzenr. IV, 23 Dc(Heft 64): 47. 1915. Dieffenbachia seguine fo. decora (Engl.) Engl., Pflanzenr. IV, 23 Dc(Heft 64): 48. 1915, nom. superfl. Dieffenbachia decora Hort. Versch. ex Engl., in DC., Monogr. Phan. 2: 446. 1878. TYPE: based on a plant of unknown origin cultivated by Verschaffelt, not designated. No type listed by Engler.
- Dieffenbachia seguine fo. nobilis Engl., Fl. Bras. 3(2): 174. 1878. Dieffenbachia seguine subvar. nobilis, Bot. Jahrb. Syst. 26: 568. 1899. Dieffenbachia seguine var. nobilis (Engl.) Engl., Pflanzenr. IV 23 Dc(Heft 64): 47. 1915. TYPE: Brazil. Pará: Barraquin based on a cultivated plant by Verschaffelt. No type listed by Engler.

- Dieffenbachia picta subvar. angustifolia Engl., Bot. Jahrb. Syst. 26: 569. 1899. TYPE: based on a cultivated plant of unknown origin, not seen. No type listed by Engler.
- Dieffenbachia seguine var. minor Engl., Bot. Jahrb. Syst. 26: 567. 1899. TYPE: No type listed by Engler.
- Dieffenbachia picta var. latior Engl., Bot. Jahrb. Syst. 26: 569. 1899. TYPE: No type listed by Engler.
- Dieffenbachia picta var. latior Engl., Bot. Jahrb. 26. 569. 1899. TYPE: Not seen. No type listed by Engler.
- Dieffenbachia picta subvar. memoria Engl., Bot. Jahrb. Syst. 26: 570. 1899. TYPE: based on living material at Berlin Botanical Garden (also Buitenzorg), not seen. No type listed by Engler.
- Dieffenbachia picta subvar. mirabilis Engl., Bot.
 Jahrb. Syst. 26: 570. 1899. Dieffenbachia mirabilis Versch. ex Engl., in DC., Monogr. Phan.
 2: 448. 1878. TYPE: based on a cultivated plant of unknown origin by Verschaffelt, not seen. No type listed by Engler.
- Dieffenbachia picta var. angustior Engl., Bot. Jahrb. Syst. 26. 569. 1899. TYPE: No type or locality listed, not seen. No type listed by Engler.
- Dieffenbachia seguine fo. viridis Engl., Fl. Bras. 3(2): 174. 1878. Dieffenbachia seguine subvar. viridis Engl., Bot. Jahrb. Syst. 26: 567. 1899.
 Dieffenbachia seguine var. viridis Engl., Pflanzenr. IV. 23 Dc(Heft 64): 45. 1915. TYPE: Not seen. No type listed by Engler.
- Dieffenbachia seguine var. lineata (K. Koch & Bouché) forma? decora (Engl.) Engl., Pflanzenr. IV.
 23 Dc(Heft 64): 48. 1915. Dieffenbachia seguine var. decora (Engl.) Engl., Pflanzenr. IV.
 23 Dc(Heft 64): 47. 1915. TYPE: based on a cultivated plant of unknown origin by Verschaffelt, not seen. No type listed by Engler.
- Dieffenbachia picta var. typica Engl., Pflanzenr. IV. 23 Dc 50. Fig. 21. 1915. TYPE: cultivated in European gardens. No type listed by Engler.

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Appendix 1

LIST OF SPECIES.

- 1. Dieffenbachia aurantiaca Engl.
- 2. D. beachiana Croat & Grayum
- 3. D. burgeri Croat & Grayum
- 4. D. concinna Croat & Grayum
- 5. D. copensis Croat

- 6. D. crebripistillata Croat
 - D. davidsei Croat & Grayum
- 8. D. fortunensis Croat
- 9. D. fosteri Croat
- 10. D. galdamesiae Croat
- 11. D. grayumiana Croat
- D. hammelii Croat & Grayum
 D. horichii Croat & Grayum
- 14. *D. isthmia* Croat &
- 15. D. killipii Croat
- 16. D. longispatha Engl. & K. Krause
- 17. D. lutheri Croat
- 18. D. nitidipetiolata Croat
- 19. D. obscurinervia Croat
- 20. D. oerstedii Schott
- 21. D. panamensis Croat
- 22. D. pittieri Engl.
- 23. D. seguine (Jacq.) Schott
- 24. D. standleyi Croat
- 25. *D. tonduzii* Croat & Grayum
- 26. *D. wendlandii* Schott
- 20. D. wenatanati Sci

Appendix 2

INDEX TO EXSICCATAE. TYPE SPECIES IN BOLDFACE

Acevedo-Rodríguez 4705 (23); Acosta Solís, M. 10896 (15); Aguilar, R. 256 (20), 2195 (4), 2380 (20), 2412 (20), 5204 (20); Aguilar et al. 4302 (20); Akers, M. 78 (18), 78A (11); Allen 5669 (4), 5669A (4), 5972 (1); Allen & Alston 1839 (6); Alvarez, A. & P. Herrera 699 (15); Alverson et al. 283 (19), 376 (15); Anaya 1 (20); André 1202 (23), 457 (15); Antonio 2994 (25), 3039 (6), 3820 (6), 4488 (18), 4546 (14), 4638 (15), 226 (15); Antonio & Hahn 4405 (15), 4406 (15); Aranda et al. 2860 (20); Archer 2215 (19); Aristeguieta 1764 (23); Asplund 15574 (15); Atha & Zanoni 770 (23); Atwood 212 (26); Augo 1693 (23); Aymard & Ortega 3090 (23); Aymard et al. 2714 (23).

