A taxonomic revision of *Monstera* Adans. (Araceae: Monsteroideae) in Costa Rica.

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ABSTRACT

Monstera Adans. (Araceae: Monstereae) is revised for Costa Rica. Thirty-five species are recognised, of which one (*M. deliciosa*) is introduced. Of them, ten have been only very recently described and *Monstera tablasensis* M.Cedeño is described as new here. A key to the species is provided, and each is illustrated. Lectotypes, epitypes or neotypes are newly designated for *Philodendron pertusum* Kunth & C.D.Bouché (the basis of *Monstera lennea* K.Koch), *P. anatomicum* J.H.Morsch, *M. borsigiana* K.Koch, *M. dubia* (Kunth) Engl. & K.Krause, *M. punctulata* (Schott) Schott ex Engl., *M. tenuis* K.Koch, and *Marcgravia paradoxa* W.Bull ex G.W.Johnson & R.Hogg. Problems with the typification of *Monstera adansonii* ssp. *laniata* (Schott) Mayo & I.M.Andrade (*Tornelia laniata* Schott) are outlined.

Keywords: Aroids, Monstereae, Revision, Talamanca mountain range, Taxonomy.

INTRODUCTION

Araceae in Costa Rica are represented by 24 genera and at least 278 species (Grayum, 2003a, 2003b; Ortiz et al., 2021; Cedeño-Fonseca et al., 2021c), distributed over five subfamilies: Lemnoideae, Lasioideae, Pothoideae, Monsteroideae, and Aroideae (Mayo et al., 1997; Cusimano et al., 2011, 2012; APG, 2016). The species are especially abundant in lowland humid tropical forest and cloud forest (Grayum, 2003a).

While *Anthurium* Schott (ca. 99 species) and *Philodendron* Schott (ca. 64 species) are generally the dominant aroid genera, *Monstera* Adans. is also a conspicuous aroid element in Costa Rican forests, occurring

from sea level to ca. 2400 m (Grayum, 2003a; Ortiz et al., 2018, 2021). It is the type genus of the subfamily Monsteroideae, which has three well-supported clades (Zuluaga et al., 2019) that may be recognised at tribal level: Spathiphylleae (mostly terrestrial, neotropical and eastern tropical Asian and western Pacific *Spathiphyllum* Schott and New Guinea *Holochlamys* Engl.); Heteropsideae (*sensu lato*; often but by no means exclusively climbing, and wholly neotropical *Heteropsis* Kunth, *Rhodospatha* Poepp., *Stenospermation* Schott and *Alloschemone* Schott); and the pantropical but predominantly palaeotropical, mostly but again not exclusively climbing Monstereae (only *Monstera* in the neotropics, to which it is restricted, the remaining genera being *Rhaphidophora* Hassk., *Epipremnum* Schott, *Scindapsus* Schott, *Amydrium* Schott and *Anadendrum* Schott).

The species of *Monstera* are generally nomadic vines — plants which begin life terrestrially, then ascend trees or rocks and eventually lose stem contact with the ground as the older parts die off, though ground connection is usually maintained by long descending feeder roots (Zotz, 2013; Sperotto et al., 2020). They characteristically have cylindric or dorsally compressed stems, distichous leaves with geniculate, smooth to rough petioles, and simple or pinnately-lobed, and commonly perforated (fenestrate) blades. The inflorescences characteristically have a zone of sterile flowers at the base of the spadix, the rest being bisexual and without a perianth, and undergo the sequential phases of female and male anthesis rapidly, usually followed immediately by the whole spathe being shed. The mature infructescence is usually a 'monsterocarp' (*sensu* Boyce et al., 2012: 4) in which the stylar caps of the crowded individual fruits are shed collectively in larger or smaller plates exposing the seeds in fleshy pulp (mesocarp) underneath.

Some *Monstera* species, (i.e. those in sections *Echinospadix* Madison and *Marcgraviopsis* Madison — see below), are markedly heteroblastic, exhibiting a very distinct juvenile phase with rotund leaf blades on short petioles very closely appressed to the substrate (Zotz et al., 2011), often referred to as the shingling stage, alluding to the fact that they sometimes overlap, like roof tiles or shingles. This stage is followed by an abrupt ontogenetic change to the early adult-leaved phase with longer petioles and free leaf blades which transition gradually into the fully adult leaf form as the shoot develops further. The majority of *Monstera* species (i.e. those in sections *Monstera* and *Tornelia* (Gutiérrez ex Schott) Madison) lack this shingling juvenile phase and exhibit a gradual transition from seedling to juvenile to adult leaves of increasing size and complexity (Strong & Ray, 1975; Madison, 1977). The adult stems, with the possible exception of those of the species in Sect. Tornelia, can revert to the juvenile phase if or when they become detached and hang, descending to the ground by transforming into elongate flagellar shoots with long internodes and reduced leaves, which forage for a new host support to climb, and when

they do, pass again through the characteristic developmental series (Strong & Ray, 1975; Madison, 1977; Grayum, 2003a). The species with shingling juveniles are usually further distinguished by having filiform, skototropic (shade-seeking) seedlings which lack foliage leaves, while those without shingling juveniles have seedlings with foliage leaves.

The first account of *Monstera* for Costa Rica was published by Schott (1858) as part of a checklist of aroids known at the time in Central America. He included two species in the country, both under the genus *Tornelia* Gutiérrez ex Schott. The next account of *Monstera* specifically for the country was presented by Standley (1937: 139–140), in his *Flora of Costa Rica*, in which seven species were recognised. Later Grayum (2003a) produced a synopsis in the *Manual de Plantas de Costa Rica*, in which he recognized 22 species, but also mentioned the existence of various other imperfectly known taxa. He pointed out that in spite of these more or less recent treatments, *Monstera* has been considered the taxonomically least understood aroid genus in Mesoamerica. Herbarium specimens are often inadequate for characterisation and identification owing to the large size of the plants, intraspecific variation and poor preservation of fleshy floral parts. Moreover, there are species which can flower precociously, when the length of the internodes and the form and size of the leaf sheaths and blades can vary significantly from well-developed adult plants.

The taxonomy of the genus has required a great deal of fieldwork to document *in vivo* characteristics which are lost in herbarium material, and the geographic variation of each species. Some important characters which had not been studied in depth include the roots, stems, seedlings, petiole markings, shape and distribution of leaf blade fenestrations, stigmatophores, style form, stigma colour, the colour of the fruit pulp (the flesh revealed after the stylar caps are shed), and the shape and colour of the seeds, among others.

With the aim of contributing to a better taxonomic understanding of *Monstera*, the Costa Rican species are here circumscribed and characterized morphologically on the basis of both living and herbarium material, and extensive field observations.

Related genera

Monstera is easily distinguished from other genera of Araceae in Costa Rica in having bisexual flowers without a perianth, a region of sterile flowers at the base of the spadix, a climbing habit, distichous leaves with sheathing and geniculate petioles and simple, entire or pinnatifid and in many cases fenestrate — naturally perforated — blades. [Note that in this paper we use 'fenestrate' to refer to leaves in which perforations are persistent in the opened leaf. Pinnatifid species are also divided by a perforation process, or intramarginal dissection (see Hay, 2019), in which threads of tissue connect the tips of adjacent lobes but break before or as the leaf unfurls.

Hence some pinnatifid species are described here as never fenestrate, despite the same developmental origin of the perforations of fenestrate leaves and the spaces between the lobes of the leaves of pinnatifid species; several species have both lobes and fenestrations in the same leaf. In Costa Rica there are no other genera of Araceae with perforated leaf blades, with the exception of the terrestrial, tuberous *Dracontium* L. (Zhu & Croat, 2004; Grayum, 2003a; Hay, 2019). The only other native Araceae genera in Costa Rica with bisexual flowers without perianth are *Heteropsis* Kunth, *Rhodospatha* Poepp. and *Stenospermation* Schott, belonging to a clade sister to the Monstereae (e.g. Zuluaga et al., 2019).

Monstera differs from *Heteropsis oblongifolia* Kunth (the only species of that genus in Costa Rica) in that the latter has a sprawling liana-like habit with thin, woody and highly branched shoots, leaves with very short petioles (<1.5 cm) and simple, narrow and sub-coriaceous leaf blades (**Figure 1: A–C**). *Rhodospatha* is distinguished by its leaf blades reddish when young, with entire margins and never perforated, inflorescences with a stipitate spadix, flowers with numerous ovules per locule, ovules with long funicles and axial or sub-basal placentation (Mayo et al., 1997: 125) (**Figure 1: D & E**). Like *Monstera*, both genera have distichous leaves and a spadix with a fully opening spathe, but the spadices of *Heteropsis* and *Rhodospatha* lack a sterile flower region at the base of the spadix in Costa Rica (Mayo et al., 1997: 116, 125, Grayum, 2003a). *Stenospermation* is distinguished from *Monstera* in its short, often self-supporting stems, thick spirally arranged leaves with indistinct venation, inflorescences usually with nutant peduncles, stipitate spadices, flowers with 4 ovules per locule, arranged in two rows, with long funicles and basal placentation (Mayo et al. 1997: 128) (**Figure 1: F & G**). It is worth mentioning that some *Stenospermation* species (for example, *S. marantifolium* Hemsl.) have a region of sterile flowers at the apex of the spadix, and many of the species are true epiphytes and some terrestrial.

In Costa Rica, three exotic species of other genera of Monstereae that resemble *Monstera* are cultivated. *Epipremnum aureum* (Linden & André) G.S.Bunting (formerly *E. pinnatum* (L.) Engl. 'Aureum'; Grayum, 2003a; Boyce, 1998, 2004) is widely cultivated in many parts of the country, including as a houseplant in containers of water. The leaves are entire or irregularly pinnatifid, with yellow-variegated blades. Similar to several species of *Monstera*, *Epipremnum aureum* has the ability to produce flagelliform hanging stems, with which they propagate vegetatively, and plants can 'take flight' from cultivation to adjacent wooded areas. This species flowers very rarely: no flowers or fruits have been recorded in Costa Rica. The second exotic species of Monstereae in Costa Rica is *Rhaphidophora decursiva* (Roxb.) Schott (*Cedeño 819 & Blanco,* USJ). This species is infrequently grown in gardens in the Valle Central and at the Lankester Botanical Garden. It is distinguished by having a

Figure 1. Araceae genera in Costa Rica similar to *Monstera*. A–C *Heteropsis oblongifolia* Kunth, (A) distichous leaves with short petiole, (B) erect inflorescence, (C) hanging immature infructescence. *M. Cedeño et al. 1101* (USJ). D & E *Rhodospatha pellucida* Croat & Grayum, (D) distichous leaves, (E) spadix in anthesis with stipe (arrow). *M. Cedeño et al. 908* (USJ). F & G *Stenospermation majus* Grayum, (F) spiral leaves with indistinct venation on the blade, (G) developing infructescence with stipe (arrow). *M. Cedeño et al. 878* (USJ).

greenish petiole sheathed throughout its length, persistent petiolar sheath, completely pinnatifid blade, with lobes less than 3 cm wide, externally deciduous creamy spathe at the end of the male phase, flowers with abundant stigmatic discharge and ovaries completely covered by raphides. The third is the neotononous (Boyce & Bogner, 2000), persistently shingling *Rhaphidophora hayi* P.C.Boyce & Bogner, known from Costa Rica only from the Wilson Botanical Garden in San Vito of Coto Brus.

Materials and methods

Observations on living plants were made during 60 field trips (by M.C.-F.) in 55 Costa Rican localities between 2015 and 2019. Collections were made in the main mountain ranges, particularly in different sectors of the Cordillera de Talamanca, on both the Pacific and Caribbean slopes, as this range contains the majority of Costa Rican *Monstera* species.

Herbarium material was studied from the following Costa Rican herbaria, amounting to 942 specimens: CR, HLDG, JVR, LSCR & USJ, and 3132 specimens from Central American countries were studied at CUVC, JAUM, MEXU, MO, PMA, NY, SEL & UCH, as well as 40 images of specimens accessible at COL, EAP, ENCB, MEXU & TEFH, for a total of 4114 specimens examined, 1015 collected in Costa Rica.

Type material used to determine the correct names and synonyms applied to the species circumscribed in this treatment have been examined, where possible, either online by consulting the virtual herbaria of particular institutions or via the JSTOR Global Plants database (https://plants.jstor.org/), or by directly examining type material at CR, MEXU, MO, PMA & USJ. Isotypes cited for some recently described Costa Rican species currently remain to be distributed from USJ.

Composite photos were prepared from living plants in the field, including representation of the habit, inflorescences in different stages of development (pre-anthesis and at anthesis), dissection of the spadix to show the morphology of the flowers (ovary, style, stigma, stigmatophore, longitudinal sections of the gynoecium and stamens), the infructescence in immature and mature states to document the colour of the stylar cap during maturation, and the form and colour of the seeds). Seeds of some species were germinated to document the morphology of seedlings.

Dimensions of morphological features were measured both in life and in herbarium material. Descriptions of colour and of the form of the spathes, spadices and florets were made from live plants and/or taken from colour notes on herbarium labels. Likewise, phenology data were gathered from field observations and herbarium labels.

Due to the recent high demand for *Monstera* species as ornamental plants, and a

rapidly growing black market that endangers native populations (even those in protected areas), the coordinates in the information of the type locality and cited specimens are omitted to reduce the possibility that the populations will be looted. Notes on conservation status is limited to listing protected forest areas of Costa Rica in which each species has been recorded. They do not correspond to assessment in terms of the IUCN conservation categories which is beyond the scope of the present work.

Some structural terms specific to Monstereae

Monsterocarp: a syncarpic infructescence derived the spadix, in which close-packed individual fruits ripen synchronously, with their stylar caps detaching together in slabs to expose the underlying fruit pulp containing the seeds.

Stigmatophore: a projection on the upper surface of the enlarged stylar region which carries the stigma above the level of the anthers when they are releasing pollen. It forms part of the stylar cap.

Stylar cap: the upper part of the stylar region of the fruit which at maturity detaches (generally more or less simultaneously throughout the infructescence), exposing the fruit pulp in which sit the seeds. (**Figure 5C**).

TAXONOMIC TREATMENT

Monstera Adans.

Monstera Adans., Fam. Pl. 2: 470. 1763. *Nom. et typ. cons.* (see Nicolson 1968, McVaugh 1969). — Type: *Monstera adansonii* Schott [based on *Dracontium pertusum* L.; non *Monstera pertusa* (Roxb.) Schott (*Pothos pertusus* Roxb.), i.e. *Rhaphidophora pertusa* (Roxb.) Schott].

Tornelia [Gutiérrez ex Schldl., Linnaea 26: 382. 1854 ('1853'), in synon.]; Gutiérrez ex Schott, Gen. Aroid. 74. 1858. — Type: *Tornelia fragrans* Gutiérrez ex Schott (= *Monstera deliciosa* Liebm.).

Serangium Wood ex Salisb., Gen. Pl.: 5. 1866. — Type: *Dracontium pertusum* L. (≡ *Monstera adansonii* Schott).

Slender to massive nomadic vines, appressed-climbing or climbing with pendent stems; growth sympodial in the adult reproductive phase. SEEDLINGS: skototropic, terrestrial; **shoots** with foliage leaves or filiform and aphyllous. JUVENILE PLANTS: **stems** cylindrical or dorsoventrally compressed, ascending with adventitious roots; leaves exserted or appressed to the substrate; **petiole** distinct or obscure; **blades** elliptic, ovate, lanceolate or oblanceolate, sometimes fenestrate, sometimes variegated greyish-green around or between the veins, oblique, attenuate, cordate, subcordate or obtuse at the base, obtuse or acuminate at apex, margins entire or pinnatilobed. ADULTS: **stems**

cylindrical or dorsoventrally compressed, sometimes sulcate; **roots** dimorphic, positively geotropic growing to penetrate substrate, appressed to substrate or pendent, occasionally with peridermal tissue; **anchor roots** along stem or only at nodes; **feeder roots** one per node on opposite side to petiole; **prophylls** deciduous, marcescent entire or becoming fibrous, 2-ribbed; **cataphylls** deciduous or marcescent, becoming fibrous, sometimes with a reduced blade at apex. LEAVES distichous; **petiole** basally alate and usually geniculate at apex; **blades** narrowly lanceolate to ovate-cordate, obtuse or long-acuminate at apex, sometimes decurrent along geniculum, entire or conspicuously fenestrate, margins entire, pinnatilobed or pinnatifid by intramarginal dissection, venation pinnate, primary lateral veins simple, bifurcated or trifurcated. INFLORESCENCE terminal, solitary or arranged in groups of up to 13 spadices, developed in ascending (adherent) stems, on pendent stems or in both types; **peduncle** straight or recurved; **spathe** equal to or longer than spadix, sometimes pruinose, without a proximal tube, tearing longitudinally at anthesis in some species, deciduous or marcescent after anthesis; stipe short (up to 2.5 cm long); **spadix** sub-cylindrical, with densely grouped flowers in spirals, white during development and cream at anthesis, with a region of sterile flowers at the base sometimes decurrent on peduncle; **flowers** hermaphrodite, achlamydeous, protogynous; androecium of 4 free stamens; filaments laminar; anthers oblong-ellipsoid, thecae with lateral dehiscence; gynoecium with a prismatic ovary, bilocular, with 2 ovules per locule, placentation axile; style cylindrical or tetragonal, usually wider than long, the upper surface quadrangular, trapezoid, pentagonal or hexagonal; stigma linear or circular, elevated by a cupuliform, columnar or conical stigmaphore. INFRUCTESCENCE with berries grouped in a syncarp ("monsterocarp"); **berries** with the stylar cap deciduous at maturity, 1–4 seeded; **seeds** obovate to ellipsoid, smooth, embryo large, endosperm absent; chromosome number 2n = 60 (24, 48, 56, 58, 70) (Mayo et al., 1997: 125).

Distribution—Wetter forests of tropical America, from southern Mexico to Panama, the West Indies, and widespread in tropical South America at low to medium elevations. Diversity is focused particularly in Costa Rica, Panama and the northern Andes. In the last revision (Madison, 1977), 22 species were recognized for the entire genus, slightly fewer than two thirds of the number of species here recognized for Costa Rica alone. Boyce & Croat (2011, onwards) estimate the total number of species in the genus, which has not yet been revised in South America, will reach ca. 80. In the present treatment, 34 native and one exotic species of *Monstera* are recognized and enumerated for Costa Rica. Of them, 10 are very recently described and a new record for Costa Rica was recently published (Cedeño-Fonseca et al., 2018; Cedeño-Fonseca et al., 2020a, 2020b, 2020c, 2020d, 2020e; Cedeño-Fonseca et al., 2021a). Two other species, neither native to Costa Rica nor truly

naturalized, have been found growing in the secondary forest of the Lankester Botanical Garden in Cartago: *Monstera acacoyaguensis* Matuda (*Cedeño 918 & Blanco*, USJ) and *M. acuminata* K. Koch (*Cedeño 952 & Blanco*, USJ). Both of these species are native in northern Mesoamerica [Mexico (Chiapas) to Belize, and Mexico (Chiapas) to Honduras, respectively]. They were probably brought in by Charles H. Lankester, (1879–1969) who lived on the property from 1924 to 1955, and who introduced several other exotic aroids in the garden (Dortort, 1981).

Some observations on frugivory and herbivory in *Monstera* were made during fieldwork (Cedeño-Fonseca et al., 2020f; Cedeño-Fonseca & Zuluaga, 2020).

Infrageneric classification

Monstera was divided by Madison (1977) into four sections, two with shingling juveniles, of which sect. *Marcgraviopsis* Madison species have erect spadices and not or shortly ligulate leaf-sheaths, and the one sect. *Echinospadix* Madison species has pendent spadices and long-ligulate leaf-sheaths; and two sections without shingling juveniles, sect. *Tornelia* (Guttierez ex Schott) Madison with large fruits and seeds, and sect. *Monstera* with smaller fruits and seeds. Whether this infrageneric classification is natural has not yet been fully tested by molecular analyses, though the results of analyses by Zuluaga et al. (2019) suggest strongly that it is not. For example, sampled species assigned to sect. *Marcgraviopsis* do not all group together in the trees they present (with *M. spruceana* and *M. acuminata* each appearing among sect. *Monstera* species), and *Monstera tuberculata* (sect. *Echinospadix*) appears nested in a group of sect. *Marcgraviopsis* species which is itself sister to a species from sect. *Monstera*. Nevertheless, we have assigned the species here to Madison's sections, while simply enumerating them alphabetically rather than organizing this account around his sections.

KEY TO THE SPECIES OF *MONSTERA* NATIVE AND NATURALIZED IN COSTA RICA

1a. Adult leaf blade without fenestrations (rarely present), entire, deeply pinnatifid or pinnatilobed; inflorescence on ascending or hanging shoots 2

1b. Adult leaf blade with fenestrations (rarely absent), entire, pinnatifid or pinnatilobed; inflorescence on ascending shoots (rarely in hanging shoots) 20

2a. Inflorescences borne on free, usually pendent shoots, never on clinging ascending shoots 3

2b. Inflorescences borne on clinging ascending shoots, rarely also on free pendent shoots 8

3a. Adult leaf blade entire (rarely perforated) 4

3b. Adult leaf blade pinnatilobed (rarely perforated) 7

4a. Petiolar sheath ligulate for 3–6 cm; spathe marcescent or falling as a single unit after anthesis, without tearing longitudinally at the base; stigmatophore broadly conical; juvenile plants with variegated leaves . . . . . ***M. tuberculata***

4b. Petiolar sheath ligulate for 1–3 cm; spathe not marcescent, falling as a single unit or tearing longitudinally at the base after anthesis before falling; stigmatophore absent; juvenile plants with non-variegated leaves 5

5a. Petiolar sheath ligulate for 1–3 cm; stem warty; spadix without style projecting and style truncate . . . . . ***M. luteynii***

5b. Petiolar sheath without ligule or ligulate ≤ 1 cm; stem smooth; spadix with or without projecting and truncate styles 6

6a. Petiolar sheath ligulate ≤ 1 cm; sheath deciduous but leaving persistent fibrous remains; adult leaf blades with 0–5 fenestrations; spathe tearing longitudinally at the base after anthesis before falling; spadix with projecting and truncate styles; Caribbean and Pacific watersheds . . . .***M. pittieri***

6b. Petiolar sheath without ligule; sheath persistent and rarely deciduous; adult leaf blades without fenestrations; spathe not tearing longitudinally at the base after anthesis before falling; spadix with truncate styles and not projecting, Pacific watershed . . . .***M. tarrazuensis***

7a. Petiolar sheath persistent or semi-persistent, reaching the base of the geniculum or the base of the leaf blade; spathe tearing longitudinally at the base after anthesis before falling, white within, externally yellowish-green and not pruinose; leaf blade, with 2–4 lobes per side, never perforate . . . .***M. molinae***

7b. Petiolar sheath deciduous, not reaching the geniculum; spathe not tearing longitudinally at the base after anthesis before falling, pale pink internally, green and pruinose externally; leaf blade with 2–6 lobes per side, usually perforated . . . .***M. tacanaensis***

8a. Adult leaf blade deeply pinnatifid; most lobes ≤ 5 cm wide 9

8b. Adult leaf blade entire or pinnatilobed; if lobed, most lobes ≥ 5 cm wide 11

9a. Adult leaf blade with 5–30 lobes per side, most lobes with one pronounced central primary vein and two basally converging or sub-parallel slightly less robust secondary veins . . . .***M. tenuis***

9b. Adult leaf blade with 3–12 lobes per side, lobe venation not so 10

10a. Vegetative parts pruinose/glaucous; petiolar sheath extending approximately to the middle of the petiole; free portion of petiole terete; peduncle subtended by a persistent mucronate cataphyll . . . .***M. croatii***

10b. Vegetative parts not pruinose/glaucous; petiolar sheath reaching the base of the geniculum or 3–6 cm short of it; free portion of petiole canaliculate; peduncle subtended by a rarely persistent acuminate cataphyll . . . .***M. pinnatipartita***

11a. Adult leaf blade with entire margin (rarely perforated) 12

11b. Adult leaf blade with pinnatilobed margin (rarely perforated) 17

12a. Petiolar sheath persistent, marcescent or deciduous leaving fibrous remains; petiole always smooth; adult leaf blade at least 15–25 × 9–15 cm 13

12b. Petiolar sheath deciduous or persistent, never leaving fibrous remains; petiole smooth or asperous; adult leaf blade at most 12–25 × 3–15 cm 15

13a. Petiolar sheath persistent; adult leaf blade not perforated (or very rarely perforated); petiole dark green, Caribbean and Pacific watersheds . . . . . .***M. standleyana***

13b. Petiolar sheath marcescent or deciduous leaving fibrous remains; adult leaf blade with or without fenestrations; petiole dark green or white-green 14

14a. Petiole green; adult leaf blade never perforated; flowers with the style prolonged and constricted in the middle, Caribbean and Pacific watersheds . . . .***M. anomala***

14b. Petiole whitish to speckled with white dots; adult leaf blade perforated or not (generally the perforations break at the margin); flowers with the conical style; Caribbean watershed . . . .***M. integrifolia***

15a. Petiole asperous; petiolar sheath persistent and involute, reaching 2–3 cm below the base of the geniculum; 50–100 m on the southern Pacific watershed . . . .***M. gambensis***

15b. Petiole smooth; petiolar sheath deciduous, reaching the base of the geniculum; Caribbean and Pacific watersheds 16

16a. Mature fruits with the stylar cap orange; adult leaf blade cuneate at the base, with 4–8 primary lateral veins per side; south of Caribbean watershed; 0–100 m . . . .***M. obliqua***

16b. Mature fruits with the stylar cap cream; adult leaf blade cordate or obtuse at the base, with more than 15 primary lateral veins per side; 900 to 2200 m on the Pacific watershed . . . .***M. wilsoniensis***

17a. Petiolar sheath persistent, reaching the geniculum or to 3 cm below it; petiole light green and pruinose 18

17b. Petiolar sheath deciduous, reaching to base of the geniculum; petiole light-green or dark green with white dots pruinose or not 19

18a. Vegetative parts pruinose/glaucous; Caribbean watershed, 0–700 m ... ***M. glaucescens***

18b. Vegetative parts never pruinose/glaucous; Caribbean and Pacific watershed, 0–700 m ***M. dissecta***

19a. Petiole not speckled with white dots; peduncle ≤ 10 cm long, shorter than the spadix . . . . . ***M. spruceana***

19b. Petiole speckled with white dots; peduncle > 10 cm long, longer than the spadix . . . . . ***M. monteverdensis***

20a. Adult leaf blade with pinnatifid or pinnatilobed margin; with or without few rounded fenestrations on each side adjacent to the midrib 21

20b. Adult leaf blade with entire margin (sometimes pinnatilobed by tearing of the fenestrations that extend close to the margin); perforated or not, with abundant rounded fenestrations on each side adjacent to the midrib. 26

21a. Adult leaf blade with each lobe (incompletely) separated from the next by a row of fenestrations, with the lobes sometimes cross-linked by filaments or very narrow bands of lamina often becoming broken with age 22

21b. Adult leaf blade with each lobe completely separated from the next by a single incision reaching or approaching the midrib 25

22a. Leaf lobes connected by mostly broader bands of laminar tissue; spathe externally yellowish or pink, without longitudinally splitting at male anthesis 23

22b. Leaf lobes connected by very fine thread-like filaments; spathe externally yellowish-green or pink, usually longitudinally splitting at male anthesis 24

23a. Geniculum winged; petiole with green warts and flattened at the apex (in Costa Rica); leaf blades ovate-cordate, with the primary lateral veins >10 mm wide; spathe yellowish externally in anthesis; cultivated, occasionally escaped ... .***M. deliciosa***

23b. Geniculum terete; petiole smooth and terete at the apex; leaf blade cuneate-truncate, with the primary lateral veins < 10 mm wide; spathe externally pink in anthesis; native plants . . . .***M. dubia***

24a. Petiolar sheath deciduous but leaving persistent fibrous remains; spathe externally pink .. ..***M. filamentosa***

24b. Petiolar sheath deciduous without leaving persistent fibrous remains; spathe externally yellowish-green.. .. ..***M. punctulata***

25a. Petiole whitish or sparsely speckled with white dots; adult leaf blade pinnatifid with abundant rounded fenestrations on each side adjacent to the midrib; stigmatophore conical; spathe pale green externally; Pacific watershed . . . . . .***M. epipremnoides***

25b. Petiole light green or strongly speckled with white dots; adult leaf blade pinnatilobed, rarely with few rounded fenestrations on each side adjacent to the midrib; stigmatophore strongly conical; spathe yellowish green externally; Caribbean watershed . . ...***M. lentii***

26a. Adult leaf blade distinctly membranous; petiolar sheath persistent, not reaching the geniculum; free portion of petiole terete; mature infructescence with the stylar caps yellow and the pulp orange . . . .***M. membranacea***

26a. Adult leaf blade more or less coriaceous; petiolar sheath deciduous or persistent, reaching the geniculum; mature infructescence with the stylar caps cream and the pulp white 27

27a. Stem, petiole and peduncle with brown, black, green or white pustules, never smooth nor asperous; leaf blade with few rounded fenestrations on each side adjacent to the midrib, rarely fenestrations larger, elongated and reaching (occasionally breaking) the margin 28

27b. Stem, petiole and peduncle asperous or smooth, never with brown, green or white pustules (rarely with white or black pustules), leaf blade with abundant rounded fenestrations on each side adjacent to the midrib and the ones located farther from the midrib much larger and elongated, reaching and breaking the margin 30

28a. Petiole sheath deciduous, not undulate; stems and petioles with large black pustules; spathe yellowish-cream externally . . ..***M. buseyi***

28b. Petiole sheath persistent or deciduous, markedly undulate; stems and petioles with large brown, black or white pustules; spathe light green or cream externally. 29

29a. Petioles with greenish white (never black) pustules; the base of petiole dark green; styles conical; Caribbean watershed . .. .***M. costaricensis***

29b. Petioles with brown, black and/or white pustules; styles truncate; Pacific watershed . . . .***M. alfaroi***

30a. Petiole and peduncle asperous (rarely smooth) .. .. .31

30b. Petiole and peduncle smooth (rarely asperous with white or black pustules) 32

31a. Spathe salmon pink inside and out, tearing longitudinally at the base and deciduous after anthesis; petiole asperous or smooth; Caribbean and Pacific watersheds, 800–2100 m . .. .***M. oreophila***

31b. Spathe pale pink within, pruinose green without, not tearing longitudinally at the base and marcescent after anthesis; petiole asperous, Pacific watersheds, 2000–2100 m ... .***M. mittermeieri***

32a. Petiole sheath persistent or deciduous, petiole always smooth; individuals growing up to 1600–2300 m, in the Cordillera de Talamanca in Pacific watershed 33

32b. Petiole sheath deciduous; petiole smooth or rarely asperous with white or dark pustules at the base; individuals growing up 0–1500 m, in Caribbean and Pacific watersheds 34

33a. Petiole sheath persistent; petiole white-green or speckled with white dots . . ..***M. juliusii***

33b. Petiole sheath deciduous; petiole light-green, sometimes white-dotted . . . .***M. tablasensis***

34a. Petiole dark green, smooth (rarely asperous with white pustules); primary lateral veins bifurcated or trifurcated or not; spathe white externally, Caribbean and Pacific watersheds . . . .***M. adansonii***

34b. Petiole white-dotted, smooth with few dark pustules in the base; primary lateral veins never bifurcated or trifurcated; spathe white-yellowish externally, Pacific watersheds .. . .***M. limitaris***

The species in Costa Rica

1. *Monstera adansonii* Schott, *Wiener Z. Kunst* 4: 1028. 1830. — *Dracontium pertusum* L., *Sp. Pl.* 2: 968. 1753. — Type: Figs. LVI & LVII, '*Arum hederaceum, amplis foliis perforatis*', in R.P.C. Plumier, Description des Plantes de l'Amerique. 1693. (lectotype, designated by Madison, 1977).

Terrestrial or nomadic vine, appressed-climbing or climbing habit. SEEDLINGS: bearing foliage leaves. JUVENILE PLANTS: root climbers; **stems** light-green or dark, smooth or slightly rough, cylindrical or flattened; **internodes** 3–5 cm long, 0.5–10 mm diam.; **petiole** distinct, dark-green, smooth or slightly rough, 10–15 cm long, sheathed to the base of the geniculum; **petiole sheath** deciduous or persistent; **blades** ovate-lanceolate, attenuate, cordate or truncate at the base, acuminate at apex, subcoriaceous, 10–15 × 5–10 cm, not appressed to the phorophyte; **fenestrations** present or absent. ADULT PLANTS: root climbers; **stem** light-brown, light-green or dark-green, smooth or with small white pustules, sometimes with white dots, cylindrical or slightly flattened; **cataphylls** light green, whitish or yellowish-green, deciduous but leaving dry fragments on the peduncle; **internodes** 1–6 cm long, 1.5–3.5 cm diam.; **anchor roots** dark brown or blackish; **feeder roots** dark brown; **petiole** greenish, sometimes with white dots, smooth or with small white pustules, scarcely verrucose at the base, 25–70 cm long, sheathed to the base of the geniculum; **petiole sheath** deciduous, sometimes with fibrous residues; geniculum smooth, flattened or sunken adaxially, convex abaxially, 2–4 cm long; **blades** ovate, lanceolate-ovate or oblong, broadly cuneate to rounded, truncate or rarely cordate at the base, acuminate at apex, coriaceous, drying blackish, reddish, yellowish or olive-green, 23–65 × 17–30 cm, 1.3–1.8 times longer than wide, undulate-decurrent on the geniculum (7–11 undulations of 0.5–1 mm wide); **midrib** flattened adaxially, convex abaxially, drying black or yellowish green on both surfaces; **primary lateral veins** 15–35 per side, emitting at a very low angle one or two robust secondary veins from near the base or to ca. 1/3rd of the way from the base of the primary veins, especially in the proximal 2/3rds of the blade, sunken to slightly sunken adaxially, raised abaxially, departing midrib at 45–80° (rarely at 90°), drying black or yellowish; **secondary veins** slightly prominent, reticulate towards the margin or parallel to the lateral nerves, undulate when dry; **collective veins** slightly visible; **fenestrations** present or absent, rounded, ovate or ellipsoid when present, and distributed along the blade near the midrib, sometimes with filaments separating the fenestrations; **margins** entire or pinnatilobed (2–5 lobes per side), due to tearing of the fenestrations that extend to the margin. INFLORESCENCES on ascending and pendent stems, 4–8 simultaneously at the flowering season, arranged in the leaf axils or into cataphylls; **peduncle** smooth or slightly rough, 12–20 cm long; 1.4–1.6 cm diam.; **spathe** short or long acuminate, light green and yellowish green during development, white or

yellowish green externally, white internally at anthesis, 13–20 × 5–14 cm, up to 5 cm longer than the spadix, slightly coriaceous or membranous, sometimes with revolute margins, completely open during anthesis or remaining convolute in the lower part, later deciduous or marcescent post-anthesis; **spadix** white or yellowish during development, cream-yellowish at anthesis, 10–15 cm long, 1.5–2 cm diam., (4.6–)7–9.2 times longer than wide; **basal sterile flowers** with a yellow stigmatic secretion, 3–5 mm long; **fertile flowers** 4–6 mm long; stamens with laminar filaments, 1–6 mm long; anther 1–2 mm long; ovary quadrangular or rectangular in longitudinal section, ribbed, 3–4 × 2–3 mm; style compressed, pentagonal or hexagonal, 0.5–2 × 2–3 mm; stigmatophore columnar, 0.5–1 mm long, absent (i.e. becoming unobservable) in dry specimens; stigma linear or linear-curved, with a transparent stigmatic secretion; **berries** creamy-white, yellowish green during development, pulp whitish; **seeds** dark green, 3–6 mm long. (**Figures 2–8**).

Distribution and habitat: From Nicaragua to Venezuela, Guyana, French Guiana, Suriname, Brazil, Trinidad & Tobago, the Lesser Antilles. In Costa Rica it is distributed on the Caribbean side, in the cordillera de Tilarán y Central, in the Sapoá River basin, Llanuras de Los Guatusos, Llanuras de San Carlos y Llanuras de Tortuguero, and on the entire Pacific slope, at 0–1500 m. It lives in *Tropical rain forest*, *Tropical wet forest*, *Tropical moist forest*, *Premontane rain forest* and *Premontane wet forest* life zones; in primary and secondary forests, and in open areas.

Phenology: In Costa Rica, flowering has been recorded from January to September and from November to December, and fruiting from January to December.

Conservation status: *Monstera adansonii* is protected in the Reserva Forestal Los Santos, Reserva Natural Absoluta Cabo Blanco, Zona Protectora Arenal-Monteverde, Zona Protectora el Rodeo, Zona Protectora Cerros de La Carpintera, Zona Protectora Cerros de Escazú, Zona Protectora Cerro de Turrubares, Parque Nacional La Cangreja, Parque Nacional Corcovado, Parque Nacional Barra Honda, Parque Nacional Carara, Parque Nacional Diriá, Parque Nacional Piedras Blancas, Parque Internacional de La Amistad, Parque Nacional Corcovado, Parque Nacional Guanacaste, Parque Nacional Rincón de la Vieja and Parque Nacional Tapantí-Macizo de La Muerte.

Comments: This species is a member of sect. *Monstera*. It is differentiated from other Costa Rican species by the combination of smooth or slightly asperous petioles, the wings of the sheath deciduous, the leaf blade perforate or not but never pinnatilobed (other than be breaking), the primary lateral veins sometimes bifurcate at the base or trifurcate at half their length, the slender spadix (less than 2 cm diam. at anthesis), on a long peduncle (to 20 cm), and the stigmas sunken on the style or

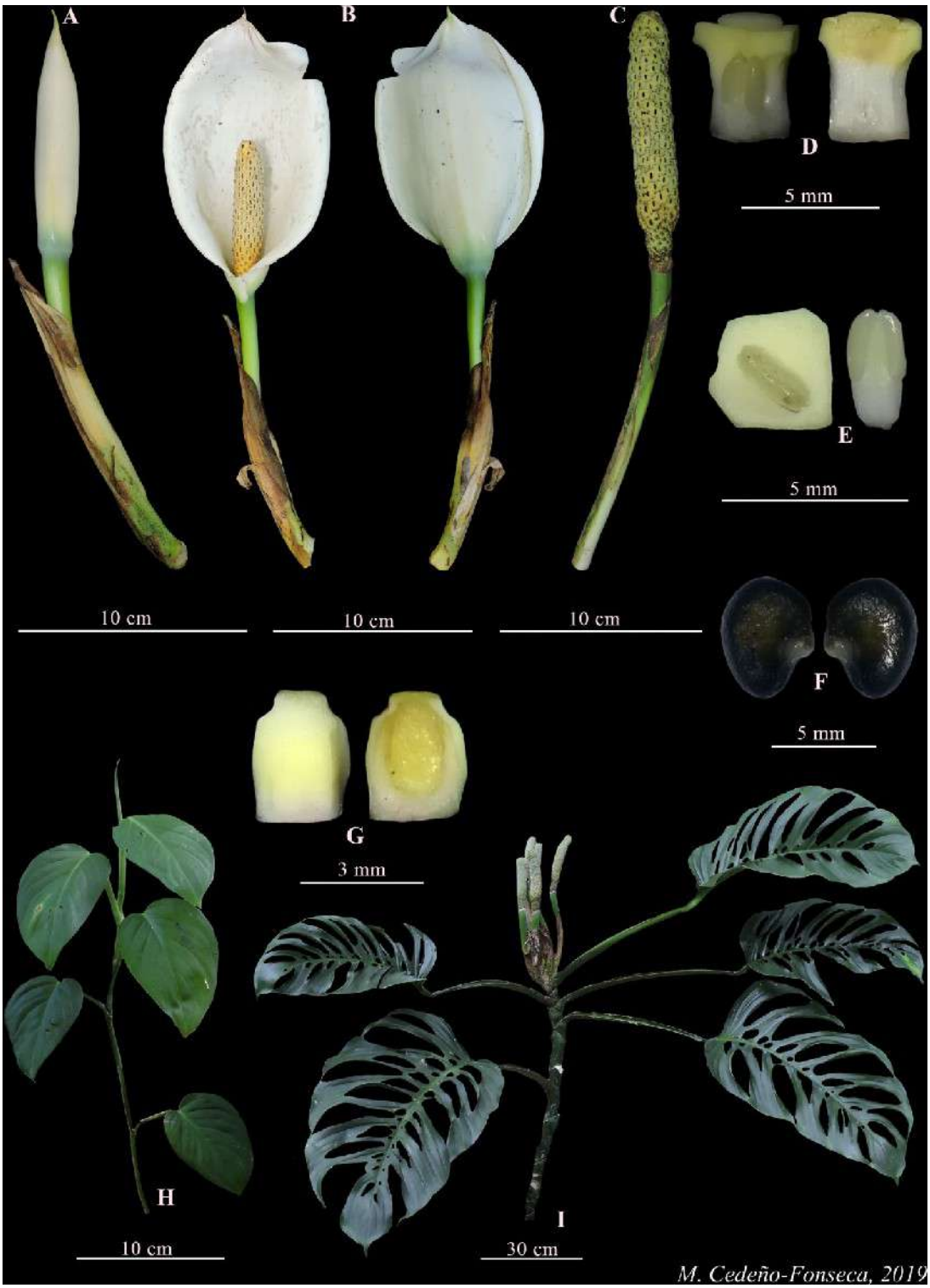

Figure 2. *Monstera adansonii* (morphotype 1: Southern Pacific watershed). (A) Developing inflorescence. (B) Open inflorescence, frontal and back views. (C) Immature infructescence. (D) Fertile flower, in lateral view (left), and longitudinal section (right). (E) Stylar plate with stigma (left) and one stamen (right). (F) Seeds. (G) Sterile flower, in lateral view (left), and longitudinal section (right). (H) Portion of juvenile plant. (I) Portion of adult plant. *M. Cedeño et al. 804* (USJ).

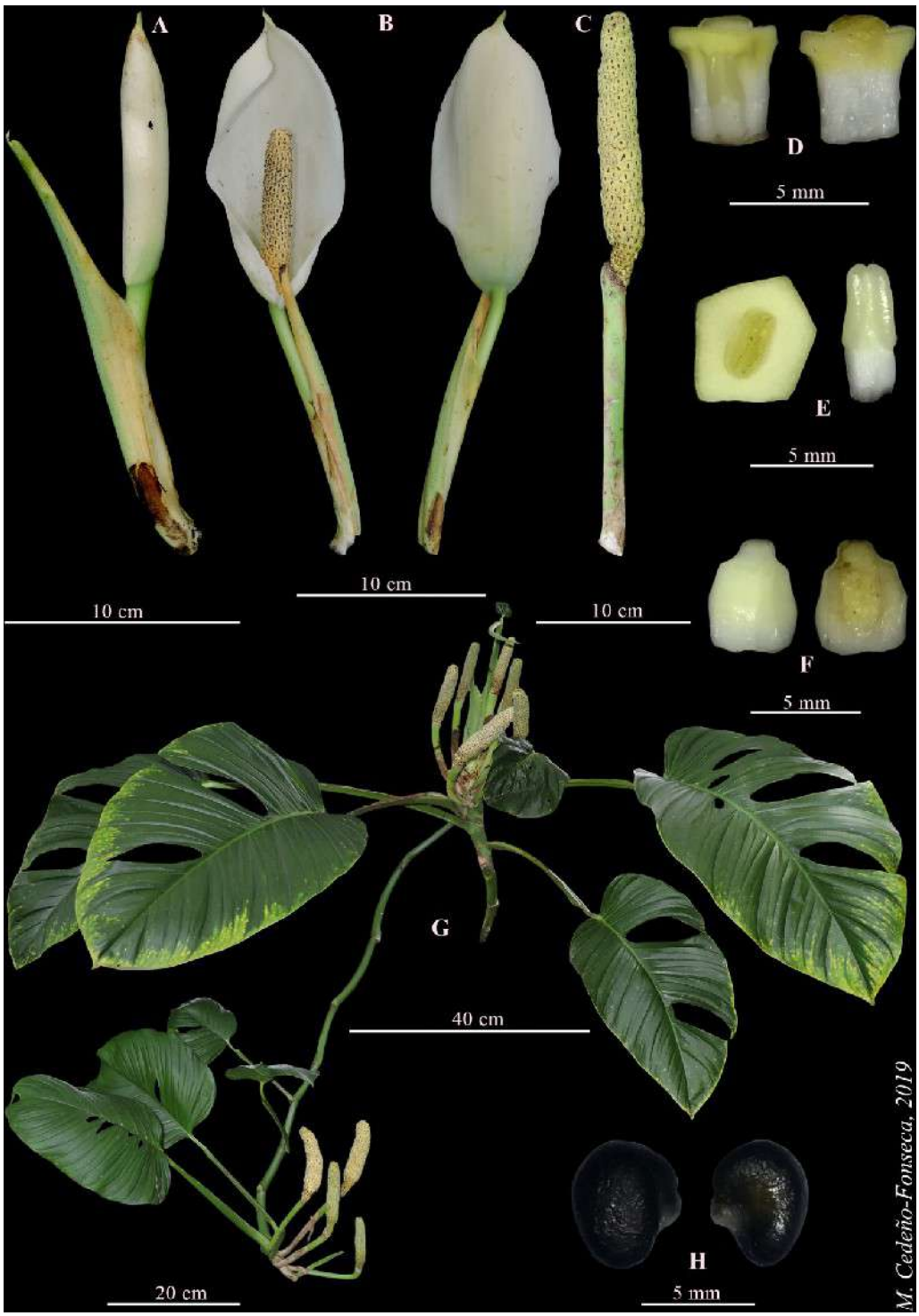

Figure 3. *Monstera adansonii* (morphotype 2: Southern Pacific watershed). (A) Developing inflorescence. (B) Open inflorescence, frontal and back views. (C) Immature infructescence. (D) Fertile flower, in lateral view (left), and longitudinal section (right). (E) Stylar plate with stigma (left) and one stamen (right). (F) Sterile flower, in lateral view (left), and longitudinal section (right). (G) Adult individual with reproductive hanging stem. (H) Seeds. Buenos Aires, Puntarenas (not collected).

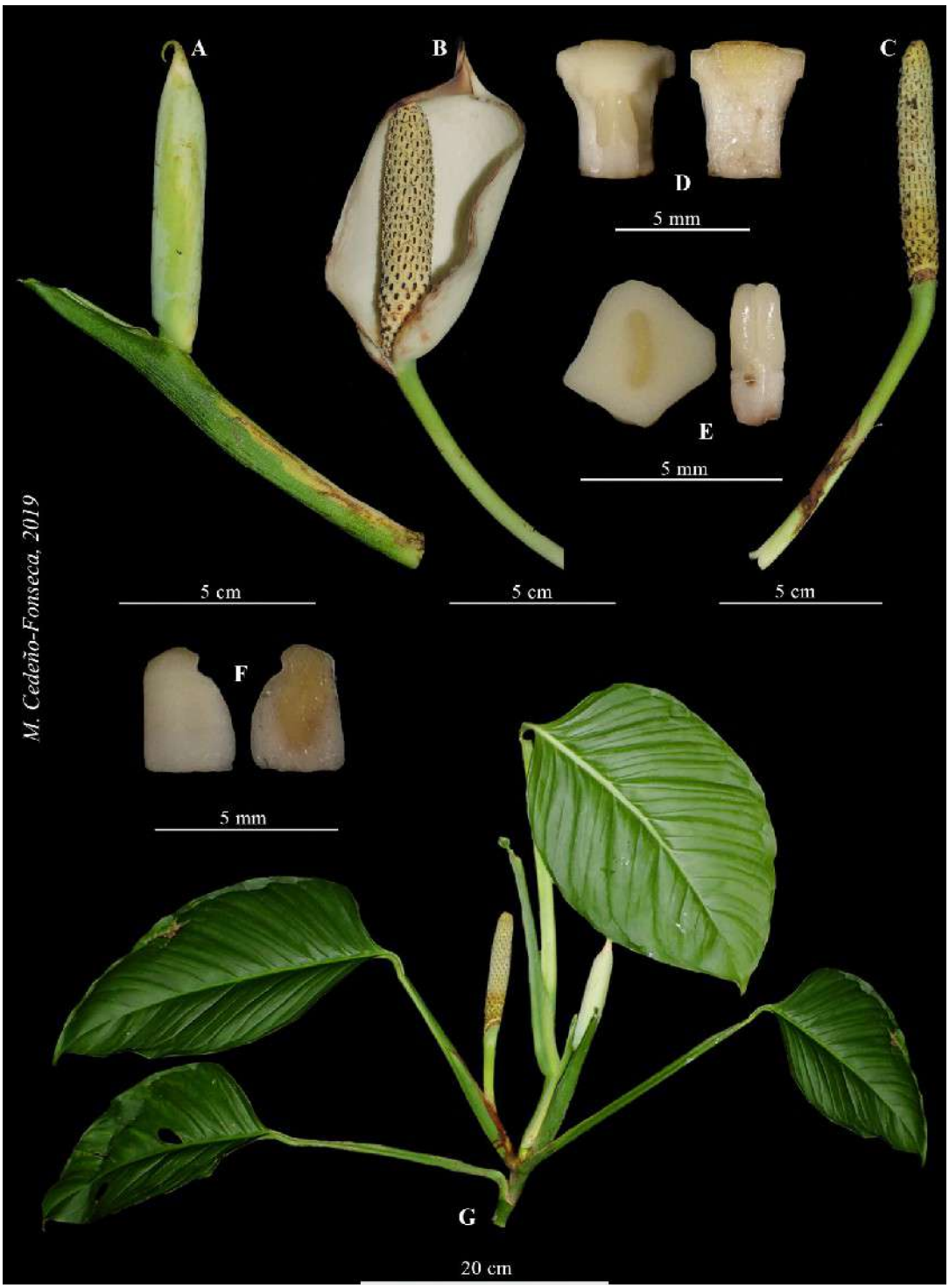

Figure 4. *Monstera adansonii* (morphotype 3: Southern Pacific watershed, La Gamba). (A) Developing inflorescence. (B) Open inflorescence, frontal view. (C) Immature infructescence. (D) Fertile flower, in lateral view (left), and longitudinal section (right). (E) Stylar plate with stigma (left) and one stamen (right). (F) Sterile flower, in lateral view (left), and longitudinal section (right). (G) Portion of adult plant. *M. Cedeño et al. 888* (USJ).

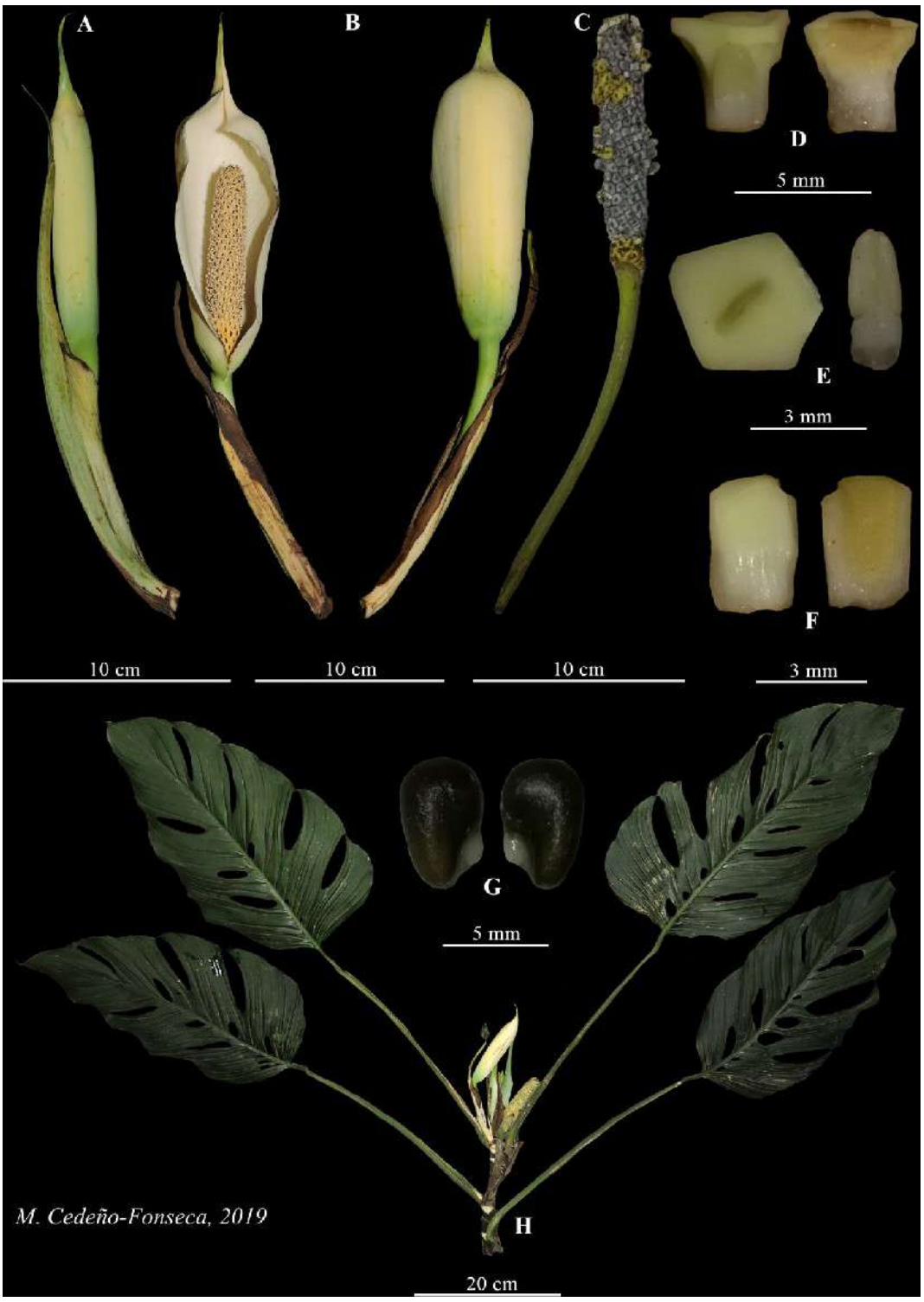

Figure 5. *Monstera adansonii* (morphotype 4: Southern Pacific watershed, Sirena). (A) Developing inflorescence. (B) Open inflorescence, frontal and back views. (C) Mature infructescence, stylar plates detached. (D) Fertile flower, in lateral view (left), and longitudinal section (right). (E) Stylar plate with stigma (left) and one stamen (right). (F) Sterile flower, in lateral view (left), and longitudinal section (right). (G) Seeds. (H) Portion of adult plant. *M. Cedeño et al. 892* (USJ).

