



Untangling the West Indian Dioscoreaceae: New combinations, lectotypification and synonymy

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Abstract

A synopsis of the West Indian Dioscoreaceae is presented. The genus *Rajania* L. is reduced to a section of *Dioscorea* L., requiring six new names, 11 new combinations, and reestablishment of two names. Explanations are provided in cases where mixed specimens or otherwise inadequate type material has led to the historical misapplication of names. Lectotypes are designated for 26 names and updated synonymy is provided for all native members of the West Indian Dioscoreaceae. Of the 121 names cited at species level and below, 26 species, one subspecies and a single variety are recognized.

Resumen

Se presenta una sinopsis de Dioscoreaceae de las Indias Occidentales. Se reduce el género *Rajania* L. a una sección de *Dioscorea* L., lo cual requiere seis nombres nuevos, 11 nuevas combinaciones, y el restablecimiento de dos nombres. Se explica los casos en que especímenes mezclados o material tipo considerado no adecuado por otras razones, ha conducido históricamente a la mala aplicación de los nombres. Se designa lectotipos para 26 nombres y se presenta sinonimia completa y actualizada para todas las especies nativas de Dioscoreaceae de las Indias Occidentales. De los 121 nombres aquí citados a nivel de especies para abajo, se reconoce 26 especies, una subespecie, y una variedad.

Key words: *Dioscorea*, Dioscoreaceae, lectotypification, new combinations, nomenclature, *Rajania*, West Indies

Introduction

Dioecy, minute flowers, and complex patterns of intraspecific variation make the Dioscoreaceae an inherently difficult family in which names and nomenclatural errors have tended to proliferate. The West Indian (WI) species are particularly challenging due to the prevalence of mixed elements in type material. Depauperate and/or erroneous descriptions have also resulted in ambiguous species concepts and propagation of misapplied names. This paper aims to link all WI Dioscoreaceae names with the elements upon which they are based and to address long standing errors in the interpretation of type material, in order to affect a clean transfer of names from *Rajania* L. to *Dioscorea* L., and to aid in the interpretation of WI yam diversity. The new names will also be included in a forthcoming treatment of the family for the series *Flora de la República de Cuba* (Raz & Pérez in prep.). Supplemental taxonomic information is provided here for non-Cuban species.

The status of Rajania

To date, the results of all phylogenetic studies that have included exemplars of *Rajania* have shown it to be a monophyletic group nested within *Dioscorea* (Caddick *et al.* 2002a, Wilkin *et al.* 2005, Raz 2007, Viruel *et al.* 2015). Furthermore, the samara, once thought to be unique to *Rajania*, is now known to occur in three *Dioscorea* species from Mexico, none of which share a recent common ancestor with *Rajania* (Raz 2007). The samara fruit type is therefore rejected as a criterion for generic circumscription in Dioscoreaceae, just as Caddick *et al.* (2002b) rejected fleshy-fruitedness as a justification for maintaining *Tamus* L. at generic rank. The latter authors sank *Tamus* into *Dioscorea* and suggested that *Rajania* be subsumed next: a deceptively simple proposal that developed into a long and complex forensic investigation.

Rajania is one of five Dioscoreaceae lineages in the West Indies. The region is also home to eight native species of *Dioscorea* s.s. distributed among four clades (Raz 2007, Viruel *et al.* 2015) and distinguishing one genus from the other has presented challenges, even for authorities on the WI flora and monographers of the Dioscoreaceae (Knuth 1917, 1924, Howard 1947, Ayala 1984). Erroneous placement in *Rajania* or *Dioscorea* was common in 19th and 20th century publications (see synopsis below), and misidentified sheets abound in US, European and Caribbean herbaria. Throughout their range in the WI, *Rajania* and endemic species of *Dioscorea* s.s. exhibit convergence in leaf shape, inflorescence architecture, floral morphology, and even pollen ornamentation, such that, in the absence of fruiting material, generic diagnosis can be particularly difficult. A classification that leads to fewer errors is therefore desirable.

Taking into account all the available evidence from molecular and morphological studies, and in the interest of producing a natural as well as a practical classification of *Dioscorea*, the taxonomic status of *Rajania* is reduced to *Dioscorea* sect. *Rajania* (L.) Raz, and new combinations (and new names as necessary) are provided for the species accepted herein.

Materials and Methods

Protologues were consulted for all published names of WI Dioscoreaceae and regional floras were examined to understand how, in practice, these names have been applied. An exhaustive physical search for specimens was beyond my means, but every effort was made to solicit curators' and librarians' assistance to locate original material and procure digital images when loans could not be sent. High resolution images were sent by curators at BM, BREM, DWC, G, GOET, JE, LD, PRC. Images from E and M were consulted via JSTOR Global Plants. Physical specimens were examined from B, BM, F, GH, HAC, HAJB, JE, K, KIEL, NY, MO, S, UCWI, US, and YU. Despite published claims to the contrary (Howard 1947, Ayala 1984), the Dioscoreaceae types at B did in fact survive WWII, and are cited herein. In rare cases, specimens could not be traced, but as herbarium digitization efforts accelerate, it is hoped that these last bits of data will eventually enter the public domain.

Synopsis of West Indian Dioscoreaceae: new combinations, lectotypification and synonymy

The Dioscoreaceae are represented in the WI by 28 native species (including two undescribed), one subspecies and one variety in the single genus *Dioscorea*. There are also five introduced species of Old World origin, cultivated for their edible tubers: *Dioscorea alata* L., *Dioscorea bulbifera* L., *Dioscorea cayennensis* Lam., *Dioscorea dumetorum* Pax, and *Dioscorea esculenta* (Lour.) Prain. The first three have become naturalized in Puerto Rico, (Acevedo Rodriguez 2005) while *D. alata* and *D. bulbifera* are naturalized in Cuba (León 1946), Jamaica (Adams 1972), and probably elsewhere in the Antilles. A *Dioscorea* research collection of over two hundred species, many of Mexican and South American origin, was maintained by Dr. Frank Martin at the USDA experiment station in Mayaguez, P.R. during the 1960's and 70's, but today it is reduced to just a handful of species; none have escaped cultivation. Herein, only the native WI yam species are considered. The reader may consult Govaerts *et al.* (2015) for complete synonymy of the domesticated food yams.

The present work includes 121 names that have been applied (or misapplied), at species level and below, to the native WI Dioscoreaceae since 1753 (plus one pre-Linnaean polynomial). The total includes six new names and 11 new combinations for those taxa formerly included in *Rajania*.

To date the most significant contribution to WI yam taxonomy has been that of German botanist R.Knuth, who published forty-two WI Dioscoreaceae names during the period 1917-37. Of this total, 29 names appeared in a single 1917 paper with abbreviated (in some cases no) descriptions, and all specimens were cited in the form of syntypes. Thirteen of the 29 names were ascribed to an unpublished manuscript written 20 years earlier by American colleague Edwin Burton Uline (author of the sectional classification of *Dioscorea* followed here). World War I created the urgency for Knuth to publish so many new taxa in abbreviated form, but he explicitly stated (1917, p. 185) he would publish a full length treatment of the family after the war. In 1924, Knuth's monograph of the Dioscoreaceae was issued as part of Engler's Pflanzreich series.

In this later work, Knuth designated a type for many of the taxa he described in the 1917 paper, selecting from among the specimens he had originally cited. Given the extenuating circumstances of the War and Knuth's explicit

statement on p. 185 (1917) connecting the two works, the type specimens designated in the later work are here interpreted to be holotypes rather than lectotypes.

Global in scope, the 1924 monograph remains the most comprehensive treatment of the family to date. The work's chief shortcomings are its narrow species concepts based on limited sample sizes, inconsistent descriptions that often lack detail, and in the case of the WI yams, conflation of disparate elements in the interpretation of individual species. By 1924 Knuth recognized a total of 45 taxa at species level or below in the WI (including four new names). In the interest of matching all names to their appropriate type elements, I have attempted to untangle the thicket of mixed collections that have long plagued the interpretation of species diversity in WI yams. Lectotypes are herein designated for 27 names and I have interpreted Howard's (1979) assessment that "typification of species described by Linnaeus and Lamarck is difficult and remains a job for a specialist," as a call to action.

In the following synopsis, sectional placement follows Uline (1897, 1898) and Knuth (1924), with the exception of *Rajania* L. (17 species treated here- an additional two are undescribed, one subspecies, and one variety), discussed above. Although published phylogenetic studies of the genus (Wilkin *et al.*, 2005; Viruel *et al.*, 2015) have used clade names (*e.g.* New World I and II) instead of sections to circumscribe broad infrageneric groups in *Dioscorea*, sampling of Neotropical remains fragmentary and is insufficient to test sectional boundaries. In practice, Knuth's (1924) sections are more relevant than clade names for interpreting morphological diversity in Neotropical Dioscoreaceae (Téllez-Váldez & Geeta 2007, Ramírez-Amezcuca *et al.* 2012). Not all will stand up to future phylogenetic testing, but the majority are on based on sound morphological criteria, and the biggest taxonomic challenges will involve sorting out species complexes within sections rather than rearrangement among sections (Couto *et al.* 2014). Apart from *Rajania*, the other four sections of *Dioscorea* represented in the WI are as follows (WI members in parenthesis): *Lychnostemon* Griseb. (*Dioscorea polygonoides* Humb. & Bonpl. ex Willd. plus five endemic species), *Chondrocarpa* Uline (*D. chondrocarpa* Griseb.), *Dematostemon* Griseb. (*D. pilosiuscula* Bertero ex Spreng.), and *Macrogynodium* Uline (*D. trifida* L.f.). The majority of species that comprise these four sections occur outside the WI, and the species explicitly named in parenthesis each have a broader Neotropical distribution. For each of the widespread species mentioned above, only synonyms that are based on type material from the WI or have been cited in literature on the WI flora, are included here (a single exception involves the erroneous use of *Rajania*: see *D. chondrocarpa*).

Below, the WI Dioscoreaceae are arranged by section, from most speciose in the region to least. Within sections, accepted species are listed alphabetically. Updated synonymy is presented for all native species.

***Dioscorea* section *Rajania* (L.) Raz, stat. nov.** *Rajania* Linnaeus (1753: 1032). Lectotype (designated by Britten & Millspaugh 1920):—*Rajania hastata* Linnaeus (1753: 1032); See *D. alainii* below for Lectotype designation)

Janraia Adanson (1763: 76). On the page cited, this name appears in a table of genera comprising Section II of Adanson's Aristolochiae.

Among the included names are *Tamus* and *Janraia*, but not *Dioscorea* (which is included in his Liliaceae). In the table, *Janraia* is inaccurately described as having "5 to 6" calyx lobes, "5 to 6" stamens, and the fruit a "capsule" with "three winged locules", while on p. 74 of the text, Adanson stated correctly that the fruit of *Janraia* is unilocular and derived from a three-locular ovary in which two of the locules abort. The name is nearly identical to Plumier's *Jan-raia* (1703: 33) which is cited by Linnaeus (1753) as a synonym of *Rajania*. It is unclear why Linnaeus chose to invert the syllables.

1. *Dioscorea alainii* Raz, nom. nov. *Rajania hastata* L. (1753: 1032). Lectotype (designated here):—HAITI. Port-de-Paix. *Bryonia fructu alato, foliis auriculatis* Plumier (1693: Tab. 98). See notes below for more about the type locality

Rajania hastata var. *angusta* Knuth (1917: 222). Lectotype (designated here):—DOMINICAN REPUBLIC. Barahona: La Loma, August, 1911, *M. Fuertes 1037* ♂. (lectotype NY!, islectotypes BM!, GH!, MO!, S!). Remaining former syntypes: DOMINICAN REPUBLIC. Barahona, July, 1910. *Fuertes 576*. GH!, NY!; HAITI. Without locality, 1890. *Picarda 104*. I was not able to locate specimens of the latter.