Bailey 335 (14); Baker & Burger 90 (25); Balick et al. 1738 (20), 2080 (20), 2359 (23), 2716 (20); Barfod & Skov 60101 (18); Barfod et al. 48154 (18), 48348 (18); Barlow s.n. (20); Barringer 1790B (13), 2416 (18), 2432 (11), 3525 (25); Barringer et al. 1973 (4), 3479 (25), 4039 (25), 4061 (20); Bartlett & Gentry 7423 (15); Bay 278 (15); Beach 1429 (20), 1430 (20), 1431 (20), 1432 (20), 1433 (20), 1434 (20), 1435 (20), 1436 (18), 1439 (18), 1440 (11), 1441 (11), 1448 (2), 1485 (2), 1518 (20); Beard 656 (23); Beck 17103 (23); Beck et al. 295 (23); Bello & Cruz 4284 (20); Bello et al. 42 (20); Benítez de Rojas et al. 4661 (23); Bernal et al. 1158 (19); Betancur et al. 1177 (18), 3054 (25); Beutelspacher s.n. (20); Billiet & Jadin 7359 (23), 7346 (23), 7347 (23), 7357 (23), 7358 (23); Billiet et al. 6257 (23); Blackmore & Chorley 4073 (24); Blackwell et al. 2704 (18); Blum & Tyson 2324 (15); Bogner 965 (23); Bourgeau s.n. (20); Brand & Ascanio 277 (14); Bravo 31 (20); Bravo s.n. (MEXU 30199) (20); Bravo & Nú 107 (20); Breedlove 12752 (20), 24166 (20), 33839 (20), 34977 (20), 40155 (20); Breedlove & McClintock 34192 (20); Breedlove & Thorne 30681 (20); Britton 447 (23), 4126 (23); Britton & Britton 7897 (23), 9664 (23), 10082 (23); Britton & Shafer 1625 (23); Bunting 1692 (23), 2026A (23), 2027 (23), 2035 (23), 2036 (23), 2044 (23), 2622 (23), 2678 (23), 2729 (23), 2738 (23), 2829 (23), 3321 (23), 11687 (23), 13515 (23); Bunting & Fernandez 3295 (23); Bunting & Holmquist 4319 (23); Bunting & Manara 2119 (23), 2120 (23), 2122 (23), 2123 (23), 2124 (23), 2124V (23), 2125 (23), 2126 (23), 2127 (23); Bunting & Trujillo 2236 (23); Bunting et al. 1937A (23), 1949A (23), 1997 (23), 2072 (23), 2074 (23), 2073 (23), 4108 (23); Burch et al. 1123 (15); Burger & Antonio 10905 (18), 11198 (18), 11224 (12), 11249 (4); Burger & Baker 9968 (11), 10121 (3), 10137 (13); Burger & Gentry Jr. 8398 (3); Burger & Liesner 7111 (20), 7196 (4), 7254 (3); Burger & Matta 4181 (11); Burger & Pohl 7825 (20); Burger & Stolze 5024 (18), 5461 (4), 5489 (3), 5753 (18), 5754 (2); Burger et al. 1323 (20), 10323 (18), 10669 (13), 10671 (3), 10699 (18), 10734 (11), 11695 (20), 11926 (20); Busey 743 (1).