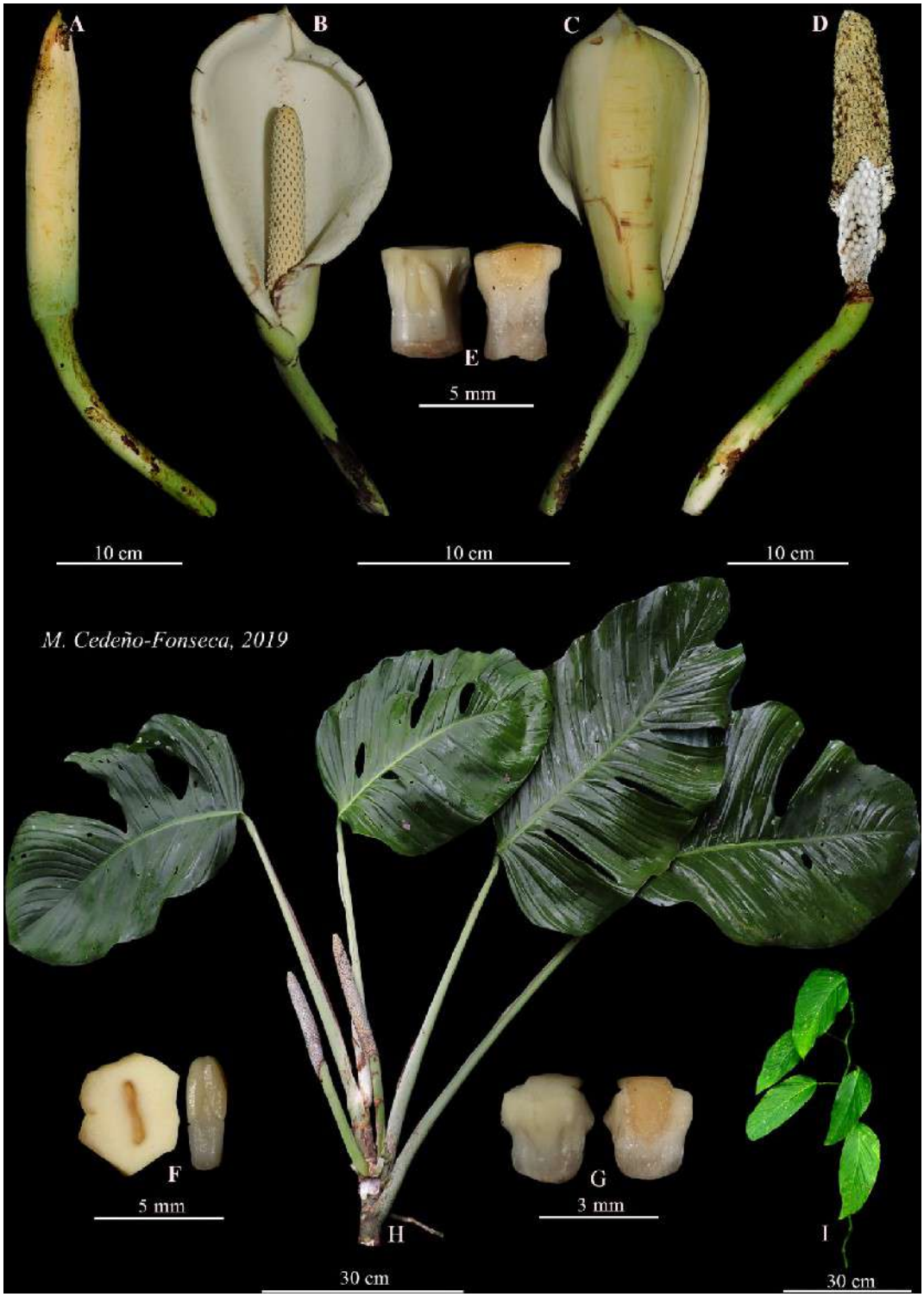

Figure 6. *Monstera adansonii* (morphotype 5: Southern Pacific watershed, Estación Biológica Piro). (A) Developing inflorescence. (B & C) Open inflorescence, frontal and back views. (D) Mature infructescence, stylar plates detached. (E) Fertile flower, in lateral view (left), and longitudinal section (right). (F) Stylar plate with stigma (left) and one stamen (right). (G) Sterile flower, in lateral view (left), and longitudinal section (right). (H) Portion of adult plant. (I) Portion of juvenile plant. *M. Cedeño et al. 1210* (USJ).

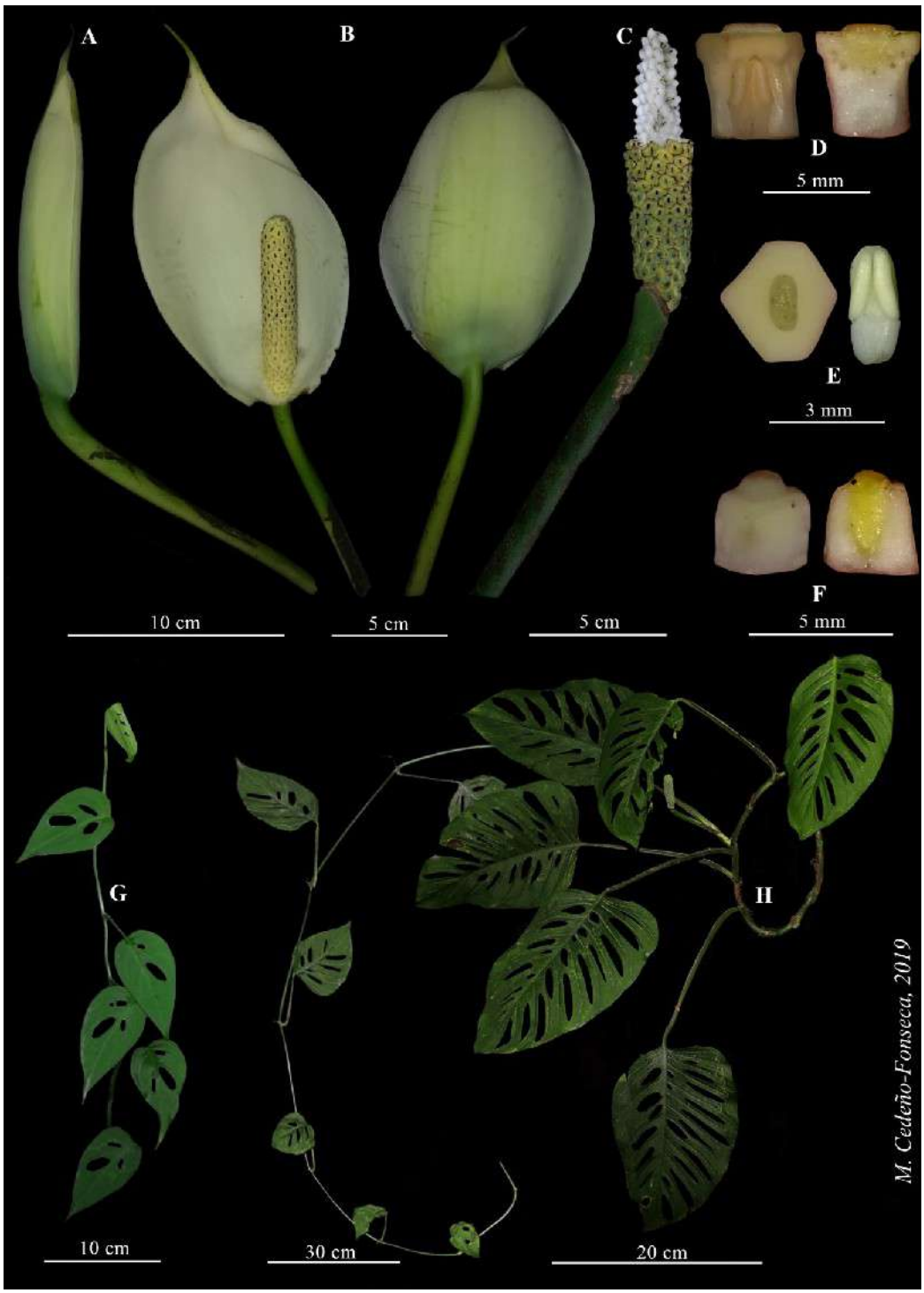

Figure 7. *Monstera adansonii* (morphotype 6: Central Pacific watershed, Ciudad Universitaria Rodrigo Facio, Universidad de Costa Rica). (A) Developing inflorescence. (B) Open inflorescence, frontal and back views. (C) Mature infructescence, stylar plates detached. (D) Fertile flower, in lateral view (left), and longitudinal section (right). (E) Stylar plate with stigma (left) and one stamen (right). (F) Sterile flower, in lateral view (left), and longitudinal section (right). (G) Portion of juvenile plant. (H) Portion of adult plant. *M. Cedeño et al. 1008* (USJ).

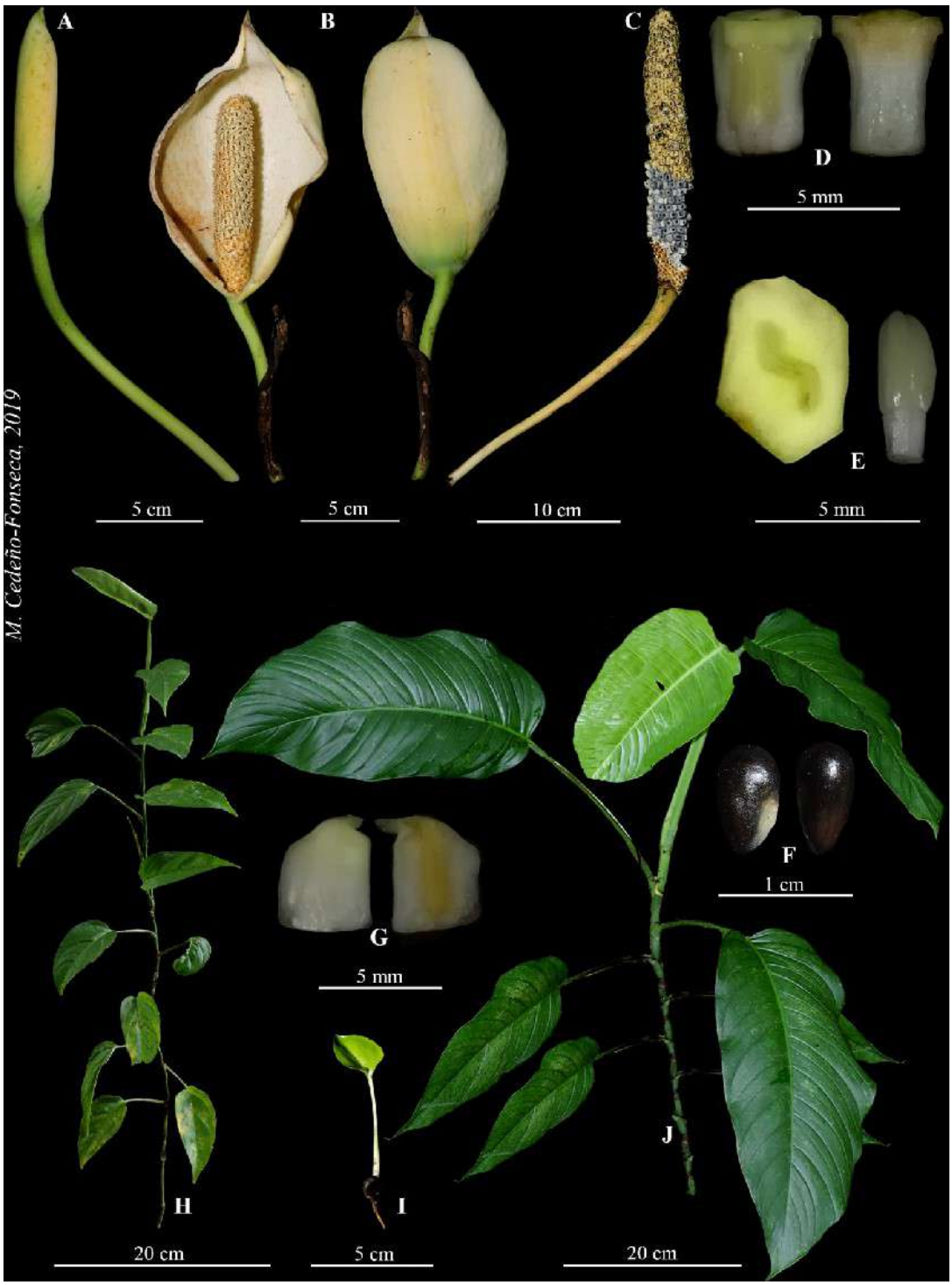

Figure 8. *Monstera adansonii* (morphotype 6: Caribbean watershed, La Tirimbina Biological Reserve). (A) Developing inflorescence. (B) Open inflorescence, frontal and back views. (C) Mature infructescence, stylar plates detached. (D) Fertile flower, in lateral view (left), and longitudinal section (right). (E) Stylar plate with stigma (left) and one stamen (right). (F) Seeds. (G) Sterile flower, in lateral view (left), and longitudinal section (right). (H) Portion of juvenile plant. (I) Seedling. (J) Portion of adult plant. *M. Cedeño et al. 925* (USJ).

slightly raised on a columnar stigmatophore. *Monstera adansonii* is widely variable in its vegetative morphology with various distinguishable morphotypes in different parts of the country. Morphotypes from the Caribbean and South Pacific slopes (Osa Peninsula) could be confused with *Monstera buseyi*, but *M. buseyi* grows in more humid habitats and has leaves with fewer fenestrations and more primary lateral veins. These same populations have slightly but consistently rough and mottled petioles, the whole leaf blade without fenestrations, primary lateral veins bifurcated at the base or trifurcated at half their length, inflorescences that frequently emerge from light green cataphylls, rarely from the leaf axils. On the other hand, in the South Pacific in the Térraba River basin, central and northern Pacific slope, they have the petiole smooth, unmottled, the leaf blade fenestrate and with the entire margin, with or without primary lateral veins bifurcated at the base or trifurcated at half their length, and inflorescences that rarely arise from cataphylls.

The form of the inflorescence is variable between the morphotypes on both slopes: the peduncle can be smooth or slightly rough; the spathe can be coriaceous, thinly coriaceous to membranaceous, deciduous or sometimes marcescent, its margins sometimes involute, the base completely open or forming a convolute tube, the apex acuminate to shortly acuminate; and the linear stigmas, sunken or raised on a stigmatophore. The infructescence is more uniform in shape and color; the fruits are always with white pulp, but the seeds can vary even within the same infructescence, in terms of form and dimension, though the colouring is constant.

Monstera adansonii, in the broad circumscription accepted here, is the most common and frequently collected *Monstera* in Costa Rica, as well as the most ecologically versatile, and it is one of the few species of Araceae found in the relatively dry parts of the Pacific slope (Grayum 2003a).

From a wider geographic perspective, Madison (1977) recognized three varieties of *Monstera adansonii*: the type variety, var. *adansonii*, restricted to the Antilles; var. *klotzschiana* (Schott) Madison, distributed from southern Venezuela and the Guyanas to southern Paraná state in Brazil, the Peruvian Amazon and Bolivia; and the extremely variable var. *laniata* (Schott) Madison, distributed from Nicaragua to Peru, Venezuela, the Guianas, and Brazil, to which all Costa Rican *Monstera adansonii* have generally been assigned (Grayum, 2003: 125). More recently, Mayo & Andrade (2014) elevated these varieties to distinct subspecies: *Monstera adansonii* subsp. *adansonii*, subsp. *klotzschiana* (Schott) Mayo & I.M.Andrade, and subsp. *laniata* (Schott) Mayo & I.M.Andrade, plus subsp. *blanchetii* (Schott) Mayo & I.M.Andrade for the state of Bahia in Brazil, a reduction in status of *Monstera blanchetii* Schott. These subspecies need to be re-evaluated in detail throughout the range of *Monstera adansonii* and, although ssp. *laniata* must have a Costa Rican type, we

have not recognized it for the purpose of this revision since, as already noted, *M. adansonii* falls into a number of morphotypes in Costa Rica alone, and it remains unclear just how useful a concept ssp. *laniata* really is. Moreover, its typification is problematic (see nomenclatural note, below). Mayo & Andrade (2014), in raising it to subspecific rank, acknowledged that they had not studied it in detail.

Subsp. *klotzschiana* may represent a different species, which has characteristics such as the petiole sheathing up to the base of the leaf blade or near the base of the geniculum, persistent, involute or revolute petiole wings, the leaf blade with entire margins, with or without fenestrations — which when present extend to the margin, and the conical style apex raised by a conical stigmatophore (Mayo & Andrade, 2014). These characteristics are not found in any population of *Monstera adansonii* subsp. *laniata* in Central America. On the other hand, subsp. *blanchetii* has similar characteristics to the morphotypes of subsp. *laniata* on the central Pacific watershed of Costa Rica: the colour and shape of the spadix, the spathe, and fenestrations in the leaf, but it differs in the petiolar sheath being persistent, whereas in subsp. *laniata* it is deciduous. Mayo & Andrade (2014) also mention that (unpublished) molecular data distinguish the population of subsp. *blanchetii* from Bahia, Brazil, from the populations subsp. *laniata* from French Guiana.

Much fieldwork is required to properly characterize the populations of each subspecies of *Monstera adansonii* throughout its entire range. Documenting characters that are not well preserved in herbarium samples and plotting their geographical distribution, needs to be combined with molecular studies to determine whether these taxa correspond to different species or whether they really do represent variation within a single species.

Nomenclatural note: The typification of *Monstera adansonii* var. *laniata* (Schott) Madison, based on *Tornelia laniata* Schott, is plagued with ambiguities and presents several problems. Madison (1977) cited the type as "Costa Rica, Candelarta [sic], *Orsted* [sic] *15795* (C; isotype B, *non vidi*)". It will be seen that the material at C was not strictly specified as the holotype, but given that an isotype is by definition a duplicate of a holotype (Turland et al., 2018: Art. 9.5), we take this omission in the citation to be an error, and that the effect was to cite the holotype as at C. [We have found no evidence of there having been a duplicate at B, contrary to Madison's citation, Engler & Krause (1908: 106) having clearly cited the Ørsted collection(s) as being at C].

Citing the type of this name in the way Madison did is problematic for several reasons. First, in the protologue, Schott (1858: 179) had cited collections from Candelaria made by Ørsted and by Hoffman (both of which he had had drawn), and thus there were (at least) two syntypes from which a lectotype should have been chosen.

The Hoffmann gathering was numbered *617,* from Candelaria, as noted on Schott's drawings 2271 and 2333 — both examined as digital scans from W — as being deposited at B (also cited with this number and as at B by Engler 1878: 115 & 1879: 263 and Engler & Krause, 1908: 106). The Hoffmann specimens are apparently lost, there is no pre-war photo at F, and no duplicates have been located by us. While the drawings can perhaps be considered part of the original material for the purpose of lectotypification, in this case there is extant syntype material collected by Ørsted, and a lectotype must be chosen from that in preference to lectotypifying with an illustration (Turland et al., 2018: Art. 9.12).

Secondly, it is not at all clear that the Ørsted specimens at C bearing the number *15795* represent a single gathering, indeed it appears to be two. There are three such sheets at C, of which two are annotated as the "holotype" by Madison (and are accessible on-line at http://daim.snm.ku.dk/digitized-type-collection-details-simple?catno=LNR-1281). A third sheet with this number (together with a fourth without a label, filed with the third, neither yet digitized) includes only a leaf, bears no indication of type status, and was merely determined (but in the end not cited) by Madison as *Monstera epipremnoides* (a species which does occur in the region around Candelaria), as was the fourth which also consists of a single leaf. Nevertheless, despite his annotations on the specimens, Madison's published typification simply gave the collection number without specifying or excluding any of the three elements bearing it, and we therefore consider he included all three labelled sheets. In all of them (which are undated), the number *15795* has been added in at some point, in exactly the same manner and hand, clearly long ago. Both the sheets Madison identified in determination slips as the holotype have on the label "Pl. Centroameric. Ørsted. [No. *15795* (inserted)] Aroideae No. 2" and no locality, while the third is identically labelled, i.e. also with that collection number inserted, but for being differentiated as "Aroideae No. 3" and with the locality Candelaria which Schott and everyone since had stated. It may be the case that Ørsted later combined these two collections under one number, and he himself gave no indication that he had collected *Tornelia laniata* anywhere else (Ørsted, 1873: 62), but even then it seems quite unreasonable to consider them as one entity for the purpose of lectotypification, all the more so given it is not clear that they are all of the same taxon. We therefore consider that Madison's type citation cannot be considered an effective (inadvertent) lectotypification to be narrowed down in a second step, because it includes two gatherings, rather than merely two duplicates. Lectotypification is therefore still required.

Thirdly, Schott's drawing of the Ørsted element(s) of *Tornelia laniata* (drawing 2272 — examined as a digital scan from W) consists only of two leaves, and is annotated "In monte Candelaría Herb. Oersted". The depicted leaves bear an extremely strong resemblance (in a plant with variable and

idiosyncratic patterns and degrees of leaf blade fenestration), not to the relatively simple entire-margined perforate leaves on the two sheets of 'Aroideae No. 2', but to the solitary more elaborately perforated and dissected blades in each of 'Aroideae No. 3' and the fourth unlabelled sheet. This provides persuasive evidence that 'Aroideae No. 3' and the fourth sheet were seen by Schott, despite not being annotated by him. The fact of the original differentiation of the specimens as 'Aroideae No. 2' and 'Aroideae No. 3' indicates that these are not duplicates, notwithstanding the later addition of the same collection number, so the question arises whether 'Aroideae No. 2' can be considered a syntype and thus be eligible for designation as a lectotype.

Fourthly, the short description in the protologue of *Tornelia laniata* clearly alludes to a plant with leaves pinnately divided to the midrib, and the more fleshed out description Schott gave in his *Prodromus*, citing only the same collections, includes that the leaves are not only pinnatisect, but also with small fenestrations along the midrib (Schott, 1860: 356) [Note that in this species pinnation may happen as a result of breaking at the margin after the leaf has opened]. This agrees only with 'Aroideae No. 3'. However, in the protologue, Schott made the qualification that the blades are 'usually' pinnately divided, as well as including Hoffmann's syntype which, according to the drawings, had more or less entire-margined, perforated blades like those of 'Aroideae 2'. Hence, allowing 'Aroideae No. 2' to be considered a syntype would not absolutely conflict with the protologue description, even if 'Aroideae No. 3' accords with it better. Given that Schott's drawing connects him with 'Aroideae No. 3' it seems most improbable that he would not also have seen 'Aroideae No. 2'. However, in the end, there is no actual link showing that 'Aroideae No. 2' is a syntype. While it would then appear more logical to lectotypify with 'Aroideae No. 3', we refrain from taking that step until it has been clarified whether plants with that leaf form occur in the Candelaria area which do in fact conform to *Monstera adansonii*, and whether there is isosyntype material in other herbaria. Because *Monstera adansonii* ssp. *laniata* in the current sense is such an enormously widespread and well-known plant, it would be unfortunate to disrupt its nomenclature possibly unnecessarily by designating a lectotype without further investigation.

Additional specimens seen: COSTA RICA: **Alajuela**. Atenas, Río Grande, Balsa de Atenas, ca 3 km southeast of Atenas on the future site of the Escuela Centroamericana de Ganadería, 400 m, 7 July 1975, (Fr.), *J. Utley & B. Utley 2618* (CR); San Carlos, La Tigra, 15 km WNW of Quebrada by air, 1 km W of Jabillos, Disturbed primary forest, 175 m, 29 April 1983, (Fl.), *R. Liesner & E. Judziewicz 15172* (CR, MO); San Carlos, Cutris, 3 km south of Boca de Arenal in remnant forest patch along río San Carlos on Hacienda Boca Arenal, 100 m, 3 June 1986, (Fr.), *B. Hammel 15323* (CR, MO); San Ramón, San Isidro, 1–3 km E of San Ramón coffee fincas,

pasture, and stream, Near Waterfall, 1000 m, 13 April 1983, (Fl.), *R. Liesner 14251* (CR, MO); San Ramón, Santiago, Finca Barranca, Bosque muy húmedo premontano, 900 m, 6 January 1984, (Fl.), *L. Gómez et al., 20762* (CR, MO); San Carlos, La Tigra, 15 km WNW of Quebrada by air, 1 km W of Jabillos, Disturbed primary forest, 175 m, 29 April 1983, (Fl., Fr.), *R. Liesner et al., 15139* (CR, MO); Upala, Bijagua, Evergreen tropical wet forest formations and pastures on eastern slopes of Volcán Miravalles, West of Bijagua, near the río Zapote, 600 m, 11 February 1982, (Fr.), *W. Burger et al., 11663* (CR, MO); San Carlos, Florencia, Directly across the river W of Muelle de San Carlos, 22 km NNE of Quebrada by air, 100 m, 8 April 1983, (Fr.), *R. Liesner 14085* (CR, MO); Upala, Aguas Claras, P.N. Rincón de la Vieja, Sector de Ríos Aguas Verdes, 2 km S aguas arriba del puente, falda NE del Volcán Santa María, 600 m, 12 February 1991, (Fl.), *G. Rivera & C. Dennis 1062* (CR); San Carlos, Fortuna, San Carlos, Fortuna, R. B. Arenal Mundo Aventura, 255 m, 5 March 2004, (Fr.), *A. Rodríguez 8500* (CR); San Carlos, Fortuna, San Carlos, Fortuna, R.B. Arenal Mundo Aventura, 255 m, 18 March 2004, (Fr.), *A. Rodríguez 8557* (CR); San Carlos, Pital, San Carlos, Boca Tapada, Bosque Ancianos, 50 m, 23 May 2004, (Fl.), *D. Solano 1060* (CR); San Carlos, Pital, Cerros Chaparrón, Acompaña D, Mena, 100 m, 8 July 2005, (Fr.), *D. Solano 2596* (CR); Along road between Cañas (Guanacaste) and Upala, 100 m, 25 June 1976, (Infer.), *T. Croat 36382* (MO); Along road between Cañas (Guanacaste) and Upala, 100 m, 25 June 1976, (Fl., Fr.), *T. Croat 36382* (MO); Atenas, Banks of Río Cacao, 800 m, 2 January 1983, (Fl., Fr.), *L. Gómez 19565* (MO); San Carlos, La Fortuna, El Tanque, 9 July 1982, (Fr.), *E. Valerio 61* (USJ); San Carlos, La Fortuna, El Tanque, 10 July 1982, (Fr.), *E. Valerio 62* (USJ), San Carlos, La Fortuna, El Tanque, 10 July 1982, (Fr.), *E. Valerio 63* (USJ); San Carlos, Florencia, San Luis, 280 m, 17 Marzo 2001, (Fr.), C. Trejos, 123 (USJ); Los Chiles; Los Chiles; Río Frio; 40 m, 1 August 1949, (Fr.), *R. Holm & H. Hugh 780* (USJ); Lago Cote, Bosque Aledaño, 800 m, 23 June 1968, (Fr.), *L.A. Fournier et al. 1448* (USJ); San Carlos, La Palmera, Extremo este del Tajo de la comunidad, 200 m, 19 February 2000, (Fr.), *A. Pérez 33* (USJ); Atenas, Concepción, Río Grande, 480 m, 30 May 1981, (Fr.), *E. Valerio s.n* (USJ); Alajuela, Orotina, Coyolar, 170 m, 1 agosto 1982, (Infer.), *R. Ocampo 3885* (CR). **Cartago**. Turrialba, Turrialba, CATIE, Confluencia del Rìo Tuis y el Rìo Reventazòn, 580 m, 15 June 1994, (Fr.), *G. Herrera 7180* (CR); La Unión, San Diego, Z.P. Cerros de La Carpintera, 1800 m, 28 September 2006, (Fr.), *A. Cascante 1586* (CR); Paraíso, Orori, Bosque primario en las faldas del Alto El Jaular, 1400 m, 20 July 1994, (Fl., Fr.), *K. Taylor 209* (CR); Turrialba, Ganadería, 10 July 1965, (Infer.), *T. Croat 257* (MO); Turrialba, Pavones, Cruce a La Suiza, En Plantación de Caña, 600 m, 12 December 1999, (Fr.), *M. Blanco 1009* (USJ); Turrialba, Turrialba, Jardín Botanico del CATIE, 616 m, 26 October 2015, (Fr.), *M. Cedeño 836* (USJ); Turrialba, Turrialba, Jardín Botanico del CATIE, 616 m, 8 December 1981, (Fr.), *E. Valerio 32* (USJ); Turrialba, Turrialba, CATIE, 675 m, 2 May 1951, (Fr.),

J. León 3388 (USJ); Turrialba, 20 July 1984, (Fr.), *C. Helfenberger s.n* (USJ). **Guanacaste**. Liberia, Liberia, P.N. Rincón de la Vieja, Cordillera de Guanacaste, Sendero de la toma de agua, a 3 km de la estación, 1000 m, 17 September 1990, (Fr.), *G. Rivera 601* (CR); Nicoya, San Antonio, P.N. Barra Honda, Península de Nicoya, Los Mesones, cerca de los tanques de captación, 350 m, 21 August 1992, (Fr.), *M. Reyes et al., 8* (CR); Bagaces, Bagaces, 1 km W of Hacienda Palo Verde, 50 m, 10 July 1976, (Infer.), *J. Salomon 2437* (CR, MO); Nicoya, San Antonio, R. B. Lomas de Barbudal, Valle del Tempisque, Estación Barra Honda, Sendero de la Flor, 300 m, 1 July 1994, (Fl., Fr.), *U. Chavarría 987* (CR); Abangares, Sierra, R.B. Monteverde, San Luis valley below comminity, premontane moist forest on Pacific slope, 1000 m, 9 May 1986, (Fr.), *W. Haber & E. Bello 5014* (CR, MO); La Cruz, Santa Elena, Along rìo Cuajiniquil, ca. 1 km SE of Rabo de Mico, 30 m, 24 January 2003, (Infer.), *R. Espinoza et al., 11503* (CR, MO); Santa Cruz, Santa Cruz, Cuenca del Tempisque, Bosque Nacional Diriá, margen del Río Enmedio de la casona a Río arriba, 300 m, 12 June 1998, (Fr.), *U. Chavarría & J. González 1868* (CR, MO); Bagaces, Bagaces, Cuenca del Tempisque, Colecta Lomas Barbudal, Sendero colegio Bagaces, 0 m, 18 July 2000, (Fr.), *G. Vargas & E. Wehncke 2024* (CR, MO); Along stream, ca. 11 km n of La Cruz, 0.5 km west of main road, 75 m, 2 February 1978, (Fl.), *R. Liesner 4840* (CR, MO); Nandayure, Bejuco, Pacífico Norte, Bejuco, Pilas de Bejuco, Finca de Benigno Mayorga, 40 m, 26 July 1994, (Fr.), *A. Estrada & A. Rodríguez 91* (CR, MO); Santa Cruz, Santa Cruz, Bosque Nacional Diría, 126 m, 25 January 2000, (Fr.), *L. Acosta 289* (CR, MO); Bagaces, Bagaces, Ojo de Agua, Papayito, Balas de Cañón, 100 m, 22 August 2000, (Infer.), *L. Acosta 2569* (CR); La Cruz, La Cruz, Cerro El Hacha, Camino a Santa Cecilia, 300 m, 23 March 1992, (Fl.), *R. Espinoza 264* (CR); Santa Cruz, Santa Cruz, Fila Vista del mar, camino a las torres de comunicación, 300 m, 23 September 1996, (Fr.), *J. Gonzáles 1252* (CR, MO); Tilarán, Tronadora, Rio Chiquito, Arenal, Zona Monteverde, 730 m, 3 March 1988, (Fl.), *W. Haber 8256* (CR); Nicoya, San Antonio, Los Mesones, cerca de los tanques de captación, 300 m, 21 August 1992, (Fl.), *M. Reyes 8* (CR); Tilarán, Tierras Morenas, Tierras Morenas, Rio Cabuyo, 685 m, 1 August 1994, (Fl.), *G. Rodríguez 298* (CR); Liberia, Curubandé, P.N. Rincón de la Vieja, sendero hacia el cráter, 1004 m, 1 June 2011, (Fl., Fr.), *L. Vargas 4573* (CR, MO); Bagases, Mogote, P.N. Rincón de la Vieja, colecta camino a San Jorge, 3 km, de la casona Sata María, 400 m, 17 February 1991, (Fr.), *G. Rivera 1149* (CR); Disturbed primary forest and open area along Río Higuerón near agricultural experimentation area near Taboga, 0–100 m, 29 June 1977, (Fl., Fr.), *R. Liesner 2709* (MO); Tilarán, Tronadora, Monteverde, 3.5 km N Santa Elena on road to San Gerardo, 0.5 km N of junction road and Rio Negro, Lower montane wet forest, 1540 m, 20 August 1988, (Fl.), *W. Haber 8619* (CR); Along Río Las Flores (identified on Tierras Morenas quadrangle as "Río Flores") 450 m, 25 January 1985, (Fr.), *M. Grayum 4913* (MO); Abangares, Cuenca del Abangares, Zona Protectora Abangares,

Sector Ecomuseo hasta Río AguasClaras, 300–500 m, 20 June 1997, (Fr.), *U. Chavarría 1737* (MO); Finca La Pacifica along Rio Corobici 13 December 1977, (Infer.), *D. Janzen 10890* (MO); P.N. Rincón de la Vieja, sendero de la toma de agua, a 3 km de la estación 17 September 1990, (Fr.), *G. Rivera 601* (USJ); Guanacaste, Cañas, Porozal, Disturbed primary forest and open area along Río Higuerón near agricultural experimentation area near Taboga, 50 m, 29 June 1977, (Fr.), *R. Liesner et al. 2717* (CR, MO). **Heredia**. Sarapiquí, Puerto Viejo, E.B. La Selva, Finca La Selva, En las parcelas de sucesión, 9 September 1983, (Fr.), *I. Chacón 1339* (CR); Sarapiquí, La Virgen, E.B. La Selva, E.B. La Selva, Along road leading to the reserve, 100 m, 16 August 1987, (Fr.), *J.F Smith & E. Frost 478* (CR); Sarapiquí, Las Horquetas, Along entry road to Finca La Selva, Puerto Viejo de Sarapiquí (from Puerto Viejo-Las Horquetas road), just before La Selva boundary, 5 m, 2 June 1985, (Fr.), *M. Grayum 5322* (CR, MO); Sarapiquí, Puerto Viejo, Near the junction of the Río Puerto Viejo and the Río Sarapiquí, 100 m, 15 July 1980, (Fr.), *B. Hammel 9215* (CR); Sarapiquí, Las Horquetas, Just n of Las Horquetas along road to Puerto Viejo, 40 m, 19 July 1984, (Fr.), *M. Grayum 3563* (CR); Santo Domingo, Tures, Lote y charral por el Río Tures, ca. 1 km al sur de San Francisco de San Isidro de Heredia, 1250 m, 29 March 2004, (Fr.), *B. Hammel 22936* (CR); Sarapiqui, 2 km south of La Virgen on Puerto Viejo-San José road, 14 June 1981, (Fl., Fr.), *B. Hammel 10886* (MO); La Selva Biological Station. 100 m, 20 June 1984, (Fr.), *B. Jacobs 2441* (MO); Sarapiqui, La Selva Biological Station 100 m, 8 June 1983, (Fr.), *I. Chacón 898* (MO); Finca La Selva, 100 m, 4 August 1980, (Fl.), *B. Hammel 9436* (MO); Finca La Selva, 100 m, 23 May 1980, (Fr.), *M. Grayum 2848* (MO); Finca La Selva, 100 m, 19 June 1981, (Fr.), *B. Hammel 10890* (MO); La Selva Biological Station, 100 m, 25 June 1984, (Fl., Fr.), *B. Jacobs 2569* (MO); Near La Selva Biological Station, 100 m, 4 July 1984, (Fr.), *B. Jacobs 2655* (MO); Sarapiquí, La Virgen, Reserva Biológica La Tirimbina, En el parqueo del Lodge, 280 m, 1 July 2013, (Fr.), *J. López 327* (USJ); Heredia, Sarapiquí, Horquetas, Estación Biológica La Selva, 50 m, 3 November 2018, (Fr.), *M. Cedeño & M. Chaves 1495* (USJ); **Limón**. Pococí, Guacimo, Forested area near Guasimo along river, 22 April 1970, (Fr.), *E. Valerio s.n* (CR). **Puntarenas**. Corredores, Corredor, Forests on main ridge and NE slopes of Fila de Cal, between San Vito and Ciudad Neilly, 550 m, 13 September 1985, (Fr.), *M. Grayum et al., 6049* (CR, MO); Montes de Oro, San Isidro, Interamerican Highway km marker 122; patch of forest west of road, 100 m, 4 August 1985, (Fr.), *B. Hammel & J. Trainer 14367* (CR, MO); Golfito, Puerto Jiménez, P.N. Corcovado, Estación Sirena, 5 m, 15 June 1990, (Fl.), *N. Obando 61* (CR); Osa, Palmar, Sitio Arqueológico, Finca 6, Unos 5,5 Km SO en linea recta de Palmar Sur, Camino del portón a los montículos principales, 100 m, 11 October 2011, (Fr.), *A. Quesada et al., 3369* (CR); Garabito, Tárcoles, P.N. Carara. Along Quebrada Bonita, Carara Reserve, 35 m, 25 July 1985, (Fl., Fr.), *M. Grayum et al.,*

5715 (CR, MO); Golfito, Golfito, Along short-cut road to Golfito from Villa Briceño on Interamerican Hwy., W side of Fila Gamba, ca. 6 km from Golfito airport, 80 m, 6 March 1985, (Fr.), *T. Croat & M. Grayum 59904* (CR, MO), Puntarenas, Paquera, Reserva Absoluta Cabo Blanco, Estación Cabo Blanco, Límite de la Reserva, Borde de bosques y potreros, 80 m, 7 November 1991, (Fl., Fr.), *U. Chavarría 320* (CR); Puntarenas, Guacimal, Monte Verde area, valley of Río San Luis just south of Monte Verde; from 1/2 km below waterfall to base of waterfall, 1050 m, 23 June 1985, (Fr.), *B. Hammel & J. Trainer 14016* (CR, MO); Puntarenas, Paquera, P.N. Cabo Blanco, Secondary forest, 30 to 50 years old, 10 m, 30 April 1994, (Fr.), *M. Blanco 2257* (CR); Osa, Sierpe, Valley of Laguna Chocuaco, ca. 9 km W of Rincón de Osa, 200 m, 8 October 1984, (Infer.), *M. Grayum et al., 4074* (CR, MO); Garabito, Tárcoles, P. N. Carara, Cuenca del Tárcoles, Quebrada Bonita sector, 25 m, 11 May 2009, (Fr.), *L. Vargas et al., 3779* (CR, MO); Golfito, Golfito, P.N. Piedras Blancas, 100 m, 6 June 2000, (Fl.), *L. Acosta et al., 1514* (CR); Garabito, Jacó, 7 m, 5 September 2001, (Fr.),*A. Ruíz et al., 545* (CR); Puntarenas, Monteverde, Monteverde, 6 km south of Santa Elena on road to highway, Los Cerros, ridge between Río Guacimal and Río Lagarto, 950 m, 19 July 1991, (Fl., Fr.), *W. Haber & W. Zuchowski 10769* (CR, MO), 8 km N of Barranca, 1 km N of Miramar turn off. W side of km 123 on the Interamerican Hwy. Quebrada Negros, 25 m, 30 April 1983, (Fl.), *R. Liesner et al., 15133* (CR, MO); Puntarenas, Guacimal, R.B. Monteverde, San Luis, Monteverde, Río Guacimal, Bosque húmedo premontano, 700 m, 24 June 1988, (Fl.), *E. Bello et al., 21* (CR); Puntarenas, Paquera, Península de Nicoya, Curú, Río Curú mouth, Pasture on flats W of ranch headquarters, 0 m, 14 August 1995, (Fr.), *A. Sanders et al., 17556* (CR, USJ, MO); Parrita, Parrita, Forest along Río Paquita, 2 m, 13 August 1936, (Infer.), *C. Dodge & V. Goerger 9763* (CR, MO); Curu, 5 November 1986, (Fr.), *R. Soto 3149* (CR); Golfito, Puerto Jiménez. P.N. Corcovado, Sirena, Ollas Trail, 0 m, 28 May 1988, (Fl.), *C. Ketnan et al., 538* (CR); Golfito, Golfito, Refugio Nacional de Fauna Silvestre Golfito, Cerro Nicuesa, 345 m, 7 April 1994, (Fl.), *G. Rivera & G. Herrera 2268* (CR); Golfito, Jiménez, Alrededor de la estación, 20 m, 11 September 1998, (Fr.), *R. Aguilar 5530* (CR, MO); Puntarenas, Lepanto, Reserva Karen Mongense, Sendero al Mirador viejo; colectado a orillas del sendero; 400 m, 9 May 2003, (Fl., Fr.), *E. Alfaro 4342* (CR); Puntarenas, Cóbano, Sendero Central, 17 December 1993, (Fl.), *A. Fernández 1320* (CR); Puntarenas, Lepanto, Jicaral, San Ramón de río Blanco, Cerro Escondido, Bosque alterados remanentes y áreas abiertas, en la cuenca de la Quebrada Pérez, 317 m, 8 May 2003, (Fl., Fr.), *J. Gonzales 3679* (CR), Puntarenas, Cóbano, Estacion San Miguel, ca. 2 km S. de Malpais, 0 m, 18 January 1996, (Fl.), *B. Hammel 20090* (CR); Buenos Aires, Potrero Grande, Bomba de Cedro, por el Río Cabagra, 200 m, 3 March 2000, (Infer.), *B. Hammel 22101* (CR); Golfito, Jiménez, Rio Piro, Playa Carate, 10 m, 15 September 1990, (Fl., Fr.), *G. Herrera*

4298 (CR, MO); Golfito, Jiménez, Estacion Sirena, 1 m, 1 September 1990, (Fl.), *J. Quesada 52* (CR, MO); Between Palmar Sur and Piedras Blancas, 20 m, 28 February 1976, (Fr.), *T. Croat 32915* (MO); La Llorona, 0–200 m, 8 August 1978, (Fr.), *D. Janzen 11043* (MO); Golfito, Jiménez, Estacion Sirena, Sendero Naranjos, 10 m, 27 July 1994, (Fr.), *R. Aguilar 3522* (CR); Aguirre, Quepos, Escuela Finca Palma al lado de Rio Naranjo, 10 m, 26 July 1995, (Fl.), *M. Chavarría 929* (CR, MO); Golfito, Jiménez, Albergue Cerro de Oro, Rio El Nino, 100 m, 18 March 1995, (Fl., Fr.), *E. Fletes 104* (CR); Golfito, Jiménez, Alrededores de la Estacion Sirena, Bosque primario, 10 m, 14 April 1995, (Fr.), *B. Gamboa 152* (CR, MO); Golfito, Jiménez, Rio Claro, 5 m, 6 August 1988, (Fr.), *C. Kernan 784* (CR); Golfito, Jiménez, Quebrada La Ignasia, del puente para el manglar, Finca de Pedro Vaca, 3 m, 20 June 1998, (Fl.), *M. Lobo 224* (CR); Golfito, Jiménez, Estacion Sirena, Recolectado a orilla del Rio Pavo, 10 m, 16 April 1995, (Fl.), *A. Picado 176* (CR, MO); Monte Verde área, valley of Río San Luis just south of Monte Verde, in woods along the river, 1000–1200 m, 18 June 1985, (Fl.), *B. Hammel 13935* (MO); Northeastern slopes of Fila de Cal, 500–620 m, 12 July 1985, (Fl.), *M. Grayum 5649* (MO); Swampy area near Interamerican Highway in vicinity of Piedras Blancas, 28 February 1978, (Infer.), *T. Croat 32954* (MO); Puntarenas, Secondary vegetation on former plantations and pasture, 0–200 m, 1 December 1969, (Fr.), *W. Burger 6657* (MO); Osa Peninsula, 19 August 1984, (Fr.), *A. Gentry 48693* (MO); Monteverde, San Luis river valley below community on Pacific slope, 1000 m, 9 May 1986, (Fl.), *W. Haber 5010* (MO); Canton OSA, along road between Rincón and Boscosa, 50 m, 11 September 1996, (Fr.), *T. Croat 79251* (MO); Buenos Aires, Potrero Grande, Las Vueltas, Centro Turístico Los Chucuacos, 295 m, 25 July 2015, (Fr.), *M. Cedeño 804* (USJ); Puntarenas, Monteverde, Reserva Biológica San Luis, Bosque secundario cercano a la rivera del Río Guacimal, 673 m, 6 December 2013, (Fr.), *P. Juárez et al., 497* (USJ); Reserva Biológica Cabo Blanco, 6 August 1993, (Fr.), *R. Soto s.n* (USJ); Parrita, Plantación vieja de palma africana, 10 m, 20 Enero 2001, (Fr.), *C. Morales 1496* (USJ); Camino del ICE de Santa Cruz a Vista de Mar, 22 July 1985, (Fr.), *H. Pittier 23671* (MO); Puntarenas, At Lindora near Monteverde, 29 September 1970, (Fl.), *H. Kennedy 571* (CR). **San José.** Puriscal, Chires, P.N. La Cangreja, Along Río Negro, E of Santa Rosa, 320 m, 21 July 1988, (Fl.), *M. Grayum et al., 8608* (CR, MO); Alajuelita, San Antonio, Z.P. Cerros de Escazú, Alrededores de Cerro Rabo de Mico, 2200 m, 22 September 1989, (Infer.), *G. Vargas et al., 765* (CR); Playa Dominical, Baru, and Tinamastes (along road to San Isidro del General), 250 m, 20 November 1975, (Fr.), *M. Burger 10165* (CR, MO); Mora, Colón, Z.P. El Rodeo, Reserva de la Universidad para la Paz, 500 m, 28 January 1994, (Fr.), *A. Cascante et al., 198* (CR); Región de El General, 850 m, 1 March 1940, (Fr.), *A. Skutch 4824* (CR); Turrubares, San Juan de Mata, No protegida, Cuenca del Tárcoles, San Luis de Turrubares, finca de Melvin Chavarría, 1200

m, 5 October 2004, (Infer.), *A. Soto 173* (CR); Pérez Zeledón Río Nuevo, R.F. Los Santos, Savegre Abajo, Márgenes del río División, 550 m, 11 November 1998, (Fr.), *A. Estrada et al., 1899* (CR); Mora, Colón, Z.P. El Rodeo, Bosque de la Universidad para la Paz, 1020 m, 13 December 2001, (Fr.), *A. Quesada et al., 925* (CR); Mora, Colón, Z.P. El Rodeo, Finca el Rodeo, camino a la Universidad para la Paz, 500 m, 27 April 1994, (Fl.), *A. Ruíz 440* (CR); Mora, Tabarcia, Zona Protectora Cerros de Escazú, cuenca del río Negro, 2 km en línea recta al noreste de la plaza de Palmichal en remanentes de bosque a la orilla del río, 1283 m, 19 August 2010, (Fr.), *J. Sánchez & R. Chacón 2166* (CR); Pérez Zeledón, Daniel Flores, San Isidro de El General, Repunta, Finca de Miguel Quesada, 700 m, 1 August 1993, (Fl.), *R. Aguilar 2077* (CR); Mora, Colón, Camino a Piedras Negras, sabanas poco antes de llegar al Río Jaris, 500 m, 1 November 2003, (Fr.), *R. Kriebel 4020* (CR); Turrubares, San Juan de Mata, San Pablo de Turrubares, 100 m, 8 December 2004, (Fr.), *D. Santamaría 331* (CR); Along Interamerican Highway, 28 February 1976, (Infer.), *T. Croat 32942* (MO); Puriscal, Along main road between Mercedes Sur and Zapotal, 900 m, 1 January 1985, (Fr.), *M. Grayum 4688* (MO); San José, Carmen, Barrio Escalante, 2 November 1984, (Fr.), *E. Valerio 121* (USJ); Curridabat, Curridabat, Granadilla, 30 August 1980, (Fr.), *E. Valerio s.n* (USJ); Curridabat, Curridabat, Granadilla, 18 September 1984, (Fr.), *E. Valerio 116* (USJ); Curridabat, Curridabat. Granadilla. 28 July 1980, (Fr.), *E. Valerio s.n* (USJ); Mora, Colón, Zona Protectora El Rodeo, Ladera Sur-Oeste de la Fila Diamante, 880 m, 25 October 2011, (Fr.), *L. Ríos 2* (USJ); Montes de Oca, San Pedro, San Pedro, 17 July 1981, (Fr.), *E. Valerio s.n* (USJ).

2. *Monstera alfaroi* Croat & M.Cedeño, *Nordic J. Bot.* 38(12): 2. 2020. — Type: COSTA RICA. San José: Cantón Tarrazú, distrito San Lorenzo, Camino de Tarrazú hacia Quepos, 1386 m, 22 October 2019, (fl.), *M. Cedeño 1702* (holotype, USJ!; isotypes, MO!, PMA!).

Robust nomadic vine with appressed-climbing habit. SEEDLINGS: bearing foliage leaves. JUVENILE PLANTS: root climbers; appressed-climbing; stem dark green, cylindrical or dorsally flattened, with whitish-green pustules making a rough-warty surface; internodes 1–15 cm long, 5–10 mm diam.; peti**oles** partly concealed by the leaf blades or not at all, light green, warty, 3–16 cm long, sheathed to the base of the geniculum; **petiole sheath** deciduous; **blades** not appressed to the phorophyte, ovate-lanceolate, acuminate at the apex, coriaceous, 9–20 × 8–13 cm, **fenestrations** absent. ADULT PLANTS: root climbers; **stem** with black and dark green pustules, cylindrical; **internodes** 1–2 cm long, 2–3 cm diam.; **anchor roots** blackish; **feeder roots** blackish; **petiole** brown or rarely light green at the base, with brown black and white pustules, 40–70 cm long, sheathed along their entire length; **petiole sheath** undulate, persistent or deciduous; geniculum warty throughout, flattened adaxially and transversally convex

abaxially, 2–2.5 cm long; **blades** narrowly ovate, rounded or asymmetric at the base, shortly acuminate at the apex, subcoriaceous, with entire margins and few fenestrations, 60–90 × 30–45 cm, drying dark brown and weakly lustrous, not decurrent on the geniculum; **midrib** concave adaxially, convex abaxially, drying black or yellowish; **primary lateral veins** 8–13 per side, diverging at 50°–70°, impressed adaxially, prominent abaxially; **secondary veins** parallel to the primary lateral veins; **collecting veins** poorly visible; **fenestrations** present (weakly perforated near the midrib); **margins** entire. INFLORESCENCES produced on ascending stems; **peduncle** with green or brown pustules, 20–35 cm long; **spathe** obtuse or acuminate, light green in developing inflorescences, internally white and externally light green at anthesis, 13–20 × 8–14 cm; **spadix** white during development, white or yellowish white at the anthesis, 10–15 cm long, 1.2–2.5 cm diam.; **basal sterile flowers** 4–5 mm long; **fertile flowers** 5–7 mm long; stamens with laminar filaments, 2–7 mm long; anthers 2–2.5 mm long; ovary quadrangular in longitudinal section, ribbed; style hexagonal, 1.2–2.5 mm long, truncate; stigma linear; **berries** with the stylar cap after anthesis white, white-cream when ripe; pulp white; **seeds** black, 3–6 mm long. (**Figures 9 & 10**).

Distribution and habitat: Endemic to Costa Rica. It is distributed in the Pacífico Central, Tarrazú, and south in the Fila Chonta and Fila Costeña, at 1100–1250 m. It occurs in *Premontane rain forest* life zone.

Phenology: In Costa Rica, flowering has been recorded in November, and fruiting in January.

Conservation status: *Monstera alfaroi* is protected in the Parque Internacional de La Amistad.