Rajania hastata var. *euastata* Knuth (1917: 222). Under article 26.3 of the Melbourne Code (2012), this name is rejected. The autonym *R. hastata* L. var. *hastata* is the correct formulation. Knuth was inconsistent in his application of the prefix "eu" to varietal names. It is unclear why he employed it in the cases of *R. hastata* L. and *R. cordata* L., but not in the case of *Dioscorea polygonoides* Humb. & Bonpl. ex Willd.

Rajania hastata var. *incisa* Knuth (1917: 222). Lectotype (designated here):—HAITI. S. Michel to Marmelade, August 6, 1905, *Nash & Taylor 1457* ♂ (lectotype NY!). Remaining former syntype: HAITI. Fessard, no date, *Christ 1716* ♂. I was not able to locate a specimen.

Rajania hastata var. *latior* Knuth (1917:222). Lectotype (designated here):—DOMINICAN REPUBLIC. Barahona, 50 m, May, 1910, *M. Fuentes* 36 (lectotype NY!, isolectotype US!). No type was designated in the original publication, but five syntypes were cited Knuth (1924). Remaining former syntypes: DOMINICAN REPUBLIC. Without locality, 1856, *Mayerhoff* 39 ♀ (n.v.); HAITI. Crete Sale, 1900, *Buch* 432 (n.v.); Plateau de la Crete a Pierrot, 1898, *Picarda* 1658 ♂ (n.v.); St. Suzanne, 1909, *Christ* 2128 ♀ (n.v.).
Rajania hastata var. *triloba* Knuth (1917:222). Type:—DOMINICAN REPUBLIC. Constanza, 1887, *Eggers* 2284 (n.v.). As yet I have not been able to locate a specimen.

Notes: Endemic to Hispaniola. When Britton & Millspaugh (1920) designated *R. hastata* as the type species of *Rajania*, they did not cite any elements upon which the name could be based. Linnaeus in his protologue of *R. hastata*, cited two elements that could serve for lectotypification: one is a wretched specimen in the Clifford Herbarium at BM (Clifford 458, BM000647488) that is annotated in the lower left hand corner (without date or attribution) in what appears to be David Prain's hand as "*R. microphylla*". The determination is correct, and can be referred to the species renamed here as *Dioscorea bahamensis*. Linnaeus (1737: 458) wrote in reference to this plant, "Crescit in insula s. Dominga", a locality inconsistent with the present day distribution of *D. bahamensis*, but the reference is most likely to Plumier's writings (see below) rather than to the specimen in the Clifford Herbarium (C. Jarvis, pers. comm.). Given the true identity of the specimen, it is here rejected for lectotypification purposes.

The second element, the Plumier illustration, selected here as the Lectotype, is based on a plant that Plumier found growing in the vicinity of Port-de-Paix, on the "Isle S. Domingue" (=Haiti; Plumier 1693, p. 84). The figure is consistent with Linnaeus' description, and unambiguously depicts the Hispaniolan species renamed here as *D. alainii*.

The varieties subsequently described by Knuth are not accepted, as they are based exclusively on variation in leaf outline, a highly plastic trait in this and many other West Indian *Dioscorea* species (see discussion under *D. cordata*). This epithet honors Alain Liogier (Hermano Alain), prolific collector and author of the *Flora of Hispaniola*. He also made significant contributions to the Flora of Cuba.

2. *Dioscorea bahamensis* (R.Knuth) Raz, comb. nov. *Rajania bahamensis* Knuth (1917: 220). Type:—BAHAMAS. New Providence, 25 January 1890, *J. I. & A. R. Northrop* 203 *pro parte* (holotype B! (♂,♀), isotypes F! (♂,♀), K! (♀), NY! (♀)). The K sheet consists of three detached leaves, a portion of a stem and a detached fruit, collectively assigned barcode number K000099309, and affixed to the same sheet as the isotype of *R. urbaniana*, (see below). The NY sheet was annotated as the lectotype in 1975 by W.T. Gillis, who believed, mistakenly, that the B sheet had been destroyed

Rajania microphylla Kunth (1850: 451). Type:—CUBA. Pinar del Río, In savannis Cubae ad sumidero, Oct. 1823, *Poeppig* s.n. (holotype B!, isotypes JE! (2 sheets), K!, MO!).

Rajania urbaniana Knuth (1917: 220). Type:—BAHAMAS. Andros Island ("Purser Point, Andros Island" on labels at K and NY), 17 June 1890, *J. I. & A. R. Northrop* 203 *pro parte* ♂ (holotype B!, isotypes G!, GH!, K!, NY!). The K sheet includes two separate fragments from Andros Island, each with its own specimen label, assigned respective barcode numbers K000099308 and K000524433 (see also *R. bahamensis*, above for description of third fragment); a fourth fragment on the same sheet is a non-type specimen of the same species: Eggers 4287, barcode number K000099310. The NY sheet was annotated as the lectotype in 1975 by W.T. Gillis, who thought, mistakenly, that the B sheet had been destroyed.

Rajania prestoniensis Knuth (1924: 337). Lectotype (designated here):—CUBA. Oriente (Holguin): Prope Preston in litore maris, 14 November, 1914, *E.L. Ekman* 3448 ♂ (lectotype S! (S05-5314), isolectotypes B!, NY!, S! (S05-5309)). The protologue states "Typus in herb. Holm", without reference to one sheet or the other.

R. hastata auct. non L. Bentham in Hooker (1882: 72, pl. 1392), Northrop & Northrop (1902), and Correll & Correll (1982).

Notes: This species is restricted to Cuba and the Bahamas. *Rajania microphylla* is the earliest name, but the specific epithet was not available in *Dioscorea* and therefore it was necessary to select from among the available synonyms.

The three species subsequently described by Knuth all reflect variation in leaf outline, as well as minor differences in the length and number of staminate inflorescences, characters that vary within this and many other *Dioscorea* species. Knuth did not describe pistillate flowers or fruits for any of the three species listed here in synonymy, even though the holotype of *R. bahamensis* does in fact include a branch with developing fruits and two detached mature samaras. Counting both the 1917 and 1924 publications, Knuth cited just a single staminate specimen each to represent, respectively, *R. bahamensis*, *R. urbaniana* and *R. prestoniensis*: an insufficient sample to adequately characterize the plasticity in this taxon.

For centuries, confusion has prevailed about what to call this species, and most commonly *R. hastata* has been

misapplied. Bentham (1882), in his description of “*R. hastata* L.,” cited a mishmash of elements that include the Plumier illustration from “San Domingo” (Lectotype of *R. hastata* L.), “Poeppig” from Cuba (probably in reference to the type of *R. microphylla*, although other Poeppig s.n. specimens are also housed at K, where Bentham was based), “L. Brace” (*D. bahamensis* from the Bahamas) and “Wright 1712” from Cuba. Among the Wright 1712 duplicates (see *D. cephalocarpa*, below), Bentham is most likely to have consulted the two sheets at K: these include a total of five elements, however none correspond to *D. bahamensis* (the K elements are K1: *D. introrsa*, K “2A”: *D. cephalocarpa* ♂, K “2B”: *D. confusa* ♂, K “2C”: *D. scorpioidea* ♀, and K “2D”: *D. cephalocarpa* ♀; this last element is at the top of the “K2” sheet- I neglected to label it when I annotated the specimen). The plate 1392 (Hooker 1882) that accompanies Bentham’s description, corresponds to *D. bahamensis*.

Northrop and Northrop (1902), also misapplied the name “*R. hastata* L.” in their Flora, citing only “Wright 1712” from Cuba (without specifying which elements of which duplicates they examined), and their own number 203 (the latter comprising material from both Andros and New Providence Islands). They made no reference to any original material cited by Linnaeus, nor did they cite Bentham (1882) or even Grisebach (1866), who described his own “*R. hastata*” in part, based on Wright 1712 (see *D. psilostachya* below). It is likely that the Northrops’ use of *R. hastata* can be traced directly to Wright’s own determination “*R. hastata*” written on the herbarium labels of his no. 1712, but it is difficult to determine which sheets they examined. The B sheet of Northrop 203 from Andros Island was subsequently designated by Knuth as the type of *R. urbaniana*, and the B sheet from New Providence Island, as the type of *R. bahamensis*.

Britton & Millspaugh (1920) in their Bahama Flora criticized “Mrs. Northrop’s” use of “*R. hastata*” in connection with the Bahamian plants that they called *R. microphylla*. They wrote that *R. hastata* was by that time understood to be a species endemic to Hispaniola, but they too failed to cite any type elements of either species. The Corrells (1982) concept of *R. hastata* is the same as that employed by the Northrops, but unlike their predecessors, the Corrells cited *R. microphylla* in synonymy, (ignoring Britton & Millspaugh’s comment). Nevertheless, they did not cite any original material for either name.

During the years 1975-6, W.T. Gillis, who was working towards a revised Flora of The Bahamas, annotated nearly all of the type material of *R. bahamensis*, *R. microphylla* and *R. urbaniana* as “*R. hastata* L.,” consistent with the Northrops’ misapplication of that name.

Ironically, there is no evidence to suggest that the Northrops, the Corrells, Gillis, Wright, Grisebach or Bentham consulted Clifford 458 (BM) in formulating their respective concepts of *R. hastata*, as the sheet was never cited by any of them. (See discussion under *D. alainii*.)

3. *Dioscorea baracoensis* (R.Knuth) Raz, comb. nov. *Rajania baracoensis* Knuth (1924: 333). Type:—CUBA. Oriente (Guantanamo): Baracoa, 1915. *E. L. Ekman 4131* ♂ (holotype S!)

Rajania tenuiflora Knuth (1917: 219). Type:—Cuba. Oriente (Holguin): Sierra de Nipe, near Woodfred, 11 December, 1909, *J. A. Shafer 3149* ♂ (holotype B!, isotypes K! (K000099316), NY!). Knuth (1917) cites two syntypes, but a holotype is clearly specified in the 1924 publication. Remaining former syntypes: CUBA. Oriente (Holguin): Sierra de Nipe, near Woodfred, 5 December, 1909, *J. A. Shafer 3016* ♂ (K! (K000099315), MO!, NY!, F!). The K sheet is mounted together with Shafer 3049.

Notes: The earlier name, *R. tenuiflora* is not available as an epithet in *Dioscorea*. Staminate plants traditionally called *R. tenuiflora* have scorpioid cymules and less robust inflorescence axes compared to those of *R. baracoensis* s.s., which Knuth described from a single specimen. Wider consultation of material across the species’ range in Cuba and Hispaniola shows continuous variation in cymule architecture and robustness of the staminate inflorescence. Knuth never described pistillate flowers or fruits from either species. The pistillate inflorescence is far less variable than the staminate.

4. *Dioscorea cephalocarpa* (Uline ex R.Knuth) Raz, comb. nov. *Rajania cephalocarpa* Uline ex Knuth (1917: 221). Lectotype (designated here):—CUBA. (Pinar del Rio), 1860–1864 Wright 1712 p.p. ♂♀ (lectotype S “3A”! (♀), isolectotypes B! (♂), BM “2A”! (♂), BREM “A”! (♀), GH “2A”! (♀), GH “2C”! (♂), HAC! (3 sheets ♀ & 1 ♂, elements to be specified), K “2A”! (♂), NY1! (♀), NY “2B”! (♂), S “1B”! (♂), S “1C”! (♀), US “2C”! (♂), US “2D”! (♀), YU “3A”! (♀).). Remaining former syntypes: CUBA. Pinar del Rio: Herradura. 1905. *Van Hermann 779* ♀ (HAC!, HAJB!, B?). There is a mysterious specimen at B (B_10_0247709) labeled *R. cephalocarpa* and annotated by Knuth as “Typus”. There is no date, collector name or number on the label, only the locality “Cuba”. It may be one of the Van Hermann collections but I have not been able to confirm this

Rajania hermannii Knuth (1917: 222). Type:—CUBA. Pinar del Rio: Herradura, 1903, *Van Hermann 740* ♂ (holotype B!).

Dioscorea rigida Knuth (1925: 79). Type:—CUBA. Pinar del Rio: Sierra del Sitio Santo Tomas, Ensenada de Vega Cuchilla, ca. 500 m, 12 June 1923, *E. L. Ekman 16681* ♂ (holotype S!, isotypes B! [2 sheets: B100247707, B100247708]).