Cadet 6030 (23); Calderon 914 (26); Callejas & Jangoux 2692 (25); Callejas et al. 4873 (19), 5661 (18), 9704 (25); Calzada 338 (20); Camp E-3599 (15), 3653 (15); Carballo et al. 47 (20); Carleton 508 (20); Carlson 153 (20); Carrasquilla 2005 (18); Carrasquilla & Mendoza 1239 (18); Carrasquilla & Rincón 304 (15); Carvajal 273 (20); Catharino et al. 1909 (23); Cedillo, T. 3645 (20); Cerón & J. Corozo 33858 (18), 33947 (18), 34097 (18); Cerón et al. 29159 (15); Chacón 364 (20), 507 (11), 553 (12), 1406 (13); Chacón et al. 1488 (25); Chavarría & Umaña 157 (13); Chavarría et al. 257 (4); Chazaro 416 (20); Chinchilla 137 (20); Churchill & Churchill 6105 (18), 6158 (8), 6159 (8), 6252 (25); Churchill & de Nevers 4333 (15); Churchill et al. 3993 (6), 4032 (15), 4125 (15); Clarke 60 (20); Clewell & Tyson 3306 (15); Clezio 221 (15); Cogollo et al. 3462 (25); Colchester 2108 (23); Conrad & Conrad 2882 (20); Conrad et al. 2863 (20); Cornejo & Bonifaz 3107 (15), 4195 (15), 4828 (15), 5191 (15), 5210 (15); Correa & Montenegro 10419 (6), 10647 (6); Cowan 2063 (20); Cowell 550 (23); Cowgill 532 (23); Cremers 9896 (23); Croat 4095 (16), 4125 (16), 4134 (16), 4576 (14), 5183 (14), 5259 (16), 5317 (14), 5709 (14), 5759 (19), 5761 (16), 5767 (16), 5819 (14), 5896 (14), 6192 (16), 6276 (16), 6308 (14), 6409 (16), 6471 (16), 6502 (14), 6775 (19), 7136 (16), 7455 (16), 7478 (6), 7712 (14), 8623 (19), 10133 (14), 10982 (14), 11291 (14), 11321 (16), 11411 (16), 11420 (6), 11514 (16), 11570 (15), 12086 (6), 12123 (6), 12229 (16), 12319 (16), 12352A (19), 12353 (15), 12401 (15), 12489 (15), 12491 (15), 12660 (19), 13403 (6), 13849 (19), 14175 (6), 14309 (15), 14388 (15), 14504 (15), 14706 (15), 14707 (6), 14789 (6), 15082 (15), 15173 (14), 16769A (18), 16803 (15), 16923 (16), 17210 (6), 17311 (15), 17394A (16), 21412 (23), 21741 (23), 21961 (1), 21999 (20), 22173 (20), 22252 (20), 24250 (20), 25213 (6), 25352 (6), 26193 (6), 26239 (6), 27161 (18), 27196 (16), 27206 (21), 27490 (25), 32955 (1), 33018 (16), 33551 (15), 33568 (6), 34442 (15), 34475 (14), 34654 (16), 34656 (14), 34745 (14), 35079 (1), 35108 (4), 35206 (20), 35210 (1), 35292 (1), 35682 (25), 35688 (4), 35702 (4), 3575(25), 35915 (6), 35951 (6), 36260 (25), 36297 (20), 36444 (20), 36472 (25), 36473 (20), 36727 (25), 36747 (25), 36821 (25), 36855 (20), 36958 (6), 37268 (17), 37351 (20), 37361 (6), 37383 (15), 37479 (15), 37605 (15), 37746 (18), 38010 (14), 38057 (14), 38120 (18), 38229 (18), 38344 (23), 38669 (15), 38947 (15), 39749 (26), 40062 (20), 40087 (20), 40089 (20), 40107 (20), 40163 (20), 40790 (26), 41855 (20), 42050 (26), 42133 (20), 42556 (24), 42625 (24), 42645 (20), 42676 (24), 43201 (25), 43217 (18), 43298 (25), 43266 (25), 43333 (25), 43368 (18), 43629 (25), 43791 (26), 43813 (26), 43931 (26), 44226 (11), 44246 (20), 44254 (18), 44283 (2), 44307 (18), 44317 (25), 44321 (11), 44558 (6), 44682 (6), 46785 (20), 46945 (25), 46947 (18), 47088 (5), 47219 (26), 47510 (26), 47868 (20), 48437 (15), 48672 (8), 48778 (25), 48816 (15), 48903 (25), 49056 (15), 49070 (25), 49124