Comments: This species is a member of sect. *Monstera*. It differs from other Costa Rican species in having light brown petioles with black or white warts throughout their length, and the sheath wavy and warty, then promptly deciduous, as well as leaf blades that are coriaceous and scarcely fenestrated, and inflorescences with the peduncle warty and the spathe light green externally. It is most closely related to *Monstera buseyi* Croat & Grayum, with which it shares tuberculate petioles. Most collections of *Monstera buseyi* differ from *M. alfaroi* in having narrowly ovate-elliptic leaf blades 2–2.5 times longer than wide which dry medium greyish yellow-brown above and much paler (yellowish green) and often matte below, although some collections have blades only 1.7 times longer than wide which dry dark brown. Also, *Monstera buseyi* has flowering spadices only 6–9 cm long and ca. 1 cm diam., versus more than 18 cm long and 2 cm diam. in *M. alfaroi*. Finally, *Monstera buseyi* has peduncles drying matte and smooth or only weakly puberulent-scurfy, whereas those of *M. alfaroi* dry grossly ridged and

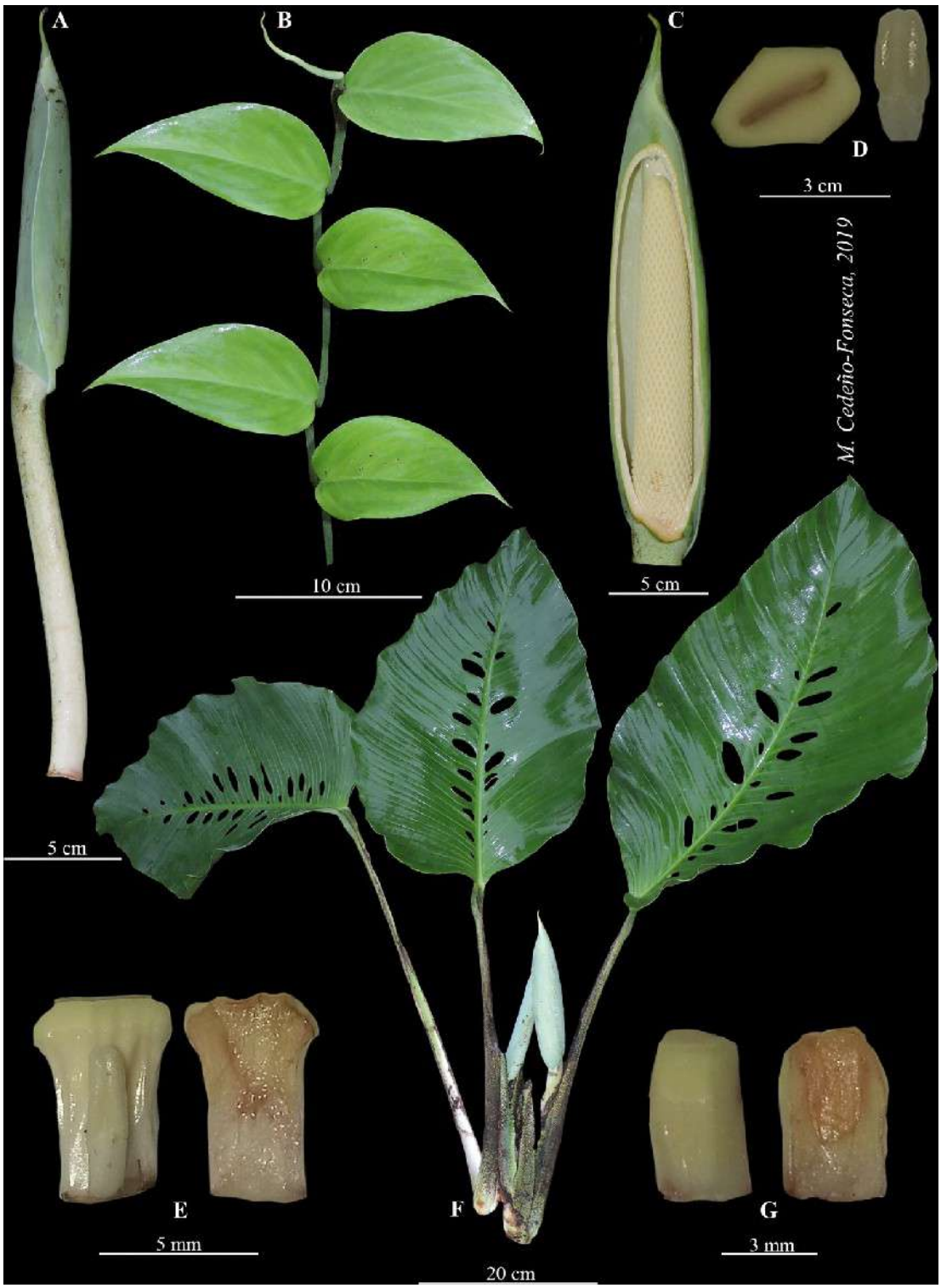

Figure 9. *Monstera alfaroi*. (A) Developing inflorescence. (B) Portion of juvenile plant. (C) Longitudinal cut of the spathe at female anthesis. (D) Stylar plate with stigma (left) and one stamen (right). (E) Fertile flower, in lateral view (left), and longitudinal section (right). (F) Portion of adult plant. (G) Sterile flower, in lateral view (left), and longitudinal section (right). *M. Cedeño 1702* (USJ).

Figure 10. *Monstera alfaroi*. (A) Adult plant in its natural habitat. (B) Leaves of adult plant (up to 190 cm long) with Mick Mittermeier and Marco Cedeño for scale. (C) Detail of petiole base, showing black warts and light brown epidermis (arrow). (D) Cataphyll (left arrow) and prophyll (right arrow), both with black and white pustules and undulate margins. *M. Cedeño 1702* (USJ).

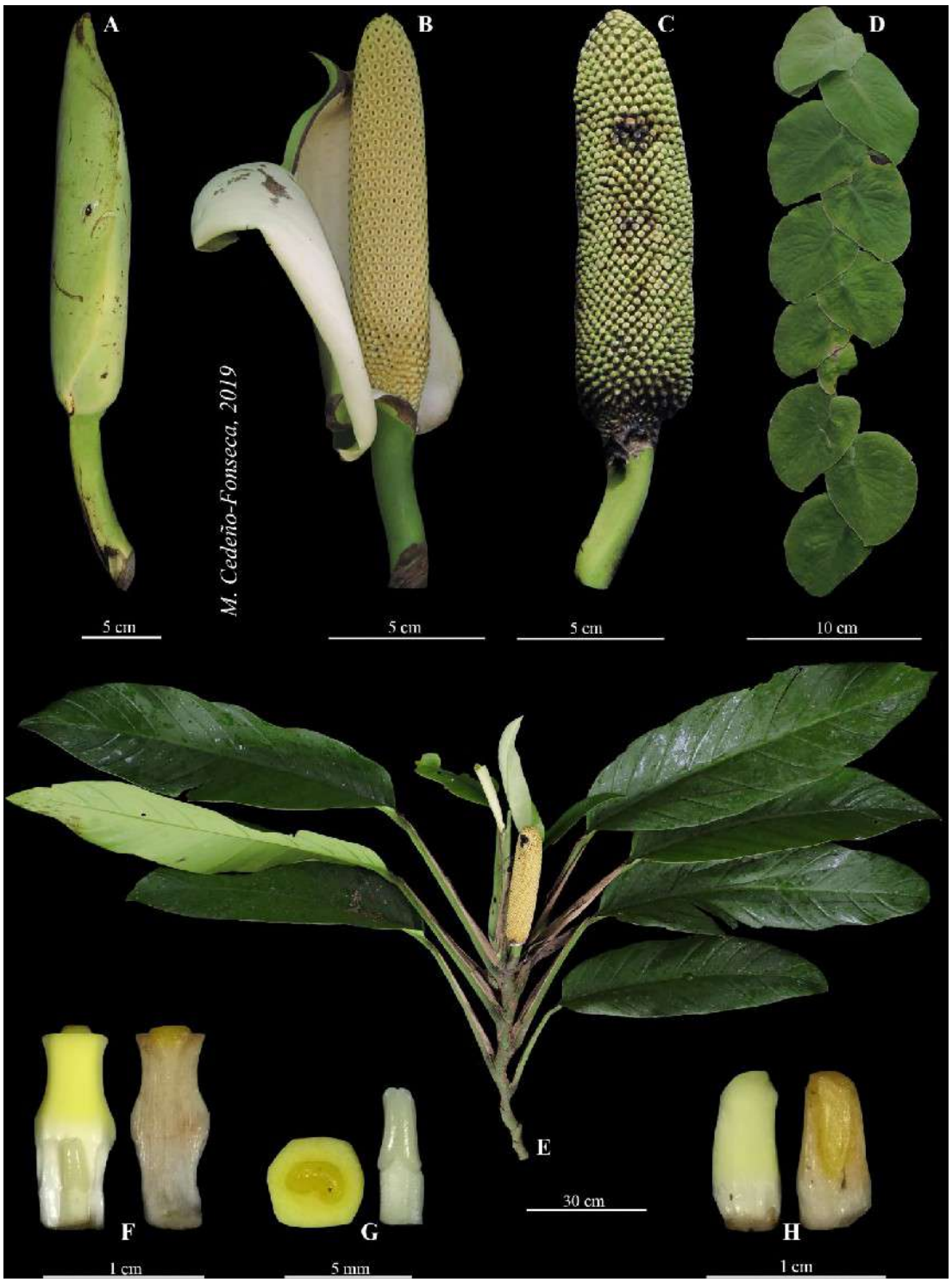

Figure 11. *Monstera anomala*. (A) Developing inflorescence. (B) Open inflorescence, frontal view, with tearing spathe. (C) Immature infructescence. (D) Portion of juvenile plant. (E) Portion of adult plant. (F) Fertile flower, in lateral view (left) and longitudinal section (right). (G) Stylar plate with stigma (left) and one stamen (right). (H) Sterile flower, in lateral view (left) and longitudinal section (right). Golfito, Puntarenas (not collected).

pitted and covered by conspicuous tubercles.

Monstera alfaroi can also be confused with *M. costaricensis* (Engl. & K.Krause) Croat & Grayum, but the latter has petioles with white pustules and markedly wavy and persistent wings, and flowers with markedly conical styles. *Monstera alfaroi* is restricted to the Pacific slope of the Cordillera de Talamanca, while *M. costaricensis* occurs only in the Caribbean lowlands (below 600 m elevation) of Costa Rica.

Additional specimens seen: COSTA RICA: **Puntarenas**. Buenos Aires, Potrero Grande, La Lucha, Punto, 1400–1500 m, 20 February 2018, (Fl.), *D. Santamaría et al., 7036* (MO); Parrita, Parrita, Fila Chonta, 1295 m, 27 November 2003, (Fl.), *A. Quesada 1264* (CR); Parrita; Fila Chonta, camino de San Marcos de Tarrazú a Cerro Cura, La Virgen y Fila Chonta, 1400 m, 31 January 1996, (Fr.), *B. Hammel & J. Morales 21189* (INB, MO). **San José**. Tarrazú, San Lorenzo, Nápoles, Estribaciones al Oeste de Cerro Toro, 1200 m, 30 November 1995, (Fl.), *G. Herrera et al., 8785* (CR); San José, Pérez Zeledón, Fila Costeña, 1100 m, 15 February 1996, (Infer.), B. *Hammel et al.,* 20161 (INB, MO); Cantón de Pérez Zeledón, Cordillera de Talamanca, Las Nubes, Estación Santa Elena, 1240 m, 15 de febrero de 1996, *E. Alfaro 508* (MO).

3. *Monstera anomala* Zuluaga & Croat, *Phytotaxa* 334(1): 2. 2018. — Type: PANAMA. Veraguas: Distrito Santa Fe, corregimiento El Pantano, Parque Nacional Santa Fe, trail between alto Los Gonzales to alto El Viro, 800–1000 m. 16 Jan 2013, *A. Zuluaga, A. Doucette, E. Brantner & E. González 888* (holotype, WIS; isotypes, PMA?, MO!).

Robust nomadic vine, appressed-climbing habit. SEEDLINGS: filiform. JUVENILE PLANTS: root climbers; **stems** light-green, smooth to slightly rough, flattened; **internodes** 3–5 cm long, 3–8 mm diam.; **petiole** distinct, dark-green, smooth, 5–7 mm long, sheathed to the base of the geniculum; **petiole sheath** deciduous; **blades** ovate, cordate at the base, obtuse to short acuminate, coriaceous, 6–9 × 6–8 cm, completely appressed to the phorophyte; **fenestrations** absent. ADULT PLANTS: root climbers; **stems** light green to greyish, slightly rough, cylindrical or slightly flattened, sulcate laterally; **internodes** 1–3.5 cm long, 1–3 cm diam.; **anchor roots** black; **feeder roots** light brown, corky; **petiole** light-green, smooth, sometimes verrucose at the base, 15–50 cm long, sheathed up to the middle of the geniculum; **petiole sheath** deciduous, with fibrous remains; geniculum smooth or pustular, slightly flattened or ribbed adaxially, 2–4.5 cm long; **blades** narrowly lanceolate or lanceolate, oblique, broadly-cuneate to attenuate at the base, acuminate at apex, subcoriaceous to thinly coriaceous, drying grey, brown, yellowish-green or olive-green, 25–55 × 10–25 cm, 2.1–4.2 times longer than wide, slightly decurrent on the geniculum (decurrent part 2–3 mm wide); **midrib** sunken adaxially, convex abaxially, drying yellowish or

blackish on both surfaces; **primary lateral veins** 4–25 per side, obscure adaxially, prominent abaxially, departing midrib at 35–50°, drying yellowish or blackish; **secondary veins** prominent and reticulate towards the margin; **collective veins** slightly visible; **fenestrations** absent; **margins** entire. INFLORESCENCES on ascending stems, 1–2 simultaneously at the flowering season, arranged in the leaf axils; **peduncle** smooth or slightly verrucose, 3–11 cm long, 0.6–1.4 cm diam.; **spathe** obtuse or mucronate, light-green during development, light-green externally and white internally at the anthesis, coriaceous, deciduous after anthesis, 10–20 × 7–10 cm, as long as the spadix; **spadix** green-yellow during development, creamy-yellowish at the anthesis, 10–24 cm long, 2–4 cm diam., 1.7–2.8 times longer than the peduncle; **basal sterile flowers** with a transparent stigmatic secretion, 4–6 mm long; **fertile flowers** 1–2.2 cm long; stamens with laminar filaments, 3–6 mm long; anthers 1.5–2 mm long; ovary quadrangular in longitudinal section, 6–10 × 2.5–5 mm; style thin and elongated at the medial part, distal region pentagonal, 4–6 × 1.5–2.5 mm; stigma linear, with a yellowish stigmatic secretion; **berries** with a yellow stylar cap, greenish during development; pulp white; **seeds** black, spherical, 4–6 mm long. (**Figure 11)**.

Distribution and habitat: From Costa Rica and western Panama. In Costa Rica it is distributed on the Caribbean side from Llanuras de San Carlos to the southern Caribbean near the Continental Division, and on the Pacific slope, North of Fila Costeña, Sierpe and Rincón de Osa, region of Golfo Dulce, at 0–1135 m. It grows in *Premontane rain forest* and *Tropical rain forest* life zones; primary, secondary forests and open areas.

Phenology: In Costa Rica, flowering has been recorded in February and September, and fruiting in May, July, and November.

Conservation status: *Monstera anomala* is protected in the Estación Biológica La Selva, Reserva Biológica La Tirimbina, Reserva Biológica Alberto Manuel Brenes, Parque Nacional Corcovado, El Refugio Nacional de Vida Silvestre Barra del Colorado and Refugio Nacional de Vida Silvestre Golfito.

Comments: The species is a member of sect. *Marcgraviopsis*. It differs from the other species of the genus in Costa Rica in having the petiole sheath deciduous with fibrous residues, the entire and acuminate leaf blade, the thick spathe deciduous after the anthesis, and the style elongate and narrowed in the middle part (the last characteristic is unique among the species of the genus in Costa Rica).

Nomenclatural note: Prior to the description of this species, herbarium material of it had been provisionally annotated with the unpublished name "*Monstera skutchii* Croat & Grayum", but it was subsequently treated by Grayum (2003a) as part of a variable *M. spruceana*

(Schott) Engl. (Zuluaga & Cameron, 2018). See notes under this last species for a comparison between the two.

Additional specimens seen: COSTA RICA: **Cartago**. Turrialba, Chirripó, Along Quebrada Platanillo near confluence of Quebrada Siripi, Platanillo de Chirripó, 1135 m, 2 March 1990, (Infer.), *M. Grayum & R. Hodel 9727* (CR). **Heredia**. Sarapiquí, La Virgen, E.B. La Selva, Finca La Selva, Puerto Viejo de Sarapiquí, Ridge near and of Pasos Perdidos, 120 m, 3 June 1985, (Infer.), *M. Grayum et al., 5356* (CR). **Limón**. Talamanca, Bribri, R.V.S.M. Manzanillo, 20 m, 3 March 2018, (Fl.), *M. Cedeño 1333* (USJ); Talamanca, Telire, Alto Urén, subiendo a Cerro Chum, siguiendo un antiguo camino de Quebrada Chaho a Alto Lari, 800 m, 24 July 1989, (Fr.), *G. Herrera 3330* (CR); Talamanca, Cahuita, Along road between Puerto Viejo de Talamanca and Manzanillo, stretch from Quebrada Ernesto to Manzanillo, 5 m, 3 November 1984, (Fr.), *M. Grayum & P. Sleeper 4352* (CR, MO); Pococí, Colorado, Hills 3 1/2 airline km S of Islas Buena Vista in the Rìo Colorado, 16 airline km SW of Barra del Colorado, Premontane wet forest on low hills, 110 m, 15 September 1986, (Fl.), *G. Davidse & G. Herrera 31269* (CR); Limón, Río Blanco, Las Brisas de Veragua, Propiedad de Veragua Rainforest, Sendero que va del serpentario hacia el Río Victoría, 356 m, 26 May 2011, (Fr.), *A. Cascante et al., 2299* (CR); Pococí, Colorado, R.N.V.S. Barra del Colorado, Forests and pastures between Río Chirripocito and pastures between Río Chirripocito and Río Sardina ("Sardinal" on Chirripó Atlántico quadrangle), 12 m, 21 April 1990, (Infer.), *M. Grayum 9809* (CR); Pococí, Rita, Cuenca Tortuguero-Sierpe, 40 m, 5 February 1988, (Infer.), *M. Grayum 11165* (CR); Limón, Valle de la Estrella, Cuenca del Estrella, Hitoy Cerere, Sendero a los alrededores de la Estación, 90 m, 19 June 1997, (Fr.), *A. Rodríguez & A. Soto 2320* (CR). **Puntarenas**. Golfito, Golfito, R.N.V.S. Golfito, Cabecerass de la quebrada Cañaza, 150 m, 3 March 1994, (Fr.), *G. Herrera & G. Rivera 7004* (CR); Osa, Sierpe, Boca Ganado, Estribaciones de Fila Ganado, 350 m, 24 November 1993, (Fr.), *G. Herrera et al., 6684* (CR); Osa, Sierpe, Along road between Rincón de Osa and Rancho Quemado and Rancho Quemado, ca. 10 km W of Rincón-Pto. Jimenez Road, 175 m, 3 March 1985, (Infer.), *T. Croat & M. Grayum 59783* (CR); Osa, Sierpe, Along road between Rincón de Osa and Rancho Quemado, ca. 10 km W of Rincón-Pto. Jiménez Road, 180 m, 3 March 1985, (Infer.), *T. Croat 59755* (CR, MO); Golfito, Golfito, Cuenca del Coto Colorado, 60 m, 10 September 1996, (Infer.), *T. Croat 67585* (CR); Osa, Sierpe, Cuenca Térraba-Sierpe, 10 m, 13 November 2002, (Infer.), *T. Croat 79200* (CR); Osa, Bahía Ballena, Ballena, 200 m, 22 January 1997, (Fr.), *J. Gonzáles 2324* (CR); Rincón de Osa; along ridge between Quebrada Aparicio and Quebrada Aguabuena, 200–400 m, 7 October 1984, (Fl.), *M. Grayum 4015* (MO). **San José**. Pérez Zeledón, Río Nuevo, Savegre Abajo de Río Nuevo, Cerro El Zoncho, 900 m, 11 February 1999, (Fl.), *A. Estrada et al., 2043* (CR).

4. *Monstera buseyi* Croat & Grayum, *Phytologia* 82: 38. 1997. — Type: COSTA RICA. Heredia: between Río Peje and Río Sardinalito, Atlantic slope of Volcán Barva. 8 April 1986. *M.H. Grayum 6877* (holotype, MO!; isotypes, B!, CR!).

Robust nomadic vine, appressed-climbing habit. SEEDLINGS: bearing foliage leaves. JUVENILE PLANTS: root climbers; stems rough-pustular at apex (with black pustules), green, cylindrical or slightly flattened; inter**nodes** 2–4 cm long, 1–1.5 cm diam.; **petiole** distinct, light-green, rough-pustular with black pustules at the base, 12–15 cm long, sheathed to the base of the geniculum; **petiole sheath** semi-persistent; **blades** lanceolate, truncate at the base, acuminate at apex, thinly coriaceous, 7–14 × 6–9 cm, not appressed to the phorophyte; **fenestrations** absent or present. ADULT PLANTS: root climbers; **stems** green, brown or grey, rough-pustular on leafy parts (with black pustules), cylindrical or slightly flattened; **internodes** 5–20 cm long, 1.0–3.0 cm diam.; **cataphylls** deciduous or marcescent, light-green with a very reduced blade, black-pustular at the base; **anchor roots** black; **feeder roots** grey and corky; **petioles** light-green, covered with black pustules along their entire length, rough-verrucose mainly at the base, white-cream to pale pinkish internally, 20–75 cm long, sheathed 7–10 cm before the base of the geniculum; **petiole sheath** semi-persistent; geniculum rough-verrucose, slightly ribbed adaxially and convex abaxially, 3–4 cm long; **unsheathed portion** flattened adaxially and convex abaxially; **blades** ovate to lanceolate-ovate or elliptic, broadly cuneate to truncate at the base, acuminate at apex, thinly coriaceous to sub-coriaceous, drying grey, blackish or olive-green (scarcely yellowish-green), 27–75 × 11–33 cm, (1.5)1.7–2.2 times longer than wide, decurrent-undulate over the geniculum (4–8 undulations of 1–4 mm wide), **midrib** slightly ribbed adaxially, convex abaxially, drying black or yellowish on both surfaces, **primary lateral veins** 35–65 per side, bifurcated or trifurcated, strongly sunken adaxially, prominent abaxially, departing midrib at 85–90°, drying black or yellowish; **secondary veins** prominent and reticulate; **collective veins** visible in blades with entire margins; **fenestrations** absent or present, arranged in a single series along the midrib when present; **margins** entire or pinnatilobed with 2–5 lobes per side. INFLORESCENCES on ascending stems, 1–3 simultaneously at flowering season, arranged in the leaf axils or into cataphylls; **peduncle** smooth or scarcely pustular, 17–30 cm long; 1–2 cm diam.; **spathe** short or long acuminate, light green to pruinose during development, white internally and cream-yellowish externally at the anthesis, 7–22 × 10–13 cm, equal or 4 cm longer than the spadix; **spadix** white during development, cream-white at the anthesis, 6–20 cm long, 1.5–2 cm diam., (5.1)6–8(9.1) times longer than wide; **basal sterile flowers** 3–5 mm long; **fertile flowers** 5–7 mm long; stamen with laminar filaments, 1.2–7 mm long; anthers 1.5–2 mm long; ovary sub-conical in longitudinal section, 3.5–5 × 2–2.5 mm; style pentagonal or hexagonal, 1.2–2.0 × 4–5 mm; stigma linear,

sunken on the top surface of the style; **berries** with a cream stylar cap, light-green during development; pulp white; **seeds** black, spherical, 5–7 mm long. (**Figures 12 & 13**).

Distribution and habitat: From Costa Rica and western Panama. In Costa Rica it is distributed on the Caribbean slope, near the continental division, Cordilleras de Guanacaste, de Tilarán and Central, and on the Pacific slope, south of Río Grande de Tárcoles and Punta Burica, at 30−1450 m. It occurs in *Tropical wet forest* and *Premontane wet forest* life zones; primary forests.

Phenology: In Costa Rica, flowering has been recorded from January to July and November to December, and fruiting in March to November.

Conservation status: *Monstera buseyi* is protected in the Reserva Biológica Alberto Manuel Brenes, Reserva Biológica del Bosque Nuboso Monteverde, Parque Nacional Rincón de la Vieja, Parque Nacional Guanacaste, Parque Nacional Braulio Carrillo and Refugio Nacional de Vida Silvestre Golfito.

Comments: The species is a member of sect. *Monstera*. It differs from other species in Costa Rica, in having the asperous-verrucate petioles with black pustules at the base, and the blade with numerous primary lateral veins, bifurcated and trifurcated from their bases. These features are shared with *Monstera costaricensis* of the Caribbean slope, which is distinguished by its markedly wavy petiole sheaths and the leaf without bifurcated veins.

It can also be confused with *Monstera oreophila*, but the latter has more distant primary lateral venation (1.5–2 vs. 0.5–1 cm) and asperous but not (or only minutely) verrucate petioles. *Monstera buseyi* occurs sympatrically with *M. adansonii* on the southern Pacific side (Osa Peninsula), but differs from it by having numerous primary lateral veins, asperous-verrucate petioles with black pustules at the base and leaves more frequently unperforated.

Monstera buseyi is common in the premontane cloud forests of the Guanacaste and Tilarán cordilleras, at elevations of 400–1300 m, growing on the edges and within primary and secondary forests. The populations of the Osa and Golfito Peninsula are below 400 m.

Additional specimens seen: COSTA RICA: **Alajuela**. San Ramón, Ángeles, R.F. San Ramón, Ca. 10 km west of Lagitos; in forest on ridge and secondary woods along Río San Lorencito, 950 m, 30 May 1986, (Fr.), *B. Hammel et al., 15257* (CR); San Ramón, Ángeles, R.B. Alberto Manuel Brenes. Sendero Volcán Muerto, 800 m, 30 April 1994, (Fr.), *V. Nilsson 456* (CR); San Ramón, Ángeles, R.B. Alberto Manuel Brenes, Sendero La Cascada, 800 m, 29 April 1994, (Fr.), *V. Nilsson 452* (CR); San Carlos, La Tigra, Reserva San Lorenzo de UCR, headwaters of the Río San Lorenzo

below the Fila Volcan Muerte, 1000 m, 14 July 1983, (Fr.), *K. Barringer & G. Herrera 3830* (CR); R.F. San Ramón, Bajos de Jamaical, Bosque tropical lluvioso, 850 m, 10 May 1985, (Fr.), *I. Chacon 1809* (CR); San Ramón, Peñas Blancas, Rio Penas Blancas, Finca de Tomas Guindon, 900 m, 10 March 1989, (Infer.), *E. Bello 761* (CR); San Ramón; Angeles; Along road between San Ramon and Bajo Rodriguez; 12 km NW of Los Angeles; 16 km NW of San Ramon; 1050 m, 3 September 1996, (Fr.), *T. Croat 78879* (CR, MO); Alajuela, Sarapiquí, SW of Cariblanco, canyon of Rio Cariblanco and W slope and summit of ridge Rio Cariblanco and Quebrada Quicuyal, 840 m, 22 January 1986, (Fr.), *M. Grayum 6185* (CR, MO); San Ramón, Angeles, Valley of Rio Peñas Blancas, 850 m, 29 February 1992, (Infer.), *M. Grayum 10200* (CR); San Ramón, Peñas Blancas, Poco Sol, 13 km South Fortuna, 700 m, 20 August 1989, (Fr.), *W. Haber 9345* (CR); Upala, Aguas Claras, Quebrada Provision, 2 Km aguas abajo del sendero hacia Colonia Blanca, 820 m, 19 January 1991, (Fr.), *G. Rivera 996* (CR); Upala, Aguas Claras, Los Zanjos, Quebrada Rancho Grande, falda SE del Volcan Santa Maria, 900 m, 1 March 1991, (Infer.), *G. Rivera 1126* (CR); Upala, Aguas Claras, Colonia Blanca, Quebrada Leiva, 4 Km aguas arriba del límite este del parque, 1000 m, 14 April 1991, (Fr.), *G. Rivera 1252* (CR, MO); San Ramón, Peñas Blancas, Fortuna, El bosque (San Martín, El Burrito), Reserva Biológica Dendrobates, Alrededores de Quebrada Piedrita, 150 m, 12 May 2007, (Fr.), *A. Rodríguez 11116* (CR); Cordillera de Tilarán, Along road between San Ramón and Bajo Rodríguez, 1100 m, 26 September 1987, (Infer.), *T. Croat 68068* (MO); Monteverde Reserve, 900–1150 m, 29 October 1986, (Fr.), *W. Haber 6158* (MO); Finca Los Ensayos, 850 m, 15 August 1977, (Infer.), *T. Croat 43582* (MO); San Ramón, Reserva Biológica Alberto Manuel Brenes, 850 m, 21 Noviembre 1998, (Fl.), *L. Gómez & V. Mora 13154* (USJ); San Ramón, Peñas Blancas, Refugio Aleman, 1005 m, 3 December 2017, (Fl.), *M. Cedeño et al., 1051* (USJ); Guatuso, Cote, Cordillera de Tilarán, 5 km al norte del Lago Arenal, Alrededores del lago Coter, 900 m, 14 October 1994, (Fr.), A. *Cascante et al., 356* (CR). **Guanacaste**. Liberia, Liberia, P.N. Rincón de la Vieja, Puesto Santa María, del mirador por la fila hasta el sesteo de la danta, de donde se baja hasta el canal, 950 m, 5 March 1988, (Fl.), *G. Herrera 1602* (CR); Tilarán, Quebrada Grande, Río Chiquito, Arenal, Zona de Monteverde, 730 m, 3 March 1988, (Fl.), *W. Haber & E. Bello 8256* (CR); P.N. Guanacaste, Estación Pitilla, 700 m, 7 November 1990, (Fr.), *C. Moraga 146* (CR); Liberia, Mayorga, Estación Cacao, Cerro Cacao, Sendero Arenales, 1100 m, 9 February 1995, (Fl.), *F. Alfaro 40* (CR); Liberia, Mayorga, Estacion Cacao, 1100 m, 28 October 1990, (Fl.), *C. Chávez 315* (CR); Liberia, Mayorga, Estacion Cacao, 1100 m, 21 November 1990, (Fl.), *R. Espinoza 17* (CR); Liberia, Mayorga, Estación Cacao, 1100 m, 23 November 1990, (Fr.), *R. Espinoza 53* (CR); Liberia, Mayorga, Estacion Cacao, 1100 m, 3 June 1990, (Fr.), *M. Zumbado 46* (CR). **Heredia**. Sarapiquí, La Virgen, Area between Río Peje and Río Sardinalito, Atlantic slope of Volcán Barva,

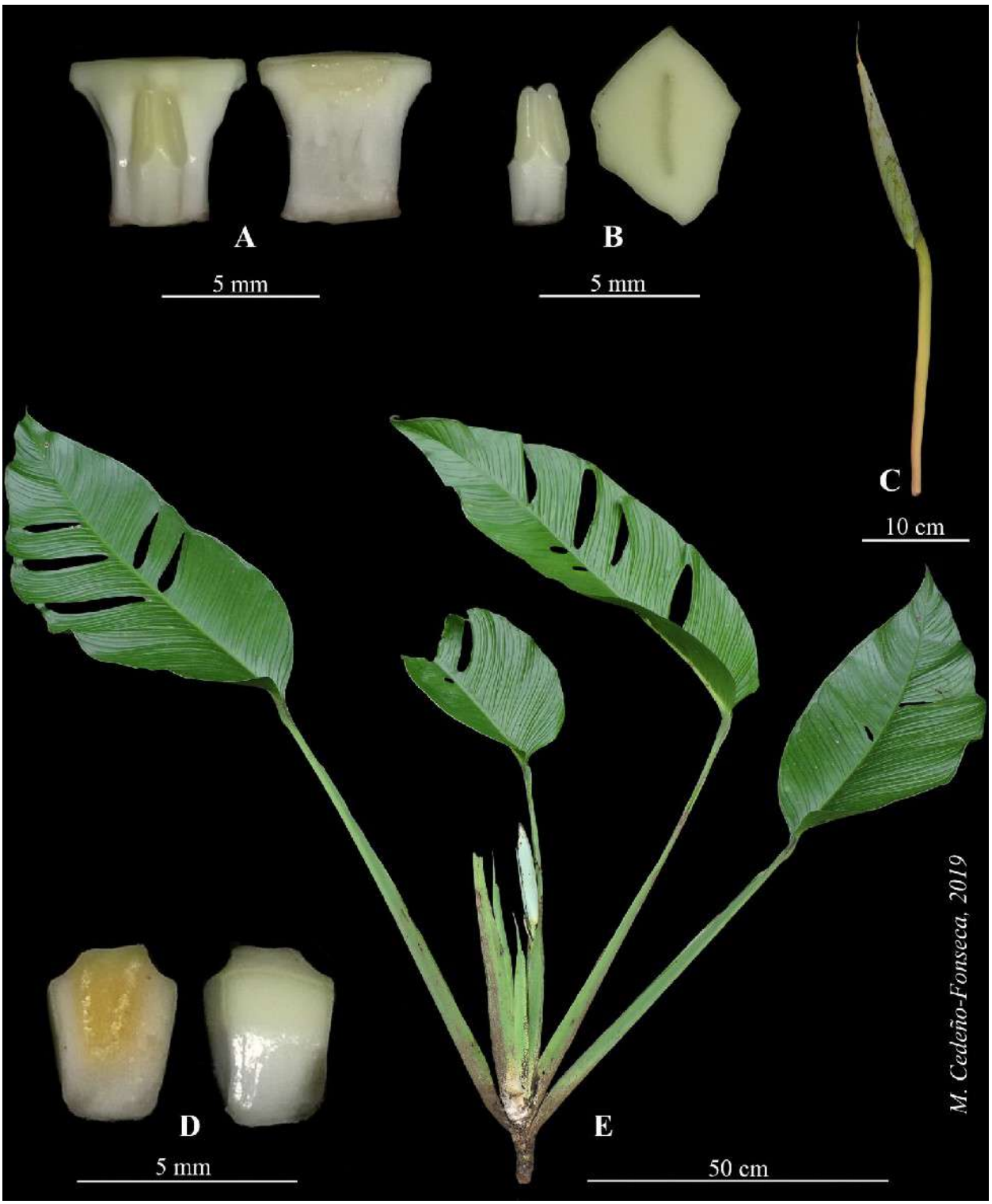

Figure 12. *Monstera buseyi*. (A) Fertile flower, lateral view (left) and longitudinal section (right). (B) One stamen (left) and stylar plate with stigma (right). (C) Developing inflorescence. (D) Sterile flower, longitudinal section (left) and lateral view (right). (E) Portion of adult plant. *M. Cedeño et al. 1052* (USJ)

Figure 13. *Monstera buseyi*. (A) Stem; (*i*) segment with short internodes, <1 cm long; (*ii*) feeder root. (B) Petioles with black warts at the base (arrow). (C) Base of the blade decurrent onto the geniculum and undulate (arrow). (D) Branched primary lateral veins (arrow). *M. Cedeño et al. 1052* (USJ)

Mostly primary forest, 495 m, 8 April 1986, (Infer.), *M. Grayum 6877* (CR); Colonia Virgen del Socorro, Cariblanco, 1000 m, 3 June 1983, (Infer.), *C. Chacón & B. Ocampo 68* (CR). **Limón**. Pococí, Colorado, P.N. Guanacaste, Estación Cacao, Bosque primario y secundario, Orilla Quebrada, bosque primario, 1100 m, 3 June 1990, (Fr.), *U. Chavarría 25* (CR). **Puntarenas**. Osa, Sierpe, about 5 km west of Rincón de Osa, 50 m, 9 January 1970, (Infer.), *W. Burger & R. Liesner 7327* (CR); Osa, Sierpe, Forested area near the airfield about 4 miles west of Rincón de Osa, 30 m, 4 June 1968, (Fr.), *W. Burger & R. Stolze 5430* (CR); Golfito, Golfito, R.N.V.S. Golfito, Cabeceras de la quebrada Cañaza, 150 m, 3 March 1994, (Fl.), *G. Herrera & G. Rivera 7005* (CR); Golfito, Jiménez, Sirena, Los Patos Forest, 1 m, 26 May 1989, (Infer.), *C. Kernan 1118* (CR); Osa, Sierpe, Along road between Rincón de Osa and Rancho Quemado, (Valley of Rìo Chocuaco). Ca. 6 km W of main Rincòn-Pto Jiménez road, 40 m, 2 March 1985, (Fr.), *T. Croat & M. Grayum 59744* (CR, MO); Osa, Sierpe, Rancho Quemado, parte plana, 300 m, 16 December 1991, (Infer.), *R. Aguilar 757* (CR); Osa, Sierpe, Vicinity of Boscosa, at Quebrada Aguabuena, 100 m, 11 September 1996, (Infer.), *T. Croat 79233* (MO); Garabito, Tárcoles, Along N Fork (known locally as 'Quebrada Mona') of Quebrada Bonita, 35 m, 11 June 1986, (Fr.), *M. Grayum 7594* (CR, MO); Golfito, Golfito, Along steep carril ascending W slope of Fila Gamba, ca. 0.5 km NE of jct. of Quebrada Gamba and Q. Rancho, 100 m, 30 January 1992, (Fr.), *M. Grayum 10079* (CR, MO); Osa, Sierpe, El Campo, Subiendo por la fila entre Aguabuena y Baneguitas, cuenca superior de Quebrada Banegas, 100 m, 14 January 1991, (Infer.), *G. Herrera 4823* (CR); Osa, Sierpe, Agua Buena, en ladera boscosa al norte de BOSCOSA, subiendo hacia la Fila Casa Loma, 15 m, 25 August 1990, (Fr.), *C. Morales 96* (CR); Osa, Sierpe, Osa, Rancho Quemado, 200 m, 31 December 2004, (Fl.), *D. Santamaría 442* (CR); Osa, Puerto Jiménez, Camino a la toma de agua, Rancho Quemado, Rincón, Bosque Primario, 200 m, 20 June 1905, (Fl.), *F. Quesada 265* (CR); Along Quebrada Bonita, 35–80 m, 25 July 1985, (Fr.), *M. Grayum 5722* (MO); Osa, Slopes above Airport, Disturbed primary forest, Rincon de Osa, 20–300 m, 11 February 1974, (Fr.), *R. Liesner 2052* (MO); Osa, Rincón de Osa, Streams and slopes adjacent to airfield, 20–200 m, 6 February 1974, (Infer.), *R. Liesner 1746* (MO); Hills above Palmar Norte, 100–200 m, 20 May 1976, (Fr.), *T. Croat 35125* (MO). **San José**. Vazquez de Coronado, Dulce Nombre de Jesús, P.N. Braulio Carrillo, Between Bajo de La Hondura and Alto La Palma, 1450 m, 19 July 1983, (Fr.), *K. Barringer et al., 4003* (CR); Perez Zeledón, Barú, Tinamaste, Finca de los Suizos, 650 m, 14 April 1999, (Fr.), *A. Estrada 2140* (CR); Perez Zeledón, Barú, Tinamaste, Faldas de Fila Tinamaste, Finca de los Suizos, 650 m, 19 August 1998, (Fr.), *O. Valverde et al., 1090* (CR); Turrubares, San Juan de Mata, Ca. 3 km NE of Bijagual de Turrubares, Western part of Montanas Jamaica, 500 m, 7 August 1985, (Fr.), *M. Grayum 5840* (CR); Aserrí, Legua, Quebrada Lajas, ca. 2.5 km al noroeste de Altos el Aguacate, 850 m, 24 September 2003, (Fr.),

R. Kriebel 3962 (CR); Puriscal, Chires, San Martin de Puriscal, bosque primario remanente en la Fila Vara Blanca, cabecera de Rio Negro, limite NW Cangreja, 800 m, 21 April 1995, (Fr.), *J. Morales 3905* (CR); Puriscal, Chires, San Martin de Puriscal, bosque primario remanente en la Fila Vara Blanca, cabecera de Rio Negro, limite NW Cangreja, 29 December 1985, (Fl.), *J. Morales 3713* (CR); Turrubares, San Luis, San Luis de Turrubares, finca de Melvin Chavarría, 1200 m, 5 October 2004, (Fr.), *A. Soto 173* (CR).

5. *Monstera costaricensis* (Engl. & K.Krause) Croat & Grayum, *Ann. Missouri Bot. Gard.* 74: 659. 1987. — *Rhodospatha costaricensis* Engl. & K.Krause in Engl., *Pflanzenr.* IV.23B (Heft 37): 95. 1908. — Type: COSTA RICA. [Limón:] Ferme de Boston, Atlantic watershed, 30 m elev., [10°01' N, 83°15'30"W], August 1901, *A. Tonduz 14628* (holotype, B!, photo F!).

Robust nomadic vine, appressed-climbing habit. SEEDLINGS: bearing foliage leaves. JUVENILE PLANTS: root climbers; **stems** dark green with greenish-white pustules which forming a rough-verrucose surface, cylindrical or dorsally flattened; **internodes** 3–13 cm long, 3–10 mm diam.; **petiole** distinct, light-green, rough, 5–13 cm long, sheathed to the base of the geniculum; **petiole sheath** deciduous; **blades** lanceolate, truncate or attenuate at the base, acuminate at apex, thinly coriaceous, 8–18 × 4–9 cm, not appressed to the phorophyte; **fenestrations** absent. ADULT PLANTS: root climbers; **stems** dark green with greenish-white pustules which forming a rough-verrucose surface, dorsally flattened; **internodes** 2–3 cm long, 2–3.5 cm diam.; **cataphylls** with thick-undulate margins, dark green with green or white pustules, marcescent; **anchor roots** greyish; **feeder roots** black; **petiole** dark green with greenish-white pustules along their entire length, rough-verrucose, 30–70 cm long, sheathed to the base of the geniculum; **petiole sheath** persistent throughout or from the medial part towards the geniculum, markedly undulate; geniculum rough-verrucose, flattened adaxially, convex abaxially, 2.0–3.5 cm long; **blades** narrowly ovate to lanceolate-ovate, broadly cuneate to truncate at the base, spiral-acuminate at apex, thin coriaceous to coriaceous, drying greyish, blackish or greenish, 40–75 × 15–35 cm, 2–2.7 times longer than wide, slightly decurrent-undulate up to medial part of the geniculum (4–6 undulations of 2–3 mm wide); **midrib** slightly ribbed adaxially, convex abaxially, drying black on both surfaces; **primary lateral veins** 30–55 per side, bifurcated, strongly sunken adaxially, prominent abaxially, departing midrib at 45–65°, drying black or yellowish, **secondary veins** slightly prominent and reticulate; **collective veins** prominent; **fenestrations** absent or present, arranged near midrib; **margins** entire (slightly undulate) pinnatilobed due to tearing of the perforations that extend to the margin, with 2 lobes per side. INFLORESCENCES on ascending stems, 1–3 simultaneously at flowering season, arranged in the leaf axils or into cataphylls; **peduncle** rough-verrucose, 10–17 cm long, 1–1.5 cm diam.;

spathe obtuse or mucronate, light green during development, white internally and cream externally at the anthesis, 9–15 × 8–13 cm, equal or 2 cm longer than the spadix; **spadix** cream during development, green to yellowish at the anthesis, 8–14 cm long, 1.2–2.5 cm diam., (4.1–)6–7(–10.6) times longer than wide; **basal sterile flowers** 3–5 mm long; **fertile flowers** 4–7 mm long; stamens with laminar filaments, 3–7 mm long; anthers 2–2.5 mm long; ovary quadrangular in longitudinal section, ribbed; style hexagonal, thickly conical, 1.2–2.5 mm long; stigma linear; **berries** with a yellow stylar cap during development, mature stylar cap unknown; pulp white; **seeds** ovoid. (**Figures 14 & 15**).

Distribution and habitat: From Nicaragua to Panama. In Costa Rica it is distributed on the Caribbean slope, at 0−600 m. It lives in *Tropical wet forest* life zone; primary and secondary forest, swamp forest, rare in open areas.

Phenology: In Costa Rica, flowering has been recorded from January to March, August and October, and fruiting in April and May.

Conservation status: *Monstera costaricensis* is protected in the Refugio de Vida Silvestre Mixto Gandoca-Manzanillo, la Estación Biológica La Selva, el Refugio Nacional Barra del Colorado and the Reserva Biológica Alberto Manuel Brenes.

Comments: The species is a member of sect. *Monstera*. It is distinguished from other *Monstera* species in Costa Rica by the stem and petiole verrucate with white pustules, the persistent and markedly undulating petiolar sheaths (unique in the genus, but see comment below), and the entire and sparsely fenestrate leaf blade, with the primary lateral veins continue and parallel. Adult individuals are robust and become fertile when they grow on trees with diameters greater than 45 cm. In swampy places at La Selva biological station the plants can grow to maturity on small trees ca. 10 m tall.

Some individuals of *Monstera costaricensis* growing in open areas on the Caribbean slope (e.g. at La Selva and La Tirimbina Biological Reserve) have characteristics intermediate with *M. adansonii*, such as minute white pustules at the base of the petiole, the deciduous petiolar sheath and unwavy petiolar sheaths, numerous primary veins bifurcated or not, white spathe with yellowish spots, and flowers with and without conical style in the same spathe. Such traits suggest that these individuals could represent natural hybrids. These characteristics were also mentioned by Grayum (2003a).

Nomenclatural notes: Some specimens of *Monstera costaricensis* at CR were originally annotated by Croat and Grayum with the unpublished name "*Monstera undulata*", prior to the realisation that this species had already been named in *Rhodospatha*.

Figure 14. *Monstera costaricensis*. (A) Adult plant. (B) Developing infructescence with warty persistent peduncle and cataphylls, with wavy margin (arrow). (C) Persistent warty cataphylls with a wavy margin (left arrow); warty prophyll with a wavy margin (right arrow); warts on both surfaces are white or greenish. (D) Infructescence with pyramidal and conical styles (arrow). *Cedeño et al. 1497* (USJ).

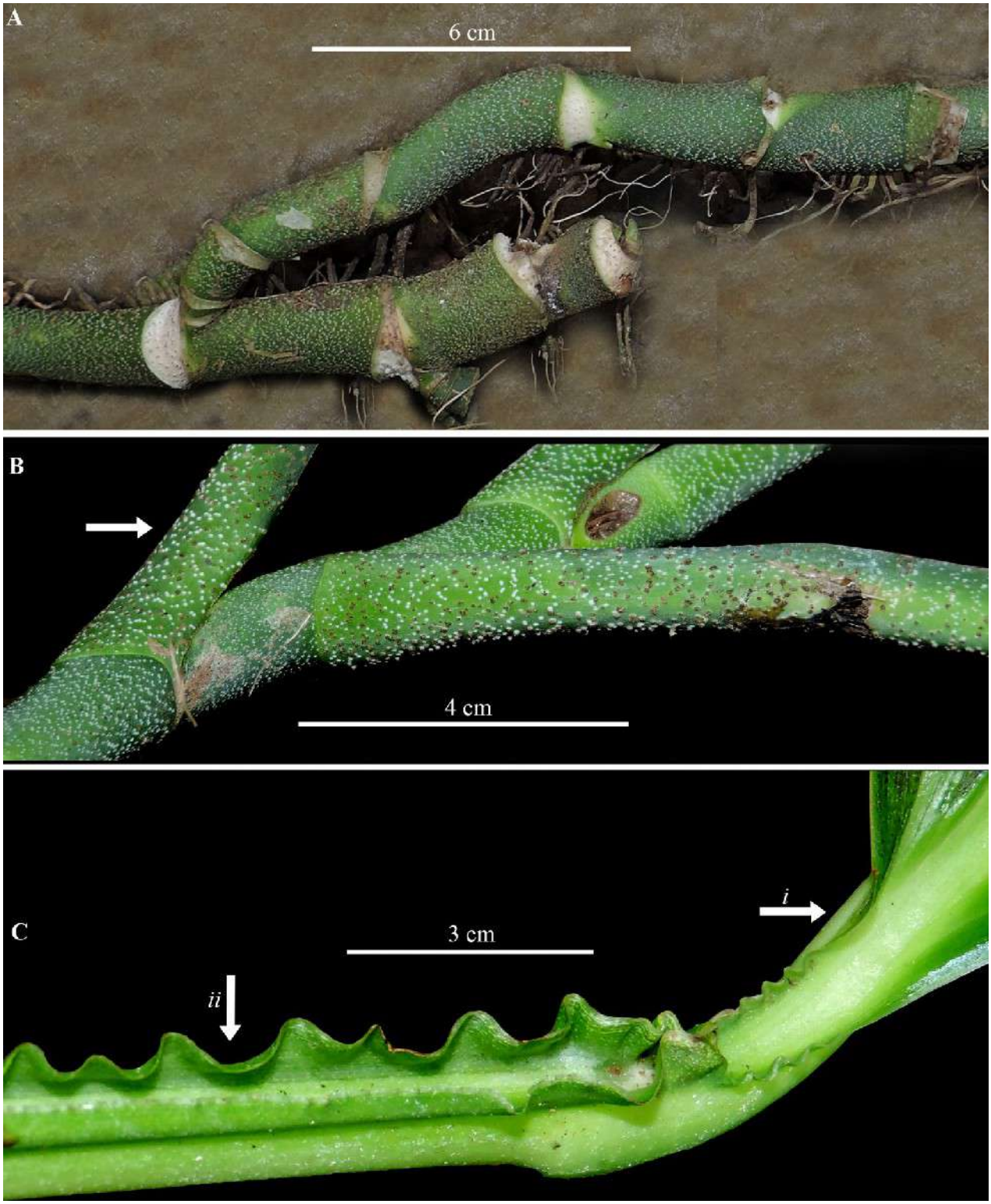

Figure 15. *Monstera costaricensis*. (A) Stem segment with short and long internodes, covered by white warts; leaves removed from the base. (B) Stem segment and petioles with white warts (arrow). (C) Base of the blade decurrent onto the geniculum and slightly wavy (arrow *i*); petiole sheath markedly wavy (arrow *ii*). *Cedeño et al. 1102* (USJ).

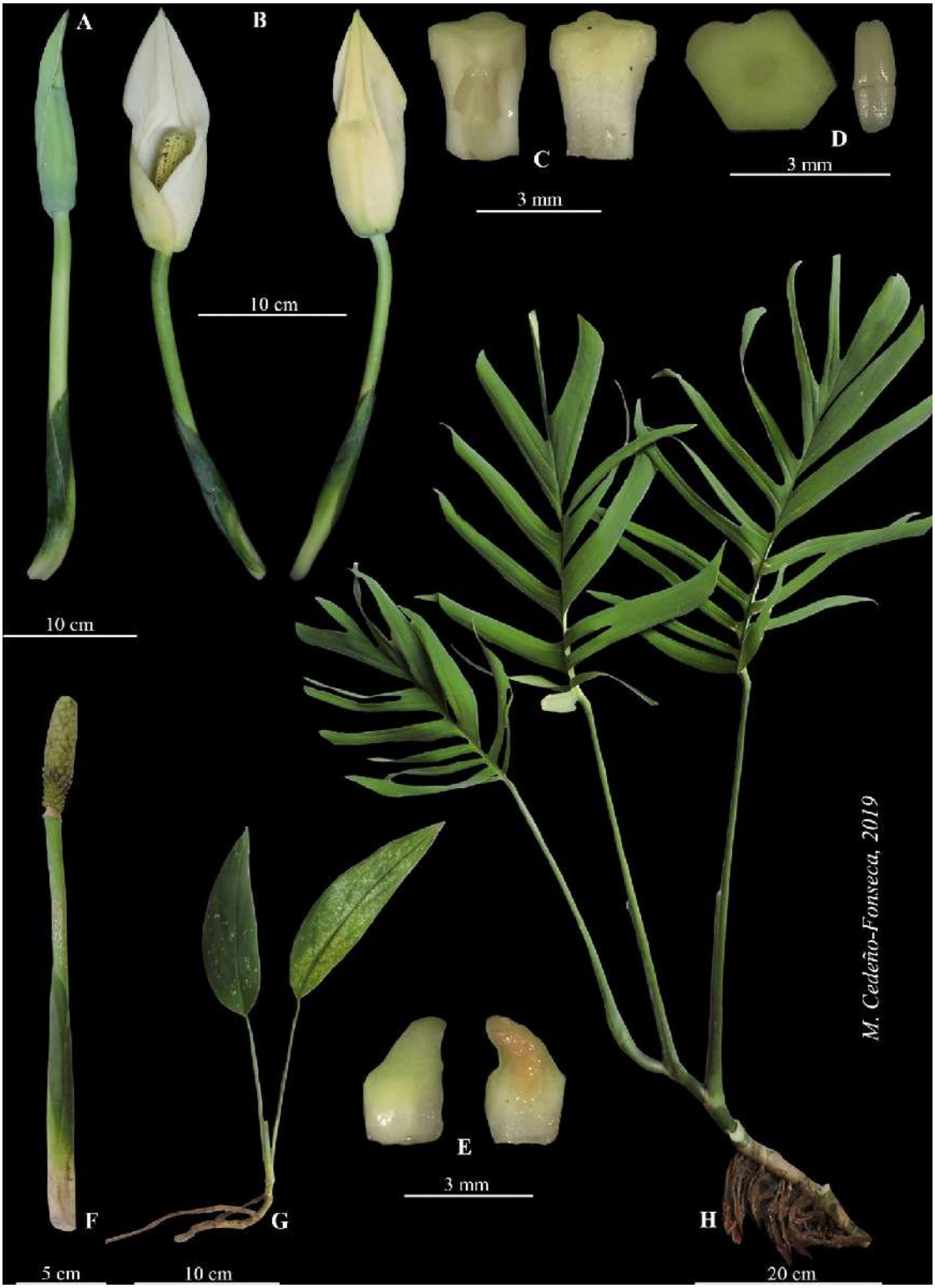

Figure 16. *Monstera croatii*. (A) Developing inflorescence. (B) Front and back views of open inflorescence. (C) Fertile flower in lateral view (left) and in longitudinal section (right). (D) Stylar plate with stigma (left) and one stamen (right). (E) Sterile flower in lateral view (left) and in longitudinal section (right). (F) Infructescence. (G) Juvenile plant. (H) Adult plant. *Cedeño et al. 1624* (USJ).