Notes: Endemic to Pinar del Rio, Cuba. Although a *Van Hermann 779* duplicate has been located at HAC with the clustered fruits typical of this species, it has somewhat anomalous leaf venation and therefore does not best represent *D. cephalocarpa*. The Wright 1712 collection, complicated as it is, better represents the typical morphology of this species. Much of the taxonomic confusion in *Rajania* can be traced to Wright 1712. This collection includes a total of six species mixed in different combinations of up to four species per sheet in at least 31 sheets (9 at HAC alone), dispersed across 12 herbaria (B, BM, BREM, F, GH, HAC, K, MO, NY, S, US, YU). There is also almost certainly a sheet at GOET, where Grisebach was based while he compiled his Cuban catalogue of Wright's material, but I haven't seen it. In all, there may be as many as 40 "duplicates" (see Howard (1988) for a history of the handling of Charles Wright specimens), each with a unique combination of elements. Nearly all the specimens I've seen are annotated simply as "*R. hastata*" by Wright himself, but the full species composition of this collection number includes what are here called: *D. cephalocarpa*, *D. confusa*, *D. introrsa*, *D. psilostachya*, *D. scorpioidea*, and *D. theresensis*.

"Wright 1712 pro parte" is cited among the syntypes of both *R. cephalocarpa* and *R. wrightii*, but Knuth never made clear which part(s) of which duplicate(s) he was referring to, and the descriptions (1917, 1924) reflect the mixed nature of the collections. As a result of this ambiguity, interpretation of all the above species has been confused, and the name *R. hastata* has been misapplied (also see discussion under *D. bahamensis* and *D. alainii*).

Rajania cephalocarpa was described primarily from pistillate material (Knuth did not see the majority of the staminate isoelectotypes cited here). Staminate plants of this species were described unambiguously, years later, under the name *Dioscorea rigida* (Knuth, 1925).

Not included in the list of synonyms is "*R. wrightii* var. *cephalocarpa* Uline", an annotation by Uline on Wright 1712 p.p. (GH "2C", my designation). The combination was never published, nor was it cited by Knuth as "in msc".

5. *Dioscorea confusa* Raz, nom. nov. *Rajania wrightii* Uline ex Knuth (1917: 221). Lectotype (designated here):—CUBA. Without locality, 1860-64, *Wright 1712* ♂ (lectotype NY "2A"!, isoelectotypes K "2B"!, S "1A"!, US "2A"!).

Notes: Cuban endemic. The interpretation of *Rajania wrightii* has been problematic from the start. The protologue includes no description and no diagnosis, just the ascription "Uline in msc." followed by a list of synonyms and specimen citations: Wright 1712 p.p. (♀♂), Valenzuela s.n. (♂♀), and Curtiss 506 p.p. (♂). Knuth did include a description in the 1924 monograph, but it is based on so many disparate elements that it is rendered meaningless.

The species represented by the Curtiss 506 duplicates from the Isle of Pines (Isla de la Juventud) in Cuba (BM, CM, F, GH) is not present among any of the Wright collections that I have seen. The Curtiss material has a rotate flower with deltate tepals as in *D. bahamensis*; it corresponds most closely to the type of *R. prestoniensis*, considered here to be a wider-leaved form of *D. bahamensis*.

I was not able to locate the Valenzuela material, but there are clues to its identity from the literature. Knuth (1924) cited among the exsiccatae of *R. psilostachya* "Valenzuela ♀", which is likely to be on the same sheet as the staminate material cited for *R. wrightii*, (there is no "p.p." appended to either citation). Richard (1850) cited a Valenzuela collection (without number or reference to the sex of the specimen) and mentioned that the species was found "near Havana". The Richard name was considered by Knuth to be a synonym of *R. psilostachya*, based on his examination of the Valenzuela material, and this determination is consistent with the narrow distribution of *D. psilostachya*. If the staminate material was also collected near Havana, then it would have to be either *D. psilostachya*, or *D. bahamensis*.

The remaining specimens cited as *R. wrightii* by Knuth (1924) are four Ekman collections from Eastern Cuba; all correspond to what is here called *D. introrsa*.

It is almost impossible to know which of the Wright 1712 elements Knuth (1917, 1924) considered in his formulation of *R. wrightii*. The elements cited here as the type collection of *D. confusa*, are those that cannot be assigned to any other species, and correspond to modern collections from southern central Cuba. The plants are unique in having staminate inflorescences congested (internodes between cymes reduced) with sessile cymes of white, globose flowers that remain light in color when dry. A full treatment is forthcoming in the series *Flora de la República de Cuba*.

6. *Dioscorea cordata* (L.) Raz, comb. nov. *Rajania cordata* L. Sp. Pl.: 1032. 1753. Lectotype (designated by Acevedo-Rodriguez & Strong 2005: 90):—DOMINICAN REPUBLIC ("Hispaniola"). Plate 491 of the Boerhaave set of Plumier

drawings in the library of Rijksuniversiteit, Groningen (used to create the composite drawing in Tab. 155 of Plumier 1758; Fig. 1)

Rajania pleioneura Grisebach (1864: 588). Lectotype (designated here):—DOMINICA. Without locality, no date, *Imray 122* (lectotype K! (♀)). Knuth (1924, p. 335) cited a staminate sheet of the same collection number, but did not cite the herbarium. There is a second *Imray* sheet at K, received in 1867 (the same year that *Imray 122* was accessioned into the Hooker herbarium): it is a staminate specimen of the same species, but it has no number; an unnumbered staminate sheet is also at GH. In his protologue, Grisebach did not cite a collection number, but since he described staminate inflorescences and samaras, he must have had access to material of both sexes.

Rajania sintenisii Uline in Urban (1902: 281). Type:—PUERTO RICO. Mayaguez: Monte Mesa, 24 Oct. 1884, *Sintenis 109* ♂ (holotype B! not destroyed, as reported in Acevedo-Rodríguez and Strong 2005). There is a mixed staminate and pistillate sheet at K. The pistillate element is a syntype of *R. cordata* var. *microcarpa*; the staminate element at K has cymules pedunculate (born on hypopodia, sensu Weberling, 1992), versus cymules sessile in the specimen at B. It is unlikely that the two staminate specimens were prepared from the same individual, and the K sheet is therefore not considered an isolectotype.

Dioscorea cyclophylla Urban (1909: 4). *Rajania cyclophylla* (Urban) Knuth (1917: 218). Type:—JAMAICA. Tyre near Troy 660 m, *Harris 9402* ♀ (holotype B!, isotypes BM!, K!, NY!, UCWI!, US!).

Rajania cordata var. *microcarpa* Uline ex Knuth (1917: 219). Lectotype (designated here):—U.S. VIRGIN ISLANDS. St. Thomas: Signal Hill 470 m, September 1880, *Eggers 184* (lectotype US! (♂), isolectotypes: FTG! (♀♂), GH! (♀♂), JE “1”! (♀♂), JE “2”! (♀), K! (♀♂), M (♀♂). The US sheet was annotated by Uline. Remaining former syntypes: CUBA. Pinar del Rio: Sierra de Anafe, 27 December 1911, *Wilson & León 11551* ♀ (K!, NY!, US!). The Cuban material is *D. psilostachya*. PUERTO RICO. Mayaguez: Monte Mesa, 24 Oct. 1884, *Sintenis 109* ♀ [GH!, K! (has both ♀ and ♂ elements: only the ♀ element was cited by Knuth, but they are the same taxon), S!, US!]; Sierra de Luquillo: in Monte Yunque, 14 July, 1885. *Sintenis 1384* ♂ (GH!, US! (mixed sheet, part *D. pilosiuscula*, part *D. cordata*); U.S. VIRGIN ISLANDS. St. Thomas: without locality, no date, *Eggers 279* ♂ (presumably at B, n.v.).

Rajania ovata var. *ehrenbergii* (Uline ex Knuth) Knuth (1917: 219). *Rajania cordata* var. *ehrenbergii* Uline ex Knuth (1917: 219). *pro syn.* Type:—HAITI. *Ehrenberg s.n.* ♀ (holotype B). I haven't seen the specimen, however Kunth (1850) provided a richly detailed description (as *R. cordata* L.), making a determination possible. Knuth (1924) ultimately chose not to recognize infraspecific taxa in *R. ovata* and sunk his own variety.

Rajania venosa Knuth (1917: 219). Type:—PUERTO RICO. Luquillo Mountains, July 1902, *P. Wilson 163* ♂ (holotype B!, isotypes K!, NY!, US!).

Rajania cordata var. *euordata* Knuth (1924: 334). Illeg. The autonym *R. cordata* L. var. *cordata*, here becomes *Dioscorea cordata* (L.) Raz var. *cordata*.

Dioscorea spiculoides Matuda (1953: 57). Type:—MEXICO. Oaxaca, 1841–1843, *Liebmann 14561* ♂ (holotype F!, isotype C!).

Notes: *Dioscorea cordata* is the most widespread and variable of the *Dioscorea* sect. *Rajania* species, occurring in both the Lesser and Greater Antilles (with the notable exception of Cuba). It exhibits complex patterns of variation across its range and further studies are needed to interpret this complexity; genetic data in particular are desirable. There is archeological evidence to suggest that this species may have been an important food plant in Puerto Rico as early as 6000 B.C. (Pagán Jiménez 2011), and it is likely that human activities (migration, trade) have influenced its distribution. The role, if any, of human selection on observed diversity, is unknown.

Across the Antilles, leaf outline in *D. cordata* varies from rounded to narrowly elliptic to deltate forms, with cordate to hastate basal lobes, however the recognition by Knuth of distinct varieties of *R. cordata* based on leaf outline seems not to be justified. Field observations of populations of *D. cordata* in Puerto Rico and Jamaica show plasticity to be the rule, not the exception, and variation is consistent with morphogenetic studies by Burkill (1960), who illustrated how differential expansion of the apex and basal lobes can produce a range of morphologies within an individual species (using *D. alata* L. and *Tamus communis* L. as case studies).

Robustness of the flowers and inflorescences also varies within *D. cordata*, particularly in Puerto Rico, where smaller flowered forms (generally lighter in flower color) are associated with serpentine and karst substrates (see below), and more robust forms occur on volcanic soils in the Luquillo Mountains at the extreme eastern end of the island.

A general description of *D. cordata* follows: it is intended to complement the information provided in regional treatments (Adams, 1972; Howard, 1979; Acevedo-Rodríguez & Strong, 2005), and for comparison with *D. cordata* var. *cymulifera*, the one variety I am currently recognizing (diagnostic characters given in 6a, below).