 $(10),\,49155\ (6),\,49243\ (6),\,49310\ (25),\,49761\ (18),\,49768$ (18), 49791 (19), 49805 (15), 49932 (25), 49971 (8), 50049 (25), 50480 (15), 50655 (15), 50684 (15), 50725 (15), 52300 (25), 5378 (14), 53921 (23), 53956 (23), 54380 (23), 54649 (23), 55549 (15), 55629 (15), 55666 (15), 56070 (18), 56112 (25), 56205 (25), 56282 (25), 56625 (25), 57000 (25), 57427 (25), 57462 (18), 59152 (2), 60567 (23), 60613 (23), 60867 (23), 62831 (25), 66533 (25), 66732 (25), 66866 (8), 66953 (2), 66993 (25), 67115 (6), 67197 (15), 67329 (19), 67379A (18), 67399A (16), 67480 (15), 67526 (21), 67533 (20), 67576 (6), 67594 (4), 67692 (3), 67700 (1), 67837 (8), 68012 (8), 68069 (20), 68097 (25), 68195 (18), 68196 (25), 68336 (25), 68358 (2), 68359 (11), 68379 (18), 68449 (20), 68494 (23), 68547A (23), 68582 (23), 68679 (15), 68699 (6), 68746 (6), 68820 (21), 68854 (18), 68961 (15), 68971 (16), 69070 (17), 69343 (15), 70099 (25), 70868 (25), 70900 (25), 71017 (25), 71119 (15), 71461 (25), 72573 (15), 73792 (15), 73826 (15), 74137 (23), 74759 (15), 74760 (6), 74789 (15), 74792 (15), 74853 (20), 74861 (6), 74930 (25), 74945 (11), 74952 (25), 74953 (11), 74958 (18), 75007 (17), 75099 (20), 75100 (7), 75149 (19), 75154 (15), 75172 (6), 75195 (16), 77281 (4), 77283 (20), 77298 (23), 78287 (23), 78318 (4), 78323 (23), 78345 (23), 78480 (26), 78678 (20), 78687 (20), 78695 (20), 78711 (26), 78720 (26), 78731 (12), 78732 (4), 78733 (11), 78758 (12), 78771 (2), 78784 (20), 78787 (25), 78788 (18), 78830 (20), 78838 (25), 78859 (20), 78905 (20), 79072 (20), 79073 (13), 79075 (20), 79076 (4), 79329 (15), 79348 (18), 79359 (15), 82829 (15), 83126 (15), 83889 (25), 87448 (18); Croat & Alba 1222 (10); Croat & Bay 75707 (15); Croat & Cogollo 52174 (15); Croat & Folsom 33989 (25), 34042 (25); Croat & Gaskin 80391 (25); Croat & Grayum 59731 (3), 59785 (4), 59814 (3), 59851 (3), 59906 (1), 59929 (20), 60002 (8), 60070 (25), 60112 (25), 60116 (18), 60130 (2), 60139 (25), 60149 (11), 60255 (2), 60346 (8), 60355 (25); Croat & D. Hannon 63129 (20), 63167 (20), 63340 (26), 64109 (24), 64317 (24), 64476 (24), 64622 (20), **64638** (24), 65370 (20), 65536 (26), 74856 (21), 79112 (3), 79115 (13), 79167 (4), 79170 (4), 79191 (4), 79193 (1), 79199 (18), 79211 (3), 79238 (4), 79284 (20), 79286 (3), 79291 (4); Croat & M. Mora 83652 (18), 83685 (7), 83696 (25), 83777 (16); Croat & Nuñez 82064 (15); Croat & M. Pérez 78686 (26); Croat & Porter 16249 (25), 16303 (18), 16375 (18), 16412 (18), 16499 (11); Croat & Zhu 76203 (16), 76253 (15), 76254 (18), 76256 (16), 76257 (16), 76259 (15), 76266 (16), 76328 (25), 76340 (8), 76422 (18), 76449 (18), 76482 (18), 76533 (7), 76560 (10), 76597 (7), 76644 (6), 76653 (25), 76666 (15), 76666A (19), 76746 (15), 76757 (6), 76794 (20), 76858 (25), 76859 (20), 76942 (18), 77017 (7), 77023 (18), 77042 (16), 77048 (15), 77101 (16), 77102 (15), 77115 (14), 77201 (20); Croat et al. 82305 (25), 82441 (25), 82520 (18), 83795 (15), 83804 (15), 84041 (18); Cruz 354 (20); Cuatrecasas 4225 (23), 15053 (25).

D'Arcy 769 (23), 770 (23), 9420 (15), 9678 (6), 10766 (20); D'Arcy & Sytsma 14498 (15); Davidse 35802 (20); Davidse & Brant 31879 (20), 32366 (20), 32410 (20); Davidse & D'Arcy 10098 (15); Davidse & González 13410 (23), 21012 (23); Davidse & Hamilton 23599 (15), 23617 (7); Davidse & Herrera 26262 (20), 31077 (12), 31154 (12), 31213 (11); Davidse & Holland 36505 (20); Davidse & Holst 36041 (20); Davidse et al. 4844 (23), 18102 (23), 20326 (20), 20440 (20), 20914 (23), 29516 (20), 34478 (24); Davidson 7164 (20); de Nevers & H. Herrera 3975 (7), 5898 (18); de Nevers et al. 4709 (7),

5727 (18), 7407 (18), **7409 (19)**, 8267 (15); Delinks 452 (15); Dillon et al. 1837 (20); Dodge 10020 (4), 10198 (4); Dodge & Goerger 9489 (25), 10157 (20); Dodson 6188 (15); Dodson & Dodson 11130 (15); Dodson & Tan 5338 (15); Dodson et al. 8415 (15), 10594 (15), 14638 (15); Donnell Smith 7813 (20); Drake 7 (23); Dressler 4688 (15), 4716 (14), 5316 (10); Dryer 1681 (11); Duke 5014 (14), 5099 (15), 5169 (15), 5260 (15), 5437 (15), 13082 (15), 13601 (15); 14346 (15), 15591 (15); Duke & Kirkbride 14019 (15); Duss, P. 3790 (23), 21496 (23); Dwyer 2077 (15), 4565 (15), 9920 (20), 11184 (20); Dwyer & Dieckman 13008 (20); Dwyer & Gentry 9479 (6).

Eggers 14183 (15), 15095 (15); Ekman 1983 (23); Engler 226 (23), 227 (23), 2389 (26), 2793 (23); Espina et al. 2902 (15); Espinosa & Guerra 3762 (15), 3939 (15); Espinosa & E. Martínez 3308 (6); Espinosa et al. 3138 (15), 3611 (15), 4478 (15), 4723 (6), 10035 (20).