Figure 17. *Monstera croatii*. (A) Hemi-epiphytic habit, ascending to only 1.5 m above the ground, showing the glaucous leaf colour especially on the youngest leaves. (B) Terrestrial habit, with the same morphology as that of reproductive individuals. (C) Young infructescences with the green stylar layer, conspicuous basal sterile zone, and persistent subtending cataphylls. (D) The base of the glaucous/pruinose petiole and persistent involute petiole sheath (arrow). (E) Part of the petiole completely terete beyond the sheath. (F) Leaf with two primary veins per lobe, sometimes bifid into lobules that divide up to 4 cm away from the costa (arrow). *Cedeño et al. 1624* (USJ).

The supposed isotypes of *Monstera costaricencis* (*Tonduz 14628* at BM and K) do not correspond to *M. costaricensis*, but rather are *Spathiphyllum friedrichsthalii* Schott; however, the holotype at B does indeed correspond to the description of *M. costaricensis*.

Additional specimens seen: COSTA RICA: **Heredia**. Sarapiquí, Las Horquetas, E.B. La Selva, Original forest near the Río Puerto Viejo, about 2 km upstream from the confluence with the Río Sarapiquí, Formerly Finca La Selva "of Holdridge", 100 m, 14 June 1968, (Fr.), *W. Burger & R. Stolze 5780* (CR); Heredia, Sarapiquí, Horquetas, Estación Biológica La Selva, 50 m, 3 November 2018, (Fl., Fr.), *M. Cedeño & M. Chaves 1497* (USJ); Heredia, Sarapiquí, Horquetas, Estación Biológica La Selva, 50 m, 3 November 2018, (Fl., Fr.), *M. Cedeño & M. Chaves 1494* (USJ); Heredia, Sarapiquí, Horquetas, Estación Biológica La Selva, 50 m, 18 November 2018, (Fr.), *M. Cedeño & M. Chaves 1496* (USJ). **Limón**. Río Tercero, 600 m, 2 May 1985, (Fr.), *J. Berrocal 77* (CR); Pococí, Colorado, R.N.V.S. Barra del Colorado, Forests and pastures between Río Chirripocito and pastures between Río Chirripocito and Río Sardina ("Sardinal" on Chirripó Atlántico quadrangle), 12 m, 20 April 1990, (Fr.), *M. Grayum 9779* (CR); Pococí, Roxana, Mata de Limón, (incorrectly identified on Agua Fría quadrangle as Milloncito") ca. 16. 5 km (as the crow flies) NE of Cariari, 21 m, 19 March 1988, (Fl.), *M. Grayum & R. Robles 8523* (CR); Talamanca, Cahuita, Forest between Punta Manzanillo and Punta Mona, E of Manzanillo de Talamanca, 10 m, 2 May 1985, (Fr.), *M. Grayum & G. Schatz 5247* (CR); Talamanca, Sixaola, Finca Asacode, Sendero La Chonta, 5 m, 2 March 1999, (Fl.), *U. Chavarría 1908* (CR); Talamanca, Sixaola, Low-lying coastal swamps and forests, Gandoca (slightly to N of trail from Mata de Limón), 1 m, 27 January 1987, (Fr.), *M. Grayum 8022* (CR); Talamanca, Cahuita, Bosques de Manzanillo, 50 m, 9 January 2017, (Infer.), *M. Cedeño et al., 1102* (USJ); Pococí, Colorado, Lomas de Sierpe, 5 km Noreste de La Aurora, Guápiles, Cerca del Río Sierpe, 30 m, 8 December 1988, (Infer.), *R. Robles 2239* (CR).

6. *Monstera croatii* M.Cedeño & A.Hay, *Webbia* 75(1): 124. 2020. — Type: COSTA RICA. Puntarenas Province, Golfito Canton, Golfito, camino hacia las antenas, 389 m, 4 February 2019 (fr.), *M. Cedeño & A. Hay 1624* (holotype, USJ! [2 sheets]).

Nomadic vine, appressed-climbing habit. SEEDLINGS: bearing foliage leaves. JUVENILE PLANTS: root climbers; terrestrial or with ascending stem; stems dark or light green, smooth, cylindrical; internodes 1–2.4 mm long, 0.5–10 mm diam.; cataphylls light green-pruinose, mucronate, persistent; petiole distinct, dark or light green, smooth, 8–10 cm long, sheathed 3–6 cm long; petiole sheath persistent; unsh**eathed portion** slightly terete or slightly ribbed; **blades** lanceolate, attenuate at the base, acuminate, thinly coriaceous, 10–20 × 4–10 cm, not appressed to the phorophyte; **fenestrations** present or absent, generally one fenestrated

side which breaks at the margin (when present). ADULT PLANTS: root climbers; **stems** dark green or bright beige, cylindrical, **internodes** 1–1.5 cm long, 1.5–2 cm diam.; **anchor** and **feeder roots** light brown; **petioles** light green, smooth and glaucous throughout, 35–45 cm long, sheathed for 20–28 cm; **petiole sheath** persistent and involute; **unsheathed portion** terete and slightly ribbed near geniculum; geniculum slightly terete, sulcate adaxially, 2–2.5 cm long; **blades** oblong-ovate, rounded or asymmetrical at the base, short acuminate at apex, subcoriaceous, 30–45 × 25–33 cm, not decurrent on the geniculum; **midrib** ribbed adaxially, convex abaxially; **primary lateral veins** 8–13 per side, departing midrib at 75–90°, sunken adaxially, prominent abaxially; **secondary veins** parallel; **collective veins** scarcely visible on the margins of each lobe; **fenestrations** absent; **margins** deeply pinnatifid, 6–12 lobes per side with 1–2 veins per lobe, 0.5–2.5 cm wide. INFLORESCENCES on ascending stems, 1–2 simultaneously at flowering time into cataphylls that cover the middle of the peduncle; **peduncle** smooth, 20–25 cm long; **spathe** long acuminate, 2-ribbed, light green during development, cream externally and white internally at anthesis, 9–14 × 3–5 cm, up to 5 cm longer than the spadix; **spadix** white in pre-anthesis and anthesis, 6–8 × 2.5–3 cm in early fruit, the basal zone of basal sterile flowers slender, very conspicuous; **basal sterile flowers** 3–5 mm long, globose and with a very prominent stigmatophore; **fertile flowers** 5–6 mm long; stamens with laminar filaments, 2–5 mm long; anthers 1–2 mm long; ovary quadrangular in longitudinal section, 1.5–3 × 1.5–2 mm; style quadrangular from above, cylindrical, or hexagonal, 0.5–1 × 2–3 mm; stigma linear; **berries** with green stylar cap during development, ripe berries color unknown; pulp unknown; **seeds** unknown. (**Figures 16 & 17**).

Distribution and habitat: Endemic to Costa Rica, where it is known only from the south on the Pacific side in the region of Golfito and the Parque Nacional Corcovado (both in the cantón of Golfito) at ca. 300–600 m. It lives in *Tropical wet forest* life zone; in primary and secondary forest, and in open areas.

Phenology: In Costa Rica, flowering has been recorded in February, and fruiting in October and November.

Conservation status: *Monstera croatii* is protected in the Refugio Nacional de Vida Silvestre Golfito and in the Parque Nacional Corcovado.

Comments: The species is a member of sect. *Monstera*. It is differentiated from all other Costa Rican species of *Monstera* by having pruinose/glaucous stems and petioles, the petioles sheathing for about half their length, with the sheath wings involute and persistent and the free (distal) part terete or only weakly channeled. It is further differentiated by the deeply pinnatifid and bluish green leaf blades, sometimes with bifid lobes, and the

pruinose peduncles with a persistent sheathing mucronate cataphyll. A particularly notable characteristic of this species is its near terrestrial habit, reaching the adult vegetative stage on the ground and climbing only to very limited height before flowering. Fertile terrestrial individuals were not found, but one plant was observed fertile after climbing only 50 cm above ground level with the same stem and leaf morphology as terrestrial examples.

Monstera croatii has basal sterile flowers with the ovary spherical, as is also the case in M. *glaucescens* Croat & Grayum, which too has glaucous stems and briefly sheathed petioles, but that species (known only from the Caribbean side of Costa Rica) has the leaves pinnately lobed (never deeply pinnatifid), the petiolar sheath persistent but not with involute margins, and the non-sheathing part of the petiole channeled (never terete). *Monstera croatii* can also be confused with *Monstera pinnatipartita*, but that species has green or speckled (never glaucous) petioles, never develops to the adult vegetative form on the ground, is fertile only after significantly ascending its phorophyte, and has acuminate and marcescent (not mucronate and persistent) cataphylls.

Additional specimens seen: COSTA RICA: **Puntarenas**. Golfito, Golfito, Camino a las Torres del I.C.E., aprox. 2 Km antes de llegar, 389 m, 29 January 1992, (Fr.), *A. Fernandez 205* (CR, MO); Golfito, Jiménez, Estación Agujas, Cerro Rincón, 600 m, 11 November 1999, (Fl.), *E. Mora 725* (CR); Puntarenas, Golfito, Golfito, Camino hacia las Antenas, 389 m, 4 February 2019, (Fr.), *M. Cedeño & A. Hay 1625* (USJ).

7. *Monstera deliciosa* Liebm., *Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn* 1: 19–20. 1849. — Type: MEXICO. Oaxaca, Western Cordillera, 5000–7000 ft. [1524–2134 m], Dec. 1842, *F.M. Liebmann s.n.* (holotype, C! LNR-1279, examined on-line; Photo: F).

Philodendron pertusum Kunth & C.D.Bouché in Kunth, Index Seminum (Berlin) 1848: 11. 1848. — *Monstera lennea* K.Koch, Bot. Zeit. 10: 277. 1852. [Non *Monstera pertusa* (Roxb.) Schott (1830), i.e. *Rhaphidophora pertusa* (Roxb.) Schott] — Type: cult. Berlin? Potsdam? from plant collected in Guatemala by J. Warszewicz, *K.S. Kunth s.n.* (?holotype, B?✝). — GUATEMALA: Dept. Huehuetenango: Paso del Boquerón, along Río Trapichillo, below La Libertad, 21 Aug 1942, *J.A. Steyermark 51186* (neotype: US! barcode 01322542, seen on-line, designated here). — See notes below.

Philodendron anatomicum [Kunth & C.D.Bouché in Kunth, Index Seminum (Berlin) 1848: 11. 1848 ('*P. anatomica* Hortul.' in synon.)]; J.H.Morsch, Verh. Vereins Beförd. Gartenbaues Konigl. Preuss. Staaten 19: 332. 1849. — Type: GUATEMALA: Dept. Huehuetenango: Paso del Boquerón, along Río Trapichillo, below La Libertad, 21 Aug 1942, *J.A. Steyermark 51186* (neotype: US! barcode

01322542, seen on-line, designated here). — See notes below.

Tornelia fragrans [Gutiérrez ex Schldl., Linnaea 26: 382. 1854 ('1853'), in synon.]; Gutiérrez ex Schott, Gen. Aroid. t. 74. 1858. — Type: MEXICO. *Gutiérrez s.n.?* [or "clonotype" of *Philodendron pertusum* Kunth & C.D. Bouché?] (holotype, W✝, see Riedl & Riedl-Dorn, 1988). — Schott, Gen. Aroid. 1858: t. 74 (lectotype, designated by Cedeño-Fonseca et al., 2020: 40).

Monstera borsigiana K.Koch, Wochenschr. Vereines Beförd. Gartenbaues Königl. Preuss. Staaten 5: 275. 1862. — *Monstera deliciosa* Liebm. var. *borsigiana* (K.Koch) Engl. & K.Krause, Pflanzenr. IV. 23B (Heft 37): 111. 1908. — Type: Cult. hort. Borsig, Moabit, Berlin, 1862, *K. Koch s.n.* (?holotype, B✝); — MEXICO. [Veracruz]: Valle de Cordoba, 20 Jan. 1865 or 1866, *E. Bourgeau 1904* (neotype, G! 4 sheets G00413452 & G00413452a–c, seen as digital scans; isoneotypes: L! L.1421839, MPU! 2 sheets MPU014356 & MPU014357, P! three sheets P02128800, P02128801 & P02128802, US! barcode 01322541, all seen on-line, designated here). — See notes below.

Robust to massive herb, terrestrial or nomadic vine, appressed-climbing habit. SEEDLINGS: bearing foliage leaves. JUVENILE PLANTS: root climbers; **stems** brown to greyish, smooth or warty, cylindrical; **internodes** 7–12 cm long, 1–2 cm diam.; **petiole** distinct, dark green, smooth, 14–17 cm long, sheathed up to half their length; **petiole sheath** semi-deciduous; **blades** ovate to lanceolate, cordate at the base, acuminate, coriaceous, 15–23 × 14–20 cm, not appressed to the phorophyte; **fenestrations** absent. ADULT PLANTS: root climbers; **stems** beige or whitish, smooth, cylindrical, **internodes** 1–9 cm in long, 3–5.5 cm diam.; **anchor roots** whitish; **feeder roots** dark brown; **petiole** light green, warty or smooth, 40–110 cm long, sheathed up to half their length; **petiole sheath** deciduous; **unsheathed portion** flattened and winged adaxially, convex abaxially; geniculum warty, flattened adaxially and convex abaxially, 2–5 cm long; **blades** ovate to lanceolate, cordate to subcordateat the base, acuminate, coriaceous, drying greyish or yellowish, 40–75(–112) × 40–55(–88) cm, 1.0–1.1 times longer than wide, decurrent-undulate over the geniculum, with 4–6 undulations of 5–7 mm wide; **midrib** flattened adaxially, convex abaxially, drying yellowish or blackish on both surfaces; **primary lateral veins** 6–11 per side, prominent on both surfaces, departing midrib at 85–90°, drying yellowish, black or dark brown; **secondary veins** slightly prominent and reticulate; **collective veins** not visible; **fenestrations** round or ovoid, numerous, which extend along the blade and near the midrib; **margins** pinnatilobed, 4–10 lobes per side, sometimes with a vein that runs along the margin which reach the middle of the blade, occasionally marginal fenestrations can break the margin and cause a bifid lobe. INFLORESCENCES on ascending stems, 2–5 simultaneously at flowering time, arranged in the leaf axils or into cataphylls;

peduncle 12–25 cm long, 2.5–3.0 cm diam., tuberculate; **spathe** short acuminate, bluish-green during development, yellowish externally and cream internally with revolute margins and closed (at apex) at the anthesis, deciduous after anthesis, 12–23 × 7–13 cm, up to 5 cm longer than the spadix; **spadix** creamy-yellowish (at both during development and anthesis), 10–20 cm long, 2.5–3 cm diam., 3.4–5.8 times longer than wide; **basal sterile flowers** with a yellow stigmatic secretion, 5–8 mm long; **fertile flowers** 7–10 mm long; stamens with laminar filaments, 1.2–9.5 mm long; anthers 2–2.7 mm long; ovary quadrangular in longitudinal section, ribbed, 5–8 × 5–7 mm; style compressed and hexagonal, 2.5–3 × 4–7 mm; stigmatophore slightly cupuliform, 0.3–0.4 mm long; stigma circular and sunken, with transparent secretion; **berries** with a light green stylar cap during development, mature stylar cap yellowish; pulp white; **seeds** dark green, 5–10 mm long. (**Figures 18 & 19**).

Distribution and habitat: From Mexico (Chiapas, Oaxaca and Veracruz) and Guatemala. In Costa Rica it is not native, but is widely cultivated as an ornamental at 0−2500 m. Apparently it has begun to colonize the forests in some botanical gardens and private reserves.

Phenology: In Costa Rica, flowering has been recorded from February to October, and fruiting during the whole year.

Comments: The species is member of sect. *Tornelia*. It differs from the other species of *Monstera* in Costa Rica by its robust habit, verrucate petiole sheathed to half its length, the sheath deciduous, the free portion adaxially flattened and winged, the coriaceous leaf with the base decurrent and markedly undulate, and with 5–11 fenestrations (of very different sizes) between each pair of primary lateral veins at the widest part of the blade.

Until recently (Cedeño et al., 2020), smaller, often terrestrial plants on cliffs, which grow wild at elevations above 800 m in Costa Rica and Panama, were considered a variant form of *Monstera deliciosa*. However, through detailed documentation of both entities during this work, it was determined that the smaller entity represents a different species (*Monstera tacanaensis*; see comments under that species for a comparison between the two). As a consequence, *Monstera deliciosa* is no longer considered a native species in Costa Rica: its wide distribution in the country is due to its easy propagation, wide tolerance to diverse growing conditions and widespread use as an ornamental plant, as well as its possible naturalization in anthropic environments.

Monstera deliciosa is one of the most cultivated ornamental plants in the world. Its large and attractive, dark and fenestrated leaves, its slow growth, in addition to its wide tolerance to different lighting and humidity environments, make it an excellent plant for indoors in temperate regions, and also for outdoor in tropical and subtropical

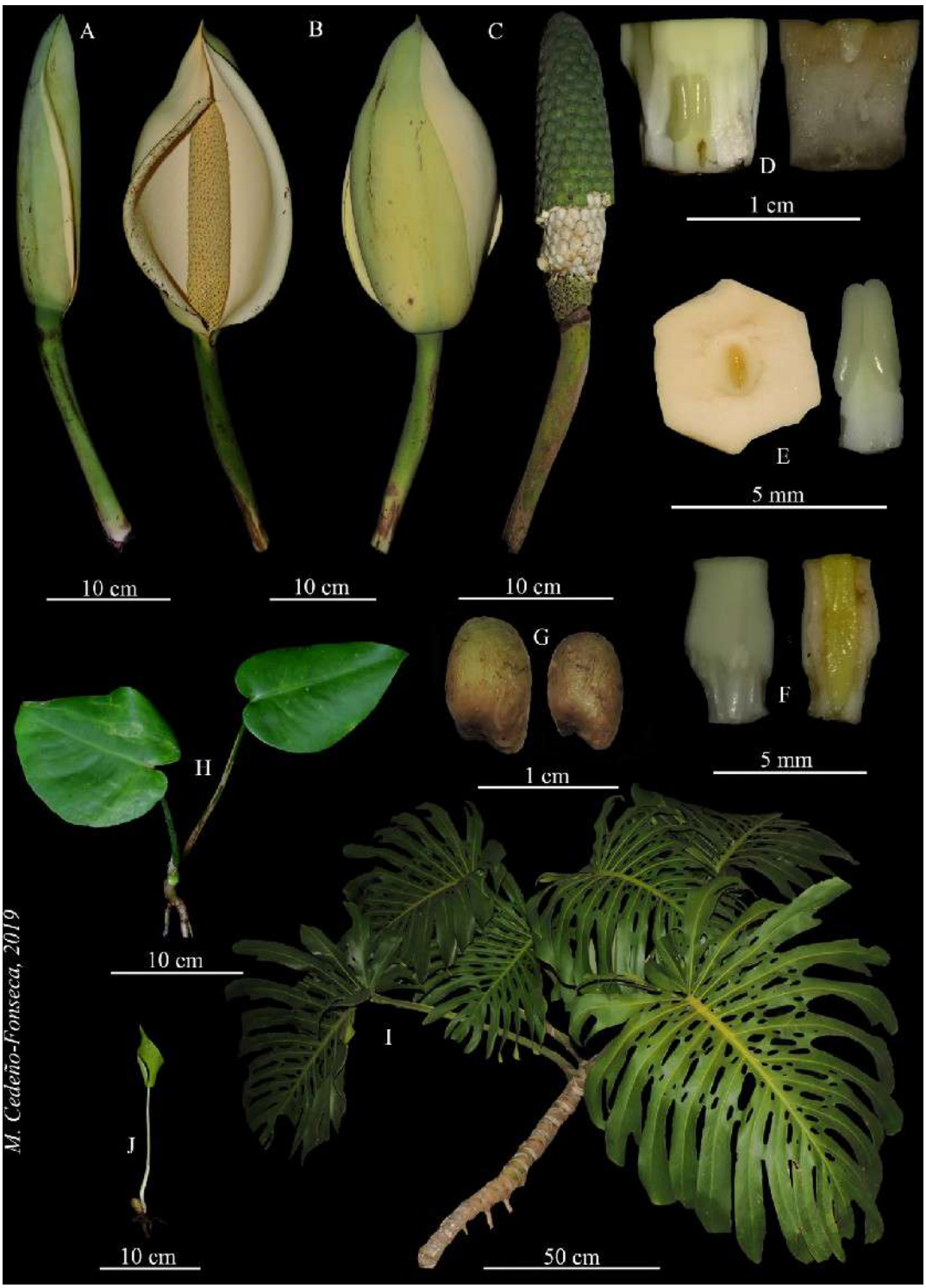

Figure 18. *Monstera deliciosa*. (A) Developing inflorescence; spathe not yet open. (B) Inflorescence with open spathe, front and back views. (C) Mature infructescence, some stylar plates detached. (D) Fertile flower in lateral view (left) and in longitudinal section (right). (E) Stylar plate with stigma (left) and one stamen (right). (F) Sterile flower; lateral view (left) and longitudinal section (right). (G) Seeds. (H) Juvenile plant. (I) Habit of adult plant. (J) Seedling. Lankester Botanical Garden (not collected).

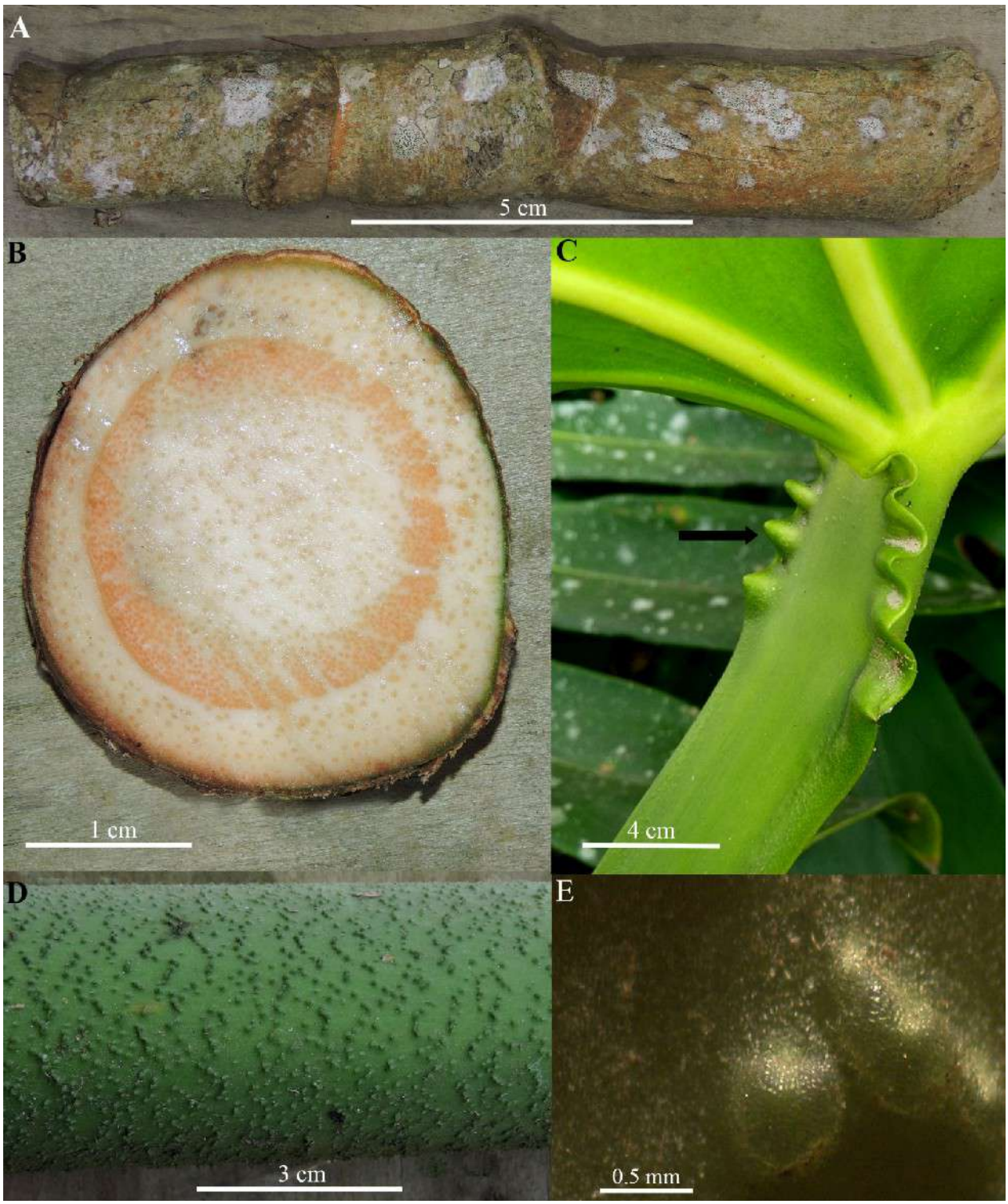

Figure 19. *Monstera deliciosa*. (A) Older stem segment. (B) Stem cross section. (C) Winged distal part of petiole and geniculum, the wings becoming undulate on the geniculum (black arrow). (D) Verrucose petiole segment. (E) Detail of petiole wart. Lankester Botanical Garden (not collected).

areas. In addition, the flavour of its fruits, described as a combination of pineapple and guanabana (soursop), from which one of its common names is derived: "Piñanona" (von Schlechtendal, 1853), has created an interest in its culinary use. In Costa Rica, some villages consume it in smoothies or prepare it as a dessert (Reinaldo Aguilar, pers. comm., 2017). It is occasionally marketed as an exotic fruit in Central America, South America and Europe.

Nomenclatural notes: The nomenclatural history of *Monstera deliciosa* and its synonyms was outlined and discussed recently by Cedeño et al. (2020). Three matters arising from that require some clarification or elaboration.

First, *Philodendron pertusum* Kunth & C.D.Bouché (the epithet is unconnected with *Dracontium pertusum* L., i.e. *Monstera adansonii*) was named in 1848 for the plant introduced to cultivation in Prussia from Guatemala by Józef Warszewicz (1812–1866) and first grown at the royal gardens at Sanssouci, Potsdam (Koch, 1853: 5). It had not at that time flowered (Kunth & C.D.Bouché, loc. cit) which likely explains its being placed in entirely the wrong genus. After seeing a dried flowering specimen [not found], Koch (1852: loc. cit.) realized the plant was a *Monstera* and, because of potential confusion with *Dracontium pertusum* L. and thence *Monstera adansonii* (q.v.) — and of course illegitimacy under today's nomenclatural rules — re-named it *M. lennea* for Peter Joseph Lenné (1789–1866), director-general of the royal Prussian parks and gardens in Potsdam and Berlin. No mention was made of the earlier *Monstera deliciosa* Liebm., so it would appear that Koch was either unaware of it at the time, or thought the Warszewicz plant was a different species: he certainly expressed the latter view later (Koch & Lauche, 1857), and was by then evidently somewhat indignant that Schott, who thought they were the same species, did not acknowledge what Koch considered his priority in naming.

The holotype of *Philodendron pertusum* (and thence of *Monstera lennea*) was cited in Cedeño-Fonseca et al. (2020), following Madison (1977), as a Koch specimen at B, presumed destroyed. It seems more likely, since Koch was not at the Berlin Botanic Garden until the year after *Philodendron pertusum* had been published, that if material had been preserved, it was by Kunth or Bouché. Either way, no type material has been found (nor a photo at F), and the treatment of *Monstera lennea* as a synonym of *M. deliciosa* is largely guided by the opinion of Schott (1854: 15), Engler (1878: 112; 1879: 266), Engler & Krause (1908: 111), and practically everyone since. Koch himself never accepted that *Monstera lennea* was the same as *M. deliciosa*, and one might wonder if his seemingly stubborn refusal was in part that it would have been embarrassing to 'sink' a species named for so important a person in Prussian horticulture as Lenné, and perhaps in part jingoistic since *M. deliciosa* was named by a Dane during the First Schleswig War. Koch & Lauche (1857) had given a detailed

comparison of *Monstera deliciosa* and *M. lennea*, but the characteristics used supposedly to distinguish *M. lennea* fall easily within *M. deliciosa*. *Monstera lennea* was illustrated in Koch & Lauche (1857: t. IV), but although the illustration is compatible with *M. deliciosa*, it is of too poor quality to serve as a neotype. Engler and Engler & Krause (ll.cc) indicated, or at least implied, they had seen a Warszewicz specimen from Guatemala, but if it was at B, it was not photographed by MacBride, as it does not appear amongst the Berlin type photos at F: it was presumably not recognised to be a type since it did not form the direct basis of these names. Warszewicz's personal herbarium is at the Institute of Botany, Jagiellonian University, in Kraków (KRA). It is in principle possible that it includes material of *Monstera deliciosa* he collected in Guatemala, which could potentially serve as a neotype, but an enquiry (by A.H.) has gone unanswered. As none of Warszewicz's specimens at KRA have provenance information, all being labelled "Reliquiae Warszewiczianae, America merid: Columbia. lg. J. Warszewicz" without date or place of gathering (Nobis et al., 2020), we prefer to designate a neotype that definitely accords with the Guatemalan origin of the material introduced to cultivation in Prussia by Warszewicz.

Although the point is largely notional as the name is virtually certain never to return to use, the epithet of *Monstera lennea*, a perfectly acceptable adjectival form in classical Latin, is strictly to be 'corrected' to *lenneana* under Art. 60.8 of the Shenzhen Code (Turland et al., 2018). The well-known name *Philodendron selloum* K.Koch, perhaps less certain to remain in synonymy (of *P. bipinnatifidum* Schott ex Endl.), is another case in point amongst the aroids, as is the currently recognised naturally occurring hybrid *Anthurium* × *selloum* K.Koch of the Lesser Antilles (Acevedo-Rodríguez & Nicolson, 2005: 28), 'corrected' in the International Plant Names Index to *A. selloanum* [cf. the 'correction' of *Furcraea selloa* K.Koch (Asparagaceae) to *F. selloana* by Figueiredo & Smith (2016)]. However, Mabberley (2020) has made a case that this rule affects a considerable number of long-used names and is thus unnecessarily disruptive, and proposed that Art. 60.8 be amended to exclude from correction epithets thus-formed in conformity with classical Latin and with currently acceptable similar usage in geographical epithets. We have therefore persisted with Koch's orthography for now.

Secondly, "*Philodendron anatomica* [sic] Hortul.", apparently a *nomen nudum* in 1848, and the name with which Warszewicz's plant had already been dubbed in cultivation, was included as a synonym in the protologue of *Philodendron pertusum*. Then, in 1849, the same year of publication of *Monstera deliciosa* Liebm., *Philodendron anatomicum* appeared with validating descriptive information in an article by J. Hermann Morsch (1809–1866), royal gardener at Charlottenhof Palace, Potsdam, describing new ornamental introductions, stating it was introduced from Guatemala by Warszewicz in 1847 and sent to the royal gardens at

Potsdam (Morsch, loc. cit.). So, there are three validly published names clearly associated with Warszewicz's introduction cultivated at Potsdam, hitherto with no extant type associated with any of them. It was stated in Cedeño-Fonseca et al. (2020) that *Philodendron anatomicum* was validated by Kunth & Bouché in 1848 (loc. cit.) by virtue of its inclusion as a synonym of *Philodendron pertusum*, but validation of a name is not effected under such a circumstance (Turland et al., 2018: Art. 36.1). However, given that *Philodendron anatomicum* was in fact validated the following year by Morsch (loc. cit.), in the same year of publication as *Monstera deliciosa* Liebm., the former may compete for priority over the latter. Despite considerable bibliographical research, we have been unable to discern when in 1849 publication of each name occurred and hence which does indeed have priority over the other. *Philodendron anatomicum* has never been transferred to *Monstera* and has long been treated as a synonym of *Monstera deliciosa* as if the latter did appear first, so that nomenclatural stability is best served by considering that *M. deliciosa*, universally long-used for such an extremely commonly cultivated plant, was indeed published first. If ever this should be found to be incorrect, there would have to be a conservation proposal to preserve the status quo.

Thirdly, Madison attributed the name *Monstera borsigiana* to Engler (1879: 266). However, Engler (loc. cit. & 1878: 112) had himself clearly attributed it to Koch ex Ender, *Index Aroidearum* (1864: 53), though it was merely listed there. Thus, it appears that Madison, who gave no reasoning, took Engler (1879: 266) to be the first valid publication of the name, and accordingly typified it with the only element Engler had cited (*Bourgeau 1904*, collected in Mexico). Madison cited the (unseen) 'holotype' as at B, whereas Engler (1878: 112 & 1879: 266) had indicated the examined specimen was at Geneva ("Herb. Boissier"), though it was cited as at B in Engler & Krause (1908: 111). It is not among the on-line Berlin type photos at F. Cedeño-Fonseca et al. (2020) correctly stated that Koch had in fact validly published *Monstera borsigiana* long before Engler, in 1862 (Koch, loc. cit.), based on a plant (of unstated origin) cultivated in the spectacular gardens of the long ago demolished Borsig Villa in Moabit, Berlin [which bore the name of the Borsig family of rich industrialists and entrepreneurs, manufacturers of locomotives, armaments and so on, whose business is still in existence]. However, their typification incorrectly followed Madison's, while also inadvertently implying that the cultivated Borsig plant that *Monstera borsiginana* was described from was derived from Bourgeau's collection in Mexico, though that had actually not yet been made, and does not appear to have been accompanied by introduction of living material anywhere. It is of course possible that Koch had preserved a type from the Borsig plant, but none has been found either at B or among the Berlin type photos at F, and neither Engler nor Engler & Krause ever mentioned it, so, we conclude that it is either destroyed or never existed, but Engler may well have been familiar with the living

plant in German cultivation. *Monstera borsigiana* is a name in widespread use at least in horticultural circles (now at varietal level) in the sense in which Madison applied it, and we have accordingly designated the collection cited by Engler (1879: 266), Engler & Krause (1908: 111) and Madison (1977) as the neotype and isoneotypes, citing a somewhat more limited set of duplicates than did Madison, including only those we have located and examined, though it is realized that further isoneotypes in all probability exist. The date of collection is indicated as 20 January 1866 on the G, P and US duplicates, and 20 January 1865 on the L and MPU duplicates.

Additional specimens seen: COSTA RICA: **San José**. Montes de Oca, San Pedro, Ciudad Universitaria Rodrigo Facio [Ornamental], 1200 m, 29 de abril 1982 (Fl., Fr.), *C.E. Valerio 53* (USJ); Curridabat, Curridabat, Granadilla [Ornamental], 1200 m, 18 de septiembre 1984, *C.E. Valerio 115* (USJ); San José, Merced, Villa Colon [Ornamental], 800 m, 19 de mayo 1968 (Fl.), *A Fournier 1421* (USJ); San José, Hospital, La Fuente Peralta, 11 de noviembre 1941 (Infer.), *A. Alfaro 30533* (CR).

8. *Monstera dissecta* [(Schott) N.E.Br. ex Donn.Sm., Enum. Pl. Guatem. 5: 88. 1899, comb. inval.]; (Schott) Croat & Grayum, *Ann. Missouri Bot. Gard.* 74(3): 659. 1987. — *Tornelia dissecta* Schott ('*Fornelia dissecta*'), *Oesterr. Bot. Z.* 8: 179. 1858. — Type: COSTA RICA. [Cartago:] Vulcan de Turialba [sic], 24 March 1857 ('1856'), *H.A. Wendland 500* (holotype, GOET!; ?isotypes, W✝ [fragm.], K *fide* Engler & Krause, 1908: 111, n.v.). — See notes below.

Monstera longipedunculata Matuda, Bol. Soc. Bot. México 14: 22. 1952, **syn. nov.** —Type: BELIZE. Middlesex: Stann Creek, 25 May 1939, *P.H. Gentle 2796A* (holotype, MICH! sheet MICH1115585, seen on-line).

Robust herb, terrestrial or nomadic vine, appressed-climbing or pendent habit. SEEDLINGS: bearing foliage leaves. JUVENILE PLANTS: root climbers; **stems** light brown to beige, smooth, cylindrical; **internodes** 3–4 cm long, 5–10 mm diam.; **petiole** distinct, light green, smooth, 7–10 cm long, sheathed to the base of the geniculum or blade; **petiole sheath** persistent; **blades** ovate to lanceolate, attenuate to subcordate at the base, acuminate, sub-coriaceous, 15–23 × 14–20 cm, not appressed to the phorophyte; **fenestrations** absent or present, only on one side of the blade when present; margins entire or lobed (due to tearing of the fenestrations that extend to the margin). ADULT PLANTS: root climbers; **stems** beige to light brown, smooth, cylindrical; **internodes** 1–3 cm long, 0.8–3 cm diam.; **cataphylls** light-green, deciduous; **anchor roots** light brown; **feeder roots** corky, dark brown; **petiole** light green, smooth, 15–55 cm long, fully sheathed or up to 5 cm long; **petiole sheath** persistent, horizontally open or revolute, fused at apex; geniculum smooth, sunken adaxially, convex abaxially, 1–3 cm long; **blades** ovate to elliptical or oblong, cuneate to rounded or truncate at the base, sub-coriaceous to coriaceous,

obtuse to short-acuminate at apex, drying bright reddish, brownish or greenish, 23–58 × 14–35 cm, (1.3)1.7–1.9(2.0) times longer than wide, decurrent on the geniculum, decurrent portion 3–5 mm wide; **midrib** ribbed adaxially, convex abaxially, drying brownish on both surfaces; **primary lateral veins** 4–20 per side, sunken adaxially, prominent abaxially, departing midrib at 50–65°, drying brownish or reddish; **secondary veins** parallel and prominent abaxially, reticulate towards margins; **collective veins** visible towards lobes; **fenestrations** absent or present; **margins** entire, pinnatilobed or scarcely pinnatifid and then 2–6 lobes per side, the lobes 2–10 cm wide, wider ones perforated and with up to 5 primary veins. INFLORESCENCES on ascending and pendent stems, 1–5 simultaneously at flowering time, arranged in the leaf axils or subtended by cataphylls; **peduncle** smooth, 12–24 cm long; **spathe** acuminate, light green during development, yellowish externally and cream internally at anthesis, with revolute margins and completely open at apex, deciduous after anthesis, scarcely marcescent, 16–24 × 12–15 cm, up to 10 cm longer than spadix; **spadix** creamy-yellowish (at both during development and anthesis), 6–15 cm long, 1.5–3.6 cm diam., 2–5.7 times longer than wide; **basal sterile flowers** 5–7 mm long, with an orange stigmatic secretion; **fertile flowers** 4–7 mm long; stamens with laminar filaments, 1–6.5 mm long; anthers 1.3–2.7 mm long; ovary rectangular in longitudinal section, ribbed, 3–4 × 2–3 mm; style hexagonal, 2–3 × 4–5 mm; stigmatophore cupuliform, 0.4–1 mm long; stigma circular, with a yellowish stigmatic secretion; **berries** with a light-green stylar cap during development, mature stylar cap creamy-yellowish; pulp white; **seeds** black with brown dots, 4–7 mm long. (**Figure 20)**.

Distribution and habitat: From Belize to the west of Panama. In Costa Rica it is distributed on the Caribbean watershed of the Cordilleras de Guanacaste, Tilarán and Central, Llanuras de San Carlos, Llanuras de Tortuguero, Baja Talamanca, and the Pacific slope of the mountain ranges of Guanacaste and Talamanca, at 0−700 (1150) m. It lives in *Tropical wet forest*, *Premontane wet* and *Lower montane rain forest* life zones; primary and secondary forest, and open areas.

Phenology: In Costa Rica, flowering has been recorded from September and November, and fruiting in February, June, July and September to November.

Conservation status: *Monstera dissecta* is protected in the Estación Biológica La Selva, Reserva Biológica La Tirimbina, Reserva Indígena Tayni, Parque Nacional Tortuguero, Parque Nacional Cahuita, Refugio Mixto de Vida Silvestre Gandoca-Manzanillo and Refugio de Vida Silvestre Barra del Colorado.

Comments: The species is a member of sect. *Monstera*. It differs from the other species of the genus in Costa Rica in its persistent and revolute petiolar sheath, its hardly perforated but often pinnatilobed

leaf blade, with a decurrent base, its externally yellowish spathe, and the stigma slightly raised by a cupuliform stigmatophore, with yellowish secretion. It is similar to *M. limitaris* and *M. monteverdensis*, but differs from the latter which has a deciduous petiolar sheath, and pinnatilobed, never-fenestrate leaves, and a light green and externally pruinose spathe. It differs from *Monstera limitaris* which has petioles with brown-dark warts on the base, leaves with pinnatilobed margins, and undulating base decurrent on the geniculum and fenestrations on each side next to the midrib, and the stigma raised by a columnar stigmatophore and with transparent secretion.

Monstera dissecta is highly variable in vegetative morphology and growth form; adult and reproductive plants can have entire and pinnatilobed leaf blades in ascending stems, or have completely entire leaves in ascending and hanging stems. Populations in the southern Caribbean (Gandoca-Manzanillo Mixed Wildlife Refuge) have some individuals with entire leaves and hanging reproductive stems, and others (less frequent) have pinnatilobed leaves in ascending flowering shoots.

Monstera dissecta material collected in Costa Rica had been determined by Madison (1977) as "*M. dilacerata* (K.Koch & Sello) K. Koch", apparently based on misinterpretation of photos of the lost type, which had been made from a sterile a cultivated plant of uncertain geographical origin (Croat & Grayum, 1987; Grayum, 1997). Grayum (1997) and then Boyce (1998) concluded that the name *M. dilacerata* is in fact a synonym of *Epipremnum pinnatum* (L.) Engl., an Asian species (see Grayum & Cedeño-Fonseca 2018 for its neotypification). Grayum (1997) further determined that all Costa Rican material previously identified as *M. dilacerata* represented not only *M. dissecta*, but also *M. glaucescens*, *M. lentii* and *M. pinnatipartita*.

Monstera longipedunculata Matuda, from Belize, is included here as a synonym as it clearly falls within the variation of *M. dissecta*.

Nomenclatural notes: Riedl & Riedl-Dorn (1988), listing Schott's aroid taxa whose associated herbarium material — much of it types — had been destroyed at W at the end of World War II, indicated there had been one sheet of *Tornelia dissecta* present, but with no other detail. Surviving the war is a line drawing of *Tornelia dissecta* (No. 2237, W! seen as a digital scan) executed for Schott by Joseph Seboth (1814–1883). It is in all but one respect an exact and detailed match, including bearing the same notes, with the specimen now at the herbarium of the University of Göttingen (GOET), annotated with the name in Schott's hand, which formed the basis of *Tornelia dissecta* and which is here cited as the holotype (as it was by Croat & Grayum, 1987). However, the one point of mismatch is that the drawing includes a second leaf not now present in the specimen. H.A. Wendland's herbarium now at GOET was unmounted until after 1969 (M. Appelhans, pers.

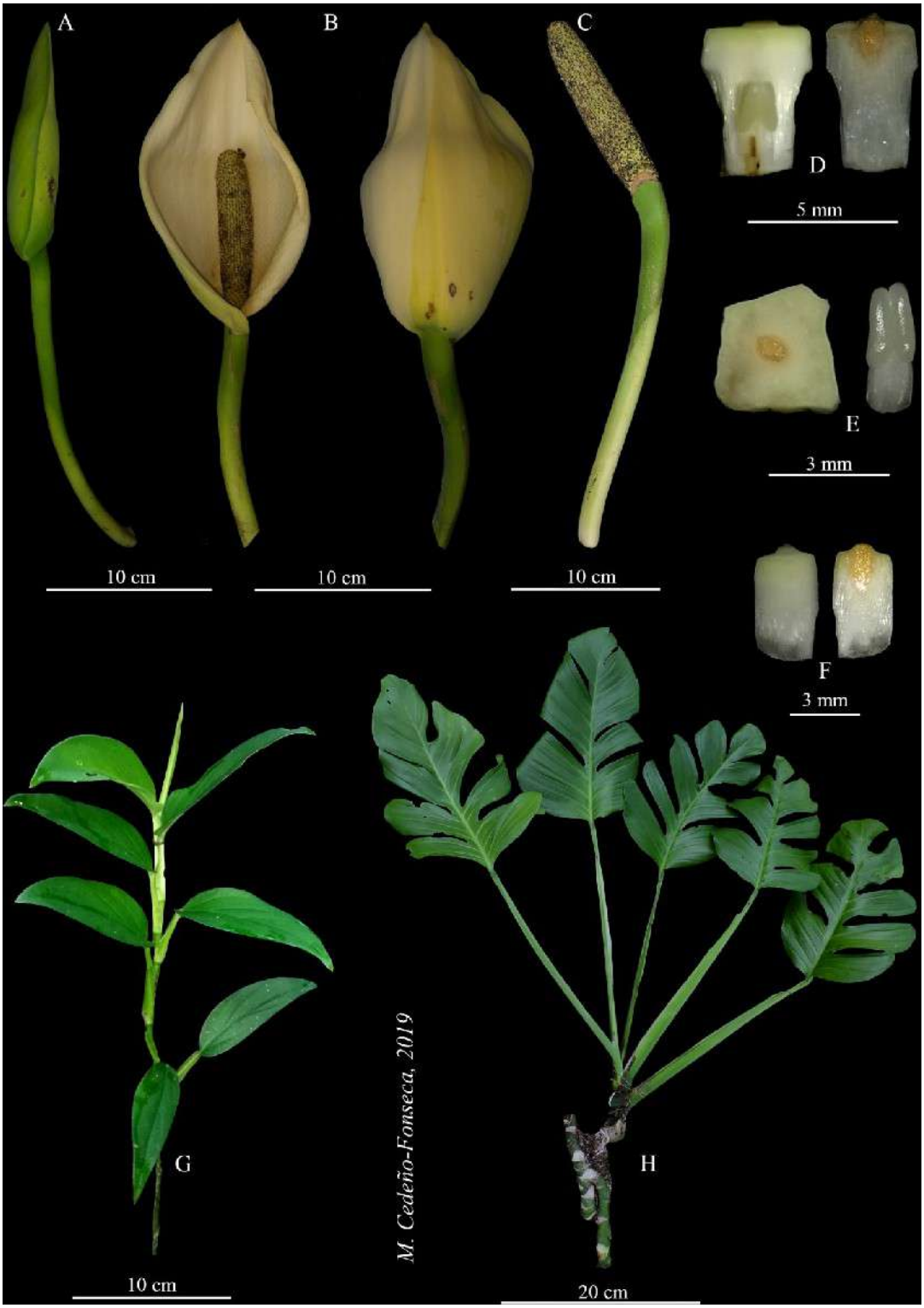

Figure 20. *Monstera dissecta*. (A) Developing inflorescence. (B) Inflorescence with open spathe frontal and back views. (C) Immature infructescence. (D) Fertile flower in lateral view (left), and longitudinal section (right). (E) Stylar plate with stigma (left) and one stamen (right) (F) Sterile flower, lateral view (left), longitudinal section (right). (G) Juvenile plant. (H) Adult plant. *Cedeño et al. 1001* (USJ).

comm., August 2021), and so we conclude, albeit somewhat speculatively, that the unaccounted for leaf in the drawing of Wendland's specimen, and the destroyed sheet at W are perhaps simultaneously explained by Schott having taken a leaf from the holotype and retained it in his own herbarium. We have therefore cited the lost sheet at W as a fragmentary isotype [see Turland et al. (2018): Art. 8.3, Ex. 8], with suitable uncertainty indicated. Engler & Krause (1908: 111) stated under "*Monstera dilacerata*", where they placed *Tornelia dissecta* Schott as a synonym, that the Wendland specimen from Turrialba that they had seen was at K, but, while there is some Wendland aroid material there, this specimen does not appear in the Kew on-line herbarium catalogue, and we have not been able to verify whether or not it really is there: it was not mentioned by Madison (1977) who had received at least some of Kew's *Monstera* material on loan for his revision. [Engler (1879: 269) had earlier cited Wendland's specimen under "*Monstera dilacerata*" but without indicating where it was deposited].

Grayum (1997) made a case that N.E. Brown had been responsible for the combination *Monstera dissecta* (Schott) N.E.Br. ex Donn.Sm. (loc. cit.), rendering *M. dissecta* (Schott) Croat & Grayum a later isonym. However, although Brown's intention to transfer *Tornelia dissecta* Schott to *Monstera* was evidently made abundantly clear in a hand-written note to the specimen for which the name was published by Donnell Smith (see Grayum, 1997), the combination was published with no reference, direct or indirect, to the basionym and hence was invalid, so *M. dissecta* (Schott) Croat & Grayum stands.