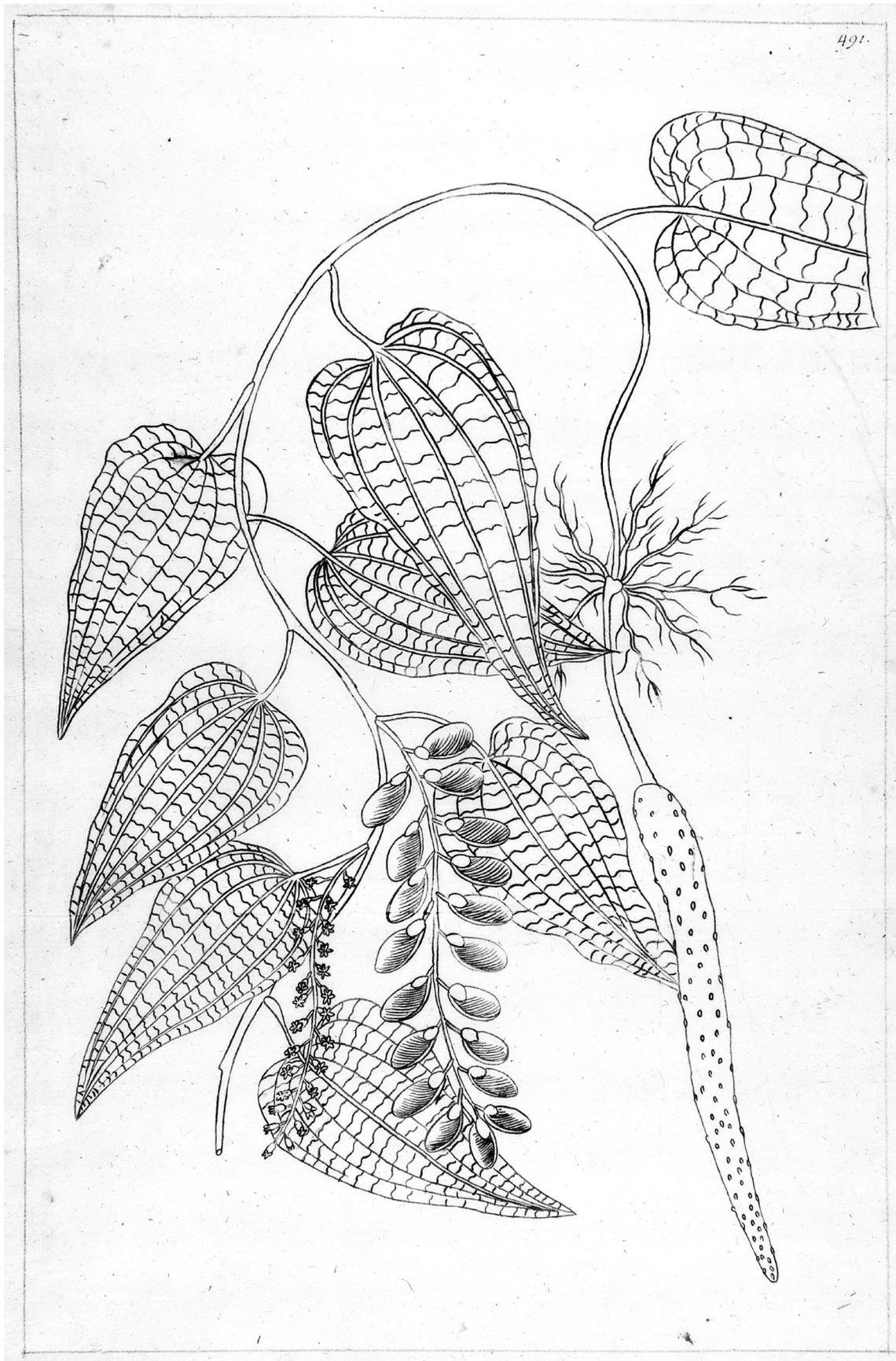


FIGURE 1. Lectotype of *Rajania cordata* L.—Plate 491 of the “Codex Boerhaavianus”. It is a copy, made for Boerhaave, of a Plumier drawing representing *Janraja scandens folius tamni* (Plumier 1703: 33), a version of which appeared subsequently in Plumier (1758: Tab. 155 Fig. 1) as “*Raja foliis simplicibus, cordatus*”. Courtesy of the library of Rijksuniversiteit, Groningen.

Tuber annual, elongate (occasionally branched) to 40 cm or more, generally wider at the distal end (to ca. 8 cm), the epidermis tan, smooth but with wiry roots, evenly distributed, these leaving circular scars < 1 mm diameter, starchy parenchyma white, mucilaginous, deeply buried at the end of a filipendulous cylindrical stalk up to 65 cm, the latter arising from the hypocotyl. Stems terete, without exudate. Leaves +/-coriaceous; primary and secondary veins frequently prominent abaxially. Inflorescences of staminate and pistillate plants are often robust and frequently tanniferous, occasionally pubescent. In the staminate inflorescences, the internodes between the cymules are frequently shortened, but may become elongated; flowers typically 3–8, in subsessile glomerules, or with floral pediments elongated (length varies continuously), sometimes becoming scorpioid; tepals (staminate and pistillate flowers) commonly light brown or yellowish (-greenish or cream), elliptic to ovate, and both whorls spreading (rotate fl.) or sometimes just the outer whorl spreading. The torus is frequently conspicuously swollen; stamens typically inserted at the periphery of the torus, the anthers stout and subsessile; pistillode inconspicuous (three minute slits in center of torus). Pollen ornamentation perforate-reticulate, the murae completely interconnected, no free ends. Samaras frequently tanniferous, the wing 2–3 cm long. Plants of serpentine and karst substrates have smaller samaras with much lower tannin content.

Plants from Hispaniola called *Rajania ovata* var. *ehrenbergii* by Knuth have attributes of both *D. cordata* and *D. haitiensis*. At the base of the stem, cordate leaves prevail, and lance-ovate leaves subtend the inflorescences. Knuth's (1917, 1924) placement of these plants within *R. ovata* was based exclusively on leaf outline, but the floral morphology is consistent with that of *D. cordata*. Pending further study of the Hispaniolan plants, I am not currently recognizing this variety.

The appearance of *Dioscorea spiculoides* in this list of synonyms is novel. It was described as an endemic species from Oaxaca, Mexico, based on the Liebmann type, but it is likely that the locality was recorded incorrectly on the label (see discussion in Téllez and Geeta, 2007). Liebmann is known to have traveled to Puerto Rico on his way to Mexico, and in fact the type of *D. spiculoides* is a *D. cordata* form that occurs on that island. The F sheet of *D. spiculoides* is the only duplicate cited by Matuda and should be considered the Holotype, not the C sheet, as cited by Téllez and Geeta (2007).

See *Dioscorea quinquefolia*, below, for discussion of lectotypification of Linnaean names.

6a. *Dioscorea cordata* var. *cymulifera* (Uline ex Knuth) Raz, comb. nov.

Rajania cordata var. *cymulifera* Uline ex Knuth (1917: 220). Type:—PUERTO RICO. Prope Maunabo, montis Malapasaca, 4 Oct. 1886, P. Sintenis 5217 ♂ (holotype B!, isotypes GH! (2 sheets), K!, US!). The sheets are annotated, presumably in Sintenis' hand, as *R. cordata* var. *scorpioides* Uline, but no published reference exists to validate this name (see *D. scorpioidea*).

Rajania hastata auct non L. in Kunth (1850: 450). Type—PUERTO RICO. Wýdler 769 (holotype B). Although I haven't seen the specimen, it is cited by Knuth (1924) among the exsiccatae of his *Rajania cordata* var. *eu cordata*. The far more detailed description by Kunth (1850) is consistent with the variety named here.

Notes: Endemic to Puerto Rico. This variety may be distinguished from other forms of *D. cordata* by the following combination of characters: leaves papery, light green, the first pair of lateral primary veins (L1) strongly arcuate, raphids often present; staminate and pistillate inflorescences on slender axes, glabrous, the cymule architecture variable, cymes often (but not always) floriferous (8–12 fls) and internodes frequently elongated, resulting in a more “open” architecture; flowers campanulate, tepals white or cream color (raphids +), oblong; stamens ca. 1/2 length of tepals; anthers minute, introrse, held just above the pistillode on slender filaments that are inserted on the tepals, just above the base; pistillode well developed, of three erect and confluent lobes. Torus not conspicuously swollen. Pollen ornamentation perforate-reticulate but with free ends of the murae projecting outward, giving the exine a tuberculate appearance. Samaras ca. 1 cm long, golden or straw colored. This variety is frequently associated with karst formations.

7. *Dioscorea haitiensis* Knuth (1926: 6). Lectotype (designated here):—HAITI. Massif de la Selle, Morne Fort Jacques between Fortes Jacques and Cadets, ca. 800 m, 7 Sept. 1924, E.L. Ekman H1821 ♂ (lectotype S!, isolectotypes B! (2 sheets: B_10_0250057, B_10_0250058), US!). The S sheet bears a holotype label by T. Clayton (1954, unpublished), however this cannot be interpreted from the protologue. The S sheet and one of the B sheets (100250058) were both annotated by Knuth as “Typus”

Rajania ovata Swartz (1788: 59). Lectotype (designated here):—DOMINICAN REPUBLIC. “Sto. Domingo”, no date, Swartz s.n. [lectotype S! (the sheet with no fragment packet), isolectotypes BM!, LD “A”! (pistillate fragment), S! (sheet with fragment packet)].

Rajania mucronata auct non Willd. Griseb (1866: 251). Lectotype (designated here):—CUBA. Oriente, 1860-64, Wright 691 (lectotype

K!, isoelectotypes BM!, BREM!, HAC! (p.p.), GH! (barcode 00030440) “MO1A”!, NY! (three sheets, one pistillate, two staminate). A second Wright specimen at K corresponding to this species (but without a collection number) from “Monte Verde” can also be considered an isoelectotype. At GH there are two duplicates of Wright 691. The second one has mixed pistillate elements of *D. haitensis* and *D. baracoensis*.

Note: *Dioscorea haitensis* occurs in Eastern Cuba and Hispaniola. It was described by Knuth from staminate material only. It is the male of *R. ovata*, described 138 years earlier from pistillate material by Swartz.

The epithet “ovata” is not available for this taxon, because it was applied by Vellozo (1827: Tab. 117) to a South American yam species. The interpretation of the WI species has been somewhat confounded by the mixed nature of the original Swartz material. Both S sheets and the BM sheet each have a single element: a fruiting specimen of what is here called *D. haitensis*. The LD isotype includes two elements: a fruiting specimen on the left hand side of the sheet (here designated “A”), and a staminate specimen on the right (here designated “B”). Only the “A” portion corresponds to *D. haitensis*; the “B” portion is *Dioscorea baracoensis*. The latter has coriaceous, generally acute leaves, and tiny flowers with erect tepals, while the former has membranaceous, acute to acuminate leaves, and larger, rotate flowers. Swartz’s description “leaf ovate, acuminate, three nerved” does not resolve the differences between the two taxa.

The Swartz name is also a homonym of a Walter name (1788: 247) published between the months of April and June of 1788; Swartz’s Prodrum was published between 20 June and 29 July of the same year. It is difficult to determine priority in this case, although Swartz’s name has been in use since its publication, while the Walter name was subsequently transferred to Polygonaceae as *Brunnichia ovata* (Walter) Shinnery.

The Grisebach name, cited here in synonymy is also based on a similarly mixed collection, Wright 691. The K sheet, designated here as the lectotype, is true *D. haitensis*. Both sheets at MO also contain elements of *D. baracoensis* (MO1B and MO2A&B). Additional sheets at NY and HAC are *D. baracoensis*.

8. *Dioscorea hyalinomarginata* Raz, nom. nov. *Rajania spiculiflora* Uline ex Knuth (1917: 219). Type:—DOMINICAN REPUBLIC. “Santo Domingo”, no date, *Poiteau s.n.* (holotype B!, isotype K!)

Rajania marginata Knuth (1935: 121). Type:—DOMINICAN REPUBLIC (“Santo Domingo”). Provincia Samaná: Loma Zaramagua, light forest on limestone, 200 m, 9 June 1930, *Ekman 15251* ♂ (holotype B!, isotypes S!, US!).

Notes: Endemic to the Dominican Republic. In the protologue of *Rajania marginata*, Knuth cited in synonymy, “ex. aff. *R. spiculiflorae* Uline,” but no such annotation appears on any of the material I examined. As the epithet suggests, this species is easily distinguished from others in section *Rajania* by its hyaline margin, especially prominent in dried specimens. The inflorescences are always arrayed in scorpioid cymes, and it is one of only three *Rajania* species with striate pollen.

9. *Dioscorea introrsa* Raz, nom. nov. *Rajania nipensis* Howard (1947: 117). Type:—CUBA. Oriente [Holguín]: Sierra de Nipe, near Woodfred, 28–9 July, 1941, *Howard 6136a* (holotype GH! (♂); isotypes GH! (3 specimens: 2 ♂ only, the third is a ♀ element mounted on the same sheet as the holotype), NY! (♂), US! (♂))

Rajania wrightii auct non Uline ex Knuth (1917: 221), Knuth (1924: 337), León (1946: 323).