Faden et al. 76/82 (20); Fallen & Ray 860 (15); Fishlock 326 (23); Folsom 1265 (6), 1444 (15), 3211 (6), 4054 (20), 6218 (6), 6247 (15), 8712 (20), 9200 (18), 9329 (12), 9724 (11), 10116 (25); Folsom & Collins 436 (15), 6486 (21); Folsom & Mauseth 7844 (15); Folsom et al. 2111 (20), 6848 (15), 6852 (15), 8264 (21); Fonnegra 1344 (25); Fonnegra et al. 2899 (18), 2907 (18); Forero 719 (25); Forero et al. 1723 (14), 4571 (18), 4659 (18), 6272 (15), 6489 (15), 9007 (15), 9047 (15); Förther 10213 (20); Foster, R. B. 865 (14); Foster et al. 14649 (9); Fuertes 367 (20); Fuertes 564 (23); Funk et al. 10626 (25), 10718 (25).

Galdames et al. 1138 (18), 1330 (7), 1570 (7), 1626 (14), 2252 (14), 2286 (14), 2486 (14); Galeano, G. 4600 (25); Galeano, G. et al. 4825 (19); Gamboa et al. 71 (15), 91 (15); Garibaldi 68 (14); Garnier 772 (26); Gentry 3035 (25), 26705 (25); Gentry & Dwyer 3643 (15); Gentry & Forero 7217 (18), 7342 (18); Gentry & Juncosa 41037 (18); Gentry & Lajones 73108 (15); Gentry & Tyson 1653 (14); Gentry et al. 3406 (15), 24700 (25), 26709 (15), 28574 (14), 72496 (15), 72955 (25), 75903 (25); Gómez 19038 (20), 19531 (4), 19532 (20), 19572 (26), 20562A (20), 20565 (20), 22016 (20), 22951 (13); Gómez & Herrera 23477 (25); Gómez et al. 20405 (25), 21108 (20); Gómez-Laurito 7792 (13), 7856 (4); Gómez-Pompa 1505 (20); Gonçalves et al. 224 (23); González 1473 (20), 6711 (20), 3341 (20), 5597 (20); Gordon 55C (18), 339 (25); Grant & Rundell 92-01928 (4); Grayum 2225 (18), 2288 (11), 2771 (20), 2772 (12), 2780 (25), 2840 (4), 4756 (13), 4765 (20), 6194 (20), 6887 (11), 6899 (2), 6918 (20), 6925 (20), 6936 (2), 7620 (12), 7698 (2), 8638 (13), 9251 (20), 9277 (20), **9773 (11)**, 9777 (4), 9804 (25), 9830 (11), 9844 (18), 10588 (4), 10858 (25); Grayum & Evans 10156 (4); Grayum & Fleming 8119 (4); Grayum & Hammel 5785 (18); Grayum & G. Herrera 7829 (20), 9139 (1), 9236 (3); Grayum & Jacobs 3524 (18); Grayum & Murakami 9939 (25); Grayum & Schatz 3174 (25), 3206 (11), 3218 (18), 3220 (2), 5279 (25); Grayum & Sleeper 6100 (20); Grayum & Warner 5710 (20); Grayum et al. 3982 (4), 3983 (4), 4014 (3), 4440 (7), 4447 (4), 4483 (7), 4961 (20), 5467 (13), 5719 (20), 5723 (13), 5862 (20), 7547 (3), 7549 (1), 7567 (4), 7657 (15), 8038 (11), 8336 (13), 8345 (20), 9250 (4), 9469 (25), 9744 (12), 9962 (4), 9973 (23), 10578 (20), 11116 (11), 11139 (4), 11163 (11), 11169 (12), 11174 (13); Grove 01 (20); Guerra & Liesner 2871 (4); Guillermo, J. & D. Cardenas L. 863 (16); Gutierrez, G. & Barkley 17115 (25).

Haber & Atwood 9163 (20); Haber & Bello 7191 (20); Haber & Hammel 1799 (20); Haber & Zuchowski 9251 (20), 11175 (25); Haber et al. 4979 (20), 10824 (25); Hahn 142 (15), 945 (23); Hammel 122 (2), 778 (21), 3140 (6), 3586 (20), 3781 (6), 4049 (18), 4101 (20), 4298 (14), 4484 (19), 5378 (14), 5607 (7), 6264 (20), 7212 (6), 8123 (18), 8167 (11), 8212 (12), 8270 (20), 8273 (12), 8415 (20), 8606 (20), 8617 (11), 8748 (12), 8784 (4), 8846 (2), 8873 (11), 8874 (25), 9688 (4), 9772 (4), 9922 (20), 10081 (4), 10082 (18), 10449 (20), 12320 (12), 13636 (5), 13685 (7), 20231 (20); Hammel & D'Arcy 5018 (15); Hammel & Grayum 14169 (1); Hammel & Kernan 16661 (4); Hammel & Trainer 13962 (20), 14211 (20), 14767 (14), 14786 (19), 15836 (25); Hammel et al. 4882 (18), 6871 (20), 14472 (15), 16262 (14), 16397 (7), 17548 (25), 20114 (20); Harling 313 (15); Harling & Andersson 16727 (15), 18898 (15), 19371 (15), 24778 (15); Harmon & Dwyer 4035 (20); Harmon & Fuentes 4740 (20), 6419 (20); Harris 8361 (23); Harris & Neal s.n. (23); Hartman R. 12488 (15); Henny 5 (2), 7 (23); Herbst & S. Ishikawa 5459 (23); Heredia, M. 60 (23); Hernández 473 (26), 542 (20), 605 (20), 1318 (26), 2586 (26); Hernández & Vazquez 551A (20); Herrera 1636 (20), 4116 (18); Herrera, G. et al. 2928 (20); Herrera, H. 245 (19); Heyde & Lux 4654 (20); Higgins, J. 119 (23); Hill, S. 24812 (23); Hitchcock s.n. (23); Hodge 2929 (23); Hodge & Hodge 3174 (23); Holm-Nielsen et al. 2769 (15), 25355 (18); Holst 62370 (23); Holstein & Armbruster 20425 (20); Hoover 1324 (15); Hoover et al. 3161 (25), 3968 (25); Horich s.n. (11), s.n. (13); Howard 11564 (23), 11744 (23); Howard & Nevling 16978 (23); Huft & Jacobs 1997 (14).