Additional specimens seen: COSTA RICA: **Alajuela**. Along road between Cañas (Guanacaste) and Upala, 100 m, 25 June 1976, (Fl., Fr.), *T. Croat 36403* (MO); San Carlos, Florencia, San Luis de Florencia, A unos 100 m al oeste de la plaza de deportes de San Luis, 280 m, 16 February 2011, (Fl.), *C. Trejos 25* (CR); San Carlos, Florencia, 9 km north of Ciudad Quesada on road to La Florencia, in patch of forest along Río Peje on property of Jose Corrales, 300 m, 3 June 1986, (Fr.), *B. Hammel & G. Nevers 15310* (CR, MO); Lower W-SW slopes of Volcan Arenal, Pre-montane wet forest, 17 September 1988, (Fl.), *V. Funk* 10474 (CR); San Carlos, Florencia, 22 km NE of Quesada by air, 4 km W of Muelle de San Carlos, Disturbed, seasonally dry primary forest, 9 April 1983, (Fr.), *R. Liesner* 14106 (CR, MO); San Carlos, Pital, San Carlos, Pital, ca. 8 km NE de Boca Tapada, ruta a Río San Juan, alrededores de Laguna Canacas, 50 m, 27 February 2004, (Fr.), *A. Rodríguez* (CR); Along road between Cañas (Guanacaste) and Upala, 100 m, 25 June 1976, (Fr.), *T. Croat 36404* (MO); Los Chiles, Refugio Nacional de Vida Silvestre Caño Negro, 30 m, 8 July 1987, (Fr.), *N. Zamora 1354* (MO); San Ramón, Peñas Blancas, Reserva Biológica Soltis Center, Sendero a la Catarata, 500 m, 29nAgosto 2016, (Fr.), *M. Cedeño et al., 929* (USJ); Upala, Aguas Claras, Sendero Cabinas Bromelia, 490 m, 15 Diciembre 2016, (Fl.), *M. Cedeño et al., 976* (USJ); San Carlos, Monterrey, Río

La Muerte, 110 m, 24 Febrero 2017, (Fl.), *M. Cedeño et al., 1001* (USJ). **Cartago**. Turrialba, Pavones, Javillo de Turrialba, 750 m, 30 November 1994, (Fr.), *V. Nilson et al., 610* (CR); Turrialba, CATIE, 525–600 m, 9 May 1983, (Fr.), *R. Liesner 15258* (MO); Turrialba, Forested slope leading down to the Río Reventazón behind main building of CATIE, 560–600 m, 30 July 1985, (Fr.), *M. Grayum 5739* (MO). **Guanacaste**. Liberia, Mayorga, Estacion Cacao, Cerro Cacao, Bosque primario, 1060 m, 8 February 1995, (Fr.), *A. Rodríguez 40* (CR); Tilarán, Río Piedra, Arenal de Tilarán, 600 m, 7 December 1983, (Fr.), *E. Valerio 69* (USJ); Tilaran, Arenal, Santuario de la Divina Misericordia, 650 m, 11 April 2016, (Fr.), *M. Cedeño et al., 872* (USJ). **Heredia**. Sarapiquí, Las Horquetas, Along main road ca. 1 km SE of Las Horquetas (Buenos Aires) de Sarapiquí, 70 m, 2 June 1985, (Fl.), *M. Grayum & B. Jacobs 5319* (CR, MO); Sarapiquí, Las Horquetas, Reserva Rara Avis, Sector Catarata, 700 m, 16 June 1995, (Fl.), *S. Marten 878* (CR); Sarapiquí, Horquetas (Buenos Aires), Finca CECAFOR, Sarapiquí, 80 m, 19 October 2006, (Fr.), *D. Beatríz 28* (CR); Sarapiquí, La Virgen, Bosques remanentes siguiendo el sendero del Río Peje, 100 m, 12 July 2003, (Fr.), *J. Gonzales 3966* (CR); Sarapiquí, Horquetas (Buenos Aires), Puerto Viejo a Rio Corinto, potreros, 100 m, 2 September 1993, (Fl.), *Hammel 18993* (CR); Finca La Selva, 100 m, 17 July 1982, (Fr.), *B. Hammel 13217* (MO); La Selva Biological Station, 100 m, 20 March 1980, (Fr.), *B. Hammel 8189* (MO); Finca La Selva, 100 m, 2 August 1979, (Fr.), *M. Grayum 2179* (MO); Finca La Selva, 100 m, 12 August 1980, (Fr.), *B. Hammel 9524* (MO); Estación Biológica La Selva At confluence of Río Sarapiquí and Río Puerto Viejo, 50–80 m, 3 May 1987, (Fr.), *M. Grayum 8297* (MO); Finca La Selva, 100 m, 22 May 1980, (Fr.), *M. Grayum 2844* (MO); Finca La Selva, 100 m, 13 July 1982, (Fr.), *B. Hammel 13159* (MO); Sarapiquí, La Virgen, Estación Biológica La Tirimbina, Sendero la Ceiba, 197 m, 19 Febrero 2016, (Fr.), *M. Cedeño et al., 1053* (USJ). **Limón**. Pococí, Roxana, Along road between Mata de Limón, (incorrectly identified on Agua Fría quadrangle as "Milloncito") and Millón, 25 m, 7 November 1987, (Fl.), *M. Grayum & B. Hammel 8406* (CR, MO); Talamanca, Cahuita, P.N. Cahuita, Sector Puerto Vargas, Sendero Las Baulas, 1 m, 24 August 2011, (Fl.), *A. Estrada et al., 5084* (CR); Pococí, Colorado, North shore of the mouth of the Río Colorado at Barra del Colorado, between the village and the Caribbean Sea, Low-land, tropical wet forest just behind the river white, 3 m, 12 September 1986, (Fr.), *G. Davidse & G. Herrera 30955* (CR, MO); Pococí, Colorado, P.N. Tortuguero, Llanura de Tortuguero, Estaciòn Cuatro Esquinas, 2 m, 18 October 1989, (Fr.), *J. Solano 17* (CR); Limón, Valle la Estrella, Along road leading south from Finca Concepción, Valle La Estrella, to Hitoy Cerere reserve (to E of Río Cerere), 100 m, 31 July 1985, (Fr.), *M. Grayum 5761* (CR, MO); Siquirres, Pacuarito, Banana and cacao plantations on level areas between Siquirres and the Río Pacuare, and remnant forest on steep hills south of the railroad bridge over the río Pacuare, 80 m, 20 December 1969, (Fr.), *W. Burger & R. Liesner 6936* (CR); Limón to Moin road, 3

m, 21 February 1984, (Infer.), *Khan et al., 1200* (CR, MO); Talamanca, Sixaola, R.V.S. Gandoca-Manzanillo, Sendero entre Gandoca y Manzanillo, Aprox. 1,2 Km de la entrada al sendero por el sector de Gandoca, 1 m, 11 April 2012, (Fr.), *A. Estrada et al., 5344* (CR); Limón, Valle la Estrella, Sea shore vegetation swamp forest cacao plantations and secondary growth along the Caribbean Coast between the río Bananito and Cahuita, 5 m, 9 February 1977, (Fr.), *W. Burger et al., 10500* (CR, MO); Limón, Matama, Limón, Valle de la Estrella, Fila Matama, Cerca de 11 km SW del pueblo de Aguas Zarcas, Punto 51, Bosque maduro dominado por *Tetragastris panamensis*, *Calatola costaricensis*, *Quaribaea*, *Sloanea* y *Billia rosea*, 800 m, 1 November 2007, (Fr.), *D. Solano 4892* (CR); Pococí, Colorado, Tortuguero, Sendero al pie del Cerro Tortuguero, entrando por Caño Palma, 4 m, 1 September 1995, (Fl.), *A. Cascante & A. Ruiz 673* (CR); Limón, Valle la Estrella, Reserva y alrededores del Hotel Colón Caribe, Borde de Estero Negro, 5 m, 25 August 2011, (Fr.), *S. Lobo et al., 3008* (CR); Pococí, Colorado, Cerro Coronel, E of Laguna Danto, Tall evergreen forest on gentle to moderately steep slopes, 75 m, 16 January 1986, (Fr.), *W. Stevens 23667* (CR, MO); Pococí, Toro amarillo, 30 August 1936, (Fr.), *F. Solís 429* (CR); Pococí, Roxana, P.N. Tortuguero, Estación Agua Fría, ca. 8 km al Sureste siguiendo el Sendero Los Raudales, hasta llegar a las primeras Lomas de Sierpe, Bosque primario, 55 m, 27 February 1988, (Fr.), *R. Robles & L. Flores 1637* (CR); Talamanca, Sixaola, Patch of slightly disturbed primary forest on level tract behind Naisa house, Ganddoca, 3 m, 4 May 1985, (Fl.), *M. Grayum & G. Schatz 5281* (CR, MO); Talamanca, Sixaola, Colecta en sendero; a orilla de la costa de Manzanillo hacia Gandoca, 10 m, 4 October 2000, (Fr.), *L. Acosta 2850* (CR); Limón, Valle La Estrella, Hitoy Cerere, Senderos en los alrededores de la estacion, 90 m, 19 June 1997, (Fr.), *A. Rodríguez 2320* (CR); Pococí, Guapiles, Finca Bosque Lluvioso, Sendero Los Helechos, Bosques secundarios, 300 m, 8 January 2008, (Fr.), *L. Vargas 2910* (CR); Bahia de Portete Parque Nacional, 10 m, 7 January 1984, (Fr.), *S. Thompson 1172* (MO); Low areas mostly in or near cacao groves, 10 m, 4 November 1984, (Fr.), *M. Grayum 4370* (MO); Refugio Gandoca-Manzanillo Along Río Gandoca from mouth ("Gandoca Bar") to ca. 2 km upstream, Mainly Rhiz- ophora toward mouth; Raphia, 5 m, 29 January 1987, (Fr.), *M. Grayum 8063* (MO); Cahuita, Abundante en el bosque y en árboles aislados, 1 May 1985, (Fr.), *E. Valerio 127* (USJ); Talamanca, Cahuita, R.V.S.M. Manzanillo, 18 m, 4 October 2017, (Fl.), *M. Cedeño et al., 1070* (USJ); Estación Carrillo de 700 a 450 m, de la Fila al Cañón del Río Sucio, Bosque muy húmedo tropical-transición a premontano, 12 November 1983, (Fr.), *I. Chacón & G. Herrera 1737* (CR, MO); Parque Tortuguero, Estación Cuatro Esquinas, 600 m al Este de la casa-estación, Sendero a la playa, Bosque secundario, 2 m, 3 December 1987, (Fl.), *R. Robles 1444* (CR, MO); Barra del Colorado, S side, between town and ocean beach; beach and fresh to blackish swamp, 1 m, 26 January 1986, (Fl.), *W. Stevens 24090* (CR,

MO); Barra del Colorado, N side, between town and ocean beach, Swamp forest, 1 m, 26 January 1986, (Fr.), *W. Stevens 24149* (CR, MO). **San José**. Hacienda Chirripó, 200 m, 1 February 1900, (Fr.), *H. Pittier 16041* (MO); 02 Octubre 1899, (Fr.), *A. Tonduz 13320* (MO); Perez Zeledon, Cordillera de Talamanca, 1150 m, 14 February 1996, (Fr.), *E. Alfaro 475* (MO).

9. *Monstera dubia* (Kunth) Engl. & K.Krause, *Pflanzenr.* IV.23B (Heft 37): 117. 1908. — *Marcgravia dubia* Kunth, *Nov. Gen. Sp.* 7: 169 [folio], 217 [quarto]. 1825. — Type: Novae Andalusiae [VENEZUELA. Sucre or Monagas], prope Cocollar et cœnobium Caripense [near Cocollar (Sucre) and Caripe monastery (Monagas)], alt. 400 hex. [≡ fathoms, i.e. ca. 730 m], [1799], *A. von Humboldt & A. Bonpland s.n.* (holotype, B✝; isotype, P! QR code P00679587, seen on-line, here designated the lectotype).

Robust nomadic vine, with appressed-climbing habit at first, then sometimes with the mature shoots free and pendent. SEEDLINGS: filiform. JUVENILE PLANTS: root climbers; **stems** light brown or beige, warty, dorsoventrally compressed; **internodes** 3–5 cm long, 5–8 mm diam.; **petiole** inconspicuous, dark green, smooth, 6–10 mm long; **blades** obovate, cordate at the base, acuminate, coriaceous, 10–18 × 6–10 cm, sometimes variegated, completely appressed to the phorophyte; **fenestrations** absent. ADULT PLANTS: root climbers; **stems** yellowish or beige, with abundant pustules that generate a warty surface, cylindrical or dorsoventrally compressed; **internodes** 2–6 cm long, 1–3.5 cm diam.; **cataphylls** slightly deciduous; **anchor roots** light brown; **feeder roots** beige, warty; **petiole** light green, white-dotted, striated and pustulate at the base, warty, 30–55 cm long, fully sheathed or up to 3 cm long; **petiole sheath** deciduous; geniculum smooth, slightly terete, 2–5 cm long; **blades** ovate to elliptical or oblong, widely cuneate to rounded or truncate at the base, sometimes peltate, obtuse to long-acuminate at apex, subcoriaceous or chartaceous, drying greenish-grey, brownish or yellowish, 55–100 × 30–35 cm, 1.6–2.1 times longer than wide, not decurrent on the geniculum; **midrib** flattened adaxially, convex abaxially, drying yellowish or dark brown on both surfaces; **primary lateral veins** 12–25 per side, decurrent on the midrib, bifurcated in the medial part of its length, obscure adaxially, prominent abaxially, departing midrib at 65–75°, drying black or dark brown; **secondary veins** reticulate and prominent; **collective veins** not visible; **fenestrations** absent or present; **margins** entire to pinnatilobed, with 3–6 lobes per side, 1.5–2.5 cm wide where the middle lobes are narrow. INFLORESCENCES on ascending and pendent stems, 1–7 simultaneously at flowering time, subtended by cataphylls which sometimes leave dry fragments on the peduncles; **peduncle** smooth, light green with white dots, 5–10 cm long, 0.7–1.2 cm diam.; **spathe** apically short-acuminate or obtuse, light green during development, pale green externally and cream internally at anthesis, coriaceous, completely open at apex, deciduous after

anthesis, 8–16 × 7–13 cm, up to 1 cm longer than the spadix; **spadix** white during development, creamy yellow at anthesis, 7–15 cm long, 1.5–3.5 cm diam., 1.5–2 times longer than wide; **basal sterile flowers** 3–5 mm long, narrow towards the base; **fertile flowers** 4–8 mm long; stamens with laminar filaments, 1–7 mm long; anthers 3–4 mm long; ovary flattened, rectangular in longitudinal section, ribbed, 4–5 × 2–4 mm; style 2–3 × 4–5 mm, compressed and hexagonal; stigmatophore slightly conical, 0.3–0.5 mm long; stigma circular, with a yellowish stigmatic secretion; **berries** with a yellowish green stylar cap during development, mature stylar cap beige-cream; pulp white; **seeds** dark brown with white dots, spherical or oblong, 5–7 mm long. (**Figure 21)**.

Distribution and habitat: From Mexico to Bolivia, Venezuela, French Guiana, Brazil, Trinidad & Tobago. In Costa Rica is distributed in the Pacific slope, from the Río Grande de Tárcoles to the south, at 0–450 m. It lives in *Tropical moist forest* and *Tropical wet forest* life zones; in primary and secondary forest, and open areas.

Phenology: In Costa Rica, the flowering has been recorded in January, May and April, and fruiting in January and April.

Conservation status: *Monstera dubia* is protected in the Reserva Forestal Golfo Dulce, Parque Nacional Corcovado and Parque Nacional Carara.

Comments: The species is a member of sect. *Marcgraviopsis*. It differs from the other species of the genus in Costa Rica by its smooth and mottled petiole with warts on the base, the deciduous petiolar sheath, the subterete geniculum, the entire or fenestrate leaf blade with the base cordate and sometimes peltate, the primary lateral veins bifurcated at about half their length, inflorescences subtended by deciduous cataphylls in a sympodial series between episodes of monopodial leafy growth, the externally pink spathe and slender flowers with circular stigmas.

Monstera dubia is similar to *M. punctulata*, but the latter has the spathes pale green externally, the petioles verrucate and grooved throughout their length, the leaf blade usually with numerous conspicuous fenestrations between each pair of primary lateral veins and grows at elevations greater than 600 m, while *M. dubia* generally has a less conspicuously fenestrate leaf and grows in the lowlands of the Pacific slope.

Monstera dubia occasionally displays necrotic regions on the inside of the spathe (**Figure 21B**), in which insect larvae are sometimes found.

Monstera dubia is one of the few species of the genus in Costa Rica that grows in open and disturbed areas. Along the Pacific coast it often grows on African oil-palm (*Elaeis guineensis* Jacq.) plantations, and less frequently in forested areas. Its abundance in this environment may be due to the

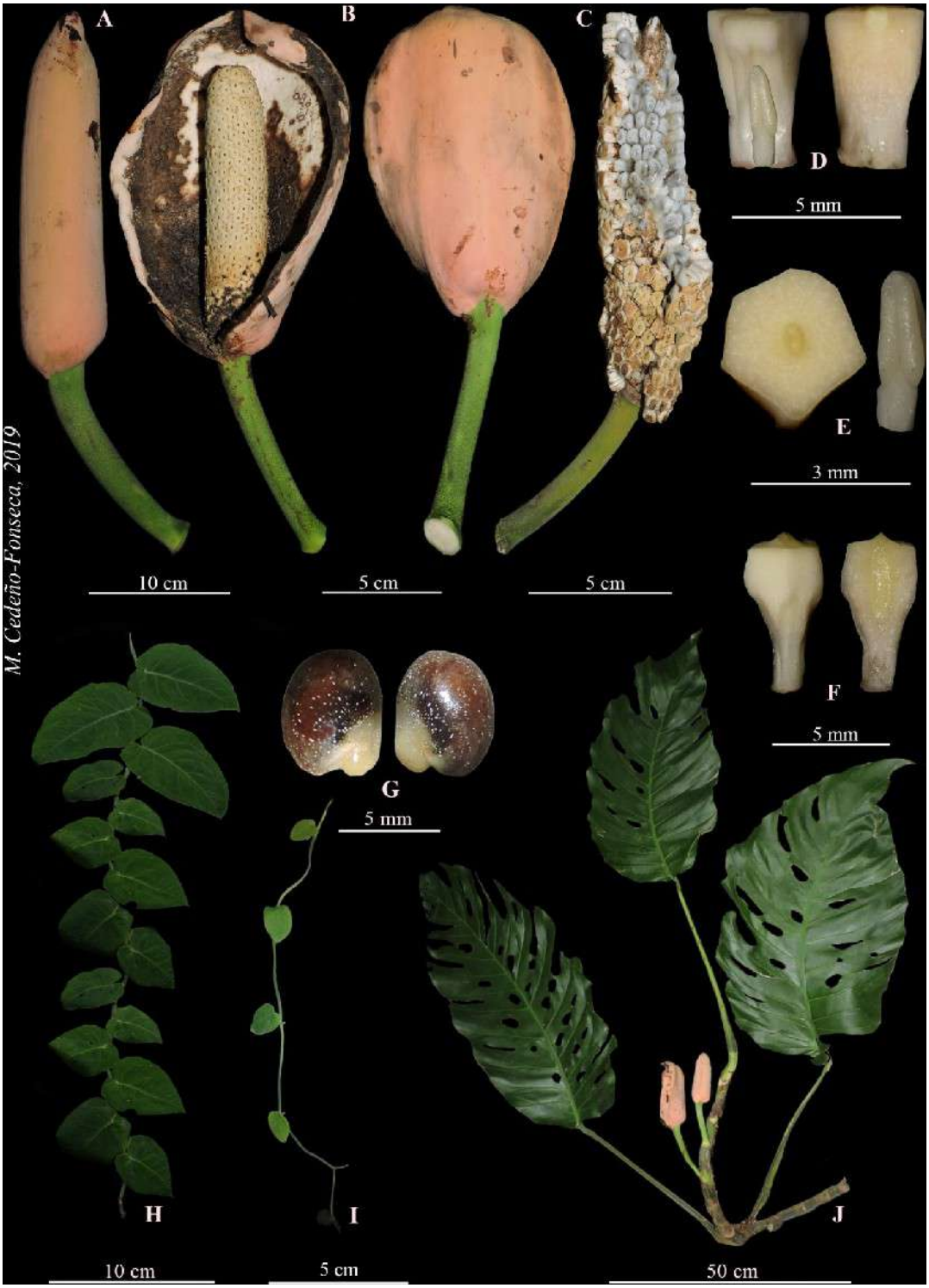

Figure 21. *Monstera dubia*. (A) Developing inflorescence. (B) Inflorescence with open spathe, front and back views. (C) Mature infructescence, stylar plates detached. (D) Fertile flower in lateral view (left) and in longitudinal section (right). (E) Stylar plate with stigma (left) and one stamen (right). (F) Sterile flower; lateral view (left) and longitudinal section (right). (G) Seeds. (H) Juvenile plant. (I) Seedling. (J) Portion of adult plant. *Cedeño et al. 891* (USJ).

accumulation of organic matter in the axils of the remnants of the palms' petioles, which allows its successful establishment as an epiphyte under these circumstances.

Nomenclatural note: The isotype of *Monstera dubia* is a piece of a very juvenile plant in the shingling phase, as doubtless was the holotype, apparently destroyed at B during World War II and not among Macbride's Berlin type photos at F. Madison (1977) noted that it could pertain to almost any shingling *Monstera* but for the fact that it was collected in a part of Venezuela in which no shingling species is known to occur apart from *M. dubia* in the widely accepted, contemporary sense here. [Engler & Krause (loc. cit.) had mistakenly attributed von Humboldt & Bonpland's specimen to Mexico and then confused this species with *Monstera tenuis* q.v.]. It should be epitypified accordingly using an adult Venezuelan specimen in order to guide the application of the name with more certainty. Apart from designating the lectotype (see above) that the epitype will support, that will be left for a revision of *Monstera* in South America and more extensive evaluation of the variation in this very widespread species, as we have not been able to locate any suitable collections from Sucre or Monagas states, in either of which the original material may have been collected (see type citation above), which would be the first preference for selection of an epitype.

Additional specimens seen: COSTA RICA: **Puntarenas**. Forest along Río Paquita, 2 m, 13 August 1936, (Infer.), *C. Dodge & V. Goerger 9764* (CR, MO); Garabito, Tárcoles, P.N. Carara, Along N fork (known locally as "Quebrada Mona") of Quebrada Bonita, 35 m, 31 August 1985, (Fr.), *M. Grayum et al., 5962* (CR, MO); Golfito, Puerto Jiménez, Along road between Rincón and Puerto Jiménez, 15 km S of Rincón, disturbed areas along road, 30 m, 4 March 1985, (Fr.), *T. Croat & M. Grayum 59797* (CR, MO); Along road between El Valle de Madraño and La Saena, 2.5 mi N of El Valle de Madroño, 3.5 mi N of turn-off To San José, 11, 6 mi N of Las Margaritas, (vicinity of Chepe, in valley of Río Mamoní, 180 m, 22 July 1994, (Fl., Fr.), *T. Croat & G. Zhu 77052* (CR); Golfito, Jiménez, Colecta en bosque junto al río Rincón, camino a la estación Los Patos, 70 m, 16 May 2000, (Fl.), *L. Acosta 1197* (CR); Osa, Sierpe, Along road between Rincon and Boscosa, 2 Km W of bridge over Rio Rincon, 50 m, 11 September 1996, (Infer.), *T. Croat 79252* (CR, MO); Golfito, Golfito, Seccion Esquinas, orilla Quebrada Arenas Bosque Esquinas, 100 m, 15 April 1994, (Fl., Fr.), *J. Quesada 886* (CR, MO); 1 mile south of Rio Claro near C.R -Panama Border, 11 August 1971, (Fr.), *J. Vaughan 621* (MO); Golfito, Serranias de Golfito, Est. Río Bonito, 450 m, 5 October 1996, (Infer.), *E. Fletes 352* (MO); Golfito, Along Interamerican Highway beside Río Grande, 8 February 1978, (Fr.), *T. Croat 32951* (MO), Parrita, 20 Abril 1985, (Infer.), *E. Valerio 132* (USJ); Parrita, 10 m, 20 Noviembre 2001, (Fl.), *C. Morales 1497* (USJ); Golfito, Puerto Jiménez, Camino a la Estación Biológica Piro, 15 m, 28 Mayo 2016, (Infrl.,

Fr.), *M. Cedeño, et al., 891* (USJ); Golfito, Puerto Jiménez, Camino a la Estación Biológica Piro, 15 m, 10 May 2016, (Fr.), *M. Cedeño et al., 950* (USJ); Golfito, Golfito, La Gamba, Río Bonito, 80 m, 28 Octubre 2017, (Fr.), *M. Cedeño et al., 1134* (USJ); Along road from San Vito (Las Cruces) to Ciudad Neily, 2 July 1984, (Fl.), *M. Grayum 3394* (MO).

10. *Monstera epipremnoides* Engl., *Bot. Jahrb. Syst.* 37: 118. 1905. — Type: COSTA RICA. '[San José,] La Uruca, 1100 m., July 1890, *P. Biolley 2846*' [(lectotype, B! seen on-line, barcode B100141893; isolectotypes, BR! [with label data of *Pittier 2486*], CR! [with label data of *Biolley 2846*, pro parte — mixtum: one un-numbered sheet of two]; designated by Madison, 1977). — See notes below.

Robust nomadic vine, appressed-climbing habit. SEEDLINGS: bearing foliage leaves. JUVENILE PLANTS: root climbers; **stems** dark green, smooth, cylindrical, white-dotted; **internodes** 4–7 cm long, 5–10 mm diam.; **petiole** distinct, light green with white dots, smooth, 7–10 cm long, sheathed to the base of the geniculum; **petiole sheath** persistent; **blades** ovate to lanceolate, obtuse or attenuate at the base, acuminate, coriaceous, 13–17 × 4–9 cm, not appressed to the phorophyte; **fenestrations** absent or present, frequently arranged on one side of the blade when present. ADULT PLANTS: root climbers; **stems** beige to dark or light green, smooth, cylindrical; **internodes** 1–7 cm long, 1.5–4 cm diam.; **cataphylls** greenish-white, deciduous; **anchor roots** dark brown; **feeder roots** beige; **petiole** light green, whitish or mottled, smooth, 30–50 cm long, sheathed to the base of the geniculum; **petiole sheath** persistent and thick; geniculum smooth, flat adaxially, convex abaxially, white spotted, 3–5 cm long; **blades** ovate to elliptical or oblong, broadly rounded or truncate at the base, short-acuminate at apex, coriaceous, drying light brown, dull beige or bright brown, 20–70 × 20–40 cm, 1.5–2.2 times longer than wide, slightly decurrent on the geniculum, decurrent portion 1–3 mm; **midrib** ribbed adaxially, convex abaxially, drying dark brown or matte-beige on both surfaces; **primary lateral veins** 9–20 per side, departing midrib at 80–90°, sunken above, prominent below, drying dark brown; **collective veins** not visible; **fenestrations** absent or present, on each side of the midrib when present; **margins** entire or deeply pinnatifid, with 3–15 lobes per side of 1.8–9 cm wide, wider lobes fenestrated with up to 4 veins. INFLORESCENCES on ascending and pendent stems, 1 or 2 simultaneously at flowering time, arranged in the leaf axils or into cataphylls; **peduncle** light green, 7–20 cm long; **spathe** acuminate, green during development, cream, yellowish green or white externally and white internally at anthesis, coriaceous, completely open at apex with the margins overlapping at the base and revolute in the medial part, deciduous or marcescent after anthesis, 15–25 × 8–13 cm, up to 13 cm longer than the spadix; **spadix** white during development, cream-yellowish at anthesis, 10–15 cm long, 1.5–3.5 cm diam., 3.4–5.5

times longer than wide; **basal sterile flowers** 4–5 mm long, with a yellowish stigmatic secretion; **fertile flowers** 4–8 mm long; stamens with laminar filaments, 3–7 mm long; anthers 3–4 mm long; ovary rectangular in longitudinal section, ribbed, 5–6 × 2–3 mm; style compressed and hexagonal, 2–4 × 3–4 mm; stigmatophore conical, 0.5–1 mm long; stigma circular, with a yellowish stigmatic secretion; **berries** with a light-green stylar cap during development, mature stylar cap creamy-white; pulp white; **seeds** black, spherical, 4–6 mm long. (**Figures 22 & 23**).

Distribution and habitat: Endemic from Costa Rica and Panama. In Costa Rica is distributed in the pacific slope of the Cordillera de Talamanca, Cerros de Escazú, Cerro Turrubares and Cerro Caraigres, at 1300–2200 m. It lives in *Tropical wet forest* and *Premontane rain forest* life zone.

Phenology: In Costa Rica, the flowering has been recorded in March, May, August, and November, and the fruiting in February–March, June, August–September and December.

Conservation status: *Monstera epipremnoides* is protected in the Zona Protectora Cerros de Escazú, Zona Protectora Cerros de Turrubares, and Parque Nacional Chirripó.

Comments: This species is a member of sect. *Monstera*. It differs from the other species of the genus in Costa Rica by the mottled or whitish petiole, the persistent petiolar sheath with open wings, pinnatifid leaf blades with fenestrations on each side next to the midrib, the green spathe yellowish externally and up to 13 cm longer than the spadix, and the circular stigma, slightly raised on a stigmatophore. It is similar to *M. monteverdensis* but differs in that the latter has green or mottled petioles with the sheath deciduous, leaves which are pinnatifid but without fenestrations on each side next to the midrib, spathes which are light green or yellowish externally.

Nomenclatural notes: Engler (loc. cit.) cited two syntypes in the protologue of *Monstera epipremnoides*: "Costa Rica, in den Wäldern von Santa Maria de Dota, um 1300 m ü. M. (*Pittier n. 2486*)"; and "La Uruca, um 1160 m ü. M. (*Biolley in Herb. inst. phys. geogr. nat. costaric. n. 2846*)". Madison (1977) designated as lectotype the specimen at Berlin (now bearing the barcode B100141893) indicated above, attributing it not to Biolley but to Pittier with the location 'Santa Maria de Dota', and the number *2486*. However, the specimen actually bears Biolley's label notes and collecting number.

Madison, perhaps correctly, considered that material of these two collections, taken in the same year with very similar numbers by Pittier and Biolley, both of whom at the time were associated with the Instituto Físico-Geográfico Nacional de Costa Rica (whose herbarium is now in the Museo Nacional: CR), had become mingled. *Biolley 2846* at CR is itself mixed, with one sheet of *Monstera epipremnoides* (see Madison, 1977: Fig 45; constituting an isolectotype) and the

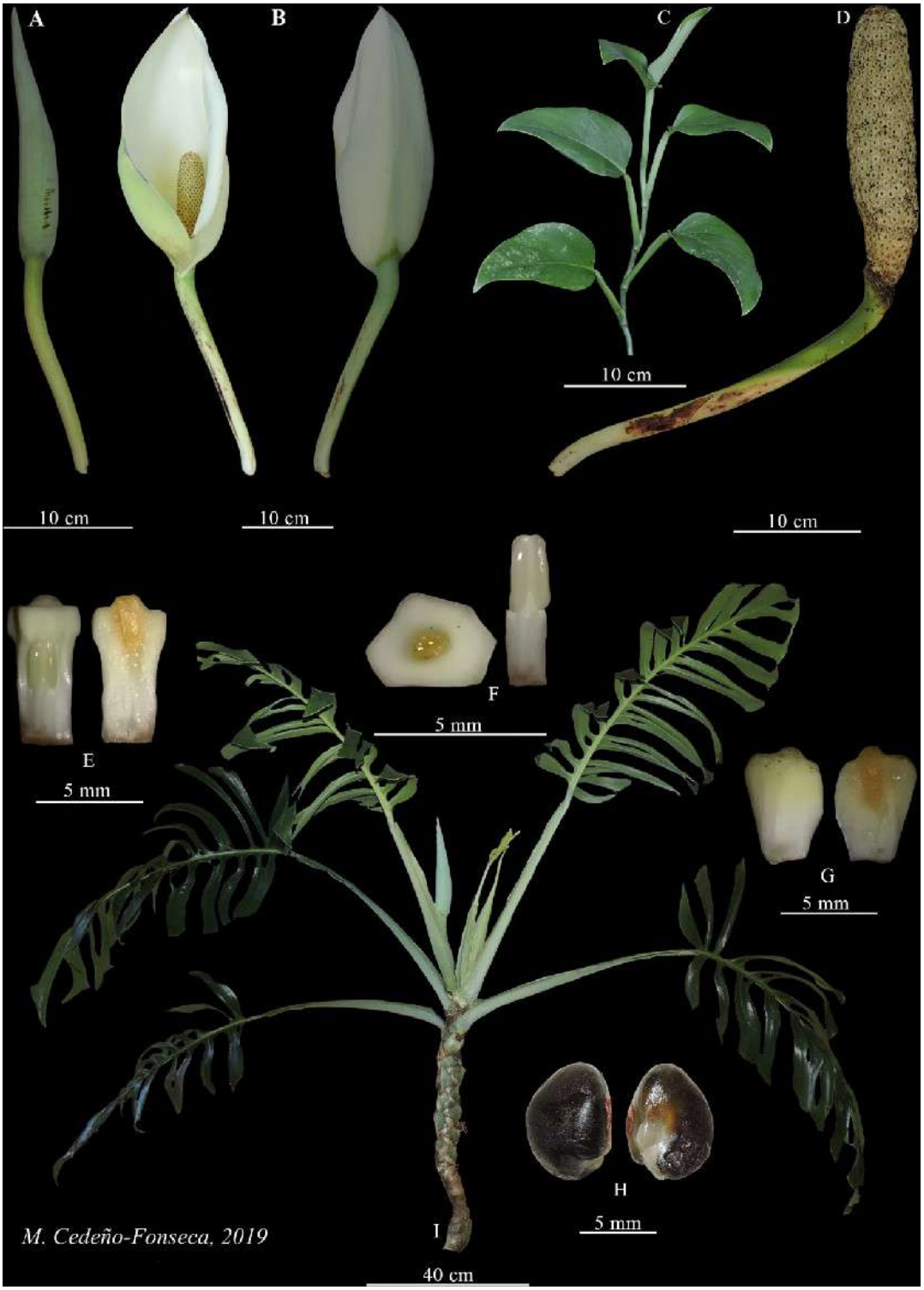

Figure 22. *Monstera epipremnoides*. (A) Developing inflorescence. (B) Inflorescence with open spathe, front and back views. (C) Juvenile plant. (D) Immature infructescence (E) Fertile flower in lateral view (left) and in longitudinal section (right). (F) Stylar plate with stigma (left) and one stamen (right). (G) Sterile flower; lateral view (left) and longitudinal section (right). (H) Seeds. (I) Adult plant. *Cedeño et al. 1275* (USJ).

Figure 23. *Monstera epipremnoides*. (A) Adult plant with developing inflorescence. (B) Perforations on each side of the midrib. (C) Adult plant with whitish petiole and inflorescence with spathe starting to open. (D) Longitudinal cut of the spathe and the spadix with yellowish stigmatic secretion. Photos A & D: *M. Cedeño 1701* (USJ). Photos B & C: *Cedeño et al. 1275* (USJ).

other of *M. adansonii* (to be excluded from the isolectotype).

In support of the idea of the collections having been mingled, *Monstera epipremnoides* has never since been collected around the locality given for *Biolley 2846*, while *M. adansonii* has been, and *M. epipremnoides* has since been collected in the area where *Pittier 2486* was gathered. Madison concluded that all of the material of *Monstera epipremnoides* distributed with Biolley's labels had in fact been collected by Pittier. The only specimen Madison cited that is of *Monstera epipremnoides and* bears Pittier's label is at BR. As Madison's interpretation, however reasonable, is still conjectural, the lectotype has been cited here just as its label indicates, so there can be no ambiguity about what is the type *object*, notwithstanding its likely mislabelling.

Soon after Engler published the new species, it was included in the *Pflanzenreich* revision of *Monstera* in which *Monstera epipremnoides* was illustrated, with exactly (and only) the same material cited as in the protologue (Engler & Krause, 1908: 114, Fig 45). The illustrated leaf is a precise match for the leaf in the lectotype, down to the number and proportions of the leaf segments and the size, shape and position of fenestrations, dispelling any lingering question deriving from these possibly mingled collections that *Monstera epipremnoides* might have been based on material of *M. adansonii.*

This ambiguity over the lectotype's origin could have been avoided if Madison had designated *Pittier 2486* at BR — as noted above, the only specimen of the right plant with the right label, and which Engler had himself annotated with the name — instead of the likely incorrectly labelled specimen at B. The Code does not allow for a lectotypification to be superseded under these circumstances, so the likely mislabelled lectotype (and isolectotype at CR) designated by Madison must stand, along with a differently labelled isolectotype at BR.

Additional specimens seen: COSTA RICA: **Puntarenas**. Parrita, Parrita, San Josecito, Finca de Marvin Abarca, Fila Chonta, 1400 m, 24 November 2003, (Fl.), *A. Quesada 1231* (CR). **San José**. Mora, Tabarcia, Z.P. Cerros de Escazú, Río Negro, entrando por Palmichal, 1500 m, 4 March 1990, (Fl.), *L. Vargas et al., 991* (CR); Pérez Zeledón, Rivas, Del límite del Parque al sendero Termómetro, 2000 m, 5 May 1997, (Fl.), *R. Aguilar 5079* (CR); Pérez Zeledón, Rivas, Sendero al Chirripo, fila cementerio La Máquina, colectado en bosque y orilla de potrero, 1900 m, 16 September 1997, (Fr.), *E. Alfaro 1437* (CR); Turrubares, San Luis, Vecindades de Llano Caite, 1500 m, 5 March 1993, (Fr.), *Q. Jiménez 1184* (CR, MO); Acosta, Cangrejal, Cerros de Caraigres, Alto Reflis, camino a Fila Aguabuena, 1600 m, 2 January 1997, (Fl.), *J. Morales 5977* (CR, MO); Mora, Tabarcia, Santa Ana, Targuá, 1300 m, 6 November 2004, (Fl.), *D. Santamaría 249* (CR); Dota, Copey, Cedro Eco Lodge, 1900 m, 9

February 2018, (Fl.), *M. Cedeño et al., 1274* (USJ); Dota, Copey, Cedro Eco Lodge, 1900 m, 9 February 2018, (Fl., Fr.), *M. Cedeño et al.,* 1275 (USJ); San José, Escazú, Escazú, Cerro Pico Alto, 1758 m, 22 September 2018, (Fl.), *M. Cedeño & K. Benavides 1476* (USJ); Turrubares, San Pedro, San Pablo de Turrubares, 300 m, 9 December 2004, (Fl., Fr.), *D. Santamaría 338* (CR); Acosta, Sabanillas, Sabanas, 2 km al sur de la Escuela, 1062 m, 30 October 2001, (Fl.), *A. Quesada et al., 760* (CR); Acosta, Cangrejal, Z.P. Caraigres, Cuenca del Pirrís-Damas, Alto Reflis, falda Norte, Fila Aguabuena, 1800 m, 16 February 2001, (Fr.), *J. Morales 7490* (CR).

11. *Monstera filamentosa* Croat & Grayum, *Phytologia* 82: 43. 1997. — Type: COSTA RICA. Heredia: S base of Cerros Sardinal, Chilamate de Sarapiqui (N side of Río Sarapiqui), 4 Jul 1985, *M. Grayum & B. Hammel 5539* (holotype, MO!; isotype, CR!).

Nomadic vine, appressed-climbing and pendent. SEEDLINGS: filiform. JUVENILE PLANTS: root climbers; **stems** dark green, dorsoventrally compressed; **internodes** 3–5 cm long, 2–4 mm diam.; **blades** appressed to the phorophyte. ADULT PLANTS: root climbers; **stems** brown to light brown, dorsoventrally compressed and markedly sulcate on one side; **internodes** 4–10 cm long, 0.6–2 cm diam.; **cataphylls** pink, marcescent and fibrous; **anchor roots** black; **feeder roots** dark brown; **petiole** brown, grooved at the base and smooth towards the geniculum, slightly terete at apex, 25–55 cm long, sheathed to the base of the geniculum or 2 cm before it; **petiole sheath** deciduous with fibrous residues; geniculum smooth or striated, grooved adaxially, convex abaxially, 3–5 cm long; **blades** narrowly elliptic to lanceolate-oblong, broadly cuneate to rounded or cordate to subcordate at the base, acuminate at apex, membranous, drying light green, yellowish or dull beige, 35–105 × 25–40 cm, not decurrent on geniculum; **midrib** flattened adaxially, convex abaxially, drying light or yellowish brown on both surfaces; **primary lateral veins** 12–30 per side, departing midrib at 80–90°, sunken adaxially, prominent abaxially, drying yellowish or light brown; **secondary veins** prominent and reticulated; **collective veins** present along the margins of the lobes; **fenestrations** present, arranged along midrib with filamentous strands connecting between the lobes; **margins** deeply pinnatifid, 6–15 lobes per side of 2–3 cm wide, each lobe with 1–2 veins and a collective vein along the margin. INFLORESCENCES on ascending stems, 1 or 2 simultaneously at flowering time, arranged into cataphylls; **peduncle** smooth, 4–10 cm long; **spathe** dark green during development, pink externally and pale pink internally at anthesis, deciduous at the end of anthesis; **spadix** white during development, cream at anthesis, 6–11 cm long, 1.5–2.5 cm diam., 4.1–4.5 times longer than wide; **basal sterile flowers** 4–5 mm, with a transparent stigmatic secretion; **fertile flowers** 5–8 mm long; stamens with laminar filaments, 2–6 mm long; anthers 2–3 mm long; ovary quadrangular in longitudinal section, ribbed, 3–4 × 2–3 mm;

style compressed and hexagonal, 1–2 × 3–4 mm; stigma linear, sunked over style; **berries** with a green stylar cap during development, mature stylar cap dark green; pulp white; **seeds** yellowish and light brown with white dots, 4–6 mm long. (**Figures 24 & 25**).

Distribution and habitat: From Costa Rica to NW Colombia. In Costa Rica it is distributed in the Caribbean watershed of the cordillera de Talamanca, Llanuras de Tortuguero, and Cordillera Volcánica Central, the South of the Pacific watershed of the Península de Osa, at 12−495 m. It lives in *Tropical wet forest* and *Premontane rain forest* life zones; primary and secondary forest.

Phenology: In Costa Rica, the flowering has been recorded in June and July, and fruiting in August-September.

Conservation status: *Monstera filamentosa* is protected in the Reserva Forestal Golfo Dulce, Refugio de Vida Silvestre Barra del Colorado, Reserva Forestal Río Pacuare, Parque Nacional Braulio Carrillo, Parque Nacional Tortuguero, and Parque Nacional Piedras Blancas.

Comments: The species is member of sect. *Marcgraviopsis*. It differs from the other species of the genus in Costa Rica by its brown petiole, grooved on the base and smooth toward the geniculum, adaxially flat and abaxially convex, the petiolar sheath deciduous with fibrous residues, the leaf blade pinnatifid (with the lobes themselves weakly pinnately lobed) and fenestrate on each side next to the midrib with very slender filaments connecting the lobes, each lobe with a distinct submarginal collective vein and the pink spathe.

Monstera filamentosa is a seldom-collected species in Costa Rica; the majority of the collections are sterile or include only the spadix. The spathe colour notes derive from the protologue and from the first author's field observations. Madison (1977) treated material of this species as *Monstera punctulata*, from which it is amply distinct.

Additional specimens seen: COSTA RICA: **Heredia**. Sarapiquí, La Virgen, Area between Río Peje and Río Sardinalito, Atlantic slope of Volcán Barva, 495 m, 8 April 1986, (Infer.), *M. Grayum 6890* (CR, MO); Sarapiqui, Zona Protectora, N slopes of Volcán Barba 300–400 m, 18 January 1983, (Fr.), *M. Grayum 3172* (MO). **Limón**. Pococí, Colorado, Cerro Coronel, E of Laguna Danto, Tall evergreen forest on gentle to moderately steep slopes, 75 m, 15 September 1986, (Infer.), *W. Stevens & O. Montiel 24366* (CR, MO); Siquirres, Pacuarito, Forested ridges and slopes between Río Pacuare and Quebrada Diablo, ca. 2.5 km E of Siquirres, 150 m, 5 October 1986, (Infer.), *M. Grayum et al., 7701* (CR); Matina, Batán, Cordillera de Talamanca, Ridge between separating Quebrada Cañabral from Río Barbilla, and slopes leading down to the latter, 300 m, 4 September 1988, (Fr.), *M. Grayum 8762* (CR, MO); Pococí, Colorado, Cerro Coronel, E

of Laguna Danto, Tall evergreen forest on gentle to moderately steep slopes, 75 m, 16 January 1986, (Infer.), *W. Stevens 23789* (CR, MO); Pococí, Colorado, R.N.V.S. Barra del Colorado, Forests and pastures between Río Chirripocito and pastures between Río Chirripocito and Río Sardina ("Sardinal" on Chirripó Atlántico quadrangle), m, 21 April 1990, (Infer.), *M. Grayum 9808* (CR, MO); Pococí, Colorado, P.N. Tortuguero, Lomas de Sierpe, 1 km al O del puesto del P.N. en el Río Sierpe, Topografía Quebrada con pendientes medianamente pronunciadas, Suelo bien drenado, 100 m, 11 August 1998, (Fr.), *R. Robles et al., 2001* (CR, MO); North end of Tortuguero National Park and near the Bocas de las Lagunas de Tortuguero, Swamp forest, 0–30 m, 23 September 1978, (Infer.), *W. Burger 11279* (MO); Hamburg Finca, 55 m, 19 February 1926, (Infer.), *P. Standley 48874* (MO). **Puntarenas**. Osa, Sierpe, R.F. Golfo Dulce, Península de Osa, Along road between Rincón de Osa and Rancho Quemado, ca. 10 km W of main Rincón-Pto. Jiménez, 100 m, 4 March 1985, (Infer.), *T. Croat & M. Grayum 59751* (CR, MO); Golfito, Golfito, Sobre Fila Golfito, 400 m, 9 June 2000, (Fl.), *L. Acosta 1676* (CR); Osa, Sierpe, Aguabuena, margen izquierda de Quebrada El Campo, 200 m, 22 September 1990, (Infer.), *G. Herrera 4352* (CR, MO); Parque Nacional, Sector Esquinas, 200–300 m, 12 September 1996, (Infer.), *T. Croat 79293* (INB, MO); Puntarenas, Golfito, Puerto Jiménez, Los Mogos, 40 m, 24 March 2018, (Fl.), *M M. Cedeño et al.1352* (USJ); Puntarenas, Golfito, Golfito, Camino hacia las Antenas, 389 m, 4 February 2019, (Infer.), *M. Cedeño & A. Hay 1627* (USJ).

12. *Monstera gambensis* M.Cedeño & M.A.Blanco, *Webbia* 75(1): 127. 2020. — Type: COSTA RICA. Puntarenas Province, Golfito Canton, Golfito, La Gamba, sendero sobre quebrada, 94 m, 27 May 2016, *M. Cedeño, A.P. Karremans & I. Chinchilla 890* (holotype, USJ!).

Nomadic vine, appressed-climbing habit. SEEDLINGS: unknown. JUVENILE PLANTS: root climbers; appressed-climbing; **stem** dark green, slightly rough; **internodes** 3–5 cm long, 4–10 mm diam.; **petioles** visible (i.e., the leaves not shingling), dark green or light, slightly rough, 3–5 cm long, sheathed to the base of the geniculum; **petiole sheath** persistent; **blades** more or less horizontal, not flattened to the substrate of the phorophyte, 4–7 × 3–4 cm, obovate or lanceolate, subcordate to truncate at the base, acuminate at the apex, thinly coriaceous, without fenestrations. ADULT PLANTS: root climbers; **stem** terete, dark green, rough, internodes 1–4 cm long, 5–10 mm diam.; **anchor roots** black and corky, 4–6 cm long, **feeder roots** black and semi-corky, both with black root hairs; **petioles** light green or whitish, rough to the geniculum, 17–22 cm long, sheathed to 2–3 cm below the base of the geniculum; **petiole sheath** involute and persistent, the free portion slightly grooved; geniculum elongate, 0.5–1 cm long; **blades** lanceolate, attenuate at the base, acuminate at the apex, subcoriaceous, 12–24 × 5–10 cm, decurrent

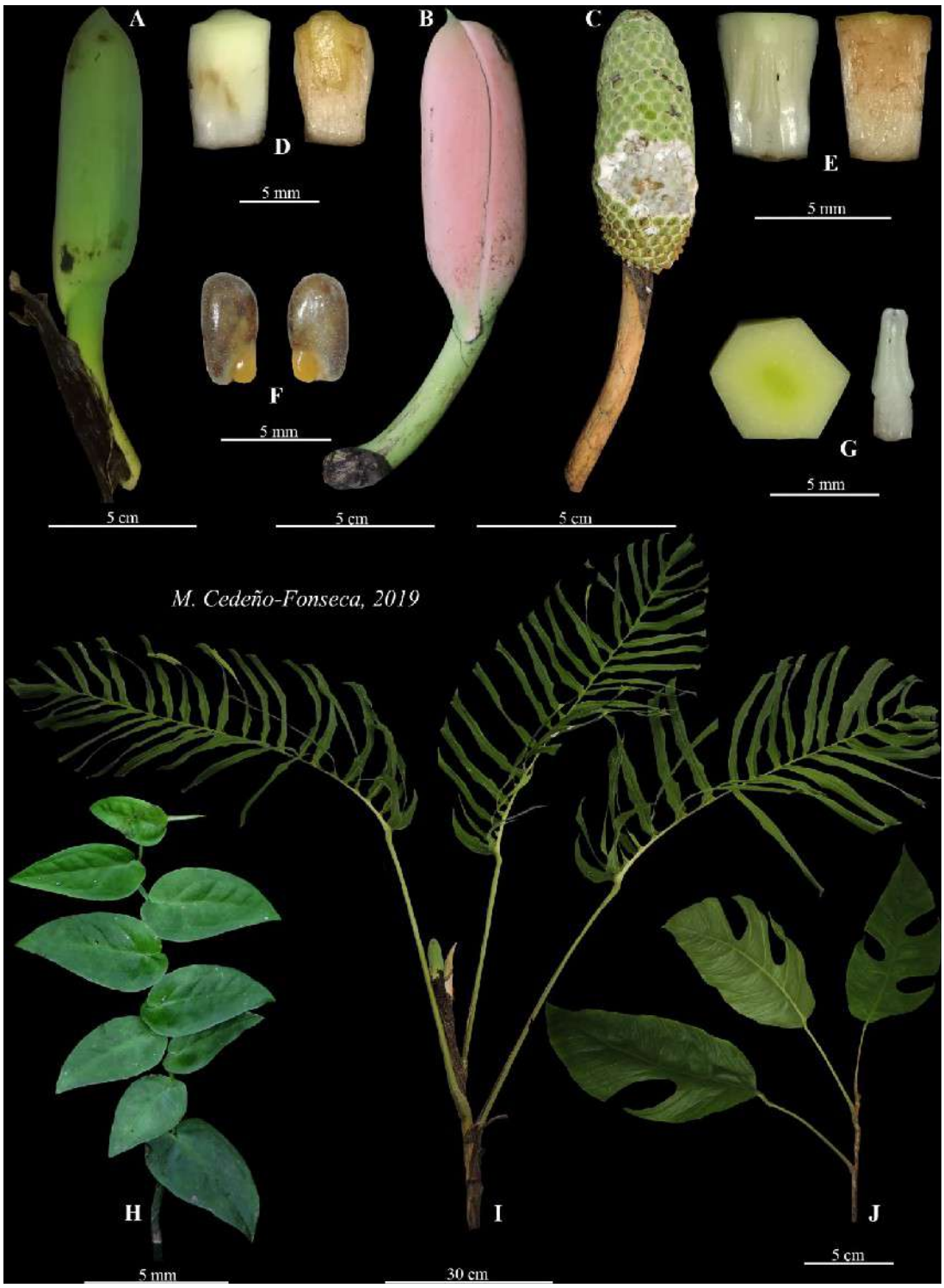

Figure 24. *Monstera filamentosa*. (A) Developing inflorescence. (B) Inflorescence in female anthesis with pink spathe. (C) Mature infructescence, stylar plates detached. (D) Sterile flower; lateral view (left) and longitudinal section (right). (E) Fertile flower in lateral view (left) and in longitudinal section (right). (F) Seeds. (G) Stylar plate with stigma (left) and one stamen (right). (H) Juvenile plant. (I) Adult plant. (I) Pre-adult plant. *M. Cedeño et al. 1352, 1627 & 1704* (USJ).

Figure 25. *Monstera filamentosa*. (A) Stem with fibrous remains of cataphylls (black arrow). (B) Petiolar sheath with fibrous residues (white arrow). (C) Part of the leaf blade shows filaments connecting the lobes (arrow *ii*) and marginal collecting veins in each lobe (arrow *i*). (D) Pale pinkish young cataphylls (white arrow). *M. Cedeño et al. 1704* (USJ).

Figure 26. *Monstera gambensis.* (A) Adult plant with non-perforated leaves. (B) Juvenile plant. (C) Adult leaf with two perforations. *M. Cedeño et al. 890* (USJ).

Figure 27. *Monstera gambensis*. (A) Support roots (*i*) and a feeding root (*ii*) both corky and blackened. (B) Petiole sheath margins persistent and involute in adult plants (arrow). (C) Petioles with sheath margins persisting, whitish and asperous (arrow). (D) Internodes of adult plant (arrow). (E) The shallowly channeled distal portion of the petiole (arrow). (F) Portions of either dead epidermis or epicuticular waxes that give a whitish appearance and an asperous texture to the surface of the petioles. *M. Cedeño et al. 890* (USJ).

on the geniculum (the decurrent part 0.5–1 mm wide); **midrib** convex to the middle of the blade abaxially, slightly rough; **primary lateral veins** 5–13 per side, impressed or indistinct abaxially, prominent on the underside, departing midrib at 35–45°; **fenestrations** (when present), one to two close to each other on the same side of the blade near its middle part; **collective veins** not visible; **margins** entire. INFLORESCENCES on ascending stems; **peduncle** rough throughout, 20–25 cm long; **spathe** unknown; **spadix** 7–10 × 1.3–1.6 cm, colour at and before anthesis unknown; **basal sterile flowers** 3–4 mm long; **fertile flowers** 4–5 mm long; stamens with laminar filaments 2–4 mm long; anther 1–2 mm long; ovary prismatic, longitudinally ribbed, 2–3 × 2–3 mm; style hexagonal, 1–2 × 3–5 mm; stigma linear; **berries** yellow when ripe; pulp white; **seeds** black, 2–3 mm long. (**Figures 26 & 27**).

Distribution and habitat: Endemic to Costa Rica, where it has been found growing low on the supporting trees (ca. 2 m above ground level), in rain forest at La Gamba Biological Station, cantón Golfito, mostly at 50–100 m.

Phenology: In Costa Rica, flowering has not been observed; fruiting was recorded in May.

Conservation status: *Monstera gambensis* is protected at the La Gamba Biological Station, the only known locality for this species.

Comments: The species is a member of section *Monstera*, and differs from other species by its rough whitish stem and petioles, persistent and involute petiole sheath, and entire adult leaf blade with or without fenestrations. It is similar in overall size to *Monstera obliqua*, but is differentiated by its distinctly longer, rough petioles and persistent petiolar sheaths. In Costa Rica, *Monstera obliqua* is found only in the extreme southeast of the country (Caribbean slope, Grayum 2003), while *M. gambensis* is only known from a single collection in La Gamba de Golfito (Pacific slope). This species is also similar to *Monstera minima* Madison but that has smaller petioles (2–6 cm), leaf blades (9–14 × 2–4 cm), and spadices (ca. 4.4 × 09–1 cm), and is only known from the northern (Caribbean) coast of Panama and along the Pacific slope of northern Colombia, in the Chocó region (Jácome & Croat 2002). In Costa Rica, *Monstera gambensis* is found in lowland tropical wet forest at elevations of up to ca. 100 m. The individuals observed were climbing in undisturbed forest on small trees no more than 2.5 m high, with abundant shade in the understorey.

13. *Monstera glaucescens* Croat & Grayum, *Phytologia* 82: 44. 1997. — Type: COSTA RICA. Heredia: Estación Biológica La Selva, at confluence of Rio Sarapiqui and Rio Puerto Viejo, Atlantic slope, 50–75 m, 5 Nov 1988, *M.H. Grayum 8972* (holotype, MO!).

Nomadic vine, appressed-climbing habit. SEEDLINGS: bearing foliage leaves. JUVENILE PLANTS: root climbers; stems dark green, smooth and pruinose, cylindrical; internodes 3–8 cm long, 3–5 mm diam.; petioles distinct, dark green, smooth, 4–7 cm long, sheathed up to half their length; **petiole sheath** persistent; **blades** lanceolate, truncate at the base, acuminate at apex, sub-coriaceous, 9–15 × 4–7 cm, not appressed to the phorophyte; **fenestrations** absent. ADULT PLANTS: root climbers; **stems** light to dark green, smooth and pruinose; **internodes** 2–10 cm long, 1–2.5 cm diam.; **cataphylls** light-green or light green-pruinose, persistent or deciduous; **anchor roots** light brown; **feeder roots** dark brown; **petiole** light green and pruinose, smooth, 25–45 cm long, sheathed to half or 3 cm below the base of the geniculum; **petiole sheath** persistent and closed; **unsheathed portion** slightly ribbed; geniculum smooth, slightly sunken adaxially, convex abaxially, 1–2.5 cm long; **blades** ovate to elliptical, broadly cuneate to rounded, truncated or subcordate at the base, acuminate at apex, subcoriaceous, drying glossy, light brown, reddish or black, 25–45 × 15–30 cm, 1.4–1.7 times longer than wide, decurrent on the geniculum, decurrent portion 1–2 mm wide; **midrib** ribbed adaxially, convex abaxially, drying reddish or black on both surfaces; **primary lateral veins** 6–18 per side, occasionally two of them emerge together from the midrib and then spreading towards the margin, sunken adaxially, prominent abaxially, departing midrib at 55–65°, drying reddish and black; **secondary veins** reticulate towards the margin; **collective veins** not visible; **fenestrations** absent; **margins** entire or deeply pinnatifid with 2–7 lobes per side. INFLORESCENCES on ascending stems, 1–2 simultaneously at flowering time, arranged in the leaf axils or into cataphylls; **peduncle** smooth, 12–25 cm long; **spathe** acuminate and completely open at apex, with overlapping basal margins, yellowish green during development, creamy white externally and white internally at anthesis, marcescent and turning dark blue at the end of anthesis, 15–22 × 9–14 cm, up to 12 cm longer than the spadix; **spadix** white during development, cream at anthesis, 4–10 cm long, 1.0–3 cm diam., 3.5–5 times longer than wide; **basal sterile flowers** with a spherical ovary and a conical stigmatophore, with an orange stigmatic secretion, 4–5 mm; **fertile flowers** 4–6 mm long; stamens with laminar filaments, 1–5 mm long; anthers 2–3 mm long; ovary cylindrical, rectangular in longitudinal section, ribbed, 3–4 × 2–3 mm; style compressed and hexagonal, 0.5–2 × 3–4 mm; stigma linear, cleft on top surface of style, with an orange stigmatic secretion; **berries** with a yellowish green stylar cap during development, mature stylar cap creamy; pulp white; **seeds** dark-brown, globose, 5–7 mm long. (**Figure 28)**.