Notes: Endemic to eastern Cuba. This is one of the species included in the mishmash of Wright 1712 collections (see *D. cephalocarpa*). Elements that correspond to *D. introrsa* include: BM “1A”, BM “1B”, GH “1”, K “1”, MO, NY “4A”, S “2A”, S “2B”, and US “1C”. It is difficult to determine which (if any) of these elements Knuth (1917) included in his confused formulation of *Rajania wrightii*, the name is included here in synonymy based on citation (1924, p. 337) of the Ekman specimens (see *D. confusa*).

When Howard described *R. nipensis* 24 years later, he cited only one collection number, and designated the “type” from GH. There are however, a total of three sheets at GH. Howard’s Latin diagnosis includes characters of the staminate flowers only, but is followed by the comment “in the collection cited above is a single pistillate specimen tangled with the staminate shoots selected as the type.” Of the three sheets at GH, only one has mixed elements. There is also a staminate-only sheet with the word “TYPE” printed on the label, but it is far inferior to the staminate specimen in the mixed sheet. Based on Howard’s comment and diagnosis, the staminate element of the mixed sheet is here interpreted to be the holotype.

10. *Dioscorea microflora* Raz, nom. nov. *Rajania angustifolia* Swartz (1788:59). Lectotype (designated here):—HISPANIOLA. Swartz s.n. [lectotype S! (♂), isolectotypes S! (the three remaining sheets (2♀ + 1♂) labeled “India Occidentali”)]. The type locality was likely from what is now the Dominican Republic, but this cannot be interpreted from the specimen

Rajania minutiflora Knuth (1917: 221). Type:—HAITI. Anse a Veau, no date, *Picarda 1283* ♂ (holotype B!, isotypes GH!, K!). The holotype was explicitly designated by Knuth in 1924.

Notes: Endemic to Hispaniola. This is the original *R. angustifolia* Sw. (see *D. quinquefolia* for a history of the misapplication of this name). The Swartz type at S consists of four sheets: they are not cross-labelled, and as such they are considered duplicates. Not having seen the Swartz material, Knuth (1917) misapplied the name to narrow leaved plants of *D. quinquefolia* and he described the Swartz species anew as *R. minutiflora*. Neither this epithet nor “angustifolia” is available in *Dioscorea*, and a new name is selected here.

Dioscorea microflora and *D. quinquefolia* converge in leaf outline, but the two can be diagnosed as follows: in *D. microflora*, the secondary veins of the leaves are reticulate, forming aerieoles, or terminating in free ends. The secondary veins of *D. quinquefolia*, are straight and parallel, departing from the midvein (and/or lateral primary veins) at acute angles and anastomosing with the adjacent primary veins. Minute pseudostipular spines are absent in *D. microflora*, but typically present in *D. quinquefolia*. The staminate flowers of *D. microflora* are sessile, arranged in scorpioid cymes, while those of *D. quinquefolia* are pedicellate, the pedicels of varying lengths. Both have tiny flowers, but *D. microflora* has striate pollen, versus the perforate-reticulate pollen of *D. quinquefolia*.

11. *Dioscorea pilifera* (Urb.) Raz, comb. nov. *Rajania pilifera* Urban (1922:17). Type:—HAITI. Dep. du Sud: between Constant and Corail near Aux Cayes, 200 m, 6 Sept. 1917, *E. L. Ekman H 799* ♂ (holotype S!; isotype B!)

Notes: A poorly known species represented by a handful of Ekman collections from Haiti and the SW Dominican Republic: leaves ovate to cordate, with stiff white hairs on the abaxial surface and small, pseudostipular spines; allied to *D. quinquefolia*.

12. *Dioscorea porulosa* (R.Knuth) Raz, comb. nov. *Rajania porulosa* Knuth (1917: 221). Type:—CUBA. Holguin: barren savannas southeast of Holguin, 28 Nov. 1909. *Shafer 2952* ♀ (holotype B!, isotypes K! (000099324), NY!)

Rajania linearis (Griseb.) [Uline ex R.Knuth] Howard (1947: 118). *Rajania linearis* (Griseb.) Uline ex R.Knuth (1924:168) *pro syn.* Lectotype (designated by Howard 1947):—CUBA. Without locality, 1860-4, *Wright 3254* [lectotype GH! ♀ (glued to sheet), isolectotypes BM! (♀), G! (♂ partial contents of packet, ♀ glued to sheet), MO! (♀ glued to sheet), S “A”! (♂)]. See *D. nipensis*. *Rajania howardii* Borhidi nom. nud. in Borhidi, A. Phytogeography and Vegetation Ecology of Cuba: 435. 1996.

Notes: Endemic to Eastern Cuba. One of several linear-leaved species from the region. The K isotype of *R. porulosa* is mounted on the same sheet with four non-type specimens (in separate packets, each individually barcoded and labeled).

Rajania linearis (Griseb.) Uline ex Knuth was an unpublished name, cited by Knuth (1924) as a synonym of *D. linearis* (see *D. nipensis* below). It is listed in synonymy here because Howard reestablished the name with a different interpretation: the one he believed Uline had originally intended, based on the *Rajania* element of the GH sheet of Wright 3254 (Howard, 1947). Under Howard’s interpretation, there is no *D. linearis*. See *D. nipensis* for the full, intertwined nomenclatural histories of these taxa.

13. *Dioscorea psilostachya* (Uline ex R.Knuth) Raz, comb. nov. *Helmia psilostachya* Kunth (1850: 429). *Rajania psilostachya* (Kunth) Uline ex Knuth (1917: 219). Type:—CUBA. In sylvis Cubae interioris, no date, *Poeppig. s.n.* ♂ (holotype KIEL!, isotypes JE!, MO!, PRC!)

Dioscorea ekmanii Knuth (1917: 191). Type:—CUBA. Havana: Tapaste, Lomas de la Jaula, Callejón del Matador, 11 June 1914, *Ekman 1336* ♂ (holotype S!, isotypes B!, NY!, phototype GH!). The holotype was explicitly designated by Knuth in 1924.

Rajania cordata var. *microcarpa* Uline ex Knuth (1917: 219). Among the syntypes cited by Knuth is Wilson and León 11551 ♀ (K!, NY!, US!) from western Havana province. The lectotype and remaining syntypes are referred to *D. cordata* (see above).

Rajania cordata auct non L. in Richard (1850: 269). Richard cited a collection by J. M. Valenzuela (s.n.) made “near Havana”. “*R. cordata* Rich.” is cited in Knuth (1917, 1924), as a synonym of *R. psilostachya*, based on a Valenzuela (♀) specimen. See *D. confusa*.

Rajania hastata L. auct non Grisebach (1866: 251). Grisebach provided no description but cited the following specimens: CUBA. Matanzas, July 1849, *Rugel 392* ♂ (NY!, BM!, FLAS!, GH!); *Wright 1712* (elements corresponding to *D. psilostachya*: BM “1C”!, GH “2B”!, NY “3”!, US “1B”!, US “2B”!; there is also likely to be a duplicate at GOET, but I’ve not seen it). While it cannot be determined with certainty which of the Wright 1712 duplicates were seen by Grisebach, the accompanying citation of *Rugel 392* dispels the ambiguity about the interpretation of his *R. hastata*. “*R. hastata* Griseb.” is also cited in Knuth (1917, 1924) as a synonym of *R. psilostachya* (and *R. wrightii*: the latter interpretation no doubt based on the mixed Wright 1712 collections; see *D. confusa*).

Notes: Endemic to NW Cuba. This species was first described in 1850 as *Helmia psilostachya*, based on a Poeppig collection cited by Kunth as “*Smilax aristolochiifolia* Poepp. en herb. Luc.” The abbreviation “herb. Luc.” refers to the private collection of A.F. Lucae, deposited in KIEL (Wilkin & Muasya 2015). See also *D. cephalocarpa* for elaboration on the Wright 1712 problem.

14. *Dioscorea quinquefolia* (L.) Raz, comb. nov. *Rajania quinquefolia* Linnaeus (1753: 1032). Lectotype (designated here):—DOMINICAN REPUBLIC (“Hispaniola”). Plate 493 of the Boerhaave set of Plumier illustrations at the library of Rijksuniversiteit, Groningen (used to create the composite drawing in Tab. 155 of Plumier 1758; Fig. 2)

Rajania mucronata Willdenow (1806: 787). Type:—HAITI. “Domingo”, no date, *Poiteau s.n.* ♂♀ (holotype B). I have not examined the specimen in person, just a black and white microfiche photo in the library at NY, supplemented by Kunth’s (1850, p. 447) exquisitely detailed description of the type.

Rajania quinquevernia Rafinesque (1840: 125). Lectotype (designated here):—CUBA. “Mt. Jalambic”, no date, *E. Durand s.n.* (lectotype DWC!).

Rajania cubensis Kunth (1850: 446). *Rajania angustifolia* Grisebach ex Kunth (1850:446) *pro syn.* Type:—CUBA. In sylvis petrorsus insulae Cubae, August, 1822. *Poeppig s.n.* (holotype B!, isotypes K!, MO!).

Dioscorea lanceolata C. Wright ex Grisebach (1866: 251). Lectotype (designated here):—CUBA. Oriente [Holguin]: Barajagua (note: this locality is likely to refer only to part of the mixed collection), 1860–64, *Wright 3253* ♂ (lectotype HAC!, isolectotypes BM “A”! (part B is a fragment of *D. alainii*, collected by Reading in “Ste. Dominique” in 1803), GH “B”! (part A is *D. haitensis*), MO!, S!).

Rajania wilsoniana Morton (1933: 85). Type:—CUBA. Santa Clara (Cienfuegos): Limones, Soledad, July 18, 1929, *J. G. Jack 7489* (holotype: NY; isotypes GH, HAC).

Rajania angustifolia auct. non Swartz in Knuth (1924: 324) and León (1946: 323).

Notes: Cuba and Hispaniola. Although it is one of the earliest names in *Rajania*, *R. quinquefolia* fell out of use shortly after its publication. The type (Fig. 2) is a schematic illustration of the leaves and fruits, but it can nevertheless be unambiguously interpreted, as there are no other *Rajania* species with both fasciculate leaves and acutely angled secondary venation. Knuth (1924) never cited the illustration and included the name in a list of unplaced and uncertain taxa at the end of his treatment. Liogier (1969) resurrected *R. quinquefolia* and listed *R. mucronata* as a synonym. He did not however comment upon the existence of narrow and wide leaved forms of this species.

The plate selected here as the lectotype appears in a modified form in Plumier (1758: Tab. 155 Fig. 2). The latter version is truncated, with only a single node, while Plate 493, reproduced here in Fig. 2, has two nodes. In Tab. 155 Fig. 2, a staminate inflorescence was also added (a highly schematic drawing that is essentially the same as the staminate inflorescence drawn for *R. cordata*), but since all Sect. *Rajania* species are strictly dioecious, it is inaccurate to represent them as monoecious. I would like to note that Tab. 155 Fig. 1 of Plumier (1758) also includes flowers and a detached fruit that were copied directly from a different Plumier source (1703: Tab. 29). In the latter work these drawings are used to represent the genus *Ian-raia*, and not any particular species; it is therefore inappropriate to depict them as specifically representing *R. cordata*, as Burman had done in his edition of Plumier (1758). The samara depicted in Tab. 29 of Plumier (1703) is slightly more stylized than that represented in plates 491 and 493 of the Codex Boerhavianus, but it is this more stylized version that was later incorporated into the drawings of the infructescences depicted in Tab. 155 (1758). Together with the above mentioned plates, in the library of the University of Groningen, there is also a proof sheet of the complete Tab. 155, plus a second, less complete version of the *R. quinquefolia* drawing. The proof sheet was almost certainly seen by Linnaeus, and while I cannot, with the same degree of certainty, assert that Linnaeus saw Plates 491 and 493 of the Codex Boerhavianus, being the original elements upon which Tab. 155 was based, these are preferred for lectotypification.

The use of *R. angustifolia* Sw. for this taxon dates to Knuth (1924) who cited primarily Cuban material as the basis for his description. It appears he did not examine the Swartz type, which differs markedly in leaf venation, floral and inflorescence morphology, and is restricted to Hispaniola (see *Dioscorea microflora* above).