İbarra 167 (20), 455 (20), 645 (20); Ibáñez et al. 1829 (26); Ibarra & Cedillo 1804 (20); Iltis et al. 30338 (20); INBio 186 (20); Ingram 1124 (15), **1146 (17)**, 1169 (23), **76452 (25)**.

Jacobs 2159 (20); Jiménez 103 (18), VI (18); Johnston, I. 1165 (14); Johnston, J. R. 305 (23). Judd et al. s.n. (23); Juncosa 619 (25), 797 (15), 1795 (18), 1898 (18), 1912 (18); Jones, A. & Tejada 275 (15).

Kennedy 455 (15), 1193 (14), 1594 (15), 2661 (15), 3253 (25); Kennedy & Foster 395 (15); Kennedy & Solomon 4629 (20); Kenoyer 188 (14); Kernan 381 (20), 748 (4); Kernan & Phillips 831 (4); Kew 70-76-494 (20); Killip 12154 (15), 35113 (18), 39979 (14); Knapp 1042 (19), 2165 (4), 2275 (15), 5758 (6); Knapp & Mallet 3089 (15); Knapp et al. 1717 (6); Koshear 59 (4); Kress 77-830 (15), 77-831 (15), 84-630 (25), 84-1622 (20), 84-1632 (11); Kufer, J. 394 (20); Kursar & Coley 4 (15); Kvist & Asanza 40756 (18); Kvist et al. 48348 (18).

Lasser 16678 (15); Lavastre 1845 (23); Lazor & Tyson 3492 (15); Lazor et al. 2578 (18); LeClezio 135a (16); Le Goff A. 95 (23); Lehmann s.n. (15), 5311 (15), 8876 (25); Leija & Garza 3341 (20), 5597 (20); Leimbeck, R. 306 (15); Lent 37 (18), 161 (1), 639 (25), 694 (25), 2789 (20), 4042 (25); Lent et al. 3374 (18), Leon 720 (25), 26573 (25); Lewis et al. 1753 (6), 2195 (14), 3251 (14); Liesner 114 (1), 1736 (3), 2871 (4), 14102 (20), 14394 (25); Liesner & A. González 10126 (23); Liesner & Judziewicz 14797 (25); Liesner & Mejía 26236 (20); Liesner et al. 7681 (23), 15035 (20), 15122 (20), 15144 (18), 15330 (25), 15365 (25); Liogier 13307 (23); Liogier & Liogier 20185 (23); Lister & Colchester 272 (23); Lloyd 237 (23); Loiselle 106 (25); (20); Løjtnant & Molau 15839 (15); Lopez Garcia & Martin 122 (26); Lotto s.n. (23); Lutevn 1010 (6), 1203 (15), 3175 (15), 3180 (15), 3188 (6), 3263 (20), 3342 (20), 3385 (18), 4043 (14); Luteyn & Croat 906 (14); Luteyn & Kennedy 1612 (6), 1837 (6); Luteyn & Wilbur 4569 (20); Luther s.n. (23).