Distribution and habitat: From Southeast of Nicaragua to Colombia. In Costa Rica is distributed across the Caribbean watershed, at 0−700 m. It lives in *Tropical wet forest* or *Premontane wet forest* life zones; primary and secondary forest.

Phenology: In Costa Rica, flowering has been recorded in January and October, and fruiting in January–February, April, June, and November–December.

Conservation status: *Monstera glaucescens* is protected in the Zona Protectora Río Banano, Estación Biológica La Selva, Reserva Biológica La Tirimbina, Reserva de Vida Silvestre Barra del Colorado, Reserva Indígena Talamanca, Reserva Indígena Tayni, Parque Nacional Tortuguero, Parque Nacional Guanacaste, Parque Nacional Barbilla.

Comments: The species is a member of sect. *Monstera*. It differs from the other species of the genus in Costa Rica by its light green, pruinose petiole, sheathed from ca. half its length up to 3 cm below the base of the geniculum, persistent and closed petiolar sheath, pinnatilobed leaf blade, without fenestrations, the externally and internally white/cream acuminate spathe, and sterile flowers with the ovary spherical and with a conical stigmatophore. It is similar to *Monstera pinnatipartita*, but the latter species has the leaf blade deeply pinnatifid, and occurs only on the Pacific slope.

Monstera glaucescens was part of the "*M. dilacerata*" complex resolved by Grayum (1997). Its populations are known only from the lowlands of the Caribbean slope, mainly growing in primary forest and less commonly in open areas. It is frequent growing to 2–3 m above ground in La Selva Biological Station and La Tirimbina Biological Reserve.

Additional specimens seen: COSTA RICA: **Alajuela**. San Carlos, Pocosol, 2 km N of San Rosa, 15 km N of Boca Arenal on Quesada, Muelle San Carlos, Los Chiles road, 100 m, 28 April 1983, (Fr.), *R. Liesner 15034* (CR, MO); Upala, Aguas Claras, Sector Caribe; colectado en bosque y charal, sendero el pantano, 395 m, 11 June 2003, (Fr.), *E. Alfaro 4480* (CR); San Carlos, Pital, Lagunas La Cureña, 100 m, 30 April 2004, (Fr.), *R. Kriebel 4525* (CR); San Ramon, Bajo Rodriguez, 300 m, 11 April 1976, (Fr.), *J. Utley 4625* (MO); San Carlos, 3 km south of Boca de Arenal in trashy patch of remnant forest in midst of cane fields of Hacienda Boca Arenal, 100 m, 6 March 1986, (Fr.), *B. Hammel 15320* (MO); Los Chiles, Los Chiles, Las Delicias, 56 m, 3 March 2017, (Fr.), *M. Cedeño et al., 1041* (USJ). **Cartago**. Turrialba, Tres Equis, Sendero Principal hacia Barbilla, por la loma, 300 m, 18 October 2000, (Fl.), *E. Mora 1608* (CR, MO). **Guanacaste**. La Cruz, Santa Cecilia, Estación Pitilla; 9 Km al S de Santa Cecilia, 700 m, 12 January 1998, (Fr.), *C. Moraga 960* (CR); La Cruz. Santa Cecilia, Estacion Pitilla, Finca Margarita, 700 m, 17 April 1995, (Fr.), *M. Moraga 162* (CR); La Cruz, Santa Cecilia, Finca Guillermo Navarro, 480 m, 24 Febrero 2017, (Fr.), *M. Cedeño et al., 1006* (USJ). **Heredia**. Sarapiquí, Puerto Viejo, Slopes of eastern spur ridge at N end of Cerros Los Arrepentidos, ca. 4 km NW of Puerto Viejo, 60 m, 3 March 1987, (Fl.), *M. Grayum et al., 8102* (CR, MO); South of Puerto Viejo, 2 km south of Magsasay Penal

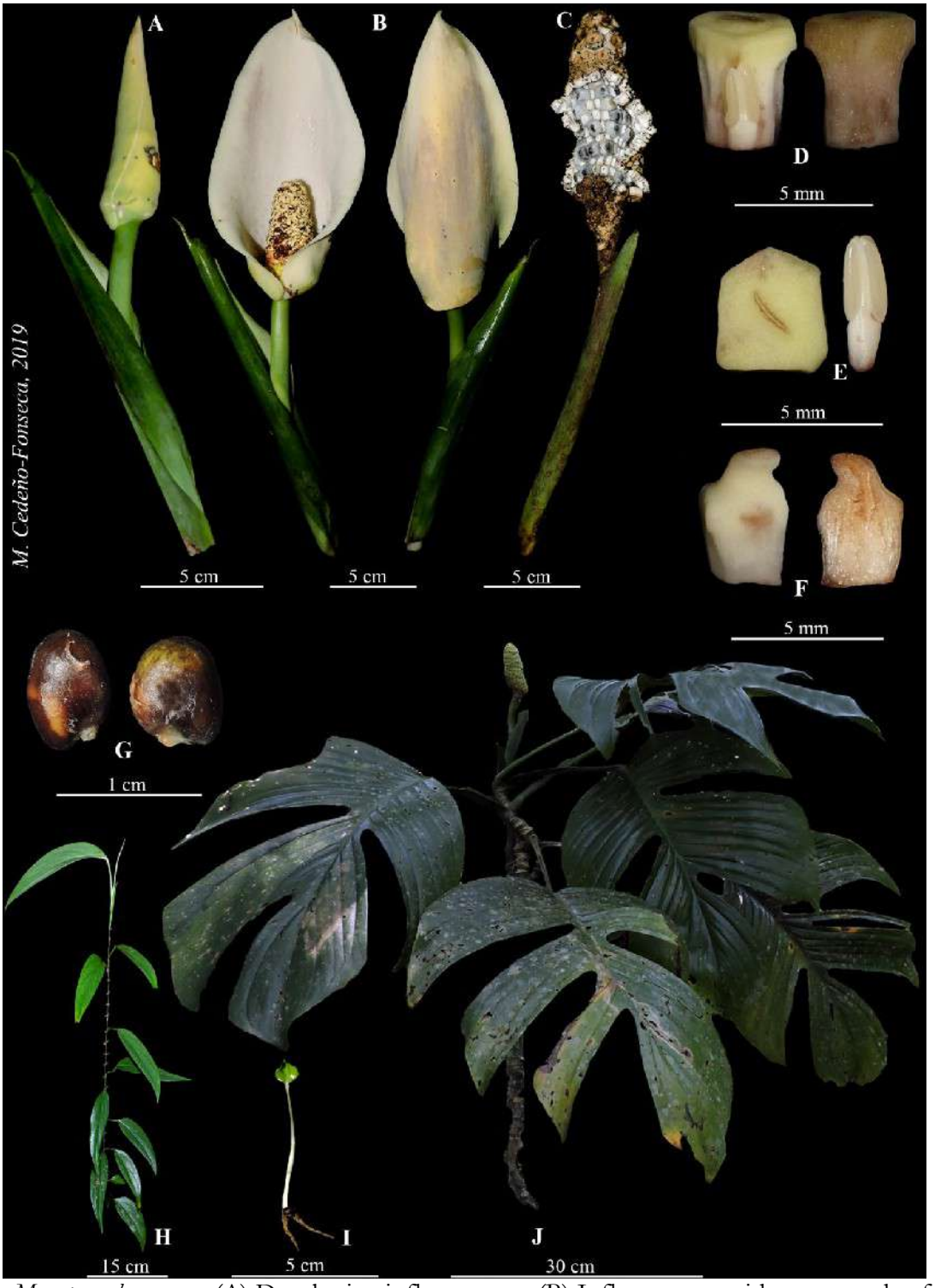

Figure 28. *Monstera glaucescens*. (A) Developing inflorescence. (B) Inflorescence with open spathe, front and back views. (C) Mature infructescence, stylar plates detaching. (D) Fertile flower in lateral view (left) and in longitudinal section (right). (E) Stylar plate with stigma (left) and one stamen (right). (F) Sterile flower; lateral view (left) and longitudinal section (right). (G) Seeds. (H) Juvenile plant. (I) Seedling. (J) Adult plant. *M. Cedeño et al. 873* (USJ).

Colony, west of the road, 200 m, 5 February 1983, (Fr.), *N. Garwood et al., 1111* (CR); Sarapiquí, La Virgen, Cuenca del Sarapiquí, Lomas de Sardinal, ca. 15 km línea recta N de Puerto Viejo, 275 m, 11 January 1997, (Fl., Fr.), *B. Hammel 20623* (CR, MO); Sendero entre el campamento Canta Rana y Río Peje, Magsasay, 400 m, 14 January 1983, (Fl.), *I. Chacón 70* (CR); Sarapiquí, Puerto Viejo, E.B. La Selva, Finca La Selva, Quebrada paralela creciendo sobre un árbol caído, 8 August 1983, (Fl.), *I. Chacón 1132* (CR); North of Puerto Viejo, 10 km down road, then 7–8 km west in forest, 2 February 1983, (Fr.), *N. Garwood et al., 848* (CR, MO); Sarapiquí, La Virgen, Sarapiquí, La Virgen, Golfito, parcela del señor Miguel Angel Picado, 0 m, 10 December 2005, (Fr.), *D. Santamaría 3604* (CR); Finca La Selva, 80 m m, 22 September 1986, (Fr.), *M. Grayum 7667* (MO); Finca La Selva, 100 m, 27 September 1982, (Fr.), *T. McDowell 222* (MO); O.T.S. La Selva Reserve, 100 m, 15 April 1986, (Infer.), *T. Croat 61217* (MO); Sarapiqui, Finca La Selva, 100–150 m, 6 January 1978, (Fr.), *T. Croat 44322* (MO); Sarapiquí, Horquetas, Estación Biológica La Selva, 50 m, 24 Jumio 2016, (Fl.), *M. Cedeño 906* (USJ); Sarapiquí, La Virgen, Reserva Biológica La Tirimbina, 150 m, 16 April 2016, (Fr.), *M. Cedeño & J. Ley 873* (USJ). **Limón**. Limón, Valle de la Estrella, Cerro Muchilla, Fila Matama, Entrando por el pueblo, El Progreso, Cordillera de Talamanca, 850 m, 9 April 1989, (Fr.), *R. Robles & A. Chacón 2735* (CR); Pococí, Colorado, R.N.V.S. Barra del Colorado, Forests and pastures between Río Chirripocito and pastures between Río Chirripocito and Río Sardina ("Sardinal" on Chirripó Atlántico quadrangle), 12 m, 21 April 1990, (Fl.), *M. Grayum 9800* (CR, MO); Pococí, Jiménez, Guápiles, Wet forest remnants on the road from Guápiles to the Río Chirripó, 300 m, 7 April 1982, (Fr.), *K. Barringer & J. Gómez 2359* (CR); Pococí, Colorado, P.N. Tortuguero, Parque Nacional Tortuguero, Estación Agua Fría, primera loma aproximadamente 6 km al SE. Cerros Azules, 70 m, 23 January 1988, (Fr.), *R. Robles 1579* (CR); Pococí, Colorado, P.N. Tortuguero, Estación Agua Fría; Segunda loma aproximadamente 7 km al sureste, Cerros Azules, 70 m, 21 January 1988, (Fr.), *R. Robles 1558* (CR); Talamanca, Bratsi, Between Cahuita and the oil drilling platforms beyond Suretka, Southern Limón, 200 m, 23 April 1982, (Fl.), *K. Barringer et al., 2643* (CR, MO); Limón, No georreferenciado, 9 June 1983, (Fr.), *K. Barringer 3043* (CR); Limón, Siquirres, Pacuarito, Forested ridges and slopes between Río Pacuare and Quebrada Diablo, ca. 2.5 km E of Siquirres, 150 m, 5 October 1986, (Fl.), *M. Grayum et al., 7702* (CR, MO); Pococí, Colorado, P.N. Tortuguero, Estación Agua Fría; Segunda loma aproximadamente 7 km al sureste, Cerros Azules, 70 m, 21 January 1988, (Fr.), *R. Robles 1553* (CR); Vicinity El Copé, 5–6 mi N of El Copé, along trail which leads into the lowlands from old Riviera saw works área, 700 m, 8 July 1994, (Fl.), *T. Croat & G. Zhu 77200* (CR); Pococí, Guapiles, Guápiles, Bosque Lluvioso, 350 m, 12 October 2005, (Fl.), *L. Acosta 3698* (CR); Pococí, Guapiles, Pococi, along Rio Corinto near Braulio Carrillo-Guapiles HWy., 1 km S of turnoff to

Puerto Viejo, 250 m, 30 August 1996, (Infer.), *T. Croat 78748* (CR, MO); Pococí, Guapiles, Guápiles, Finca INBio, Sendero de Las Aves, 300 m, 7 June 2007, (Infer.), *A. Soto 1593* (CR); Pococí, Guapiles, R.B. Bosque Lluvioso, Sendero Los Gigantes, 315 m, 21 February 2008, (Fr.), *L. Vargas 3047* (CR, MO); Hacienda Tapezco-Hacienda La Suerte, 40 m, 14 March 1978, (Fl.), *C. Davidson 6938* (MO); Talamanca, 7 km SW of Bribrí, 100–250 m, 4 May 1983, (Fr.), *L. Gómez 20372* (MO); Parque Nacional Tortuguero Estación Agua Fría, Aproximadamente 12 Km al Noreste, 80–100 m, 2 March 1988, (Fr.), *R. Robles 1672* (CR, MO); Finca Montecristo, 25 m, 18 February 1926, (Fr.), *P. Standley 48938* (MO); Finca Montecristo, 25 m, 18 February 1926, (Fr.), *P. Standley 48945* (MO); Finca Montecristo, 25 m, 18 February 1926, (Fr.), *P. Standley 49010* (MO).

14. *Monstera integrifolia* Zuluaga & Croat, *Phytotaxa* 334(1): 6. 2018. — Type: PANAMA. Chiriquí: Distrito Gualaca, corregimiento Hornito, Reserva Forestal Fortuna, trails near to research center Jorge L. Arauz, 1200–1500 m elevation, 31 Jan 2013, *A. Zuluaga 916* (holotype, WIS; isotypes, PMA?, MO!).

Nomadic vine, appressed-climbing habit. SEEDLINGS: bearing foliage leaves. JUVENILE PLANTS: root climbers; **stems** dark green with white dots, cylindrical; **internodes** 2–8 cm long, 4–10 mm diam.; **petiole** distinct, dark green with white dots, smooth, 8–10 cm long, sheathed to the base of the geniculum; **petiole sheath** deciduous or slightly persistent; **blades** lanceolate, truncate at the base, acuminate at apex, 8–14 × 5–8 cm; not appressed to the phorophyte; collective veins visible; **fenestrations** absent. ADULT PLANTS: root climbers; **stems** dark green or yellowish, sometimes white-spotted, cylindrical; **internodes** 2–4 cm long, 1.4–2 cm diam.; **anchor roots** and **feeder roots** dark brown; **petioles** dark green, whitish or with white dots, smooth, 10–30 cm long, sheathed to the base of the geniculum; **petiole sheath** slightly persistent or deciduous with fibrous fragments; geniculum smooth with white dots, sulcate adaxially, convex abaxially, 1–3 cm long; **blades** lanceolate, cuneate or attenuate at the base, acuminate at apex, coriaceous, 9–13 × 30–40 cm, 2–2.6(3.3) times longer than wide, slightly decurrent on geniculum, decurrent portion 1–2 mm wide, drying black with light brown dots; **midrib** ribbed adaxially, convex abaxially, **primary lateral veins** 5–10 per side, slightly sunken adaxially, prominent abaxially, departing midrib at 35–45°; **secondary veins** parallel across primary lateral veins, reticulate towards the margins; collective veins slightly visible; **fenestrations** absent or present, generally the fenestrations breaks at the margin; **margins** pinnatilobed with 2–3 lobes per side. INFLORESCENCES on ascending stems, arranged in the axils of the leaves; **peduncle** smooth, 6–15 cm long, 0.6–1.2 cm diam.; **spathe** acuminate, light green during development, white to creamy internally and green externally at anthesis, 15–18 × 8–9 cm, up to 8 cm longer than

the spadix; **spadix** white (at both during development and anthesis), 8–10 cm long, 1.7–2.0 cm diam., 0.6–0.9 times longer than peduncle; **basal sterile flowers** 4–5 mm long; **fertile flowers** 4–5 mm long; stamens with laminar filaments, 2–4 mm long; anthers 1.5–2 mm long; ovary rectangular in longitudinal section, ribbed, 2–4 × 2–3 mm; style hexagonal, 2–4 × 3–4 mm; stigmatophore conical, 0.5–1 mm long; stigma circular, with a yellowish stigmatic secretion; **berries** with a white stylar cap during development, mature stylar cap unknown; pulp unknown; **seeds** unknown. (**Figure 29)**.

Distribution and habitat: From the north of Costa Rica to west of Panama. In Costa Rica is distributed in the region of the Caribbean watershed of the Volcán Barba and the Parque Internacional de La Amistad (Moravia, Chirripó), at 1500−1700 m. It lives in *Premontane rain forest* life zones.

Phenology: In Costa Rica, flowering has been recorded in November, and fruiting in December.

Conservation status: *Monstera integrifolia* is protected in the Parque Nacional Braulio Carrillo (región of Volcán Barba), and the Parque Internacional de La Amistad (Moravia, Chirripó).

Comments: The species is a member of sect. *Monstera*. It is distinguished by having narrow leaf blades with primary lateral veins that arise from the midrib at an angle of 35°, whitish and mottled petioles, with a petiolar sheath that disintegrates as fibrous residues, and flowers with a conical stigmatophore. It could be confused with *Monstera anomala* Zuluaga & Croat and *M. standleyana* G. Bunting. *Monstera anomala* never has fenestrate leaf blades and the flowers have an elongated style with a constriction in the middle, and *M. standleyana* plants are usually more robust, have a columnar stigmatophore, and inhabit at lower elevations (0−1360 m).

Nomenclatural note: The paratype cited for Costa Rica (*Croat 66170,* MO) in the protologue of *Monstera integrifolia* is actually *Monstera epipremnoides* Engl.

Additional specimens seen: COSTA RICA: **Cartago**. Turrialba, Chirripo, Moravia de Chirripó, Bosque nuboso, 1602 m, 20 December 2019, (Fr.), *M. Cedeño et al., 638* (USJ); Turrialba, Chirripo, Moravia de Chirripó, Bosque nuboso, 1602 m, 20 December 2018, (Fr.), *M. Cedeño etb al.,1639* (USJ); Turrialba, Chirripó, Tayutic, Jicotea, Siguiendo la Fila Vereh, entre la Cueva del Sapo y Fila Vereh, 1634 m, 22 December 2018, (Fl., Fr.), *G. Herrera 8005* (CR, MO). **Heredia**. Sarapiqui, La Virgen, Primary forest along Rio San Rafael, Atlantic slope of Volcan Barva, 1500 m, 12 April 2019, (Fr.), *Grayum 7017* (MO).

15. *Monstera juliusii* M.Cedeño & Croat, *Phytotaxa* 461(3): 186. 2020. — Type: COSTA RICA. Puntarenas: Buenos Aires, Biolley, Parque Internacional de La Amistad,

Figure 29. *Monstera integrifolia*. (A) Adult plant. (B) Juvenile plant. (C) Whitish petioles, with somewhat persistent sheaths (arrow). (D) Developing infructescence with short, conical styles (left); whitish petiole with green sheath speckled with white dots (arrow). *M. Cedeño et al. 1638* (USJ).

Cerro Frantzius, 2000 m, 5 February 2018, *M. Cedeño, I. Chinchilla, J. Jiménez & J. Porras 1220* (holotype, USJ!; isotype, MO!).

Robust nomadic vine, appressed-climbing habit. SEEDLINGS: bearing foliage leaves. JUVENILE PLANTS: root climbers; **stem** smooth, dark green with white spots; internodes 4–7 cm long, 4–6 mm diam.; **petioles** conspicuous, dark green with white spots, smooth, 7–12 cm long, sheathed throughout, sheath margins convolute, persisting; **leaf blades** ovate, without fenestrations, acuminate at apex, sub-cordate to truncate at base, coriaceous, 9–15 × 7–10 cm, not flattened against the phorophyte. ADULT PLANTS: root climbers; **stem** dark, opaque beige, smooth, terete, internodes 1–3 cm long, 1.5–2.5 cm diam.; **support roots** light brown, 2–4 cm long, **feeder roots** dark brown; **petioles** white-green or with minute white spots, smooth, 25–60 cm long, sheathed to within 2 cm before or up to the base of the geniculum; **petiole sheath** thick and persistent; **geniculum** smooth, 5–10 mm long; **blade** lanceolate to ovate in outline, entire or partially pinnatilobed, narrowly rounded, shortly acuminate at apex, sub-cordate to obtuse at base, decurrent onto the geniculum, the decurrent portion 1–2 mm wide, coriaceous, 25–60 × 15–30 cm; midrib grooved adaxially, transversally convex abaxially; primary lateral veins 13–17 per side, moderately sunken above, prominently raised below; collective veins not visible; **fenestrations** rounded near the midrib, oval toward the margin; **margin** sometimes breaking. INFLORESCENCES on ascending stems; **peduncle** smooth, 15–23 cm long; **spathe** acuminate, light green in developing inflorescences, greenish-yellow externally and white internally at anthesis, thick, completely open at the apex, the margins slightly overlapping at the base, deciduous after the anthesis, 15–30 × 7–11 cm, up to 15 cm longer than the spadix; **spadix** white in developing inflorescences, yellowish cream at anthesis, 8–14 cm long, 1.5–3.0 cm diameter; **basal sterile flowers** 4–5 mm long with a transparent secretion; **fertile flowers** 5–7 mm long; stamens with filament laminar, 2–6 mm long; anther 2–3 mm long; ovary rectangular in longitudinal section, ridged, 4–5 mm long, 2–3 mm wide; style hexagonal, 2–3 × 3–4 mm; stigmatophore cupular, 0.5–1 mm long, stigma linear, with yellowish discharge; berries with the stylar layer white-cream at maturity; pulp white; **seeds** smooth, green or light brown, sub-elliptical, 5–7 mm long. (**Figure 30)**.

Distribution and habitat: Endemic to Costa Rica (Cerro Frantzius of the Cordillera de Talamanca), at 1600–2250 m. It occurs in *Premontane rain forest* life zone.

Phenology: Flowering and fruiting has been recorded in January, February and September.

Conservation status: *Monstera juliusii* is safely conserved in the Parque Internacional de La Amistad.

Comments: The species is a member of sect. *Monstera*. It differs from other species in Costa Rica by the combination of leathery leaves with whitish or mottled petioles, thick and persistent petiole sheath margins, and by spathes yellowish green externally and white internally.

Herbarium material of *Monstera juliusii* has been confused with *M. standleyana* G.S.Bunting, but the latter species has deep green petioles with white dots, usually non-perforate (rarely with few fenestrations), usually entire (rarely with few lobes), lanceolate to ovate leaf blades, creamy yellow spathes with brown spots on the outside, cream on the inside, and laterally flattened stigmatophores.

Additional specimens seen: COSTA RICA: **Puntarenas**. Coto Brus, P.I. La Amistad, Cordillera de Talamanca, Estación Pittier, Sendero Altamira, 1700 m, 28 January 1995 (fl.), *A. Mora 12* (CR-INB, MO); Buenos Aires, Biolley, Cordillera de Talamanca, Cerro Frantzius to Valle de Silencio, Oak-Podocarpus-laurel forest with *Chusquea longifolia* understory, 2250 m, 7 September 1984, (fl.), *G. Davidse et al. 28563* (MO); Buenos Aires, Biolley, Camino a Casa Coca, 1600 m, 5 February 2018, (fr.), *M. Cedeño et al. 1219* (USJ); Coto Brus, Pittier, P.I. La Amistad, Cordillera de Talamanca, Estación Pittier, Sendero Fila Pittier, 1900 m, 27 January 1995 (fl., fr.), *A. Mora 1* (CR, MO).

16. *Monstera lentii* Croat & Grayum, *Phytologia* 82: 46. 1997. — Type: COSTA RICA. Cartago: 10 km S of Cartago by air, along confluence of Río Empalme and Río Estrella, 1 km S of Palo Verde by road, 1450 m, *R.L. Liesner & E.J. Judziewicz 14549* (holotype, MO!; isotype, RSA).

Robust nomadic vine, appressed-climbing habit. SEEDLINGS: bearing foliage leaves. JUVENILE PLANTS: root climbers; **stems** dark green, smooth, cylindrical; **internodes** 3–10 cm long, 2–5 mm diam.; **petiole** visible, dark or light green, smooth, 8–14 cm long, sheathed to the base of the geniculum; **petiole sheath** persistent; **blades** obovate, subcordate to truncate at the base, acuminate at apex, sub-coriaceous, 8–14 × 7–11 cm, collective veins distinct, not appressed to the phorophyte; **fenestrations** absent or present. ADULT PLANTS: root climbers; **stems** light green, dark or light brown, smooth, cylindrical; **internodes** 2–35 cm long, 1–3.5 cm diam.; **cataphylls** light green, deciduous but leaving dry fragments on the peduncle; **anchor roots** black; **feeder roots** light-brown; **petiole** light green or strongly speckled with white dots, smooth, 25–75 cm long, sheathed to the base of the geniculum; **petiole sheath** persistent, revolute, open or closed; geniculum smooth, slightly sulcate adaxially, convex abaxially, 1–2.5 cm long; **blades** ovate to oblong, broadly cuneate to rounded or subcordate at the base, acuminate at apex, sub-coriaceous, drying reddish, black with reddish dots, light-brown or shiny-black, 25–60 × 17–45 cm, 1.4–1.6 times longer than broad, decurrent

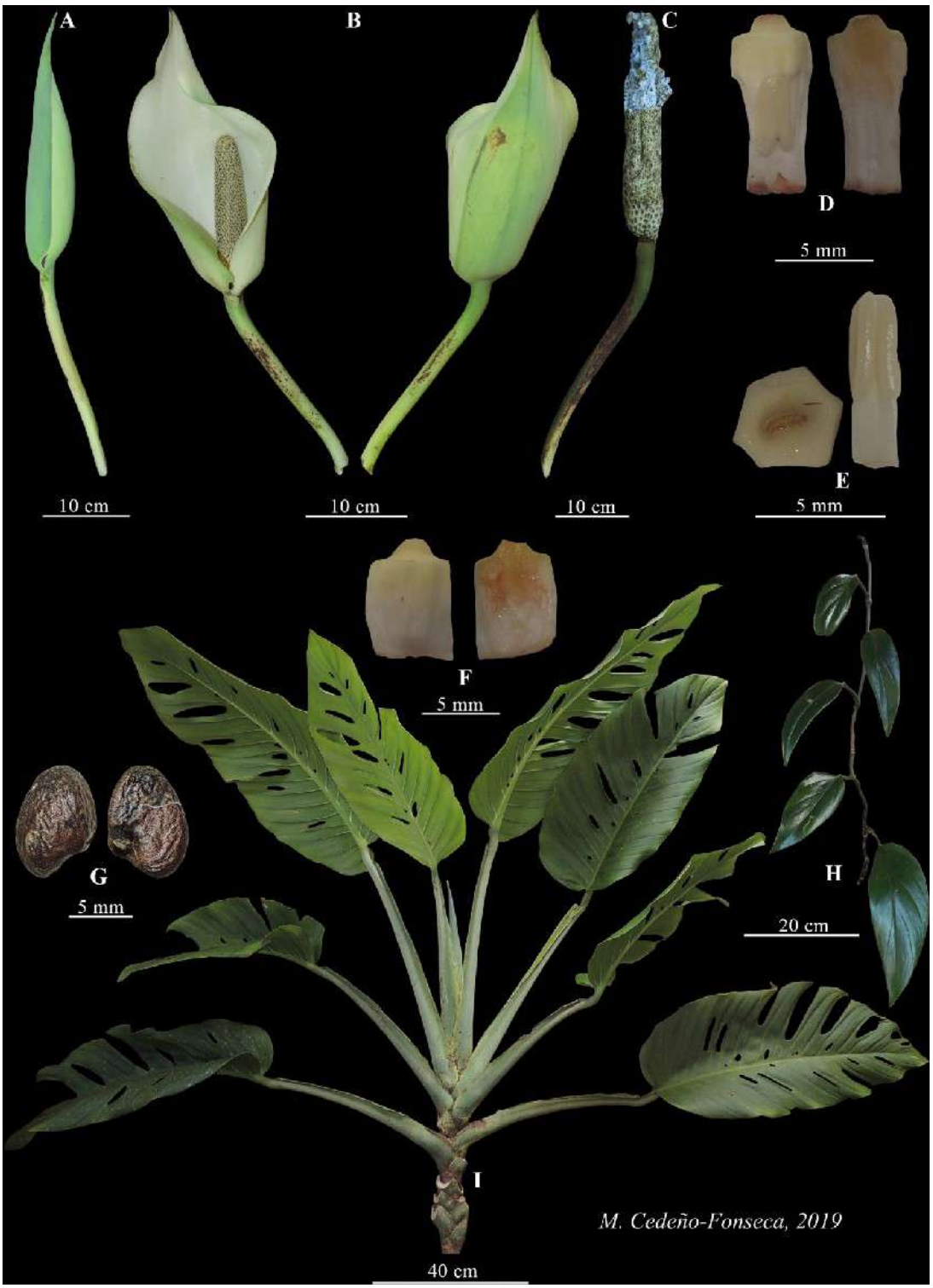

Figure 30. *Monstera juliusii.* (A) Developing inflorescence. (B) Open inflorescence, front and back views. (C) Mature infructescence, stylar plates detached toward the apical part. (D) Fertile flower, in lateral view (left), and longitudinal section (right). (E) Stylar plate with stigma (left) and one stamen (right). (F) Sterile flower, in lateral view (left), and longitudinal section (right). (G) Seeds. (H) Portion of juvenile plant. (I) Portion of adult plant. *M. Cedeño et al. 1220* (USJ).

on geniculum, decurrent portion 1–3 mm wide; **midrib** ribbed adaxially, convex abaxially, drying reddish, light brown, or black on both surfaces; **primary lateral veins** 10–25 per side, forked or trifurcated, sunken adaxially, strongly prominent abaxially, departing midrib at 65–75°, drying reddish, black or light brown; **secondary veins** parallel, reticulate towards the margin, undulate in most of its length when dry; **collective veins** not visible; **fenestrations** absent or present, arranged along the midrib; **margins** entire, pinnatilobed or deeply pinnatifid, with 2–9 lobes per side of 2–15 cm wide. INFLORESCENCES on ascending stems, 2–4 simultaneously at flowering time, arranged in the axils of the leaves or into cataphylls; **peduncle** smooth, 7–25 cm long; **spathe** acuminate, light-green during development, yellowish green externally and white internally at anthesis, completely open at apex, light-brown marcescent at the end of anthesis, 12–20 × 6–10 cm, up to 10 cm longer than the spadix; **spadix** white during development, cream at anthesis, 5–15 × 1–4 cm, 3.5–5 cm times longer than wide; **basal sterile flowers** 4–5 mm long, with a rust-red stigmatic secretion; **fertile flowers** 5–8 mm long; stamens with laminar filaments, 2–7 mm long; anthers 1.5–2 mm long; ovary flattened, rectangular in longitudinal section, ribbed, 4–5 × 2–3 mm; style hexagonal, 4–5 × 3–4 mm; stigmatophore strongly conical, slender, 2–5 mm long; stigma circular, with a transparent stigmatic secretion; **berries** with a light-green stylar cap during development, mature stylar cap creamy-yellow; pulp white; **seeds** black with reddish dots, globose, 4–6 mm long. (**Figure 31)**.

Distribution and habitat: from Costa Rica to western Panama. In Costa Rica it is almost restricted to the Caribbean watershed, at the southern part of the Cordillera Volcánica Central and the northern part of the Cordillera de Talamanca (at whose junction it crosses the continental divide into the Pacific watershed in some restricted places), at 1000–1650 m. It lives in *Premontane rain forest* life zone; primary and secondary forest.

Phenology: In Costa Rica, flowering has been recorded in February–April, July, and December, and fruiting in February–March, July–August, and November.

Conservation status: *Monstera lentii* is protected in the Reserva Indígena Chirripó, Zona Protectora Cerros de La Carpintera, Zona Protectora Río Navarro-Río Sombrero, Zona Protectora Río Tiribi, Parque Nacional Tapantí, Parque Nacional Braulio Carrillo, and Parque Internacional de la Amistad.

Comments: The species is a member of sect. *Monstera*. It differs from the other species of the genus in Costa Rica by the petiole mottled or light green, the petiolar sheath persistent with open wings, the leaf blade entire or pinnatilobed with few fenestrations, externally yellowish spathe and slender flowers toward the base with circular stigma, elevated by strongly and

narrowly conical stigmatophore (a unique characteristic among species of the genus).

Previously, *Monstera lentii* was confused with *M. dissecta*, but the latter is distinguished by the cupuliform stigmatophores and its distribution in cloud forests in the Pacific sector of the Talamanca mountain range.

Populations of *Monstera lentii* in the foothills of the Turrialba Volcano have white or speckled petioles, pinnatilobed leaf blades without fenestrations, the spadix stipitate for 1–2 cm and without a region of sterile flowers, and cylindrical stigmatophore with round stigma. These populations could represent a different species, as the populations around the type locality and the Central Valley do not have these characteristics.

Monstera lentii is another of the species of the "*M. dilacerata*" complex resolved by Grayum (1997). In Costa Rica it is common in the Cerros de la Carpintera and the Seven Manantiales Reserve in the Central Valley, while in Panama it is known from the La Fortuna region in Cerro Hornito and Cerro Colorado. Most of the samples from that Panamanian locality have completely pinnatifid leaves, with lobes 2–5 cm wide, but the morphology of the flowers is similar to that of populations present in Costa Rica.

Additional specimens seen: COSTA RICA: **Cartago**. El Guarco, San Isidro, 10 km Sof Cartago by air, Along Confluence of rio Empalme and rio Estrella, 1 km S of Palo Verde by road, Paloverde is 1.5 km S of Panamerican High way on road to Estrella, 1450 m, 21 April 1983, (Fr.), *R. Liesner & E. Judziewicz 14549* (CR); Cartago, Llano Grande, Z.P. Río Tiribí, Zona de bosque de jaúl, 1826 m, 10 August 2009, (Fl.), *S. Lobo et al., 2467* (CR); Along road between Moravia and Quebrada Platanillo, 3–5 km from Finca Racine in Moravia, Disturbed primary forest (marketable lumber trees removed), 30 June 1976, (Fr.), *T. Croat 36615* (CR, MO); La Unión, San Rafael, Z.P. Cerros de La Carpintera, Laderas hacia Tres Ríos, 1560 m, 23 January 2007, (Fr.), *A. Cascante & J. Sánchez 1670* (CR, USJ); Paraíso, En bosque secundario del que se abastece de agua a la ciudad, 24 October 1986, (Infer.), *R. Hernández 861024* (CR); El Guarco, San Isidro, Hills above El Muñeco, along Río Sombrero, disturbed forest, 1500 m, 28 July 1983, (Infer.), *K. Barringer & E. Christenson 4144* (CR, MO); R.F. Río Macho, Sendero número 4. 1400 m, 26 March 1992, (Fl.), *V. Nilsson & R. Manfredi 125* (CR); Paraíso, Orosi, R.F. Río Macho, Sendero Atraz da casa, lado oeste para a direita, 1250 m, 30 April 1993, (Fl.), *V. Nilsson et al., 345* (CR); La Unión, San Diego, Z.P. Cerros de La Carpintera, Bosque del campo Escuela Istarú de los Scouts, 750 m, 3 August 2006, (Fl.), *A. Cascante et al., 1608* (CR); Cartago, San Nicolás, Z.P. La Carpintera, Propiedad de Campo Escuela Iztarú, Bosque por canchas al sur del área administrativ, 1623 m, 19 July 2007, (Fr.), *A. Cascante 1775* (CR); La Unión, Dulce Nombre, Z.P. Río Tiribí, Faja

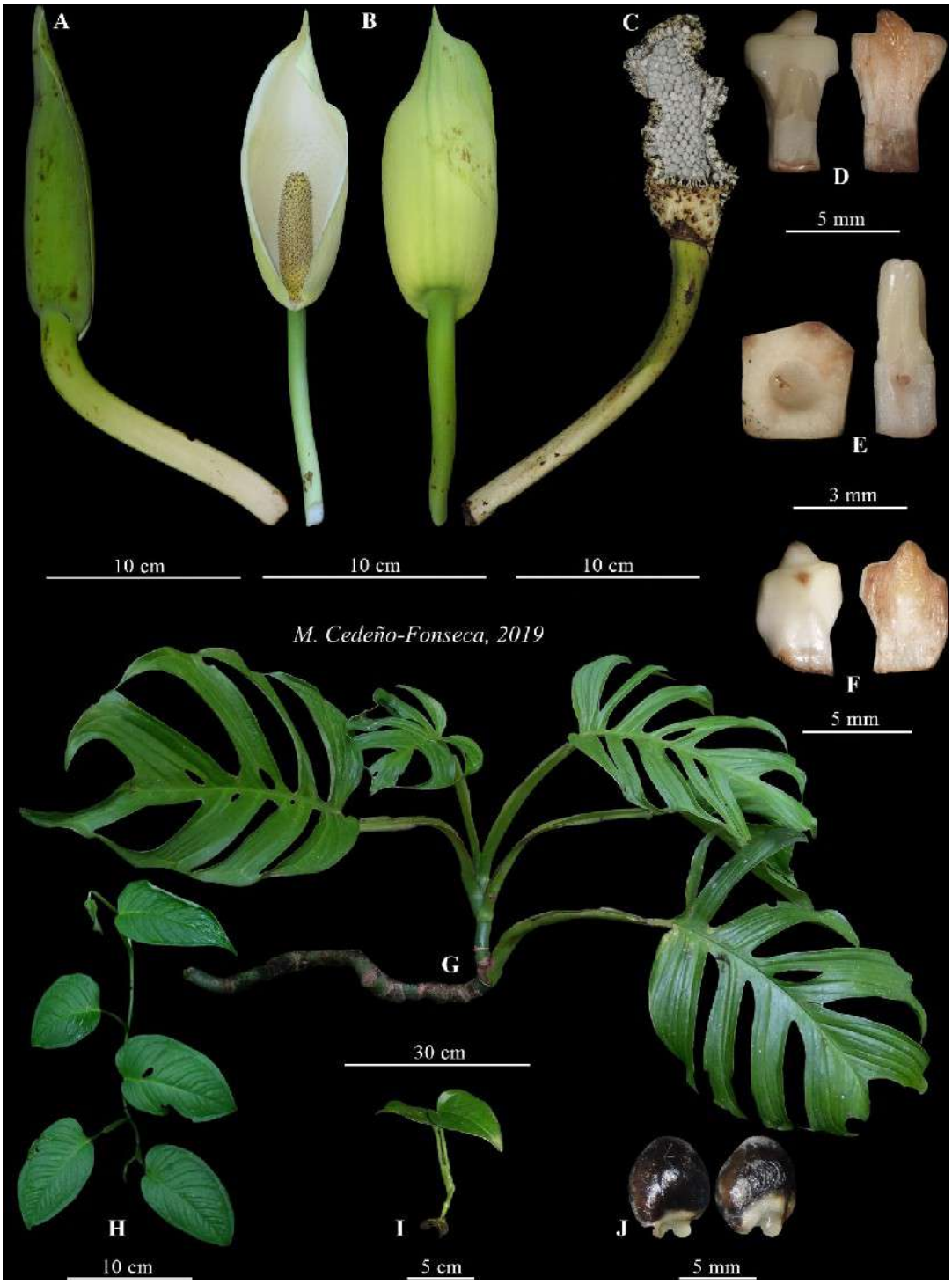

Figure 31. *Monstera lentii*. (A) Developing inflorescence. (B) Inflorescence with open spathe, front and back views. (C) Mature infructescence, stylar plates detaching. (D) Fertile flower in lateral view (left) and in longitudinal section (right). (E) Stylar plate with stigma (left) and one stamen (right). (F) Sterile flower; lateral view (left) and longitudinal section (right). (G) Adult plant. (H) Juvenile plant. (I) Seedling. (J) Seeds. *M. Cedeño et al. 912* (USJ).

de bosque ripario, alrededores de puesto Pizote (AyA), 1600 m, 23 April 2008, (Fl.), *A. Cascante & A. Quesada 1925* (CR); Paraíso, Orosi, P.N. Tapantí, Margen izquierda Río Grande de Orosí, Estribaciones Alto Peralta, 1800 m, 17 December 1992, (Fl.), *G. Herrera 5766* (CR); Paraíso, Orori, Sendero La Pavas, 1400 m, 7 March 2000, (Fr.), *L. Acosta 543* (CR); Paraíso, Orori, Estacion Tapanti, camino Alto Patillos, cerca del mirador, Sendero Los Palmitos, 1350 m, 21 July 1994, (Fl.), *D. Garcia 340* (CR, MO); Paraíso, Orori, Rio Humo, Camino al túnel, 1600 m, 20 July 1994, (Fr.), *E. Lepiz 489* (CR); Paraíso, Orori, Sector Quebrada Segunda, 1300 m, 1 February 1995, (Fl.), *G. Mora 501* (CR); Paraíso, Orori, Estacion Tapanti, Rio Grande de Orosi, Sector a Segunda, 300 m, 13 March 1995, (Fr.), *G. Mora 568* (CR); Turrialba, Along camino Raíz de Hule, 1200–1400 m, 1 July 1976, (Fr.), *T. Croat 36723* (MO); Turrialba, Along camino Raíz de Hule, 1200–1400 m, 1 July 1976, (Fl.), *T. Croat 36748* (MO); Turrialba, Santa Cruz, Santa Cruz de Turrialba, hacia Bajos Bonilla, 1931 m, 19 December 2019, (Fr.), *M. Cedeño et al., 1628* (USJ); Turrialba, Chirripo, Moravia de Chirripó, bosque primario, 1196 m, 21 December 2019, (Fr.), *M. Cedeño et al., 1635* (USJ); Turrialba, Chirripo, Moravia de Chirripó, bosque primario, 196 m, 22 December 2019, (Fr.), *M. Cedeño et al., 1636* (USJ); Turrialba, Chirripo, Moravia de Chirripó, bosque primario, 1196 m, 23 December 2019, (Fr.), *M. Cedeño et al., 1637* (USJ); Alvarado, Capellades, Carretera a Pacayas, 728 m, 8 November 2018, (Fr.), *M. Cedeño et al., 1498* (USJ); Alvarado, Capellades, Carretera a Pacayas, 1728 m, 8 November 2018, (Fr.), *M. Cedeño et al., 1500* (USJ); Paraiso, Reserva de Tapantí, 1300–1800 m, 1 November 1982, (Fr.), *L. Gómez 18772* (MO); Paraiso, Along tributary of Quebrada Casa Blanca Tapantí, 1350 m m, 6 August 1984, (Fl.), *M. Grayum 3696* (MO); Paraiso, Hill just to north of Quebrada Casa Blanca, 1350 m, 26 August 1984, (Fr.), *M. Grayum 3889* (MO); Paraiso, Disturbed primary forest, 1400 m, 16 April 1967, (Fl.), *R. Lent 824* (MO); Paraiso, Tapantí Hydroelectric Reserve, 1600–1700 m, 23 June 1976, (Infer.), *T. Croat 36192* (MO); Paraiso, Hacienda Queverí, 1630 m, 15 July 1984, (Fr.), *M. Grayum 3490* (MO); Turrialba, Tayutic, 1500 m, 26 July 1995, (Fl.), *G. Herrera 8130* (CR); Turrialba, Along road between Juan Viñas and Turrialba, 1 July 1976, (Infer.), *T. Croat 36827* (MO); Paraiso, Tapantí Reserve, 1500–1800 m, 29 September 1987, (Fr.), *T. Croat 68291* (MO); Turrialba, Alvarado, Capellades, Santa Cruz, Linderos del Río Turrialba, 1750 m, 19 June 2015, (Fr.), *M. Cedeño 794* (USJ); Paraíso, Orosi, Parque Nacional Tapantí, Proyecto Tapantí-Micorriza de Melania Fernández, 1260 m, 29 Junio 2016, (Fl.), *M. Cedeño & M. Fernández 912* (USJ); Paraíso, Paraíso, Bosque secundafrio municipal, calle Mero, 1400 m, 6 July 2015, (Fl.), *M. Mata et al., 3* (USJ); La unión, San Ramón, Finca Siete Manantiales, 1450 m, 3 December 2017, (Fr.), *M. Cedeño 1178* (USJ). **Limón**. Limón, Valle La Estrella, N flank of Fila de Matama in headwaters of Rio Boyei, 1200 m, 16 August 1995, (Fr.), *M. Grayum 11025* (CR, MO); Talamanca, Bratsi, Amubri, Alto Lari, Kivut, Subiendo entre las cabeceras del Rio

Lari y Rio Dapari, 1550 m, 15 March 1992, (Fl.), *G. Herrera 5358* (CR). **San José**. San José, Near Río Tiribí along road to Planta Eléctrica María del Rosario, SW of Rancho Redondo, Montes de Oca m, 24 June 1984, (Infer.), *M. Grayum & P. Sleeper 3304* (CR); Curridabat, Tirrases, Remnant forest above río Tiribi, near Maria del Socorro Power Plant, 5 km NW of Tres Ríos, 1700 m, 28 May 1967, (Fr.), *R. Lent 1006* (CR); Vázquez de Coronado, Cascajal. P. N. Braulio Carrillo, Bajo La Hondura, 800 m después del portón, 1400 m, 2 November 2005, (Fr.), *L. Acosta 3777* (CR); Vázquez de Coronado, Cascajal, Bajo La Hondura, entrendo por antiguo camino de mulas, 1400 m, 10 February 2000, (Fr.), *A. Rodríguez 5734* (CR); Desamparados, San Miguel, Camino rural entre pequeños fragmentos de bosque y potreros arbolados a 4.5 km E de Tobosi, siguiendo la carretera 228, 1850 m, 8 April 2015, (Fl.), *A. Cascante & C. Trejos 2538* (USJ).

17. *Monstera limitaris* M.Cedeño, *Phytotaxa* 376: 37. 2018. — Type: COSTA RICA. Puntarenas: Corredores, Canoas, Barrio el Triunfo, margen del Río, 130 m, 27 September 2017, *M. Cedeño 1129, I. Chinchilla, A.P. Karremans & G. Rojas-Alvarado* (holotype, USJ! [2 sheets]; isotype, PMA! [2 sheets]).

Robust nomadic vine, appressed-climbing habit. SEEDLINGS: bearing foliage leaves. JUVENILE PLANTS: root climbers; **stems** smooth, light green; **internodes** 3–4 cm long, 4–10 mm diam.; **blades** not appressed to the phorophyte. ADULT PLANTS: root climbers; **stems** beige, cylindrical; **internodes** 2–3 cm long, 1.5–3.5 cm diam.; **cataphylls** light-green with a very reduced blade; **anchor roots** brown; **feeder roots** corky, light-beige; **petiole** whitish with dark pustules at the base, smooth towards the base of the geniculum, 30–55 cm long, fully sheathed; **petiole sheath** deciduous or semi-persistent, convolute, forming a ligule of 2–4 mm; geniculum concave, smooth, sulcate adaxially, convex abaxially, 3–4.5 cm long; **blades** sub-ovate to sub-orbicular, oblique, cordate to obtuse at the base, acuminate at apex, subcoriaceous, drying yellowish, 35–55 × 20–35 cm, decurrent-wavy on the geniculum, with 5–7 undulations of 3–5 mm wide; **midrib** ribbed adaxially, convex abaxially, drying yellowish or pale on both surfaces, **primary lateral veins** 17–23 per side, sunken adaxially, prominent abaxially, departing midrib at 75–85°, drying yellowish or pale; **secondary veins** reticulate; **collective veins** visible; **fenestrations** present along each side near to the midrib; **margins** pinnatilobed due to tearing of the perforations that extend close to the margin, 3–6 lobes per side, reaching to the middle of the blade. INFLORESCENCES on ascending stems, 1–3 simultaneously at flowering time, arranged in the axils of the leaves or into cataphylls; **peduncle** smooth, 10–15 cm long; **spathe** acuminate, white during development, white-yellowish externally and white internally at anthesis, thin membranous, open at apex, forming a tube in the base, deciduous after anthesis, 13–18 × 6–10 cm, up to 8 cm longer than the spadix; **spadix** white during

development, cream at anthesis, 9–12 cm long, 1–2.5 cm diam.; **basal sterile flowers** 3–5 mm long with a transparent stigmatic secretion; **fertile flowers** 5–6 mm long; stamens with laminar filaments, 2–5 mm long; anthers 1.5–2 mm long; ovary rectangular in longitudinal section, ribbed, 4–5 × 2–3 mm; style hexagonal, 1–3 × 4–5 mm; stigmatophore columnar, 0.5–1.5 mm long; stigma linear, with a transparent stigmatic secretion; **berries** with a light-green stylar cap during development, mature stylar cap creamy; pulp white; **seeds** black, lung-shaped, 4–6 mm long. (**Figure 32)**.

Distribution and habitat: This species is known only from the border between Costa Rica (Puntarenas province) and Panama (Chiriquí province), at 130 m. The collection sites consist of isolated trees in open agricultural areas (potreros), on the banks of a small rivers.

Phenology: In Costa Rica, flowering and fruiting have been recorded in September.

Conservation status: In Costa Rica, *Monstera limitaris* is restricted to isolated populations in a small geographic area. The habitat where it grows, in both countries, is strongly impacted by human activities, especially due to agricultural expansion.

Comments: The species is a member of sect. *Monstera*. It differs from the other species of the genus in Costa Rica by the petiole with white dots, sheathing throughout its length, the sheath semi-persistent, the leaf blade fenestrate on each side next to the central nerve, with pinnatilobed margins, the spathe internally white and externally yellowish, with overlapping margins (forming a tube) in the basal part.

Monstera limitaris is similar to *M. dissecta*, but the latter species differs in having leaves with smooth petioles (not verruculose) with persistent and revolute sheaths, non-crenate geniculum margins, blades with entire to pinnatifid margins without fenestrations along the midrib, an externally yellow-cream spathe, semi-conical stigmatophores and orange stigmatic secretion.

18. *Monstera luteynii* Madison, *Contr. Gray Herb.* 207: 89. 1977. — Type: COSTA RICA. Alajuela: along road to and around the edge of Laguna Hule, NE of Cerro Congo, and about 8 km NW of the village of Cariblanco, 20 km N of Vara Blanca, alt. 740–900 m, June 1972, *J. Luteyn 3227* (holotype, MO!; isotypes, US!, DUKE!).