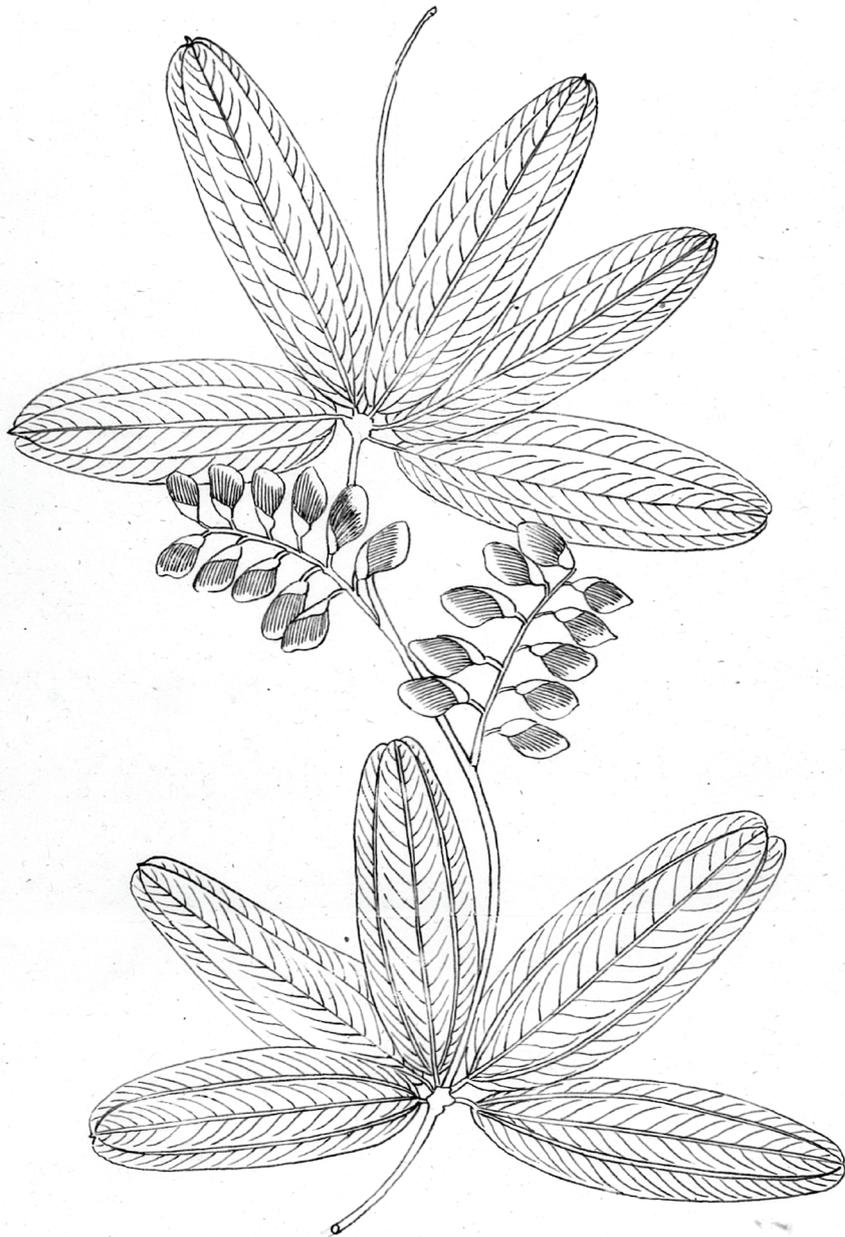


FIGURE 2. Lectotype of *Rajania quinquefolia* L.—Plate 493 of the “Codex Boerhaavianus”. It is a copy, made for Boerhaave, of a Plumier drawing representing *Janraja scandens quinquefolia* (Plumier 1703: 33), a version of which appeared subsequently in Plumier (1758: Tab. 155 Fig. 2) as “*Raja foliis quinis*”. Courtesy of the library of Rijksuniversiteit, Groningen.

Leaf width of *Dioscorea quinquefolia* varies across a continuous spectrum, but all forms are identical in their floral morphology. Narrow-leaved specimens from Cuba (associated with serpentine formations) and Hispaniola have traditionally been interpreted as “*R. angustifolia*”, while specimens with leaves of intermediate width from Cuba and Hispaniola have been called *R. mucronata*, and broad-leaved specimens from Cienfuegos, Cuba have been treated as *R. wilsoniana*. The latter are restricted to karst formations in and around what is today the Jardín Botánico de Cienfuegos (formerly the site of the Atkins Biological Station of Harvard University). At this locality the leaves are ovate, thin, membranaceous with conspicuous raphids, and an indumentum of fine white hairs, abaxially. Morton (1933) believed it to be more closely related to *R. pilifera*, but the flowers don’t accord. Morphological and molecular studies by Raz (2007) place it squarely within *D. quinquefolia*.

In Hispaniola *D. quinquefolia* appears to be introgressing with *D. alainii*.

15. *Dioscorea richardhowardii* Raz, nom. nov. *Rajania tenella* Howard (1947: 119). Type:—CUBA. Sierra de Nipe, south of Woodfred, in dense woods with yellow flowers, 28–9 July 1941, *Howard 6134* ♂ (holotype GH! (marked as “Type”), isotypes BM!, GH!, NY!, S!, US!)

Notes: Endemic to eastern Cuba. The GH sheet that is marked on the label in pen and stamped above the label as “Type” should be considered the holotype. The second GH sheet is unmarked: it is a comparatively poor specimen, discolored and somewhat degraded. This epithet honors the late Richard Howard, who was, in all senses, a giant of West Indian botany.

16. *Dioscorea scorpioidea* Wright (1871: 74). *Rajania cordata* var. *scorpioidea* (C. Wright) R. Knuth Notizbl. Bot. Gart. Berlin-Dahlem 7: 220. 1917. *Rajania scorpioidea* (Wright) Uline ex R. Knuth *pro syn.* in Notizbl. Bot. Gart. Berlin-Dahlem 7: 220. 1917. Type:—CUBA. Pinar del Río: en la loma pelada cerca del Retiro, San Cristobal, 1864, *Wright 3746* ♂ (holotype HAC!, isotypes GH!, K!). The number 3746 appears only on the K sheet, with a note stating that the specimen was issued with a serial number in 1869. The remaining duplicates are not numbered

Rajania ekmanii Knuth (1925: 80). Type:—CUBA. Pinar del Río: Pinar de Cajalbana, 28 August 1923, *E.L. Ekman 17348* ♂♀ (holotype S!, isotypes B!, NY!).

Note: Western Cuban endemic. The application of the name *D. scorpioidea* to this species is novel. Wright’s description was based exclusively on the type collection (staminate); the specimens are quite old and fragile and it hasn’t been possible to do any in-depth morphological or genetic studies with the material, but details of the flowers have been meticulously recorded and illustrated on the K sheet by David Prain (annotated 1916). Except for its slightly more robust inflorescences, the *D. scorpioidea* type is identical to that of *R. ekmanii*. The types of both have leaves dotted with irregularly shaped macroscopic black glands, staminate inflorescences in scorpioid cymes, tepals highly tanniferous (seen as red spots under the dissecting microscope), and stamens with long, slender filaments. The type locality of *D. scorpioidea* is slightly southeast of the Cajalbana locality where the Ekman type was collected. This species is one of the six represented among the Wright 1712 collections.

17. *Dioscorea theresensis* (R. Knuth) Raz, comb. nov. *Rajania theresensis* Uline ex Knuth (1917: 221). Type—UNKNOWN. Ile Ste. Therese, pres Cuba, 1848, *Gibollet s.n.* ♂ (holotype G!, isotype B!, phototype of the G sheet at NY!). The protologue does not include a holotype designation, but the 1924 monograph (p. 337) explicitly states, “Typus in herb. Barbey-Boissier”

Notes: The locality of the type collection remains something of a mystery. “Ile Ste. Therese” is not registered in English, French or Spanish in any gazetteer in Cuba or elsewhere in the West Indies. The only known island of this name is off the east coast of Canada, but the *R. theresensis* type is most certainly of West Indian origin. The same Gibollet locality has been cited for collections of three Cyperaceae taxa, included in Clarke (1900). The locality is considered in that work to be an independent island in the West Indies, not a territory of any sovereign nation.

Despite having been described from only the type collection, this species does appear to represent a distinct biological entity. The Wright 1712 duplicate that I have designated “YU 2B” is consistent with the type of *R. theresensis*, with its turbinate flower and narrow, elongate tepals. Unfortunately its locality is also uncertain, (the label states only “Cuba”) and it is mounted on a sheet that also includes species from Pinar del Río and south central Cuba.

Undescribed species in *Dioscorea* sect. *Rajania*

Not included here is an undescribed species from Sancti Spiritus, Cuba (Raz & Pérez in press).

The species from Western Hispaniola require further study. There is what appears to be an undescribed species with ovate adult leaves and sessile flowers from the Independencia province of the Dominican Republic. A densely ferruginous-pubescent morphotype of *R. cordata* from Pedernales province may also merit taxonomic status at an infraspecific rank.

***Dioscorea* sect. *Lychnostemon* Grisebach** (1842: 42). Lectotype (designated here):—*Dioscorea polygonoides* Humbolt & Bonpland ex Willdenow (1806:795). Knuth (1924) erroneously attributed authorship of the section to Uline (1897)

1. *Dioscorea cubensis* R.Knuth (1917:209). Type—CUBA. Without locality, 1860–1864, *Wright 3252 pro parte* [holotype B! (♂), isotypes BM! (♂ element only), MO! (♂ element only)]

D. cuspidata auct. non Willdenow in Grisebach (1866: 251).

Notes: Eastern Cuban endemic. The type collection is cited as “*pro parte*” in the protologue; the holotype consists of a single staminate element, and Knuth did not describe the pistillate flowers or inflorescences for this species. The BM and MO sheets each include a detached infructescence of *D. tamoidea* Griseb. Knuth (1924) cited “Wright 3252 p.p.” among the exsiccatae of *D. tamoidea*, citing both staminate and pistillate material, however I have not seen any staminate material of this collection number that corresponds to *D. tamoidea*. Grisebach’s (1866) *D. cuspidata* is based on Wright 3252.

2. *Dioscorea nipensis* Howard (1947: 119). Type:—CUBA. Oriente (Holguin): Moa, 15 km. southwest of Compañía de Moa mill, 25 Jul 1941, *Howard 5873* ♂ (holotype GH! [30362], isotypes GH! [30361], US!)

Dioscorea linearis Grisebach (1866: 251). *Dioscorea grisebachii* Britton ex León (1946: 321). *Dioscorea raveni* Ayala (1984: 296). Type:—CUBA. Without locality, 1860–1864, *Wright 3254* ♀ (holotype GOET!, isotypes G! (♀ and ♂, partial contents of the fragment packet, see below), S! (♀ part “B”, right hand side, designated here), BM! (♀ part “B”, designated here), GH! (♀ part “II”, right hand side, designated by Uline), MO! (♀ part “B”, left hand side, designated here), phototype NY! [of the G isotype, packet closed]).

Dioscorea montecristiana Hadač (1970: 430). Type:—CUBA. Oriente (Guantanamo): jugo Montecristo dicto, solo calcáreo, 27 Jan.1968, *Hadač 1322* ♀ (holotype PR!).

Rajania linearis auct. non (Griseb.) Uline ex R.Knuth in Knuth (1924: 168; see discussion below).