Maas et al. 7834 (1); MacDougal 1027 (18), 1090 (20),

3193 (20), 3299 (20), 3303 (24); Madison 589 (20), 627 (20), 705 (24), 712 (20); Madison et al. 5008 (15); Maguire et al. 36461 (23); Marten 789 (4), 831 (20), 848 (3); Martínez 3016 (20); Martínez et al. 22713 (20), 23175 (20), 23474 (20), 23693 (20); Martínez, E. 2287 (26), 13445 (20), 13630 (20), 16131 (20); E. Martínez S. & Aguilar 12435 (20); Matuda 16369 (26), 16765 (26); Maxon et al. 6812 (14), 6820 (14); Mayo & Madison 301 (20); McAlpin 85-33 (4); McDade s.n. (16); McDonagh et al. 433 (15), 439 (15); McDowell 148 (20), 769 (11), 1012 (20); McPherson 7371 (25), 9176 (15), 9829 (18), 9865 (25), 10725 (7), 10958 (14), 11129 (25), 11381 (18), 11401 (18), 11591 (14), 11816 (2), 15037 (14); McPherson & J. Aranda 10095 (2); McPherson & Merello 8143 (19), 8235 (18); Meier et al. 5164 (23); Mejia & Ramirez 9929 (23); Mejia & Zanoni 6614 (23); Mena 190 (20); Mendieta 1-10 (15), 1-101 (15), 1-121 (15); Miller & Schmidt 5551 (23); Miller & Taylor 5937 (23); Miller et al. 753 (15); Miranda, F. 7546 (20); Miyashiro s.n. (23); Montenegro, D. & Chung 1462 (20); Montes s.n. (23); Moore, J. W. 451 (23); Moore Jr. & Bunting 8928 (20), 8933 (20); Mora 51 (25), 70 (18); Moraga 173 (20); Morales 1047 (26), 2035 (13); Morales et al. 5413 (20); Moreno 15290 (26), 16421 (26), 16464 (26), 17142 (24); Moreno & Henrich 8427 (26); Moreno & Robleto 20526 (24); Moreno & Sandino 12855 (25), 12891 (25), 12917 (25), 12955 (25), 12976 (18), 15160 (18); Mori & Bolten 7698 (15); Mori & Gracie 18717 (23); Mori & Kallunki 3591 (15), 6026 (6); Mori et al. 3817 (25), 4184 (7), 6814 (25); Murphy & Jacobs 1289 (20); Moreno, P. & J. Sandino 15160 (18).

Nash, G. 611 (23); Nee 9023 (16), 22595 (20), 23733 (20), 29752 (20), 29993 (20), 41364 (23), 99121 (20); Nee et al. 24759 20), 26103 (20); Neill 1571 (24), 1657 (26), 3629 (24); Neill & Vincelli 3484 (12); Neill et al. 11683 (15); Nelson & Andino 16247 (24); Nelson & Cruz 9215 (20), 9291 (24); Nevling & Gómez-Pampa 1505 (20); Nicolson 2060 (23), 3393 (4); Nilsson & Manfredi 505 (20); Nilsson et al. 377 (25), 632 (25); Noriega & H. Vasquez G. 1353a (20).

Ocampo 3411 (20); **Oersted s.n. (20)**; Opler 246 (20); Oppenheimer 67-1-3-1244 (16).

Palacios 11452 (25), 13626 (25); Palacios & Tirado 1287 (25), 11327 (15); Paredes et al. 940 (7); Penéis, D. 633 (25); Pérez 1 (25); Pérez, J. & M. Sosa 671 (23); Peterson 6405 (16); Peterson & Annable 6768 (15); Pfeifer 2124 (24), 2163 (20); Philcox 8231 (23); Picado & Gamboa 134 (20), 138 (1); Pipoly 4479 (24); Pitman & Bass 995 (25); Pittier 2600 (15), 2715 (16), 2836 (20), 3754 (14), **3766 (22)**, **3838 (16)**, 3847 (19), 6845 (15); Pittier & Durand s.n. (1); Plowman 14121 (15); Polanco 1485 (15), 1591 (18); Polanco et al. 1905 (15); Porter et al. 4282 (15); Prance et al. 30247 (23); Prevost 3258 (23), 3382 (23), 3580 (23); Proctor 20987 (23), 32251 (20), 38601 (23).

Quesada 51 (4), 175(20); Quishpe & Dávila 82 (15).

Ramamoorthy et al. 3763 (20); Raven 21532 (4); Read & Watson 84-75 (21); Renson 266 (26); Rentería 10680 (15); Ríos et al. 109 (20); Rivera 623 (20), 758 (20), 1560 (20), 1718 (25); Robles, R. 815 (20), 1142 (25), 1158 (25), 1234 (2), 2090 (4); Robles et al. 2050 (25); Rodríguez, A. & Estrada 142 (20); Rodríguez, G. 32 (20); Rodríguez, J. 262 (15); Rojas et al. 607 (23); Roldan et al. 1199 (18); Romero-Castaneda 6436 (16); Rose et al. 4375 (23); Rueda et al. 4070 (4); Rueda & Coronado 6557 (24).