Nomadic vine, appressed-climbing and pendent habit. SEEDLINGS: filiform. JUVENILE PLANTS: root climbers; **blades** appressed to the phorophyte. ADULT PLANTS: root climbers; **stems** light brown, warty with pustules, cylindrical and sulcate; **internodes** 3–10 cm long, 1–1.5 cm diam.; **anchor roots** 2–4 cm long; **feeder roots** whitish and corky; **petiole** smooth and striated at the base, 8–13 cm long, sheathed to the base of the geniculum,

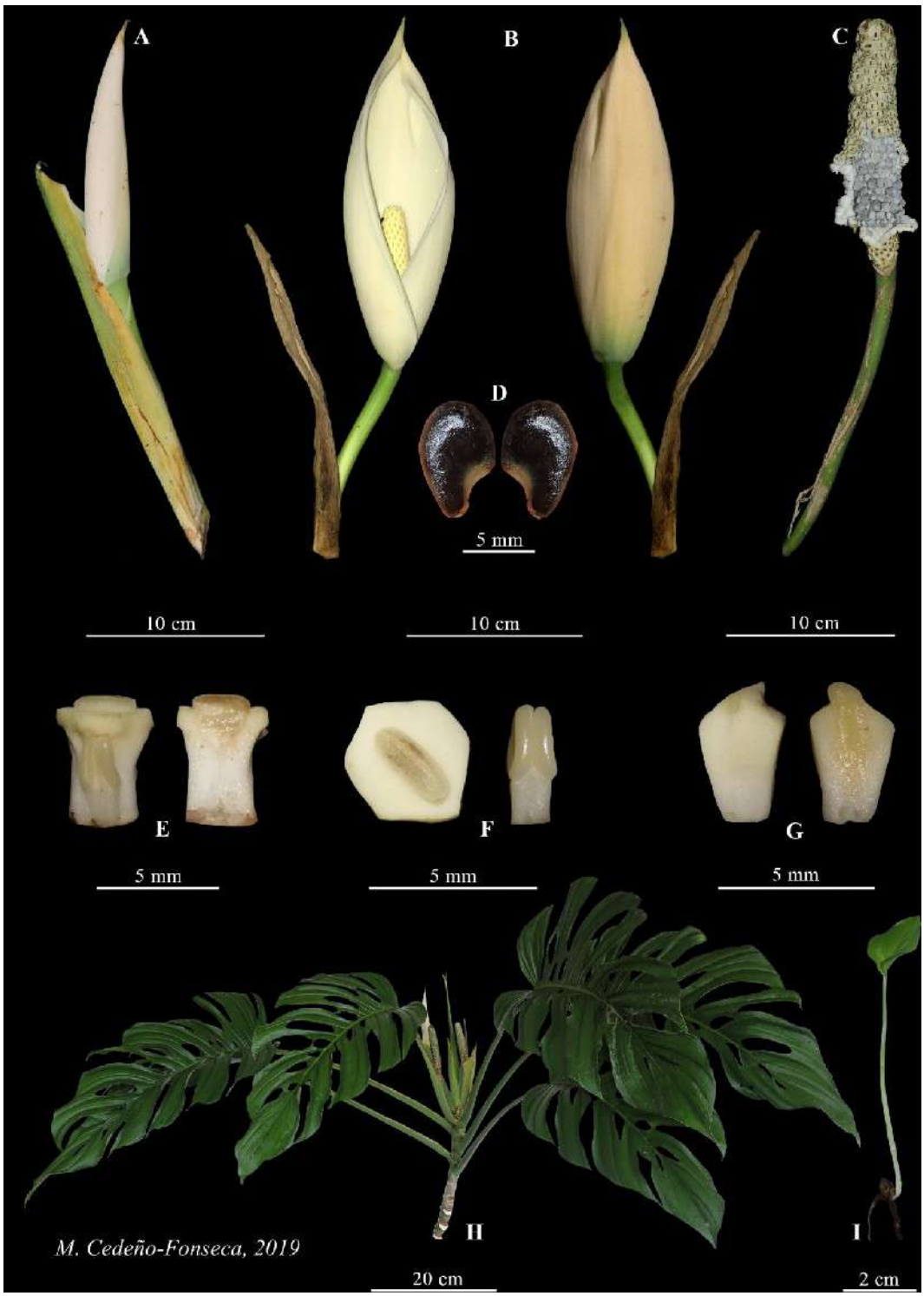

Figure 32. *Monstera limitaris*. (A) Inflorescence development. (B) Front and back views of open inflorescence. C. Mature infructescence, stylar plates detached. (D) Seeds. (E) Fertile flower, in lateral view (left), and longitudinal section (right). (F) Stylar plate with stigma (left) and one stamen (right). (G) Sterile flower in lateral view (left) and in longitudinal section (right). (H) Adult plant. (I) seedling. *M. Cedeño et al. 1129* (USJ).

prolonged into a free ligule 1–3 cm long; **petiole sheath** deciduous; geniculum striated abaxially, terete, 0.5–1 cm long; **blades** ovate to broadly elliptic, rounded to truncated, cordate or subcordate at the base, acuminate at apex, coriaceous, drying yellowish or black with yellowish green, 12–16 × 9–13 cm, not decurrent on geniculum; **midrib** flattened adaxially, convex abaxially, **primary lateral veins** 4–6 per side, obscure adaxially, prominent abaxially, departing midrib at 35–50°; **secondary veins** prominent and reticulated towards the margin; **collective veins** not visible; **fenestrations** absent; **margins** entire. INFLORESCENCES on pendent stems; **peduncle** smooth, 3–5 cm long, 5–8 mm diam.; **spathe** obtuse, unknown color; **spadix** unknown during development, creamy-white at anthesis, 6–8 cm long, 1.7–2 cm diam., 1.6–3.4 times longer than wide; **basal sterile flowers** 3–5 mm long; **fertile flowers** 3–6 mm long; stamens with laminar filaments, 1–6 mm long; anthers 1–2 mm long; ovary unknown; style compressed and hexagonal, 1–2 × 3–4 mm; stigma linear or circular; **berries** with a olive-green stylar cap during development, mature stylar cap unknown; pulp unknown; **seeds** unknown. (**Figure 33)**.

Distribution and habitat: Endemic from Costa Rica. Is distributed in the Carribean watershed of the Cordillera de Tilarán (La Balsa de San Ramón), Volcánica Central (Laguna Hule), and the Talamanca (Las Vueltas de Tucurrique), at 360–900 m. It lives in a *Tropical wet forest* life zone; primary and secondary forest.

Phenology: In Costa Rica, the flowering has been recorded in November, and fruiting in March.

Conservation status: *Monstera luteynii* is protected in the Zona Protectora Arenal-Monteverde, and the Reserva Biológica Monteverde.

Comments: The species is a member of sect. *Marcgraviopsis*. It is known from the type locality in Cariblanco (around the Hule Lagoon), the sector of Peñas Blancas in San Carlos and the Monteverde Biological Reserve on the Quebrada Celeste in the basin of the Peñas Blancas River. It resembles *Monstera pittieri* (both bloom on hanging stems), but that species has flowers somewhat separated on the spadix. Madison (1977) distinguished *Monstera luteynii* by having ovate leaves less than twice as long as wide, verrucate stems and petioles, whereas *M. pittieri* has lanceolate leaves, 2–5 times longer than broad, and smooth stems and petioles.

Additional specimens seen: COSTA RICA: **Alajuela**. San Ramón, Ángeles, Remnant trees in pasture, 2 km N.E. of La Balsa de San Ramón, 900 m, 26 September 1976, (Fl.), *R. Lent 3889* (CR, MO); San Ramón, Peñas Blancas, Quebrada Celeste, Rio Penas Blancas, Campo, 900 m, 6 November 1989, (Fl.), *E. Bello 1468* (CR). **Cartago**. Jiménez, Lurtes arbres a Las Vueltas, 635 m, 1 Enero 1898, (Fr.), *A. Tonduz 12841* (MO). **Limón**. Limón, Valle La Estrella, Fila Carbón, Buena Vista;

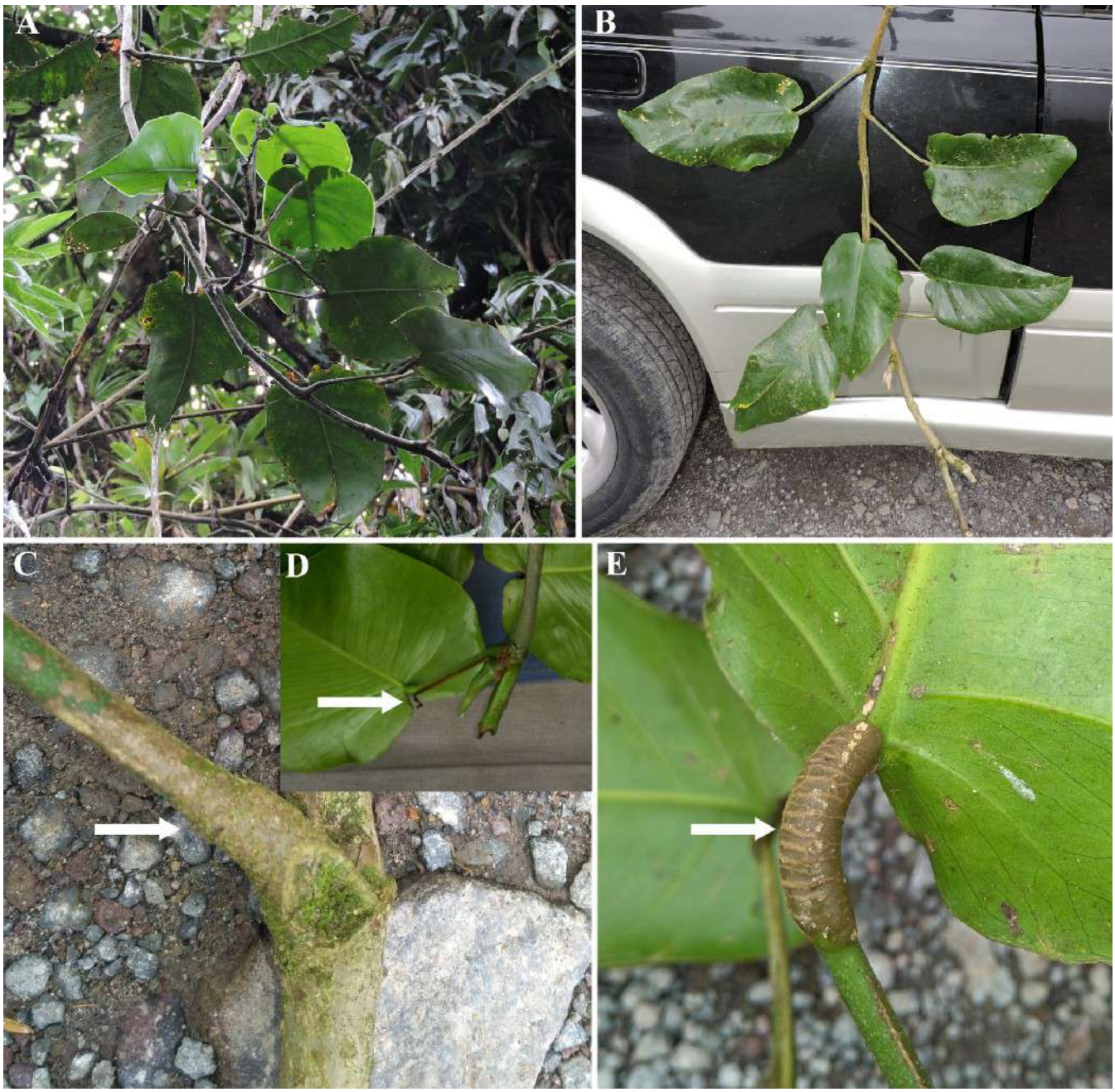

Figure 33. *Monstera luteynii*. A. Branching pendent habit. (B) Stem with entire cordate leaves. (C) Stem and base of petioles densely verrucose with light brown pustules. (D) Leaves on a hanging stem with a persistent but dry sheath and a 2 cm long ligule (arrow). (E) Densely striate and terete scaly geniculum. *M. Cedeño et al. 1672* (USJ).

pastizales arbolados y ecotonos boscosos, 360 m, 26 March 2003, (Fr.), *J. González 3272* (CR).

19. *Monstera membranacea* Madison, *Contr. Gray Herb.* 207: 55. 1977. — Type: COSTA RICA. Prov. San José: [Puriscal], western slope of Cerro Tufares, 800 m, 2 October 1972, *M. Madison 738* (holotype, GH! [2 sheets]; isotypes, CR!, MO!).

Nomadic vine, appressed-climbing habit. SEEDLINGS: bearing foliage leaves. JUVENILE PLANTS: root climbers; **stems** dark green, smooth, cylindrical; **internodes** 3–8 cm long, 2–4 mm diam.; **petiole** distinct, light green, smooth, 3–6 cm long, sheathed up to half its length, **petiole sheath** persistent; **blades** ovate, cordate at the base, acuminate at apex, membranous, 7–10 × 3–6 cm, not appressed to the phorophyte; **fenestrations** absent. ADULT PLANTS: root climbers; **stems** bright green, glossy, smooth, cylindrical; **internodes** 1–3 cm long, 1–2.5 cm diam.; **cataphylls** with a very reduced blade, light green, deciduous; **anchor roots** black; **feeder roots** light brown; **petiole** light green, smooth, 25–60 cm long, sheathed up to the medial part or 5–7 cm before the base of the geniculum; **petiole sheath** persistent; **unsheathed portion** terete; geniculum smooth, slightly terete, 1.0–2.5 cm long; **blades** ovate or elliptic, subcordate to cordate at the base, obtuse at apex, membranous, drying greenish, yellowish, greyish or blackish, 18–55 × 15–30 cm, 1.1–1.8 times longer than wide, decurrent on geniculum, decurrent portion 1–2 mm wide; **midrib** ribbed adaxially, convex abaxially, drying reddish, blackish or yellowish on both surfaces; **primary lateral veins** 8–12 per side, bifurcated or trifurcated, markedly reticulated towards the margin, strongly sunken adaxially, prominent abaxially, departing midrib at 65–70°, drying yellowish, blackish; **secondary veins** reticulate; **collective veins** not visible; **fenestrations** absent or present, arranged in a single series near the midrib, on one or both sides; **margins** entire or pinnatilobed, 4–10 lobes per side. INFLORESCENCES on ascending stems, 1–5 simultaneously at flowering time, arranged in the axils of the leaves or subtended by cataphylls; **peduncle** smooth, 9–20 cm long, **spathe** long-acuminate, light green during development, yellowish-green externally and cream internally at anthesis, coriaceous, open in the medial part, closed at the base and apex, deciduous as fragments post-anthesis, 10–17 × 5–9 cm, up to 5 cm longer than spadix; **spadix** white during development, cream at anthesis, 7–11 cm long, 1.0–3.5 cm diam., 5.4–5 times longer than wide; **basal sterile flowers** 4–5 mm long, with a yellowish stigmatic secretion; **fertile flowers** 5–7 mm long; stamens with laminar filaments, 1–2 mm long; anthers 1.5–2 mm long; ovary square in longitudinal section, ribbed, 2–3 × 3–4 mm; style compressed and hexagonal, 2–3 × 3.5–4 mm; stigmatophore slightly cupuliform, at the base slightly cleft on the style; stigma circular, with a yellowish stigmatic secretion; **berries** with a yellowish-green stylar cap during development, mature stylar cap yellow; pulp

orange; **seeds** globose, green with reddish dots, 4–7 mm long. (**Figure 34)**.

Distribution and habitat: From Costa Rica to Panama (Chirquí). In Costa Rica it is distributed from South of Caribbean watershed (Manzanillo and Arenal de Bribri) and the Pacific watershed (from the Río Grande de Tárcoles to Punta Burica), at 0–800 m. It lives in *Tropical wet forest* life zone; primary and secondary forest.

Phenology: In Costa Rica, flowering has been recorded in November, and fruiting from March to July.

Conservation status: *Monstera membranacea* is protected in the Refugio de Vida Silvestre Mixto Gandoca-Manzanillo, Reserva Indígena de Talamanca, Reserva Forestal Golfo Dulce, Parque Nacional Carara and Parque Nacional Corcovado.

Comments: The species is a member of sect. *Monstera*. It differs from the other species of the genus in Costa Rica by its light green petiole sheathed to half of its length with persistent wings, the bright green, distinctly membranous leaf blade, the spathe yellow externally and cream internally, with its margins overlapping at the base and apex (open only in the middle), and its infructescence with the stylar layer yellow green and the fruits with orange pulp. In the pre-adult state, *Monstera membranacea* can be confused with *M. filamentosa*, but the latter has brown petioles, sheathed to the base of the geniculum and with the wings of the sheath deciduous.

Grayum (2003a) reported *Monstera membranacea* only from the Pacific watershed, but it has since also been collected on the southern Caribbean side. The population of the Gandoca-Manzanillo Wildlife Refuge (discovered during the field work of this study) has more than 35 adult individuals, which grow on the edge of the road in a patch of forest 2 km from the center of Manzanillo town.

Additional specimens seen: COSTA RICA: **Limón**. Talamanca, Between Bri Bri and Sixaola, 20–70 m, 5 July 1983, (Fl.), *K. Barringer 3500* (MO); Talamanca, Bríbri, R.V.S.M. Manzanillo, 20 m, 3 March 2018, (Fr.), *M. Cedeño & M. Jiménez 1332* (USJ); Talamanca, Telire, Camino a Sibody, 130 m, 30 Abril 2017, (Fr.), *M. Cedeño et al., 1088* (USJ); Talamanca, Cahuita, Bosques de Manzanillo, 50 m, 9 January 2017, (Fl., Fr.), *M. Cedeño et al., 1106* (USJ). **Puntarenas**. Slopes above airport, disturbed priamary forest, Rincón, 150 m, 11 February 1974, (Fr.), *R. Liesner 2061* (CR, MO); P.N. Carara, Estación Quebrada Bonita, 30 m, 29 September 1983, (Fr.), I. *Chacón 1408* (CR); Garabito, Tárcoles, P.N. Carara. Estación Quebrada Bonita, Bosque primario, 50 m, 27 July 1990, (Fl.), *E. Bello 2379* (CR, MO); Golfito, Puerto Jiménez, P.N. Corcovado, Lower Lookout Trail, 25 m, 31 July 1988, (Fr.), *C. Kernan 744* (CR); Osa, Sierpe, 50 m, 24 March 1973, (Fr.), *W. Burger & J. Gentry 8865* (CR, MO); Golfito, Jiménez, Sector Los Patos, colecta en bosque a orilla del río

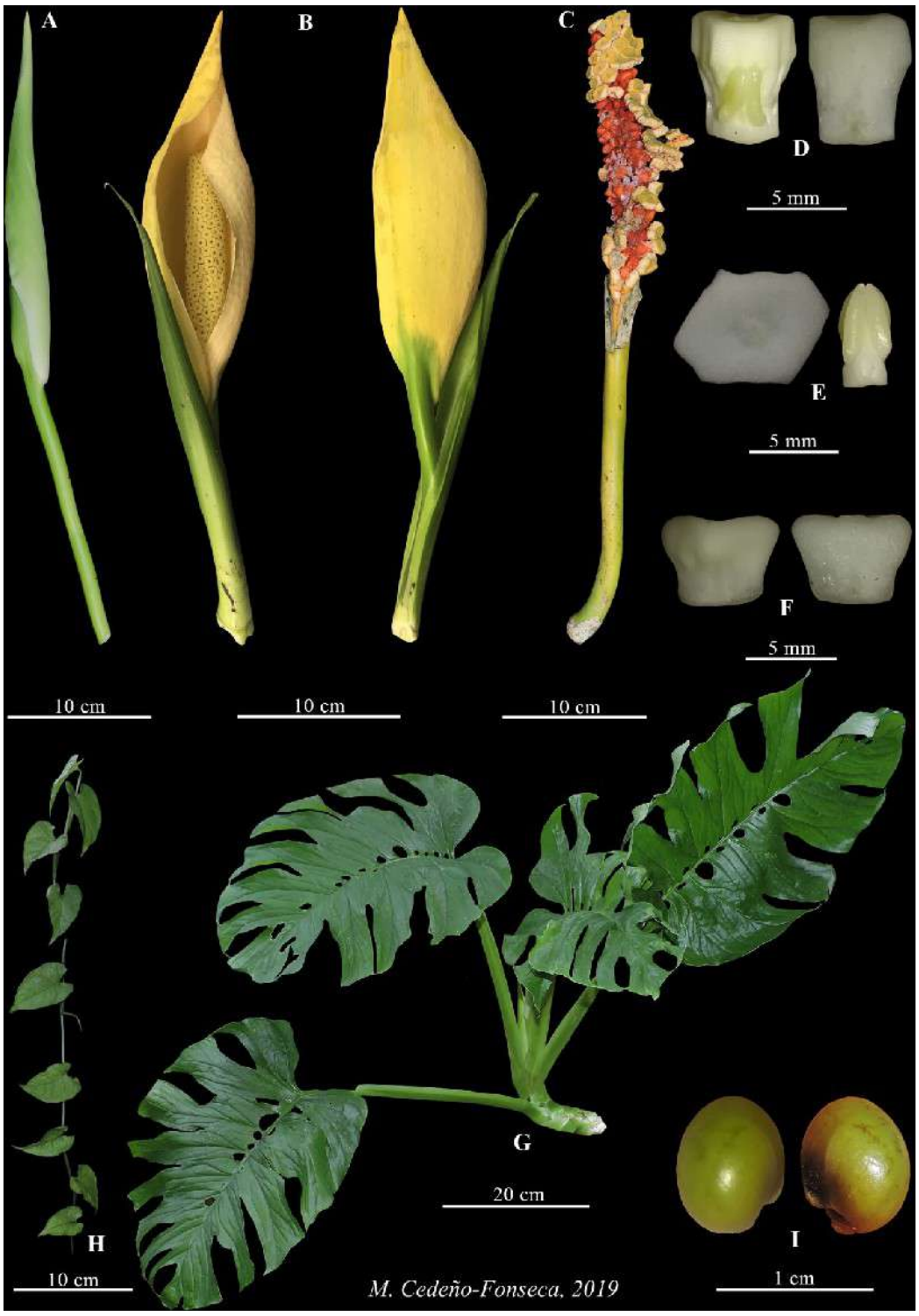

Figure 34. *Monstera membranacea*. (A) Developing inflorescence. (B) Inflorescence with open spathe, front and back views. (C) Mature infructescence, stylar plates detaching. (D) Fertile flower in lateral view (left) and in longitudinal section (right). (E) Stylar plate with stigma (left) and one stamen (right). (F) Sterile flower; lateral view (left) and longitudinal section (right). (G) Adult plant. (H) Juvenile plant. (I) Seeds. *M. Cedeño et al. 1532* (USJ).

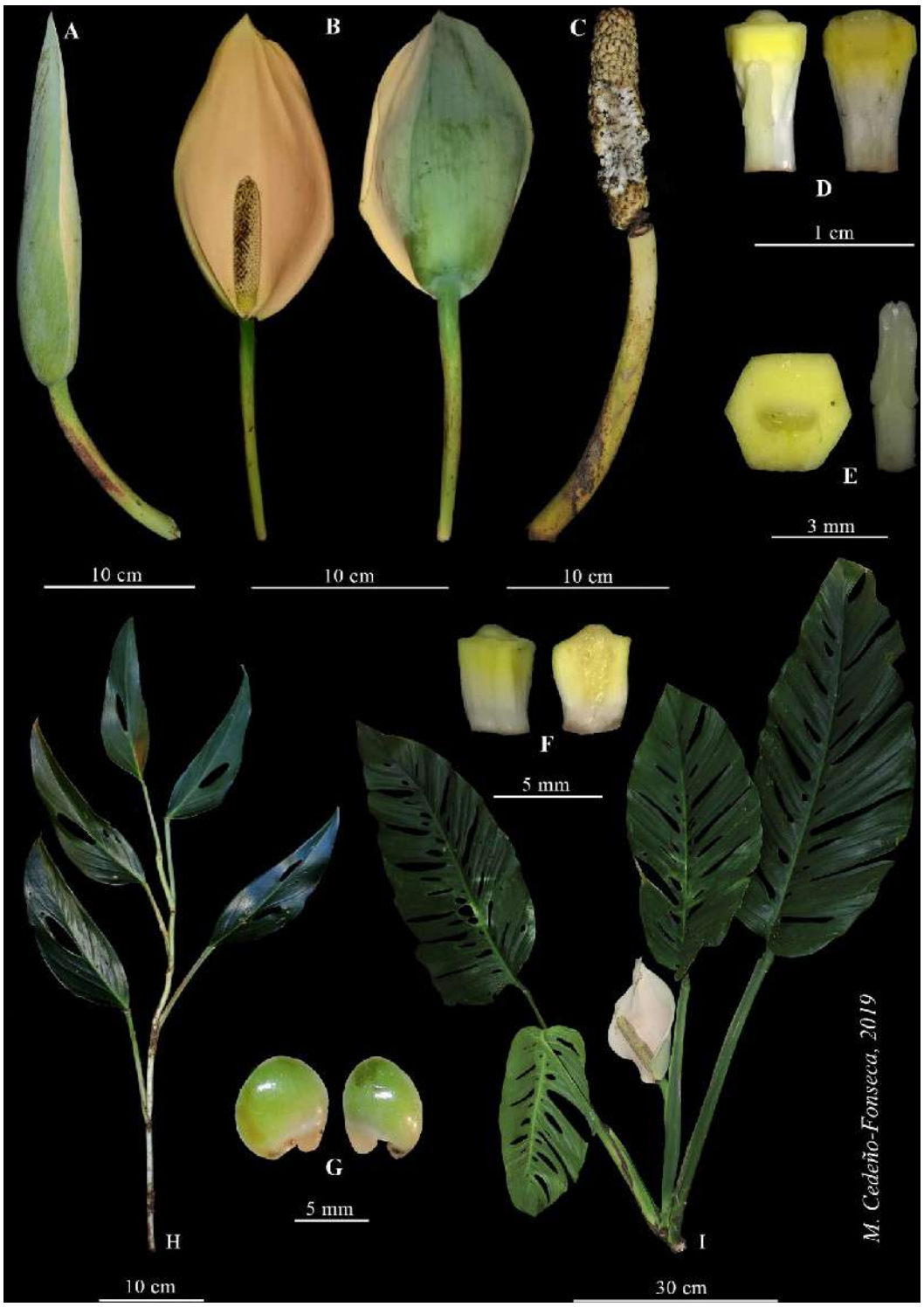

Figure 35. *Monstera mittermeieri*. (A) Developing inflorescence. (B) Front and back views of open inflorescence. (C) Mature infructescence, stylar plates detached. (D) Fertile flower, in lateral view (left), and longitudinal section (right). (E) Stylar plate with stigma (left) and one stamen (right). (F) Sterile flower in lateral view (left) and in longitudinal section (right). (G) Seeds. (H) Juvenile plant. (I) Adult plant. *M. Cedeño et al. 1013* (USJ).

Rincón, 70 m, 17 May 2000, (Fl.), *L. Acosta 1248* (CR, MO); Golfito, Jiménez, Sector Los Patos, colecta en bosque a orilla del río Rincón, 70 m, 17 Mayo 2000, (Fr.), *L. Acosta 1252* (CR); Golfito, Jiménez, In low, flat forest from Rio Sirena to Rio Pavo, 25 m, 2 April 1988, (Fl., Fr.), *B. Hammel 16638* (CR, MO); Golfito, Jiménez, La Palma, Rio Rincon aguas arriba, camino a Cerro de Oro, 100 m, 30 July 1990, (Fr.), *G. Herrera 4062* (CR, MO); Golfito, Jiménez, Sirena, Pavo Trail to old airstrip, 1 m, 21 June 1989, (Fr.), *C. Kernan 1173* (CR); Osa, Moist forest in valley-bottoms, 50–200 m, 1 September 1970, (Fr.), *W. Burger 7212* (MO); Along highway to Golfito from Panamerican Hwy. at Río Claro, 60 m, 14 September 1987, (Infer.), *T. Croat 67592* (MO); Forest at eastern base of Fila Barriganes. Ca. 1 km S and 3 km W of Clañasas, 60 m, 4 March 1985, (Infer.), *T. Croat 59821A* (MO); Lowland forest between guard station and Quebrada Bonita, 40 m m, 25 July 1985, (Fl.), *M. Grayum 5706* (MO); Osa, Corcovado National Park, Primary forest on hills 0 km to 1 km W of the park headquarters at Sirena, 0–200 m m, 4 July 1977, (Fl., Fr.), *R. Liesner 2828* (MO). **San José**. Acosta, Sabanillas, Acosta, Las Vegas, Rio Parritilla, camino a Alto Pitales, 200 m, 3 May 1997, (Fr.), *J. Morales 6179* (CR, MO); Puriscal, Chires, Camino viejo a Quepos, A orillas del camino, 700 m, 21 May 2005, (Fr.), *D. Santamaría 2052* (CR).

20. *Monstera mittermeieri* M.Cedeño, *Phytotaxa* 514(3): 217. 2021. — Type: COSTA RICA. Puntarenas. Buenos Aires. Buenos Aires. Olan, Sendero a Cerro Arbolada, 2000 m 15 January 2017, *M. Cedeño, I. Chinchilla, A. Karremans & D. Bogarin 1013*, (holotype, USJ!; isotype, MO!).

Robust nomadic vine, with appressed-climbing habit. SEEDLINGS bearing foliage leaves. JUVENILE PLANTS: root climbers; **stems** light green with white dots, smooth; **internodes** 4–6 cm long, 3–5 mm diam.; **petiole** conspicuous, dark or light green, smooth, 7–12 cm long, sheathed to the base of the geniculum; **petiole sheath** semi-persistent; blades lanceolate, attenuate or truncate at the base, acuminate at apex, coriaceous, 8–13 × 2–5 cm, not appressed to the phorophyte; **fenestrations** 1 or 2 elongate. ADULT PLANTS: root climbers; **stems** light-gold, cylindrical; **internodes** 1–5 cm long, 1–2.5 cm diam.; **anchor roots** beige; **feeder roots** brown; **petiole** dark green, finely asperous, 40–60 cm long, sheathed to the base of the geniculum; **petiole sheath** thin and semi-persistent; geniculum smooth, flattened adaxially, convex abaxially, 1–2 cm long; **blades** lanceolate or oblong, rounded, subcordate to obtuse at the base, acuminate at apex, sub-coriaceous, 35–55 × 14–30 cm, decurrent on geniculum (continuous with petiole sheaths), decurrent portion 2–4 mm wide; **midrib** grooved adaxially, convex abaxially; **primary lateral veins** 20–28 per side, sunken adaxially, prominent abaxially, departing midrib at 75–85°; **secondary veins** reticulate; **collective veins** visible along the margin; **fenestrations** present, the ones located along each side of the midrib small and roundish, the ones located farther from the midrib much larger and elongated;

margins entire or pinnatilobed, due to tearing of the fenestrations that extend to the margin. INFLORESCENCES produced on ascending stems; **peduncle** smooth, 15–35 cm long; **spathe** acuminate with revolute margins, light green and pruinose externally and pale pink internally at anthesis, turning whitish after female anthesis, thick, completely open at apex, marcescent after anthesis, 15–20 × 9–12 cm, up to 5 cm longer than the spadix; **spadix** white during development, yellowish-cream at anthesis, 13–17 cm long, 1.5–2.5 cm diam.; **basal sterile flowers** green, 4–6 mm long, with a transparent stigmatic secretion; **fertile flowers** 5–7 mm long; stamens with laminar filaments, 2–6 mm long; anthers 2–3 mm long; ovary rectangular in longitudinal section, ribbed, 4–5 × 2–3 mm; style hexagonal, 2–3 × 3–4 mm; stigmatophore columnar, 0.5–1 mm long; stigma linear, with a transparent secretion; **berries** with a yellowish-green stylar cap during development, mature stylar cap white-cream; pulp white; **seeds** green, spherical, 6–8 mm long. (**Figure 35)**.

Distribution and habitat: *Monstera mittermeieri* is endemic to Costa Rica. It is present in the Pacific watershed in the Cordillera of Talamanca, at 2000–2100 m. It lives in the *Premontane rain forest* life zone, in the internal part of the forest, on trees with abundant bryophytes.

Phenology: In Costa Rica, the flowering and fruiting has been recorded in January.

Conservation status: *Monstera mittermeieri* is not found in any protected areas.

Comments: The species is a member of sect. *Monstera*. It differs from the other species of the genus in Costa Rica by the rough petiole, sheathing throughout its length with the sheath persistent, the leaf blade with elongated fenestrations towards the margin, and the light green spathe, glaucous externally and pale pink internally. It could be confused with *Monstera epipremnoides*, but that has a mottled or whitish petiole, a deeply pinnatifid leaf blade with fenestrations on each side next to the midrib or reaching the margin, and a spathe yellowish-green externally and cream internally. In the light pink spathe colouration it could be confused with *Monstera oreophila*, but *M. mittermeieri* differs in having the spathe thicker and persistent (vs. thin and deciduous spathe).

Additional specimens seen: COSTA RICA: **Puntarenas**. Buenos Aires, Buenos Aires, Olan, Sendero a Cerro Arbolada, 2000 m, 15 Enero 2017, *M. Cedeño 1012 et al.,* (USJ); Buenos Aires, Buenos Aires, Olan, Sendero a Cerro Arbolado, 2000 m 15 Enero 2017, *M. Cedeño et al., 1011* (USJ); Puntarenas, Buenos Aires, Buenos Aires, Gira Transtalamanca, 2060 m, 24 April 2017, (Fl.), *M. Cedeño et al., 1071* (USJ).

21. *Monstera molinae* Grayum, *Phytologia* 82: 48. 1997. — Type: COSTA RICA. Guanacaste: Parque Nacional Rincón de la Vieja, the SE slopes of Volcán Santa María,

above Estación Hacienda Santa María, 900–1200 m, 27–28 January 1983, *G. Davidse, L.D. Gómez, M. Sousa, C.J. Humphries, N. Garwood, R. Hampshire & M. Gibby 23344* (holotype, CR!; isotype, MO!).

Nomadic vine, appressed-climbing and pendent habit. SEEDLINGS: filiform. JUVENILE PLANTS: root climbers; **stems** dark green, smooth, cylindrical; **internodes** 4–6 cm long, 3–5 mm diam.; **petiole** distinct, dark green, smooth, 6–10 cm long, sheathed to the base of the geniculum; **petiole sheath** persistent; **blades** obovate, subcordate to truncated at the base, acuminate at apex, coriaceous, 7–10 × 5–8 cm, slightly appressed to the phorophyte; **fenestrations** absent. ADULT PLANTS: root climbers with free lateral branches; **stems** beige to light brown, smooth, cylindrical or dorsoventrally compressed and slightly sulcate; **internodes** 2–14 cm long, 6–5 mm diam.; **anchor roots** whitish; **feeder roots** dark brown; **petiole** light green, smooth, 10–25 cm long, sheathing to the base of the geniculum or the base of the leaf blade; **petiole sheath** persistent or semi-persistent; geniculum smooth, sunken adaxially, convex abaxially, 6–15 mm long; **blades** ovate, oblique, cordate to subcordate or obtuse at the base, acuminate at apex, coriaceous, drying reddish with black or brownish dots, 10–30 × 11–25 cm, 1.06–1.4 times longer than wide, decurrent on the geniculum, decurrent portion 1–2 mm wide; **midrib** ribbed adaxially, convex abaxially, drying dark or reddish brown on both surfaces, **primary lateral veins** 7–10 per side (occasionally 2 of them can emerge at once and then spread to the margin), strongly sunken adaxially, prominent abaxially, departing midrib at 75–80°, drying black up to the medial part; **secondary veins** prominent, reticulate towards the margin; **collective veins** not visible; **fenestrations** absent; **margins** entire or pinnatilobed with 2–4 lobes per side. INFLORESCENCES on free lateral shoots and ascending stems, 1–5 simultaneously at flowering time, arranged in the axils of the leaves; **peduncle** smooth, 4–5 cm long; **spathe** obtuse to short acuminate, light green during development, yellowish green externally and white internally at anthesis, completely open at apex, deciduous post-anthesis (tearing in several parts), 8–12 × 5–9 cm, up to 1 cm longer than the spadix; **spadix** white during development, cream at anthesis, 7–15 cm long, 2–3 cm diam., 3.2–3.4 times longer than wide; **basal sterile flowers** 4–5 mm long, with an orange stigmatic secretion; **fertile flowers** 4–7 mm long; stamens with laminar filaments, 1–2 mm long; anthers 1–3 mm long, the filaments do not exceed the styles at anthesis; the flowers on the spadix are separated, allowing exposure thecae; ovary square in longitudinal section, ribbed, slender than style, 2–4 × 2–3 mm; style square, cylindrical or hexagonal, 3–5 × 3–4 mm; stigma linear, cleft on style, black at anthesis; **berries** with a creamy stylar cap during development, mature stylar cap moss-green; pulp greyish; **seeds** light-brown with pale dots, elongated, 5–10 mm long. (**Figures 36 & 37**).

Distribution and habitat: Endemic to Costa Rica, in the Caribbean watershed, near to the continental divide, and on the Pacific side on Guanacaste, Tilarán and Central cordilleras, at 0–1200 m. It lives in *Tropical wet forest*, *Tropical wet forest transition to Premontane wet forest* life zones; in primary and secondary forest.

Phenology: In Costa Rica, flowering has been recorded in January to March, May, and November, and fruiting in June and December.

Conservation status: *Monstera molinae* is protected in the Estación Biológica La Selva, Reserva Biológica La Tirimbina, Parque Nacional Guanacaste, Parque Nacional Rincón de la Vieja, Parque Nacional Volcán Tenorio and Parque Nacional Braulio Carrillo.

Comments: The species is a member of sect. *Marcgraviopsis*. It differs from the other species of the genus in Costa Rica by the petiole sheathing to the base of the geniculum, semi-persistent wings of the petiolar sheath, the leaf blade pinnatilobed, with 1–4 lobes per side, inflorescences with the spathe tearing longitudinally, and the infructescence with the stylar cap moss green at maturity. It could be confused with *Monstera pittieri* and *M. tuberculata*, but these species have entire leaves (though *M. pittieri* has fenestrations in some populations in the south of the Caribbean side).

The populations of *Monstera molinae* are distributed only in the Caribbean slope and are located mainly in primary forests. Adult plants develop hanging reproductive stems. In La Tirimbina Biological Station, the reproductive hanging stems reach the ground, eventually becoming creeping.

Additional specimens seen: COSTA RICA: **Alajuela**. Upala, Aguas Claras, Cuenca del Pizote, 800 m, 4 March 1999, (Infer.), *G. Herrera 1517* (CR, MO); Upala, Dos Ríos, P.N. Guanacaste, Cordillera de Guanacaste, Estación San Ramón, Dos Ríos, Límite del parque a 2 km de la casa, 550 m, 27 January 1995, (Fr.), *F. Quesada 191* (CR, MO); Camino entre la estación de la Reserva Forestal de San Ramón y el camino a la colonia Palmareña, 1 February 1987, (Fr.), *G. Herrera 499* (MO); Along road between Cañas and Upala, 400 m, 24 June 1976, (Infer.), *T. Croat 36259* (MO); San Carlos, Llanura de San Carlos, 100 m, 21 February 1966, (Fr.), *A. Molina 17685* (MO); Remnant evergreen forest and secondary growth in the tropical-premontane wet forest transition zone about 3 km NNE of Bijagua along the new road to Upala, 450 m, 7 November 1975, (Fl., Fr.), *W. Burger 9882* (CR); Upala, Aguas Claras, Sendero Cabinas Bromelia, 600 m, 15 Diciembre 2016, (Fr.), *M. Cedeño et al., 983* (USJ). **Guanacaste**. Liberia, Mayorga, Estacion Cacao, Sendero casa de Fran, 1000 m, 9 February 1995, (Fr.), *E. Fletes 52* (CR); La Cruz, Santa Cecilia, Estacion Pitilla 9 km, S. de Santa Cecilia, 700 m, 14 July 1997, (Fr.), *C. Moraga 910* (CR, MO); Parque Nacional Rincón de la Vieja, 900–1200 m,

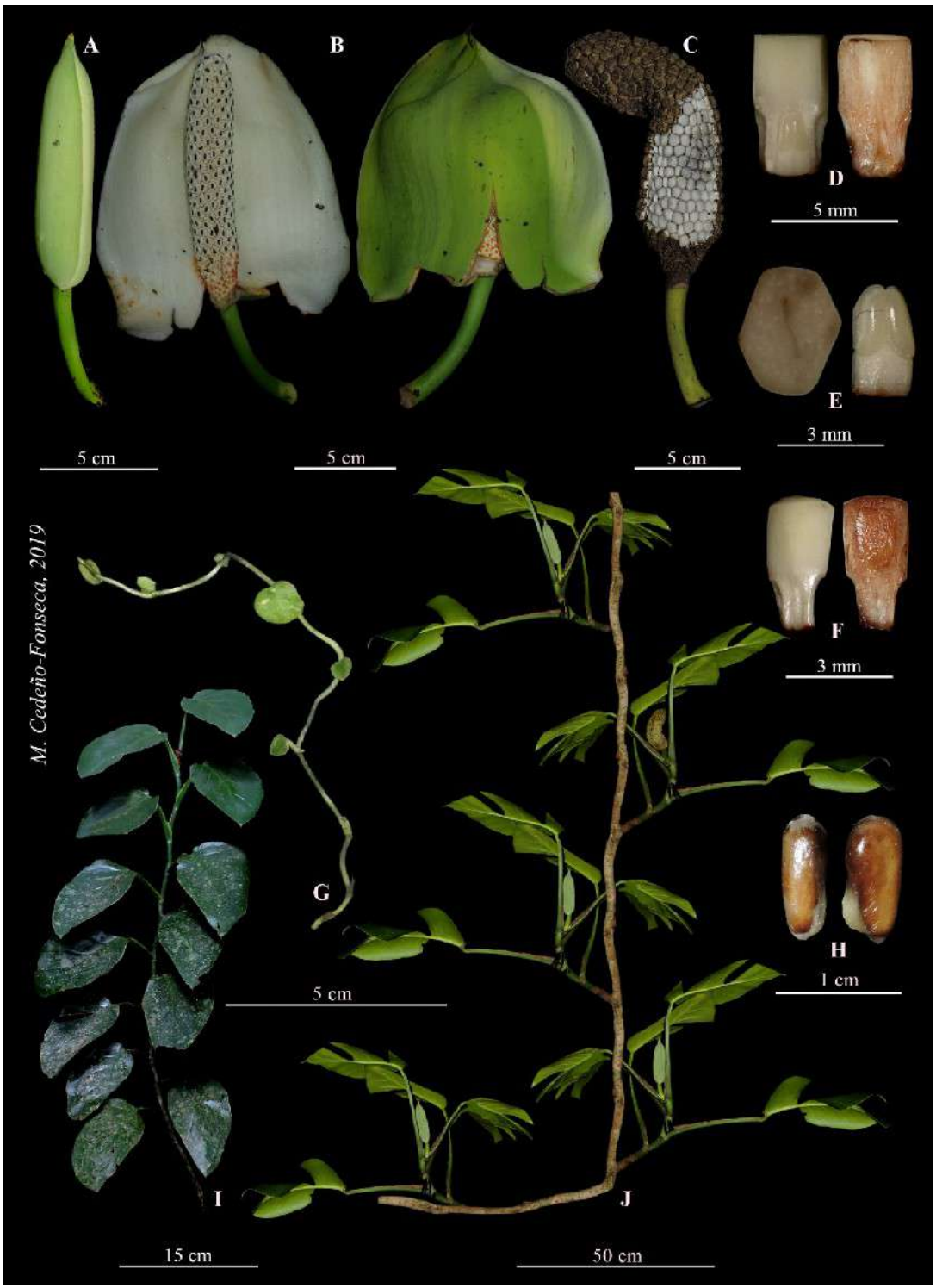

Figure 36. *Monstera molinae*. (A) Developing inflorescence. (B) Inflorescence with open spathe, front and back views. (C) Mature infructescence, stylar plates detached. (D) Fertile flower in lateral view (left) and in longitudinal section (right). (E) Stylar plate with stigma (left) and one stamen (right). (F) Sterile flower; lateral view (left) and longitudinal section (right). (G) Seedling. (H) Seeds. (I) Juvenile plant. (J) Adult plant flowering on free lateral shoots. *M. Cedeño et al. 899* (USJ).

Figure 37. *Monstera molinae*. Adult plant with hanging stems growing 20m above the ground. Tilaran, Guanacaste (not collected).

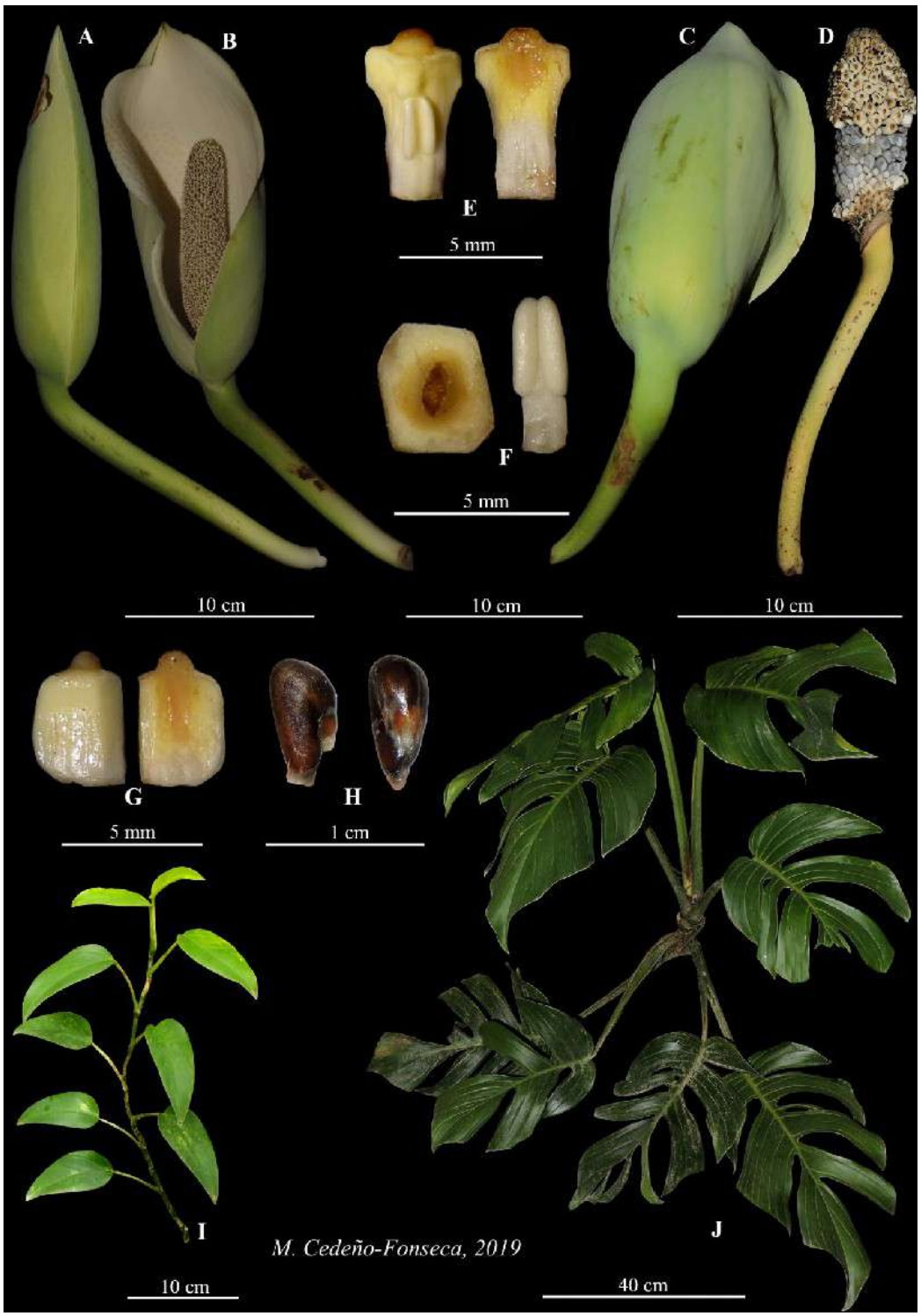

Figure 38. *Monstera monteverdensis*. (A) Developing inflorescence. (B) Open inflorescence, frontal view. (C) Open inflorescence, back view. (D) Mature infructescence, stylar plates detached in the middle part. (E) Fertile flower, in lateral view (left), and longitudinal section (right). (F) Stylar plate with stigma (left) and one stamen (right). (G) Sterile flower, in lateral view (left), and longitudinal section (right). (H) Seeds. (I) Portion of juvenile plant. (J) Portion of adult plant. *M. Cedeño et al. 1045* (USJ).

Figure 39. *Monstera monteverdensis*. Adult plant growing in the forests around Monteverde, Puntarenas (not collected).

27 Enero 1983, (Fr.), *G. Davidse 23344* (MO); Rincón de la Vieja National Park, 800 m, 28 January 1983, (Fr.), *N. Garwood 755* (CR, MO); El Dos de Tilaran, 1000 m, 12 April 1986, (Fr.), *W. Haber 4446* (CR, MO). **Heredia**. Sarapiqui, Near Puerto Viejo along road near the Río Sucio, 20 m, 27 May 1976, (Fr.), *T. Croat 35689* (MO); Sarapiqui, Sendero entre el campamento Canta Rana y Río Peje, 400 m, 14 January 1983, (Fr.), *I. Chacón 82* (MO); Heredia, Fila Carrillo, 700 m, 30 March 1984, (Fr.), *L. Gómez 21131* (CR, MO); Sarapiquí, La Virgen, Estación Biológica La Tirimbina, Sendero la Ceiba, 150 m, 6 June 2016, (Fr.), *M. Cedeño et al., 899* (USJ).

22. *Monstera monteverdensis* M.Cedeño & Croat, *Phytotaxa* 461 (3): 188. 2020. — Type: COSTA RICA. Puntarenas: Monteverde, Santa Elena, Camino a Selvatura, 1530 m, 11 March 2017, *M. Cedeño, M. Fernández & I. Chinchilla 1045* (holotype, USJ!; isotype, MO!).

Nomadic vine, appressed-climbing habit. SEEDLINGS: bearing foliage leaves. JUVENILE PLANTS: root climbers; **stem** light green with white dots; internodes 3–5 cm long, 3–5 mm diam. Leaves with **petioles** conspicuous, dark green or light green, smooth, 8–14 cm long, sheathed throughout its length, petiole sheath deciduous; **leaf blades** ovate or lanceolate, acuminate at apex, sub-cordate to truncate at base, with or without fenestrations (when present, usually on one side of blade, breaking the margin if very close to it), coriaceous, 7–14 × 3–9 cm, not flattened against the phorophyte. ADULT PLANTS: root climbers; **stem** light brown or beige, smooth, terete; internodes 1.5–3.5 cm long, 1–3.5 cm diam.; support roots light brown to brown, 3–6 cm long; feeder roots light brown; **petiole** dark green with white dots, smooth, 25–50 cm long, sheathed to the middle of the geniculum; **petiole sheath** involute in young leaves, becoming deciduous; **geniculum** smooth, flattened adaxially, rounded abaxially, 2–3 cm long; **blade** ovate to lanceolate in outline, oblique, acuminate at apex, sub-cordate to obtuse at base, decurrent to the middle of the geniculum, the decurrent portion 1–2 mm wide, coriaceous, 25–60 × 20–30 cm; midrib grooved above, transversally convex below; primary lateral veins 10–15 per side, impressed above, prominently raised below; collecting veins slightly visible; margins pinnatifid with 2–8 lobes per side, fenestrations sparse, rarely near the midrib. INFLORESCENCES on ascending stems; **peduncle** smooth, 14–20 cm long; **spathe** acuminate, light green and pruinose in developing inflorescences, externally light green and pruinose at anthesis, internally white, leathery, open at the apex, the margins overlapping at the base, deciduous after the anthesis, 15–20 × 9–14 cm, up to 7 cm longer than the spadix; **spadix** cream-colored during development, yellowish cream at anthesis, 6–14 cm long, 1.5–4 cm diameter; basal sterile flowers 4–6 mm long, with an orange or rusty-red secretion; **fertile flowers** 5–7 mm long; stamens with filament laminar, 1–6 mm long, anther 2–3 mm long; ovary rectangular in longitudinal section, ridged, 4–5 mm long, 2–3 mm

diameter; style hexagonal, 2–3 mm long, 4–5 mm diameter, stigmatophore cupular, 0.5–2 mm long, stigma linear to rhombic, with orange or rusty-red discharge. **berries** with the stylar layer light green during development, maturing white-cream; pulp white; **seeds** smooth, brown to dark brown, obliquely obovate, 8–10 mm long. (**Figures 38 & 39**).

Distribution and habitat: Endemic to Costa Rica, occurring on both Caribbean and Pacific slopes of the Cordillera de Guanacaste and Cordillera de Tilarán, and the extreme northwestern part of the Cordillera Central, at 500–2300 m. It lives in *Tropical rain forest*, *Premontane rain forest* and *Lower montane rain forest* life zones.

Phenology: In Costa Rica, the flowering has been recorded from December to June and in August, and fruiting has been recorded throughout the year.

Conservation status: *Monstera monteverdensis* is protected in the Reserva Biológica Alberto Manuel Brenes, Reserva Biológica del Bosque Nuboso Monteverde, Parque Nacional Rincón de la Vieja, Parque Nacional Volcán Tenorio and Parque Nacional Guanacaste.

Comments: The species is a member of sect. *Monstera*. It is characterized by its moderately slender stems, nearly fully sheathed petioles with the sheath mostly deciduous or persisting as fragments or fibres, small yellowish brown, narrowly ovate weakly perforated short-acuminate moderately inequilateral leaf blades as well as by the solitary inflorescence with the spathe much longer than the stubby spadix.

Monstera monteverdensis has been confused with *M. dissecta* but that species has larger more prominently pinnate leaves and petioles with a persistent sheath. Other species with which *Monstera monteverdensis* has been confused are *M. epipremnoides* and *M. lentii*, but it differs from *M. epipremnoides* by its deciduous (*vs.* persistent) petiolar sheaths, and pinnatifid leaves with few lateral lobes (2–8 per side) and few fenestrations or none (*vs.* pinnatifid with numerous lateral lobes (8–15 per side) with several fenestrations at either side of the midrib). It differs from *Monstera lentii* by its deciduous (*vs.* persistent) petiolar sheaths, thicker spathes, and styles with a cupular stigmatophore of 0.5–2 mm (*vs.* a conical stigmatophore of 3–4 mm).