Notes: Endemic to eastern Cuba. The nomenclatural history of this taxon is particularly complex. The binomial *Dioscorea linearis* Bertero ex Colla (1836: 11) is the earliest publication of this name, referring to a species of Chilean origin (*Bertero 1787*, holotype TO) that had already been described three years earlier as *D. saxatilis* Poepp.; Colla’s name was therefore reduced to a synonym. “*Dioscorea linearis*” reappeared in Grisebach (1866) with a brief description based on “Wright 3254” from Cuba. The type collection includes at least six duplicates (those cited here), of which five have mixed elements belonging to two different species with convergent leaf morphologies. Grisebach’s protologue does not specify which duplicate(s) he examined, but at the time of his preparation of the Catalogue he was based in Göttingen. The GOET sheet alone bears his handwritten diagnosis, as well as a label from the “Herbarium Grisebachianum”. The GOET sheet was also annotated as the Holotype by Richard Howard in 1984. At that time Howard was researching an article on the Cuban collections of Charles Wright (37 years after the publication of *D. nipensis* and *R. linearis*). The GOET sheet is the only one of the six known duplicates that is 100% consistent with Grisebach’s description, which includes only characters of the leaves and capsules; there is no description of a staminate inflorescence, just the symbols “♂...”. The GOET sheet is also the only duplicate that is not composed of two species. It bears a single element: a stem segment with leaves and infructescence attached. Yet, in his monograph of the Dioscoreaceae, Knuth (1924) cited the “typus” as Wright 3254 (♀) pro parte, from “herb. Berol.” There remains some uncertainty as to whether a duplicate was ever stored at B. As of September 2013, none could be found, but even if such a duplicate exists (or existed), it should not be considered the holotype.

The G sheet has an annotation label from the Museum Botanicum Berolinense but this cannot be considered evidence of the existence of a duplicate at B. The annotation was written by Uline who was at the time a doctoral

student in Berlin (with access to the Museum's annotation labels). Of the six known duplicates, only the S sheet bears an annotation by Knuth (no date, no "typus"). It consists of a staminate specimen of *Dioscorea porulosa* (part "A", designated here, left hand side) and a fruiting specimen of *Dioscorea nipensis* on the right (part "B"). Yet the only specimen cited by Knuth (1924) as supporting material for his treatment of *D. linearis* Griseb. (p. 168), is the pistillate "type". He made no reference to any staminate material, and yet he described a male inflorescence with pedicillate flowers bearing six fertile stamens, consistent with the flowers of *D. porulosa*. Aside from the S sheet, the only other staminate material from Wright 3254 is in the packet of the G sheet (not annotated by Knuth), which includes a small fragment each of a male inflorescence of *D. porulosa* and *D. nipensis* (the only male fragment of the latter species in any of the duplicates). The packet also contains loose leaves of both species and a few capsules of *D. nipensis*. Affixed to the G sheet is a pistillate specimen of *D. porulosa* (det. by Uline as *R. microphylla* Kunth).

On the basis of the androecium with six stamens, Knuth assigned *D. linearis* Griseb. to *Dioscorea* sect. *Apodostemon* Uline. It was subsequently excluded from this section by Téllez and Geeta (2007). Since there is apparently no B sheet, it remains unclear what the source material was for Knuth's description (1924) of *D. linearis*, or if any of it was adapted directly from Uline's unpublished work (see below for discussion of GH sheet).

The BM sheet was determined by me in 2004 as *R. porulosa*, but at the time I failed to open the packet, which contains mature capsules of *D. nipensis*. There is also a very small piece of *D. nipensis* on the right side of the sheet: one leaf and a deteriorated pistillate inflorescence with sessile flowers. It is mixed in with what is mostly pistillate *D. porulosa* and is difficult to distinguish from the mass.

The remaining sheets require explanation because they are the base elements of three more names published after Knuth. In León's Flora de Cuba (1946) the illegitimate name *Dioscorea linearis* Griseb. was replaced by the new name *D. grisebachii* Britton ex León, with no citation of a holotype or lectotype (only "Wright 3254"). Ayala (1984) pointed out that the León name was also illegitimate, because it had already been applied by Kunth (1850) to an unrelated *Dioscorea* species from Brazil. At this time, Ayala was based at MO and the only sheet of Wright 3254 that he examined was the MO sheet: it includes a pistillate *Rajania* element and a fragment of an infructescence consistent with the fruits of *D. nipensis*. Having never seen the GOET sheet, Ayala selected a new name for the Grisebach species, *D. raveni*, without recognizing the *Rajania* element, and designating the MO sheet (in its entirety) as the lectotype.

The GH sheet includes a pistillate *Rajania* element and a detached infructescence of *Dioscorea nipensis*. The latter was determined a century ago by Uline, as *D. tamoidea* Griseb., but at the time he was unaware of the existence of two (as yet undescribed) endemic *Dioscorea* species from Eastern Cuba. Howard (1947), who was the first to acknowledge the mixed character of this Wright collection, recognized the *Rajania* element and published a formal description based on the GH sheet, giving it the new combination: *R. linearis* (Griseb.) R.A. Howard (see *D. porulosa*).

There are three problems with Howard's name: 1) Not having seen the holotype of *D. linearis* Griseb. (at the time he thought it was destroyed in WWII), and having accepted Uline's determination of the capsules on the GH sheet, Howard was under the impression that Grisebach had mistakenly described the fruits of *D. linearis* from capsules of *D. tamoidea*, and the leaves from *D. porulosa*. Had he been aware of the *D. linearis* holotype in 1947, it is unlikely that he would have sunk the Grisebach name. 2) Howard was not the first to describe the *Rajania* element. *Rajania porulosa* was described in 1917 by Knuth (not based on Wright 3254); it corresponds morphologically and geographically to the *Rajania* element of the GH sheet. Howard never mentioned *R. porulosa* and it appears that he never saw any of the material cited by Knuth under this name. 3) Knuth (p. 168, 1924) cited "*Rajania linearis* Uline in msc. p. p." as a synonym of *D. linearis*, thereby establishing the name, even though he misapplied it. It seems that Uline's intention (based on his annotation of the GH sheet), was to apply this name only to the *Rajania* element of Wright 3254 (GH). A half century later, Howard (1947) published the combination as his own: *Rajania linearis* (Griseb.) [Uline in msc. ex Knuth in syn.] Howard *comb. nov.*

Ironically, in the same 1947 paper, Howard also described a new *Dioscorea* species from Eastern Cuba, giving it the epithet *D. nipensis*. The species was described only from the type, collected by Howard, himself. This "new" *Dioscorea* had been documented by numerous collections in NY, US and HAC, from the early 1940s and earlier, but Howard did not cite any of this material, nor any of the Wright 3254 duplicates that contain a linear leaved *Dioscorea* element. His type is a staminate specimen, and he never described a pistillate plant because he hadn't seen one, nor had he seen a large enough sample to interpret intraspecific variation. This species is highly variable in width and outline of the leaf base, but inflorescence morphology of both male and female specimens remains constant, independent of the variation in leaf outline. Howard had actually described the mate of the Wright 3254 GOET sheet without realizing it, and his is now the correct name for this species. *Dioscorea raveni* is superfluous, not because there is no species that corresponds to "*D. linearis* Griseb." as argued by Téllez and Geeta (2007) who were also unaware of the other Wright duplicates, but because it was published 37 years after *D. nipensis*.

Finally, there are two duplicates of Wright 3254 at HAC, but both are unmixed sheets of *D. porulosa*, one with staminate inflorescences, the other sterile.

3. *Dioscorea polygonoides* Humb. & Bonpl. ex Willdenow (1806: 795). Type:—Venezuela, Orinoco River. Humboldt & Bonpland s. n. (holotype: B-W; isotype: P-HBK)

Dioscorea lutea G. Meyer (1818: 282). Type:—Suriname. Essiquibo, E.K. Rodschied 262 (holotype: GOET).

Dioscorea martinicensis (1822: 17). Lectotype (designated here):—MARTINIQUE. Without locality, Jun 1822, *Sieber 27* (lectotype K!, isolectotype MO!). *Dioscorea sieberi* Kunth (1848: 58). *Dioscorea polygonoides* var. *sieberi* (Kunth) Uline ex Knuth (1917: 208).

Dioscorea polygonoides var. *martinicensis* (Sprengel) Knuth (1924: 217). The type is attributed to Sieber, but the K sheet is marked “legit. Kohaut”, referring to an associate of Sieber, who collected in Martinique from 1819–1821.

Dioscorea altissima Sieber ex Presl (1845: 546), *nom. illeg.* (cited in synonymy of the following).

Dioscorea multiflora Presl (1845: 546). *nom. illeg.*

Dioscorea polygonoides var. *aperta* Knuth (1917: 208) Type:—TRINIDAD & TOBAGO. Tobago: Campbleton Woods, 13 Nov. 1912, *Broadway 4278* ♂ (holotype B!, isotypes E!, K!).

Dioscorea polygonoides var. *scorpioides* Uline ex Knuth (1917: 208). Lectotype (designated here):—PUERTO RICO. Sierra de Luquillo: Monte Jimenes, 1885, *Sintenis 1729* ♂ (lectotype B!, isolectotypes LD!, S!). Remaining former syntypes: DOMINICAN REPUBLIC. Puerto Plata, no date, *Eggers 2496* ♂ (B!); GRENADA. Without locality, 1905, *Broadway 1747* ♂ (B!).

Dioscorea polygonoides var. *cabreana* Stehlé (1976: 447). *nom. illeg.*

Dioscorea altissima auct. non Lamarck in Sieber ex Presl (1845: 546).

Notes: This species has essentially the same distribution as *D. cordata* in the Greater and Lesser Antilles, and also occurs throughout the lowland neotropics. While *D. polygonoides* is highly variable, the leaf outline is more stable than in *D. cordata*. Knuth’s varieties reflect differences in cymule architecture and width of the basal sinus, but do not correspond to any clearly observable patterns in either geographical or morphological space. Howard (1979) described local variants in the Lesser Antilles (without assigning to them formal taxonomic ranks), but further studies of this species are needed on a region-wide basis, including South and Central America. See Govaerts *et al.* (2015) for non WI synonyms.

Knuth (1917) described *D. polygonoides* var. *sieberi* and then cited it in synonymy under *D. polygonoides* var. *martinicensis* (Knuth 1924), the latter epithet being the older of the two. Knuth (1917, 1924) also cited “*D. lutea* Griseb. nec Mey” in Grisebach (1864: 588) as a synonym of *D. p.* var. *martinicensis*, while he interpreted the Meyer name to be a synonym of “*D. polygonoides*” with no varietal name. Grisebach’s (1864) use of *D. lutea* was based primarily on examination of material from Antigua and Trinidad. Here no distinction is made between Meyer’s and Grisebach’s interpretations of this species in the Lesser Antilles.

Neither the 1917 protologue nor the 1924 monograph includes an explicit citation of the herbarium where the type of *D. p.* var. *aperta* is stored, however the B sheet is the only one annotated by Knuth, and is here interpreted to be the holotype.

Acevedo & Strong (2012) chose to include *D. kegeliana* Grisebach (1848: 279) among the synonyms of *D. polygonoides*, a decision apparently based on Govaerts *et al.* (2015). This name was based on material from Northern S. America (including Trinidad & Tobago) but is not mentioned in other sources of literature on the WI flora, and thus it has not been included here.

4. *Dioscorea subnigra* Knuth (1934: 126). Type:—DOMINICAN REPUBLIC. Santo Domingo: Cordillera Central, Villa Altigracia, Loma Marian Chicle, 800 m, *Ekman 14248* ♀ (holotype B!, isotype S!)

Notes: This taxon is known only from the type collection; no staminate specimens are known. The organization of the higher vein orders in the leaves is similar to that found in some forms of *D. polygonoides*, but it is unusual in having a slightly lobed margin and the leaves drying black. In these latter aspects it somewhat resembles *D. tamoidea* Grisebach but the fruits are unusually large and round. Further study is required to determine whether it merits recognition at species level, if at all. Characters of the androecium are important in species delimitation in *Dioscorea* sect. *Lychnostemon*. Not having seen any staminate specimens that correspond to this phenotype, it is premature to make a decision about synonymy.