Salick 8092 (12), 8153 (25); Sanchez 539 (2); Sanders et al. 19322 (20); Sandino 1248 (26); Sandoval & Chinchilla 352 (20); Sargent 340 (23), 643 (23); Schatz 1079 (15); Schatz & Grayum 700 (20), 701 (20), 706 (25); Schipp 386 (20); Schmalzel 1212 (15); Schmalzel & Alverson 1199 (15); Schubert & Rogerson 619 (20); Schultes & Cabrera 17890 (23); Schwerdtfeger 21422 (25); Seler 2389 (26), 2398 (26); Shank & Molina 4288 (25); Shattuck 397 (14); Shepherd 438 (19); Simmonds s.n. (23); Sinaca 830 (20); Sintenis, P. 2793 (23); Skutch 5328 (1); Slane 634 (23); Smith 2239 (20); Smith, C. E., Jr. & H. M. Smith 3389 (6); Smith, D. A. 134 (20); Smith, D. et al. 1059 (25); Smith, H. H. & G. W. Smith 1411 (23); Soejarto & Rentería 3556 (19); Solomon 5761 (23); Sparre 14122 (15), 14556 (15), 15182 (15), 15499 (15), 18326 (18), 19397 (15), 19488 (15); Sparrow & Brewster 108 (20); Spellman et al. 164 (20); Sperry 517 (20), 525 (20), 567 (20), 570 (20); Standley 7700 (20), 7935 (20), 18786 (24), 20085 (20), 21077 (26), 21414 (20), 25700 (24), 26156 (16), 26305 (20), 27224 (15), 27413 (15), 28238 (16), 28732 (16), 29867 (14), 31266 (14), 32242 (20), 32794 (20), 36314 (25), 36739 (4), 36840 (2), 38942 (20), 40223 (20), 40960 (14), 41107 (14), 44754 (20), 52702 (20), 52924 (20), 53146 (24), 53990 (20), 55444 (20), 58291 (20), 60715 (20), 63529 (20), 63620 (20), 65041 (20), 66844 (20), 68724 (26), 72447 (20), 75669 (20), 78161(26), 78523 (20), 79561 (26), 87180 (20), 88988 (20); Standley & Chacón 6701 (24); Standley & Valerio 45008 (20), 45206 (25), 45262 (25), 45592 (20), 46000 (20), 48960 (4), 48997 (25); Stein & Hamilton 990 (6); Stergios et al. 7940 (23); Stern et al. 433 (15); Stevens 6027 (26), 6420 (25), 7457 (24), 8044 (24), 11786 (24), 12311 (24), 13564 (25), 13761 (20), 23642 (11), 24257 (12); Stevens et al. 17591 (26), 20998 (24), 24699 (12); Stevenson, P. 379 (16); Stevermark 31763 (20), 34555 (20), 37153 (20), 37456 (20), 38647 (20), 38775 (20), 41699 (20), 44754 (20), 45410 (20), 45869 (20), 47684 (26), 47908 (20), 49321 (20), 49637 (26), 52070 (20), 60796 (23), 88864 (23), 91896 (23), 94331 (23); Stevermark & Bunting 97728 (23), 105293 (23); Steyermark & Davidse 116647 (23); Stevermark & Liesner 118891 (23), 121834 (23); Stevermark & Rogers 119364 (23); Stevermark et al. 100213 (23), 100239 (23), 100318 (23), 102036 (23), 122412 (23), 124629 (23), 124955 (23), 127204 (23); Stimson 5277 (16); Stone 3317 (20); Stricker 342 (20); Sturrock 352 (23); Sullivan 59 (15), 537 (6), 745 (15); Sytsma 1658 (15), 1695 (18); Sytsma et al. 2414 (15), 4398 (6); Sytsma & Andersson 4573 (6); Sytsma & Antonio 3006 (25).

Taylor 216 (20); Taylor, N. 48 (23); Taylor & Taylor 11660 (18); Tellez et al. 4466 (20), 4875 (25); Thompson 128 (15), 160 (15), 441 (26), 3238 (23), 4593 (15), 4816 (15), 4874 (6), 4937 (2), 4951 (8), 5028 (18); Thorne & Lathrop 40559 (20); Tipaz et al. 2280 (18); Tonduz 503 (25), **9961 (1)**, 12874 (25); Trujillo et al. 17397 (23); Tyson 1438 (16), 1443 (15), 4632 (14), 6700 (16); Tyson et al. 4486 (15), 4631 (14), 4701 (16), 4834 (14).

Utley & Utley 1100 (3).

Valerio s.n. (20), 246 (20), 462 (1), 1355 (20), 1356 (20); Valverde 741 (13); Vanderveen 590 (20); Vasquez, M. et al. V-907 (20); Villacorta et al. 314 (20), 408 (20); von Wedel 1438 (2), 2892 (18).

Wagner, R. 558 (23); Webster et al. 12581 (24), 12624 (20), 12625 (20); Wendland s.n. (26), 410 (26); White-foord 1176 (20), 3284 (20); Whitefoord & Eddy 136 (15), 372 (25); Whitehill 8 (23); Wilbur 28249 (20), 37243 (20), 37337 (20); Wilbur & Jacobs 34819 (20), 34962 (20); Wilbur et al. 15664 (6), 15861 (26); Williams, L. et al.

28479 (13); Witherspoon & Witherspoon 8401 (15); Won s.n. (23); Woodbury et al. s.n. (23); Woodson Jr. & Schery 861 (1); Woodson Jr. et al. 1909 (25). Yanez et al. 1387 (25); Yuncker 4961 (24); Yuncker et al. 8395 (20), 8551 (24), 8826 (20).

Zak et al. 5383 (15), 5414 (15), 5726 (15); Zambrano & Delgado 1336 (14); Zanoni & Pimentel 23420 (23), 23456 (23); Zanoni et al. 23113 (23), 25159 (23), 27170 (23); Zapata et al. 289 (19); Zent, E. & S. 2189 (23); Zuñiga 216 (20).