5. *Dioscorea tamoidea* Grisebach (1842: 42). Type:—CUBA. Sancti Spiritus: ufer San Juan, 24 July 1839, *Otto 349* ♂ [holotype B!, isotypes S! (2 sheets)]

Notes: Cuba and Hispaniola. The protologue (as “*D. tamoideam*” with a final “m”) consists of a three word description

of the leaves, followed by the type citation. It appears in *Flora Brasiliensis* as a species affine to Grisebach's *D. hederifolia*, from eastern Brazil, however it does not appear in Grisebach's Cuban catalogue (1866), as the latter refers only to material collected by Wright. An orthographic variant, *D. thamnoidea* hort. ex Correns was cited by Knuth (1924; the source cited by him is "Sitzungsber. Akad. Wien 97 (1): 672-3, 1889," but I have not been able to track down a copy, digital or hardcopy). Knuth (1924) also cited among the exsiccatae of *D. tamoidea*, Ekman 1105 and "Wright 3252 p.p." The former is actually a specimen of *Dioscorea psilostachya*, and in the case of the latter, it remains unclear which duplicate(s) Knuth was referring to (see *D. cubensis*). A single subspecies of *D. tamoidea* is recognized below. Described as a variety, it is here elevated to the rank of subspecies as it is geographically restricted to Eastern Cuba and Western Hispaniola.

5a. *Dioscorea tamoidea* subsp. *lindenii* (R.Knuth) Raz, stat. nov. *Dioscorea tamoidea*. var. *lindenii* Uline ex Knuth (1917: 209). Type:—CUBA. Santiago de Cuba: Pinal de Nimanima, Aug. 1844, *Linden 2077* ♂ (holotype B n.v., isotypes BM!, G! (3 sheets: G00098812, G00098813, G0098814), K!)

Notes: Cuba and Haiti. Knuth (1924) cited *Linden 2077* as the type, but did not explicitly name the source herbarium. I have not seen the B sheet, but evidence for its existence comes from the K sheet, which bears a hand written note stating that the locality information was taken from the sheet at the Herb. Berol. Since none of the isotypes were annotated by Knuth, the B sheet is here interpreted as the holotype. G00098812 was annotated by Uline, and in the event that the B sheet cannot be found, it would become the lectotype.

6. *Dioscorea wrightii* Uline ex Knuth (1917: 208). Type:—CUBA. Pinar del Río, 29 Sept. 1860–64, *Wright 3255* ♂♀ (holotype B!, isotypes GH!, K!)

Rajania herradurens Knuth (1917: 220). Type:—CUBA. Pinar del Río: Vicinity of Herradura, 26–30 Aug. 1910, *N. L. Britton, E. G. Britton, F.S. Earle, and C. S. Gager 6390* ♂ (holotype B!, isotype NY!). *Dioscorea herradurens* (Knuth) Wilson ex Alain in León (1946: 321).

D. lutea auct non Mey in Grisebach (1866: 251); Knuth (1917: 208).

Notes: Endemic to western Cuba. Although *Rajania herradurens* was described in the same publication as *D. wrightii*, Knuth did not include a description of the androecium of the former, suggesting he did not open the flowers. When Wilson transferred the *Rajania* name to *Dioscorea*, he too gave only a superficial description with no detail of the flowers.

Grisebach's (1866) use of *D. lutea* Mey. was based on examination of *Wright 3255*, the type specimen of *D. wrightii*. He also treated "*Dioscorea lutea* Mey" in his *Flora of the British West Indies* (1864), citing primarily specimens from the Lesser Antilles, however he also included Cuba in the species' range. *Dioscorea polygonoides* does not in fact occur in Cuba, but Grisebach did not distinguish the Cuban *Wright* material from the non-Cuban material (see also *D. polygonoides*).

Although a holotype specimen is not explicitly cited in either the 1917 or 1924 works, the B sheet is the only one annotated "Typus" by Knuth.

***Dioscorea* sect. *Chondrocarpa* Uline** (1897: 84). Lectotype (designated here):—*Dioscorea chondrocarpa* Grisebach (1842:34)

***Dioscorea chondrocarpa* Grisebach** (1842: 34). Lectotype (designated here):—BRAZIL. [near Rio de Janeiro], without date, *Sellow 54* ♂ (lectotype K!). Remaining former syntypes: BRAZIL. *Schott 4573* ♀ (specimens not found)

Dioscorea altissima Lamarck (1789: 231). *Dioscorea alata* var. *altissima* (Lamarck) Grisebach (1864: 587). Lectotype (designated in Pedralli 2004: 12):—MARTINIQUE. *Surian 816* (P! 00307100), misapplied in Kunth, 1850; Knuth, 1924; León, 1946; Adams, 1972; Howard, 1979; Acevedo-Rodriguez, 2005. See below.

Rajania cordata Vellozo (1881: 124). Lectotype (designated here):—(icon) *Fl. Flum.* Vellozo (1827: Pl. 116). There are no specimen citations in either work; the material upon which the illustration was based was apparently lost in transit from Rio de Janeiro to Paris.

Dioscorea cayennensis var. *altissima* pro syn in Knuth (1924: 81). Knuth erroneously ascribed this name to Grisebach (1864: 587), where it is not to be found.

Notes: This species, distributed in tropical South America and the Antilles, had traditionally been called *Dioscorea*

altissima Lamarck. Doubts about the name arose when Acevedo- Rodriguez (2005) called into question the identity of the type, suspecting it to be *D. cayennensis* Lamarck (1789). The two species were published simultaneously, based on different specimens. Lamarck described *D. altissima* as having opposite leaves, cylindrical stems and small, campanulate flowers, however none of these characters applies to *Dioscorea altissima* as it has been understood in modern treatments. In all references dating from Kunth (1850) to the present, “*D. altissima*” has been applied to a plant with prickly, quadrangular stems, aerial tubers (towards the base of the stem), mixed subopposite and alternate leaves, and large, rotate flowers, from the West Indies and lowland tropical South America. Lamarck’s description of *D. altissima* corresponds perfectly to Surian 816 in the Jussieu herbarium, but it does not represent the neotropical species in question.

The identity of the Surian specimen was a matter of debate some 75 years ago, although there is no published commentary on the issue. I. H. Burkill, the foremost authority on paleotropical *Dioscorea* in the first half of the 20th century, annotated the specimen as *D. cayennensis* (without date). Burkill worked extensively with cultivated yams and although he probably would not have been very familiar with *D. altissima*, he would have had ample experience with *D. cayennensis*. A second determination is attributed to Aug. Chevalier with the date October 18, 1936, and reads “*Dioscorea altissima* Lamk. (non *Dioscorea cayennensis* Lamk.)”, although in front of *Dioscorea altissima* the word “Not” appears, in an anonymous hand. Chevalier, a contemporary of Burkill, worked in tropical West Africa, where *D. cayennensis* is native, and he published several articles on cultivated yams from that region, but he is not likely to have been familiar with *D. altissima* (apart from the specimen citation in Lamarck). The final annotation (undated) reads “*Dioscorea berteriana*” written in one hand, and below it, in a different hand “(Sagot Impr.)”, a reference to Paul Antoine Sagot, who worked extensively in French Guiana (where the type of *D. cayennensis* was collected). *Dioscorea berteriana* Kunth is today treated as a synonym of *Dioscorea cayennensis* subsp. *cayennensis* (Govaerts *et al.* 2015). Pedralli (2004), though he did not annotate the specimen, did examine it in person, and cited it as the “holotype” of *D. altissima*, without questioning its identity. Acevedo-Rodriguez was the last person to see the specimen before bringing the issue to my attention. He corrected Pedralli’s “holotype” to “lectotype” (2005), because Lamarck cited multiple elements.

Such is the difficulty of *Dioscorea* that even specialists’ opinions are divided, but based on the characters cited above, as well as my own field observations of both species in the West Indies, it is clear that Surian 816 is in fact *D. cayennensis*. This specimen cannot therefore be used to represent *Dioscorea altissima*.

The other element cited by Lamarck is an illustration by Plumier (1757: Tab. 117 Fig 2). The figure depicts a single inflorescence axis with campanulate flowers, a cylindrical stem, and opposite leaves armed at the nodes with a pair of pseudostipular spines. While *D. altissima* is generally armed at the base of the petioles, *D. cayennensis* often has petiolar spines. Lamarck, however, did not mention spines at all. Regardless, the drawing is too schematic to resolve the ambiguity and would not be an appropriate element upon which to lectotypify *D. altissima*.

As the definition of *Dioscorea altissima* cannot be clearly established from Lamarck’s protologue, nor from the elements used to substantiate his description, selection of a synonym is preferable to conservation. Grisebach’s description of *Dioscorea chondrocarpa* is complete and accurate, and the type is consistent with modern collections from both the West Indies and South America.

***Dioscorea* sect. *Dematostemon* Grisebach (1842: 27). Lectotype (designated here):—*Dioscorea pilosiuscula* Sprengel (1825: 152)**

***Dioscorea pilosiuscula* Bertero ex Sprengel (1825: 152). *Helmia pilosiuscula* (Bertero ex Sprengel) Kunth (1850: 434). Type:—HISPANIOLA. Without locality, no date, *Bertero s.n.* (holotype TO!). Most likely from the Dominican Republic.**

Dioscorea cuspidata Balbis ex Kunth (1850:434). *Pro syn.*

Dioscorea duchassaingii Knuth (1924: 67). Type:—GUADELOUPE (?), without date, *Duchassaing s.n.* (♂) (holotype B!).

Notes: This species is known from the Greater and Lesser Antilles, Central America and lowland tropical South America. Consult Govaerts *et al.* (2015) for complete synonymy. Staminate specimens from the WI are unknown and in all pistillate specimens the ovaries are immature. It flowers and sets fruit in other parts of its range, suggesting a recent introduction to the WI. Knuth described *D. duchassaingii* as a distinct species on the basis of differences in leaf outline alone, and in Acevedo & Strong (2012), it is listed as an accepted name, but this is an error that was carried over from Govaerts *et al.* (2015).

***Dioscorea* sect. *Macrogynodium* Uline** (1897: 84). Lectotype (designated here):—*Dioscorea trifida* Linnaeus (1782: 427)

***Dioscorea trifida* Linnaeus** (1782: 427). Type:—SURINAME. Napis, no date, *Allamand s.n.* (holotype LINN-1184.1!)

Dioscorea triloba Lamarck (1789: 234). Type:—FRENCH GUIANA. Cayenne, no further information given (holotype: MPU 012349!).

The protologue refers to a specimen in the Jussieu herbarium. No sheet has been discovered there, however the MPU specimen bears the annotations “D. triloba- Willdenov” and “ex herbaris musei Paris,” (musoi is my transcription, but it the writing is illegible) suggesting it is the original material consulted by Lamarck. It is thus interpreted here as the holotype.

“*Dioscorea tuberosa*” auct. non Vellozo in Duss (1897: 566).

Dioscorea trifida var. *tuberosa* (Vell.) Stehlé (1976: 447). *nom. illeg.*

Notes: Widely distributed throughout the lowland neotropics. Specimens from the Greater and Lesser Antilles are probably all of cultivated origin (this information is not always explicit on herbarium labels). The species does not appear to be naturalized in the West Indian flora, although it does flower and set fruit in cultivation. It has been recorded in the West Indies from starch grains (Pagan-Jiménez 2011), and may have been brought by earlier migrants from S. America. Consult Govaerts *et al.* (2015) for complete synonymy.

Unplaced names

1. *Rajania cordata* var. *retusa* Knuth (1917: 219). Type:—UNKNOWN. “Vaterland Unbekkant” (holotype B n.v.)

Notes: It’s not clear what this name refers to. The lack of collection data (“fatherland unknown”) makes the specimen difficult to locate, although most likely it is still at B, perhaps filed in the general collection. Knuth (1917, 1924) provided only scant details: no other specimens are cited, and without a locality, the description: “leaf-blade triangular-oblong, base +/- retuse, moderately firm, fruit 13 mm. long,” is too generic to determine if the specimen is in fact *D. cordata* or a different species.

2. *Smilax hastata* Jacquin (1760: 33). Neotype:—[illustration] “*Smilax hastata*” in Jacquin (1763: Tab. 179, Fig. 103)

This name is based on an illustration that depicts a single detached leaf of what appears to be a species of *Dioscorea* sect. *Lychnostemon*, possibly *Dioscorea tamoidea* Griseb. The source material for the illustration is reportedly from Hispaniola, but there are no specimens cited in connection with the figure. The level of detail in the drawing is insufficient to permit a definitive identification at species level.

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