Additional specimens seen: COSTA RICA: **Alajuela**. San Ramón, Peñas Blancas, Evergreen cloud forest and wet wind-gap formations (lower montane and premontane rain forest life zone) on and near the Continental Divide about 2 to 5 km east and southeast of Monteverde, 1650 m, 17 October 1978, (Fr.), *M. Thomas 738* (CR, MO); Woods on Atlantic side of Alto Palomo, 1900 m, 3 January 1970, (Fr.), *R. Lent 1846* (CR); San Carlos, La Fortuna, Finca El Jilguero, Cumbre del Volcán Chato, 1140 m, 25 November 1992, (Fr.), *G. Herrera 5647* (CR); R.F. Grecia, En bosque secundario, Bosque del Niño, 1700 m, 2

October 1986, (Fr.), *G. Umaña 104* (CR); Reserva Forestal Grecia, 1000 m, 16 Enero 1987, (Fl.), *G. Herrera 405* (MO); San Ramon, Small patch of primary cloud forest on N slope of Cerros Pata de Gallo, 1480 m, 18 November 1988, (Fr.), *M. Grayum 9093* (MO); San Ramon, Along road from San Ramón northward through Balsa, 700–800 m, 29 August 1979, (Fr.), *W. Stevens 13860* (MO); San Ramon, Along road from San Ramón northward through Balsa, 1100–1150 m, 10 September 1979, (Infer.), *W. Stevens 14129* (MO); Along road between San Ramón and Balsa, 1200 m, 2 February 1979, (Fr.), *T. Croat 46841* (MO); San Ramón, Ángeles, R.F. San Ramón, Ca. 10 km west of Lagitos; in forest on ridge and secondary woods along Río San Lorencito, 950 m, 30 May 1986, (Fl.), *B. Hammel et al., 15239* (CR, MO); San Ramón, Angeles, Estacion Rio San Lorenzo, 800 m, 22 April 1994, (Fl., Fr.), *Z. Fuentes 757* (CR). **Guanacaste**. Cañas, Palmira, Agua Caliente, subiendo el Volcán Tenorio, 1326 m, 19 December 2015, (Fr.), *M. Cedeño & M. Campos 847* (USJ); Liberia, Curubandé, Estacion Las Pailas; sendero a Santa Maria, 1200 m, 29 May 1994, (Fr.), *D. Garcia 259* (CR); Cañas, Palmira, Agua Caliente, subiendo el Volcán Tenorio, 1326 m, 19 December 2015, (Fr.), *M. Cedeño & M. Campos 846* (USJ); Tilarán, Quebrada Grande, R.B. Monteverde, 1 km N Las Nubes Village, 8 km NW Monteverde, premontane rain forest, 200 m, 31 August 1989, (Fl.), *W. Haber & W. Zuchowski 9520* (CR); Tilarán, Tronadora, R.B. Monteverde, 3.5 km N Santa Elena on road to San Gerardo, 0.5 km N of junction road and Río Negro, Lower montane wet forest, 1540 m, 20 August 1988, (Fl.), W. *Haber & W. Zuchowski 8619* (CR); Tilarán, Tronadora, R.B. Monteverde, Trayecto de la Torre a Río Negro, división entre Alajuela - Puntarenas y Guanacaste, en tre las vertientes Pacífica y Norte, 1650 m, 21 January 1988, (Fr.), *W. Haber & E. Bello 8021* (CR); Tilarán, Quebrada Grande, Quebrada Grande, Tilaran, Sendero Esperanza-Las Nubes, Division Continental, Bosque pluvial premontano, 1300 m, 24 February 1987, (Fr.), *W. Haber 6685* (CR, MO); La Cruz, Santa Cecilia, P.N. Guanacaste, La Cruz - 9 km al sur de Santa Cecilia, Estación Pitilla, 700 m, 28 September 1990, (Fr.), *C. Chávez 187* (CR, MO); La Cruz, Santa Cecilia, P.N. Guanacaste, La Cruz - 9 km al sur de Santa Cecilia, Estación Pitilla, 700 m, 24 October 1990, (Fr.), *C. Chávez 297* (CR); La Chirripa ridge, 1000 m, 8 May 1986, (Fl.), *W. Haber 4858* (MO); Río Chiquito valley, 700 m, 12 April 1986, (Fr.), *W. Haber 4456* (MO); Río Chiquito de Tilaran, Río Negro, 1450 m, 1 July 1986, (Fr.), *W. Haber 5168* (MO); Guanacaste, Cañas, Palmira, Agua Caliente, subiendo el Volcán Tenorio, 1326 m, 19 December 2015, (Fr.), *M. Cedeño & M. Campos 843* (USJ); Guanacaste, Cañas, Palmira, Agua Caliente, subiendo el Volcán Tenorio, 1326 m, 19 December 2015, (Fl.), *M. Cedeño & M. Campos 845* (CR); Guanacaste, Tilarán, Tilarán, Camino a Tilarán, 1325 m, 21 November 2018, (Fr.), *M. Cedeño & A. Cascante 1502* (USJ). **Heredia.** Colonia Virgen del Socorro, Cariblanco. 1000 m, 3 June 1983, (Fl.), *C. Chacón & B. Ocampo 67* (CR); Heredia, Barva, Concepción, Subiendo al Parque

Nacional Braulio Carrillo, sector Volcán Barva, 2300 m, 26 February 2018, (Fl., Fr.), *M. Cedeño et al.,1353* (USJ); San Isidro, Heredia and San José provinces, 1600–1800 m, 13 September 1978, (Fr.), *W. Burger 11023* (MO). **Puntarenas**. Puntarenas, Monteverde, Santa Elena, Camino a Selvatura, 1530 m, 11 Marzo 2017, *M. Cedeño et al. 1045* (USJ, MO); 2 km NE Santa Elena on border of Monteverde Reserve, Upper San Gerardo, 1550 m, 20 November 1988, (Fr.), *W. Haber 8795* (CR, MO); Monteverde community, 1400 m, 15 May 1986, (Fr.), *W. Haber 4927* (MO); Hills above Santa Elena, 1450 m, 11 June 1986, (Fr.), *W. Haber 5054* (MO); Puntarenas, Monteverde, Monteverde community, Pacific slope, 500 m, 28 August 1989, (Fr.), *W. Haber 9336* (CR, MO); Monteverde Cloud Forest Reserve,1600 m, 14 January 1986, (Fr.), *W. Haber 4274* (MO); Puntarenas, R.B. Monteverde; Cordillera de Tilarán, Cerro Ojo de Agua, 1600 m, 24 August 1993, (Fl.), *E. Bello 5235* (CR, MO); Puntarenas, Monteverde, Community, En faja de bosque perturbado cerca de Divis de Reserva, 1540 m, 23 junio 1977, (fl.), *V. Dryer 1521* (CR).

23. *Monstera obliqua* Miq., *Linnaea* 18: 79. 1844. — Type: SURINAME. [Wanica]: Vredenburger-Zandrits, October 1842, *H.C. Focke 719* (holotype, U n.v.; photos: BH, SEL! sheet 006766).

Nomadic vine, appressed-climbing habit. SEEDLINGS: bearing foliage leaves. JUVENILE PLANTS: root climbers; **stems** smooth, dark green; **internodes** 3–5 cm long, 2–5 mm diam.; **petiole** conspicuous, dark green, smooth 5–11 cm long, sheathing to the base of the geniculum; **petiole sheath** deciduous; **blades** lanceolate, truncate at the base, acuminate at apex, sub-coriaceous, 7–13 × 2–4 cm, not appressed to the phorophyte; **fenestrations** absent. ADULT PLANTS: root climbers; **stems** smooth, light to dark green; **internodes** 2–10 cm long, 3–5 mm diam.; **cataphylls** light-green, deciduous but leaving dry fragments on peduncles; **anchor roots** black; **feeder roots** black; **petiole** light green, smooth, 5–18 cm long, sheathing to the geniculum, **petiole sheath** deciduous; geniculum smooth, 3–5 mm long; **blades** lanceolate to narrowly elliptical, cuneate at the base, acuminate at apex, membranous to sub-coriaceous, drying blackish, reddish, light brown or greyish, 12–23 × 3–10 cm, not decurrent on geniculum; **midrib** ribbed adaxially, convex abaxially; **primary lateral veins** 4–8, obscure adaxially, prominent abaxially, departing midrib at 35–50°; **secondary veins** inconspicuous; **collective veins** not visible; **fenestrations** absent or scarcely developed (in Central America); **margins** entire. INFLORESCENCES on ascending stems, 1–3 simultaneously at flowering time, arranged in the axils of the leaves or cataphylls; **peduncle** smooth, 10–17 cm long, 5–6 mm diam.; **spathe** acuminate, light-green during development, yellow externally and white internally at anthesis, the margins towards the apex involute, deciduous at the end of the anthesis, up to 4 cm longer than the spadix; **spadix** with green style margins and white at the medial

part during development, cream at anthesis, 3–5 × 0.5–1 cm; **basal sterile flowers** scarce or absent; **fertile flowers** 4–7 mm long; stamens with laminar filaments, 1–2 mm long; anthers 1–2 mm long; ovary square in longitudinal section, ribbed, 1.5–2 × 1.5–2 mm; style square or hexagonal, 1.5–2 × 2.5–3 mm; stigma linear; **berries** with a moss-green stylar cap during development, mature stylar cap orange; pulp white; **seeds** black, 3–5 mm long. (**Figures 40 & 41**).

Distribution and habitat: From Costa Rica to Bolivia, Venezuela, the Guianas, Brazil, Trinidad & Tobago. In Costa Rica is distributed in the Southeast of the Caribbean watershed, Cordillera de Talamanca (Alto Urén), at 0–100 m. It lives in the *Tropical rain forest* life zone.

Phenology: In Costa Rica, the flowering has been recorded from July to November, and the fruit in January, March July and November.

Conservation status: *Monstera obliqua* is protected in the Refugio de Vida Silvestre Mixto Gandoca-Manzanillo, Reserva Indígena Talamanca Bribri and Reserva Biológica Hitoy Cerere.

Comments: The species is a member of sect. *Monstera*. It differs from the other species of the genus in Costa Rica by its slender petioles (<0.5 cm diam.), sheathed to the base of the geniculum, the entire, narrowly lanceolate, not or hardly fenestrate leaf blade; the infructescence with the stylar layer orange with white pulp beneath. Vegetatively, individuals of *Monstera obliqua* with fenestrate leaves can be confused with the dry forest morphotype of *M. adansonii*. However, *Monstera obliqua* is found at the southeastern end of the Caribbean slope, while that morphotype of *M. adansonii* grows in the seasonal forests of the northern, central and southern Pacific watershed. Another species with which it could be confused is *Monstera gambensis*, which has the petiole rough, persistent petiolar sheaths with involute wings, and is only known from a collection on the Pacific side in the area of La Gamba, Golfito.

In Costa Rica, *Monstera obliqua* is only found in the extreme southeast of the Caribbean watershed. These populations frequently have narrowly lanceolate leaves lacking fenestrations, uniquely amongst Costa Rican *Monstera*.

In its current conception, *Monstera obliqua* is a very variable and widespread species, including forms with widely varying and sometimes extreme leaf fenestration patterns, occurring across much of lowland wet tropical South America. It may be that further study will show that it covers several species. There are a number of synonyms based on South American and West Indian representatives which it is beyond the scope of this paper to evaluate.

Additional specimens seen: COSTA RICA: **Limón**. Talamanca. Sixaola. San Miguel de Sixaola. Finca -albergue de

ASACODE, 35 m, 28 July 1994, (Fr.), *J. Sánchez et al., 340* (CR); Talamanca, Bratsi, Suretka, Bosques cercanos al sitio de exploración petrolera, 200 m, 19 July 1995, (Fl., Fr.), *A. Cascante et al., 551* (CR); Limón, Talamanca, Cahuita, Between Bri Bri and Sixaola, NW of Paraíso, Disturbed forest, 50 m, 5 July 1983, (Fr.), *K. Barringer et al., 3489* (CR, MO); Talamanca, Sixaola, Hills between headwaters of Quebrada Mata de Limón and upper branches of Quebrada Tigre, and lowland forest of Quebrada Tigre drainage, Finca Anai, (Sixaola region), 28 m, 18 November 1984, (Fl., Fr.), *M. Grayum et al., 4458* (CR, MO); Talamanca, Sixaola, Headwaters of quebrada Mata de Limón, westernmost fork, Finca Anai, (Sixaola region), 23 m, 17 November 1984, (Fr.), *M. Grayum et al., 4439* (CR, MO); Talamanca, Cahuita, Gandoca, El Llano entre Fila Manzanillo y Río Creek. Atrás de la playa, 80 m, 27 March 1995, (Fr.), *G. Herrera & E. Sandoval 7600* (CR); Limón, Valle La Estrella, Fila Espavel, 200 m, 3 July 2000, (Fr.), *L. Acosta 2117* (CR); Talamanca, Sixaola, Sendero Cerillo, 1 m, 3 March 1999, (Fr.), *U. Chavarría 1920* (CR); Talamanca, Sixaola, San Miguel, senderos en la ruta a Manzanillo, 30 m, 16 January 1997, (Fr.), *J. González 1582* (CR); Lugar, Camino entre Fila Dimat y Río Uren, 22 October 1985, (Fr.), *L. Gómez 23765* (MO); Ca. 10 miles S of Punta Cahuita, 70 m, 11 August 1977, (Infer.), *T. Croat 43199A* (MO); Talamanca, Bribri, Proyecto ARA, 4 m, 30 September 2018, (Fl., Fr.), *M. Cedeño et al., 1481* (USJ); Talamanca, Bribri, Proyecto ARA, 4 m, 30 September 2018, (Fr.), *M. Cedeño et al., 1482* (USJ).

24. *Monstera oreophila* Madison, *Contr. Gray Herb.* 207: 54. 1977. — Type: PANAMA. Chiriquí: vicinity of Boquete, Finca Collins, 5500 ft., oak-laurel cloud forest, 24 July 1959, *W.L. Stern, K.L Chambers, J.D. Dwyer & J.E. Ebinger 1104* (holotype, MO!; isotypes, GH! seen on-line, LE, US!).

Robust nomadic vine, with appressed-climbing habit. SEEDLINGS: bearing foliage leaves. JUVENILE PLANTS; root climbers; **stems** light or dark green, smooth or rough; **internodes** 2–8 cm long, 3–6 mm diam.; **petiole** distinct, light or dark green, smooth or warty, 7–15 cm long, sheathed to the base of the geniculum; **petiole sheath** persistent or deciduous; blades lanceolate, ovate, subcordate to rounded at the base, acuminate at apex, 8–16 × 3–11 cm, not appressed to the phorophyte; **fenestrations** present or absent. ADULT PLANTS: root climbers; **stems** dark or light green, smooth or warty, cylindrical; internodes 1–5 cm long, 2–4 cm diam.; **anchor roots** black, **feeder roots**, suberose; **cataphylls** light-green, warty or smooth, deciduous; **petiole** dark or light-green, smooth or distinctly warty, 25–70 cm long, sheathed to the base of the geniculum; **petiole sheath** deciduous with fibrous residues; geniculum smooth, sulcate adaxially, convex abaxially, 2–5 cm long; **blades** ovate to lance-ovate or oblong, asymmetrically cuneate to rounded or sub-cordate at the base, short to long-acuminate at apex, sub-coriaceous, drying yellowish, brownish, or very dark brown to almost black, 25–75 × 20–35 cm, 1.3–2.0 times longer than wide, decurrent on the

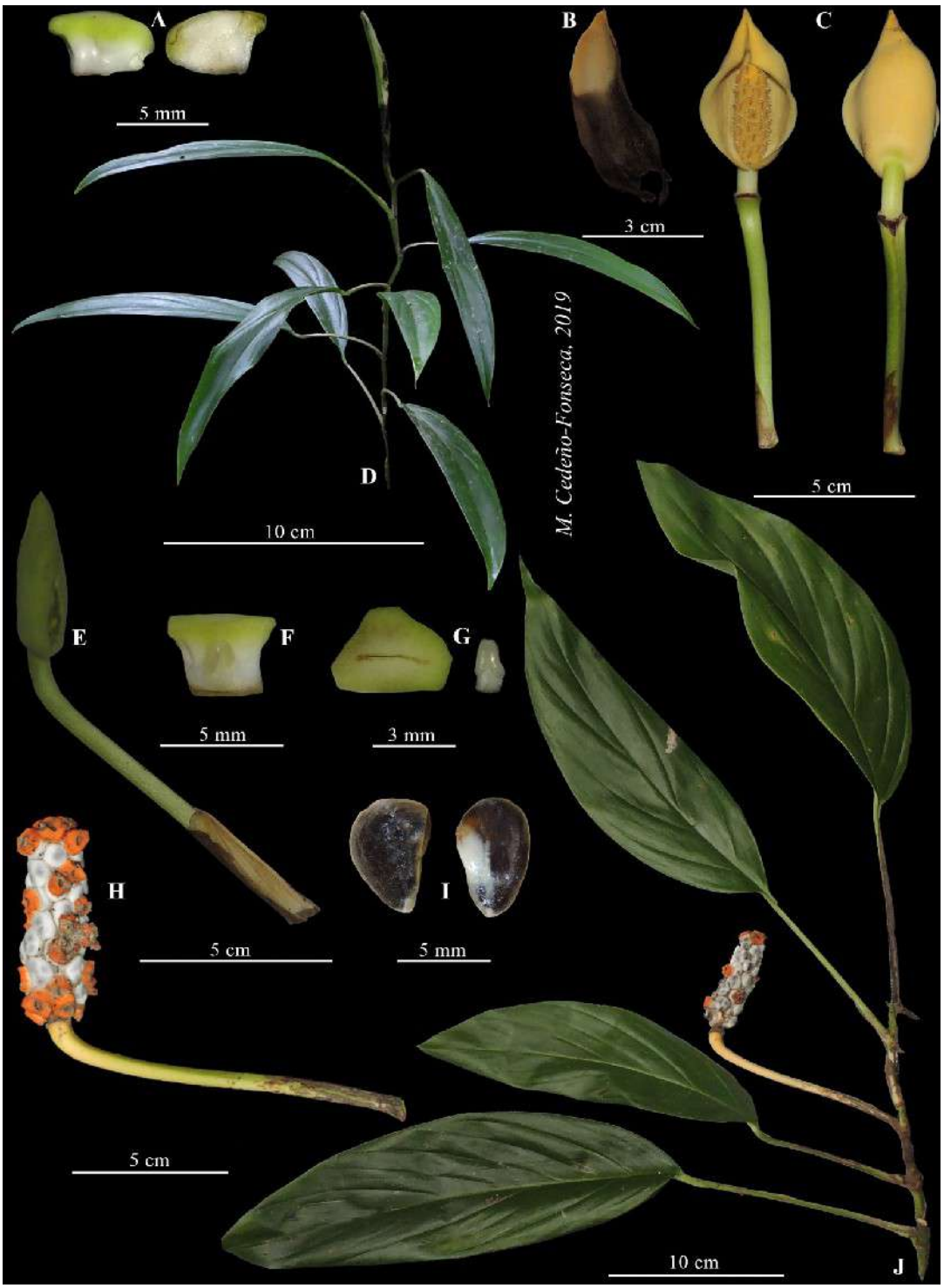

Figure 40. *Monstera obliqua*. (A) Sterile flower in lateral view (left) and in longitudinal section (right). (B) Spathe anomaly: a small second spathe. (C) Front and back views of open inflorescence, with scar of atypical second spathe on the peduncle. (D) Juvenile plant. (E) Developing inflorescence. (F) Fertile flower. (G) Stylar plate with stigma (left) and one stamen (right). (H) Mature infructescence, stylar plates detached toward the apical part. (I) Seeds. (J) Adult plant. *M. Cedeño et al. 1481* (USJ).

Figure 41. *Monstera obliqua*. Adult plant growing in the forests around Manzanillo. *M. Cedeño et al. 2201* (USJ).

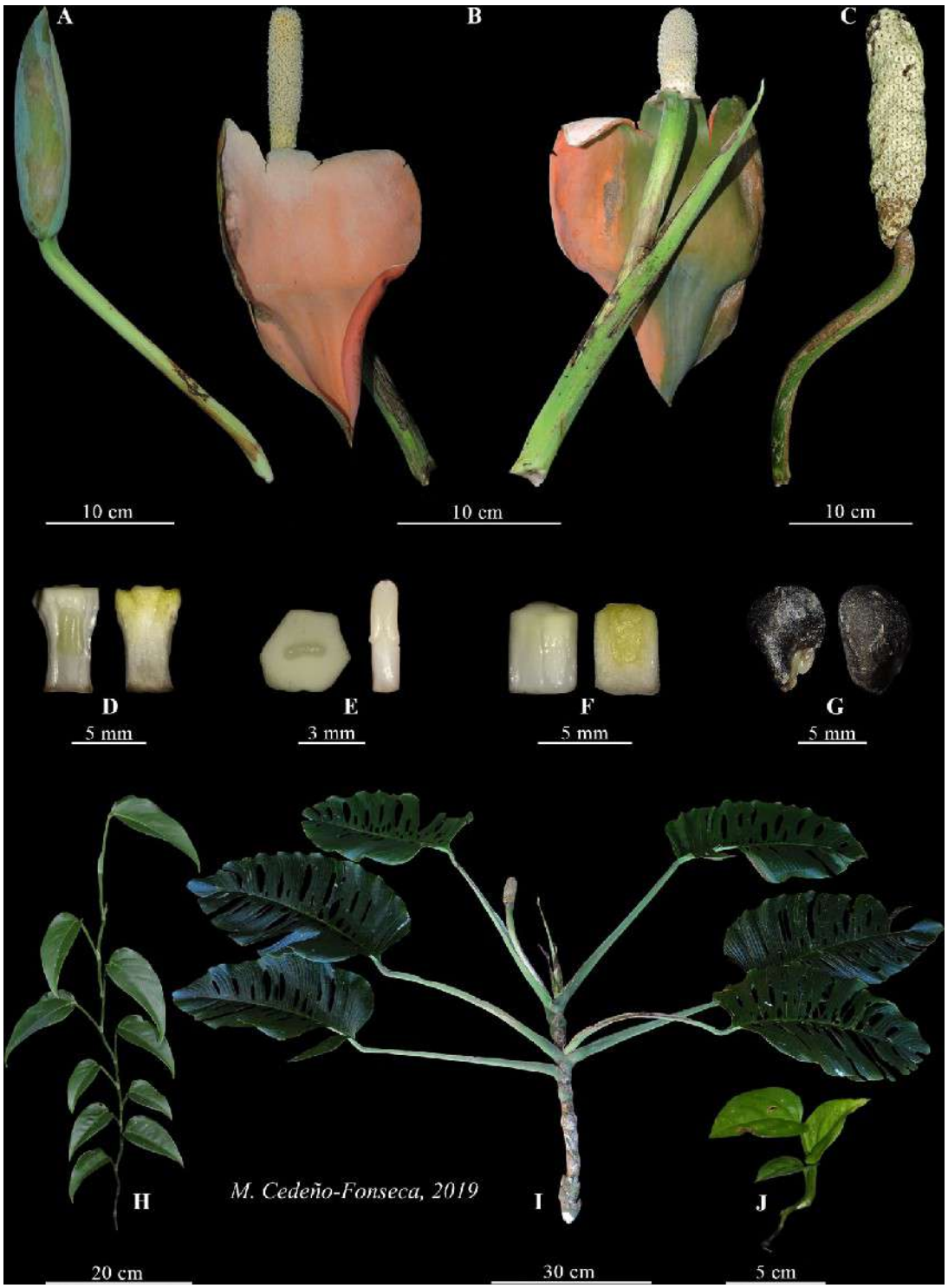

Figure 42. *Monstera oreophila*. (A) Developing inflorescence. (B) Front and back views of open inflorescence with pendent spathe. (C) Mature infructescence. (D) Fertile flower, in lateral view (left), and longitudinal section (right). (E) Stylar plate with stigma (left) and one stamen (right). (F) Sterile flower in lateral view (left) and in longitudinal section (right). (G) Seeds. (H) Juvenile plant. (I) Adult plant. (J) seedling. *M. Cedeño et al. 1272* (USJ).

Figure 43. *Monstera oreophila*. (A) Adult plant. (B) Inflorescence with intact pale pink spathe. Telire, Limon (not collected).

geniculum, decurrent portions 0.5–2 mm wide; **midrib** sulcate adaxially, convex and smooth to markedly warty abaxially, drying blackish or yellowish; **primary lateral veins** 11–45 per side, departing midrib at 75–90°, rarely forked, sunken adaxially, prominent abaxially, drying blackish or yellowish; **secondary veins** parallel but becoming reticulated toward the margin; **collective veins** not visible; **fenestrations** present (rarely absent), the ones located along each side of the midrib small and roundish, the ones located farther from the midrib much larger and elongated; **margins** entire or pinnatilobed due to tearing of the fenestrations that extend to the margin, 3–7 lobes per side, the sinuses reaching halfway or all the way to the midrib, 0.5–6 cm wide. INFLORESCENCES produced on ascending stems, 1–5 per synflorescence, with or without subtending cataphylls; **peduncle** smooth or warty, 13–40 cm long; **spathe** acuminate to long-acuminate, glaucous-green externally during development, glaucous-green or pinkish externally and light orange-yellow internally at anthesis, becoming torn at base and hanging (reflexed) from the midrib base during the staminate phase of anthesis, deciduous soon after anthesis, 10–16 × 8–11 cm, up to 6 cm longer than the spadix; **spadix** white during development, yellow at anthesis, 7–15 cm long, 1.3–3 cm diam., 4.4–5.5 times longer than wide; **basal**

sterile flowers 4–6 mm long, with a transparent secretion; **fertile flowers** 5–7 mm long; stamens with laminar filaments, 1.5–7 mm long; anthers 1.5–3 mm long; ovary rectangular in longitudinal section, ribbed, 3–5 × 2–3.5 mm; style hexagonal, 1.5–2 × 2–4 mm; stigmatophore absent or present, slightly columnar; stigma linear; **berries** with light green to creamy-white stylar caps during development, mature stylar caps creamy-white; pulp white; **seeds** black, oblong, 5–7 mm long. (**Figures 42 & 43**).

Distribution and habitat: From Costa Rica to eastern Panama. In Costa Rica in distributed in both slopes of the cordilleras de Tilarán, Volcánica Central and Talamanca, Pacific watershed of the Monte del Aguacate and Cerros de Escazú, at 800–2200 m. It lives in *Tropical wet forest*, *Premontane wet forest*, *Premontane rain forest* and *Lower montane rain forest* life zones.

Phenology: In Costa Rica, the flowering has been recorded in February–March, May, and October-November, and fruiting in February–April, August, October, and December.

Conservation status: *Monstera oreophila* is protected in the Refugio de Vida Silvestre Jaguarundi, Reserva Forestal Cordillera Volcánica Central, Reserva Forestal Los Santos, Zona Protectora Cerros de Escazú, Zona Protectora Cerros de La Carpintera, Zona Protectora Las Tablas, Zona Protectora Río Banano, Reserva Indígena Chirripó, Reserva Biológica Alberto Manuel Brenes, Parque Nacional Barbilla, Parque Nacional Guanacaste and Parque Internacional de La Amistad.

Comments: The species is a member of sect. *Monstera*. It differs from the other species of the genus in Costa Rica by the petiole asperous in its entire length and with deciduous wings, leaf blades fenestrate throughout and sometimes pinnatilobed, the asperous midrib, and the spathe papaya-coloured externally and internally (this latter characteristic is unique among the species of the genus in Costa Rica). It could be confused with the allopatric *Monstersa buseyi*, but that has the petioles verrucate-asperous, the leaf blade with the midrib smooth, and an externally cream-coloured spathe.

Outside Costa Rica, Panamanian populations of *Monstera oreophila* in Boquete and La Fortuna, Chiriquí Province (where the type was collected) exhibit asperous petioles and midribs, salmon to papaya pink spathes, drying yellowish, blackish or dark brown, similar to the populations in the Central and Talamanca cordilleras of Costa Rica. However, Costa Rican populations in Tilarán and Guacanaste show certain differences, such as the smooth stem, smooth green petioles with the sheath semi-persistent, smooth midribs, heavily fenestrate or pinnatilobed leaf blades, the spathe externally glaucous green and internally papaya pink, and the prophylls and cataphylls smooth and drying completely yellow (Cedeño-Fonseca et al., 2021a). These populations may represent a

distinct species, but for now they are provisionally treated as being within the range of variation of *Monstera oreophila*.

Additional specimens seen: COSTA RICA: **Alajuela**. San Carlos, at terminus of road out of Sucre toward Cerro Porvenir, 2000 m, 24 December 1974, *Luteyn 4504* (MO); San Ramón, Ángeles, R.B. Alberto Manuel Brenes, Las Rocas, 2 Km al Oeste de Finca de Carlos González, 1000 m, 16 February 1994, *Herrera & Mora 6898* (CR, USJ); San Ramón, San Rafael, N slope of Cerros Pata de Gallo, near summit, Montes del Aguacate, 1495 m, 18 November 1988, *Grayum et al. 9098* (CR, MO); Valverde Vega, North of Grecia, 1800 m, 2 June 1984, *Murphy 1375* (MO). **Cartago**. Paraíso, Orosi, Parque Nacional Tapantí, 1260 m, 14 June 2016, *Cedeño & Fernández 900* (USJ); San Nicolás, Z.P. La Carpintera, ladera sur, finca Hacienda La Lima, 1816 m, 4 October 2007, *Cascante 1823* (CR); Aguacaliente o San Francisco, Camino entre Navarro y Muñeco, ca. 3.0–3.5 km del pueblo de Muñeco, 1530 m, 23 February 2010, *Cascante & Chacón 2209* (CR); Mountains south of Muñeco, 5 April 1974, *Utley et al. 790* (CR); La Unión, Río Azul, Quebrada Quebradas, 9 km SE of San José, 1450 m, 19 December 1976, *Lent 4005* (CR); Turrialba, Chirripó, P.N. Barbilla, Cuenca del Matina, Sendero Barthon, Quebrada Avispa, 1600 m, 8 March 2001, *Mora 1888* (CR); La Unión, San Diego, Z.P. La Carpintera, Ladera norte con vista a Tres Ríos, entrando por finca de los Tinoco, 1520 m, 26 March 2008, *Cascante et al. 1904* (CR); Tapantí, 1500 m, 22 October 1983, *Chacón 1454* (CR, MO); Jiménez, Pejibaye, El Copal, Sendero Gárvula, saliendo a Senderos Ron Ron y Mariposas, 900 m, 29 May 2005, *Solano 2484* (CR); El Guarco, La Sierra, 2000 m, 14 January 1983, *Gómez 19742* (MO); Turrialba, Along road between Moravia and Quebrada Plantanillo, 1200–1300 m, 30 June 1976, *Croat 36642* (MO); Turrialba, Along camino Raíz de Hule, 1200–1400 m, 1 July 1976, *Croat 36729* (MO). Paraiso, Tapantí Reserve, 1500–1800 m, 29 September 1987, *Croat 68244* (MO); Quebradilla, camino hacia poblado de Corralillo, ruta 228, 1890 m, 2 February 2017, *Cascante & Trejos 2633* (USJ); Quebradilla, camino hacia poblado de Corralillo, ruta 228, 1890 m, 2 February 2017, *Cascante & Trejos 2634* (USJ); Turrialba, Chirripo, Moravia de Chirripó, 1602 m, 20 December 2019, *Cedeño et al. 1639* (USJ); La Unión, San Rafael, Z.P. La Carpintera, límite de propiedad del Campo Escuela Iztarú, 1854 m, 13 June 2007, *Cascante et al. 1754* (CR). **Guanacaste**: Tilarán, Tronadora, 5 km N Monteverde, Western margin of Reserva Biológica Monteverde, junction of road to San Gerardo valley with Río Negro, 1550 m, 23 December 1988, *Haber & Zuchowski 8948* (CR); La Cruz, Santa Cecilia, Trail above Estación Pitilla, on east slope of Volcán Orosi 710 m, 30 December 1989, *Gereau & Taylor 3475* (CR, MO); Tilarán, Camino a Tilarán, 1325 m, 22 November 2018, *Cedeño & Cascante 1511* (USJ). **Heredia**. Barva, San José de la Montaña, Vicinity of Porrosatí, S slope Volcán Barva, 1980 m, 3 April 1987, *Grayum et al. 8248* (CR, MO); Cerro del Gallito, 1800 m, 20 November 1940, *León*

326 (CR). San Rafael, Road between San Rafael and Río Las Vueltas, 2100–2200 m, 4 September 1979, *Stevens 13992* (MO); San Rafael, Ángeles, Cordillera Volcánica Central, aprox. 0.7 km NE del Hotel El Tirol, 1820 m, 12 September 2017, *Cascante et al. 2623* (USJ); Vara Blanca vicinity, 1800 m, 25 May 1972, *Luteyn 3026* (MO); Sarapiqui, 7.5 km north of Vara Blanca in the vicinity of Río La Paz Grande, 1270–1350 m, 22 June 1976, *Croat 36018* (MO); 4 miles north of Vara Blanca, 1350 m, 26 May 1976, *Croat 35560* (MO); Varablanca, R. F. Cordillera Volcánica Central, Cuenca del Sarapiquí, 9 km NE de la casa de Pablo Serrano, Proyecto ALAS, 1450 m, 16 April 2005, *Santamaría 1811* (CR, MO); Varablanca, Cerro Chompipe (falda norte) San Rafael, 2100 m, 16 December 1993, *Cascante et al. 137* (CR); Varablanca, Alto del Roble, ladera norte del Cerro Chompipe, por entrada a torres del ICE, 2044 m, 11 November 2008, *Cascante et al. 2049* (CR); Forest along ridge between Río Sardinal and headwaters of Quebrada Arrayanes, 1850–2000 m, 20 April 1986, *Grayum 7302* (MO). **Puntarenas**. Buenos Aires, Potrero Grande, Estacion Tres Colinas, Finca Benito Acuna, 1700 m, 10 September 1996, *Alfaro 765* (CR); Buenos Aires, Potrero Grande, Puesto Tres Colinas, Sendero Rompe Fuegos, 2100 m, 20 September 1996, *Gamboa 711* (CR); Buenos Aires, Potrero Grande, Potrero Grande, La Lucha -Tres Colinas, Fila entre Cerro Seno y Cerro Kebé, 2100 m, 24 February 2008, *Santamaría 7197* (CR); Coto Brus, Upper Río Burú, 2010 m, 19 August 1983, *Gómez et al. 21704* (CR, MO); Coto Brus, Sabalito, I Campamento ACLA, Camino a Cerro Echandi, 1900 m, 12 April 1998, *Alfaro 1561* (CR); Coto Brus, Upper Río Burú, 2010 m, 19 August 1983, *Gómez 21415* (MO); Coto Brus, Sabalito, Zona Protectora Las Tablas, Finca Sandí-Hartmann "El Capricho", camino a El Surá, 2000 m, 30 April 2016, *Cedeño et al. 883* (USJ); Coto Brus, San Vito, E.B. Las Cruces, Las Cruces Tropical Botanical Garden, 6 km W of San Vito de Java, 1200 m, 6 March 1984, *Croat 57250* (CR, MO); Coto Brus, Sabalito, Sendero a Cerro Echandi, 1580 m, 11 February 1998, *Gamboa 2144* (CR); Coto Brus, San Vito, Along trail between Las Cruces Botanical Garden and Rio Jaba, ca. 3.5 Km SE of San Vito de Coto Brus, 1200 m, 12 September 1985, *Grayum 5976* (CR); Coto Brus, San Vito, Fila Cruces. 1150–1200 m, 22 May 1995, *Chacón 131* (USJ); Guacimal, Ojo de Agua, 1600 m, 20 April 1989, *Bello 803* (CR, MO); Puntarenas, Monteverde, Camino a Selvatura, 1590 m, 22 November 2018, *Cedeño & Cascante 1507* (USJ); Puntarenas, Monte Verde, R.B. Monteverde, Cordillera de Tilarán, 1520 m, 19 August 1984, *Grayum 3876* (CR, MO); Puntarenas, Monte Verde, R.B. Monteverde, Cordillera de Tilarán, Sendero Tranquilo, 1.5 km SE of Cerro Amigos, 1400 m, 19 August 1995, *Penneys et al. 671* (CR, MO). **San José**. Acosta, Palmichal, Cedral, Cerro Rabo de Mico, 2100 m, 25 July 1991, *Morales 87* (CR, MO); Aserrí, Tarbaca, Tranquerillas, 1500 m, 2 February 1941, *Echeverría 237* (CR); Aserrí, San Gabriel, Tranquerillas-Aserrí, 1500 m, 2 February 1946, *Echeverría 238* (CR); Dota, Copey, Quebrada Grande, Finca Cedrela Eco-Lodge, 1800 m, 9 February 2018, *Cedeño et*

al. 1272 (USJ); Dota, Copey, San Gerardo de Dota, Sendero Los Robles, 2200 m, 21 May 1997, *González 1908* (CR); Dota, Copey, Cedro Eco Lodge, 1900 m, 9 February 2018, *Cedeño et al. 1272* (USJ); Dota, Copey, Cedro Eco Lodge, 1900 m, 9 February 2018, *Cedeño et al. 1273* (USJ); Desamparados, San Miguel, Altos Tablazo, área no protegida, Aprox. 2.5–3.0 km al Oeste del pueblo de Jericó, por la cruz de la avioneta, 1915 m, 5 March 2008, *Cascante & Quesada 1877* (CR); Alto de la Palma on finca Porvenir Ca 5 km north of San Jeronimo, 1500 m, 18 August 1975, *Utley et al. 2904* (CR, MO); Montes de Oca, Cultivo en La Paulina [cultivated], 26 August 1971, *Rodríguez 1311* (CR); Mora, Tabarcia, Cedral, 2250 m, 22 April 2004, *Quesada 1404* (CR); Pérez Zeledón, Páramo, Hills around Rio Savegre, near Finca Zacatales, 2000 m, 1 August 1991, *Gay 1559* (CR); Pérez Zeledón, Páramo, Cerca al Rio Quebradas; Carretera Interamericana km 117; 1750 m, 9 December 1996, *Hammel 20583* (CR, MO); Santa Ana, Salitral, Cuenca alta del Río Uruca, arriba de Matinilla, 1950 m, 5 May 2009, *Cascante et al. 2114* (CR); Tarrazú, San Carlos, No protegida, Cuenca del Pirrís-Damas, Región Tarrazu, 1500 m, 28 December 1998, *Hammel & Morales 21834* (CR, MO); Vázquez de Coronado, Dulce Nombre de Jesús, Entrando por San Jerónimo, Camino rural, conocido localmente como calle la torre, 1517 m, 24 February 2009, *Cascante & Solano 2090* (CR); Vazquez de Coronado, Boundary between Province of San José and Province of Cartago, 1800–1900 m, 30 May 1985, *Grayum 5292* (MO).

25. *Monstera pinnatipartita* Schott, *Oesterr. Bot. Wochenbl.* 7: 197. 1857. — Type: Dried leaf ex Venezuela, Caracas, sent by *H.G. Reichenbach* to Schott (holotype, W✝; see Schott, 1860: 363; Riedl & Riedl-Dorn, 1988 ['pinnatifida']). — VENEZUELA. Zulia: Distrito Perijá, ca. 13 airline km NE of intersection of the Maracaibo-La Fría Hwy. (Hwy. 6) and the Río Aricuaisá (near intersection of LAGOVEN picas 80–2 and 19), 40 m, 20 June 1980, *G. Davidse, A.C. González & R.A. León 18286* (neotype, MO!; isoneotype, VEN, designated by Grayum, 1997: 49).

[*Monstera dilacerata* auctt. non (K.Koch & Sello) K.Koch. (i.e. *Epipremnum pinnatum* (L.) Engl.): Standley, *Fl. Panama* 2(3): 31. 1944 (pro parte); Madison, *Contr. Gray Herb.* 207: 57. 1977 (pro parte); Croat, *Fl. Barro Colorado Isl.*: 207. 1978.]

Nomadic vine, appressed-climbing habit. SEEDLINGS: bearing foliage leaves. JUVENILE PLANTS: root climbers; **stems** dark green with white dots, smooth, cylindrical or flattened; **internodes** 3–6 cm long, 3–5 mm diam.; **petiole** distinct, dark green, smooth, 4–12 cm long, sheathed to the base of the geniculum; **petiole sheath** persistent; **blades** lanceolate, subcordate to truncate at the base, acuminate at apex, coriaceous, 10–15 × 3–8 cm, not appressed to the phorophyte; **fenestrations** absent or present. ADULT PLANTS: root climbers; **stems** smooth, cylindrical, or slightly dorsoventrally compressed, dark green with white dots; **internodes** 1–3 cm long, 1–3 cm diam.; **cataphylls** light or dark, mottled

or whitish, persistent or occasionally deciduous; **anchor roots** dark brown; **feeder roots** dark brown; **petiole** light or dark-green, mottled to whitish, smooth, 15–65 cm long, sheathed up to 3–6 cm before the geniculum or to the base of the geniculum; **petiole sheath** persistent, involute; geniculum smooth, sunken adaxially, convex abaxially, 2–3 cm long; **blades** ovate to lanceolate-ovate, broadly cuneate to rounded or truncate at the base, obtuse to short-acuminate at apex, sub-coriaceous to coriaceous, drying yellowish, blackish or light brown, 20–70 × 20–35 cm, (1.2)1.7 –2.1 times longer than wide, decurrent on the geniculum, decurrent portion 1–2 mm wide; **midrib** ribbed adaxially, convex abaxially, drying black or yellowish on both surfaces; **primary lateral veins** 6–20 per side, slightly sunken adaxially, prominent abaxially, departing midrib at 35–75°, drying black or yellowish; **collective vein** not visible; **fenestrations** absent or present; **margins** deeply pinnatifid, 3–10 lobes per side, 1.5–5 cm wide, 1–3 veins per lobe. INFLORESCENCES on ascending stems, 1–3 simultaneously at flowering time, arranged in the axils of the leaves or into cataphylls; **peduncle** smooth, mottled, 10–25 cm long, 1–1.5 cm diam.; **spathe** acuminate to long-acuminate, yellowish green externally during development, white yellowish externally and white internally at anthesis, overlapping basal margins, deciduous after anthesis; 12–20 × 6–9 cm, up to 7 cm longer than the spadix; **spadix** white during development, creamy-yellow at anthesis, 6–15 cm long, 1.3–2.5 cm diam., (4.4)5.5–9.1 times longer than wide; **basal sterile flowers** 3–5 mm long, with a red-rusty stigmatic secretion; **fertile flowers** 4–7 mm long; stamens with laminar filaments, 2–6 mm long; anthers 1.5–2 mm long; ovary rectangular in longitudinal section, ribbed, 4–6 × 3–4 mm; style hexagonal, 2–3 × 3–5 mm; stigmatophore columnar, 0.3–0.5 mm long; stigma linear, with an orange stigmatic secretion; **berries** with a yellowish-green stylar cap during development, mature stylar cap cream-white; pulp white; **seeds** oblong, black, 5–6 mm long. (**Figure 44)**.

Distribution and habitat: From Costa Rica to Bolivia, Venezuela and Brasil. In Costa Rica it is distributed in the lowlands of the Pacific watershed, from the Península de Nicoya to the south, and in the western part of the Valle Central, at 0–920 m. It lives in the *Tropical wet forest* life zone; in primary and secondary forest.

Phenology: In Costa Rica, flowering has been recorded in January, September–November and fruit in January, March–June and October.

Conservation status: *Monstera pinnatipartita* is protected in the Reserva Natural Absoluta Cabo Blanco, Zona Protectora El Rodeo, Reserva Forestal Golfo Dulce, Reserva Biológica Isla del Caño, Parque Nacional Carara and Parque Nacional Corcovado.

Comments: The species is a member of sect. *Monstera*. It differs from the other species of the genus in Costa Rica by the

light or dark green petiole, speckled to whitish, the persistent petiolar sheath with involute wings, the deeply pinnatifid leaf blade, and externally yellowish-white and internally white spathe. It can be confused with individuals of *Monstera dissecta* but that has pinnatilobed leaves with wider lobes (4−10 cm vs. 1.5−5 cm in *M. pinnatipartita*).

Monstera pinnatipartita is distributed throughout the Pacific slope, being the most frequent species in the Osa Peninsula, growing by estuaries, open areas and primary forest. This species develops hanging stems when the plant cannot continue its ascent, but these hanging stems are never reproductive. Moreover, pre-adult plants can develop inflorescences in ascending stems when they have fenestrate and not pinnatifid leaves.

Nomenclatural note: *Monstera pinnatipartita* is a name that had long been doubtful. It was originally based on a sterile specimen (and only a leaf blade at that) from Caracas (Venezuela), now lost. No other original material has been found, and apparently Schott had no illustration made. The name seems to have been entirely overlooked (or ignored) by Engler & Krause. Madison (1977) treated *Monstera pinnatipartita* as a synonym of his "*M. dilacerata"* (noted above to have included no less than four species, and the name being in fact a synonym of Asian *Epipremnum pinnatum*). In unravelling "*Monstera dilacerata*", Grayum (1997) designated a fertile neotype for *M. pinnatipartita* from the region of Venezuela in which the type had been collected and representing the only species in the region corresponding to "*M. dilacerata*" sensu Madison. Grayum also noted that for some time the unpublished name "*Monstera involuta*" had been applied to Costa Rican material of this species.

Additional specimens seen: COSTA RICA: **Guanacaste**. Hojancha, Puerto Carrillo, Finca Dyalá, Puerto Carrillo, Bosque situado en el nacimiento de la Quebrada Zapotal, 20 m, 26 December 1988, (Fr.), *L. Flores & C. Herrera 12* (CR, MO); Hojancha, Puerto Carrillo, Along Quebrada Zapotal (not on current maps), from Finca Dyalá upstream to near summit of ridge (ca. 2 km ENE of Puerto Carrillo), Península de Nicoya, 60 m, 30 April 1989, (Fr.), *M. Grayum et al., 9438* (CR, MO), Santa Cruz, Cuajiniquil, Cerro Vista al Mar, 750 m, 16 March 2008, (Fr.), *B. Hammel 24541* (CR). **Puntarenas**. Montes de Oro, San Isidro, Interamerican Highway km marker 122; patch of forest west of road, 100 m, 4 August 1985, (Infer.), *B. Hammel & J. Trainer 14369* (CR, MO); Osa Sierpe, P.N. Corcovado, Llorona Forest, 75 m, 29 May 1988, (Fr.), *C. Kernan et al., 549* (CR); Secondary vegetation on former plantations and pasture and remnants of original tall evergreen forest on steep slopes and stream edges in the Cabo Blanco Nature Reserve, Southern tip of the Nicoya Península, 100 m, 1 December 1969, (Fr.), *W. Burger & R. Liesner 6607* (CR, MO); Golfito, Puerto Jiménez, P.N. Corcovado, Near estación Corcovado, 10 m, 7 December 1989, (Fr.), *Merz 454* (CR); Golfito, Puerto Jiménez. P.N. Corcovado, Pavo forest, Poorly drained

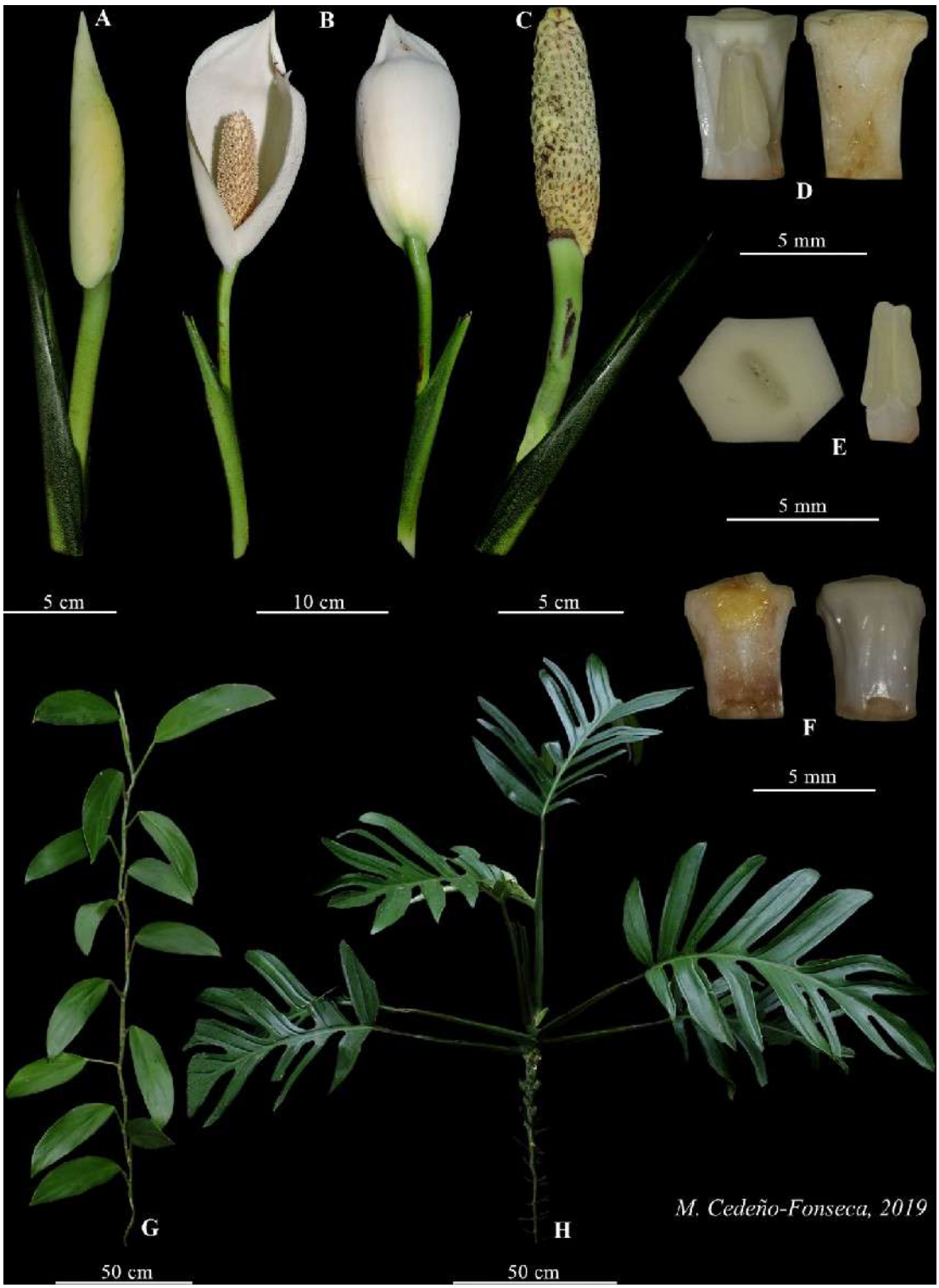

Figure 44. *Monstera pinnatipartita*. (A) Developing inflorescence. (B) Inflorescence with open spathe, front and back views. (C) Immature infructescence. (D) Fertile flower in lateral view (left) and in longitudinal section (right). (E) Stylar plate with stigma (left) and one stamen (right). (F) Sterile flower; lateral view (left) and longitudinal section (right). (G) Juvenile plant. (H) Adult plant. *M. Cedeño et al. 950* (USJ).

lowland forest, 70 m, 14 July 1988, (Fr.), *C. Kernan 693* (CR); Osa, Sierpe, Pasture and forest edge along Quebrada Banegas, ca. 4 km W of Rincón de Osa, 40 m, 8 October 1984, (Fr.), *M. Grayum 4118* (CR, MO); Golfito, Puerto Jiménez, Along road between Rincón and Puerto Jiménez, 15 km S of Rincón, disturbed areas along road, 30 m, 4 March 1985, (Fr.), *T. Croat 59796* (CR, MO); Golfito, Puerto Jiménez, P.N. Corcovado, Sirena Woods, 50 m, 30 April 1989, (Fr.), *C. Kernan 1062* (CR); Garabito, Tárcoles, P.N. Carara, Along Quebrada Bonita, Carara Reserve, 35 m, 25 July 1985, (Fr.), *M. Grayum et al., 5736* (CR, MO); Isla del Caño, 25 July 1985, (Infer.), *R. Soto 2421* (CR); Osa, Sierpe, Ridge between Quebrada Banegas and Río Riyito, ca. 7 Km W of Rincón de Osa, 200 m, 8 October 1984, (Fr.), *M. Grayum 4085* (CR, MO); Area del Faro en el lomo de la fila, Isla del Caño, 26 July 1985, (Infer.), *R. Soto 2457* (CR); Sendero al chorro, Isla del Caño, 13 March 1986, (Fr.), *R. Soto 2886* (CR); Golfito, Puerto Jiménez, Jiménez, cuenca inferior del Río Piro, 20 m, 16 September 1990, (Fl.), *G. Herrera 4300* (CR, MO); Golfito, Puerto Jiménez, P.N. Corcovado, Sirena Woods, 50 m, 30 April 1989, (Fr.), *C. Kernan 1065* (CR, MO); Osa, Bahía Ballena, Uvita, San Josecito, Faldas de la fila Alivio, Lado Pacífico de la fila Costeña, Finca Oro Verde, 300 m, 12 January 2000, (Fr.), *M. Blanco 1245* (CR); Golfito, Jiménez, Estacion Sirena, sendero Rio Claro, 10 m, 11 October 1993, (Fr.), *R. Aguilar 2456* (CR); Golfito, Jiménez, Alrededor de la Estacion Los Patos, 200 m, 7 June 1994, (Fr.), *R. Aguilar 3356* (CR); Golfito, Jiménez, Alrededor de la estación, 20 m, 11 September 1998, (Fr.), *R. Aguilar 5534* (CR, MO); Osa, Sierpe, Isla del Caño, 0 m, 30 August 2000, (Infer.), *J. Azofeifa 26* (CR); Osa, Sierpe, Vicinity of Boscosa, at Quebrada Aguabuena, 100 m, 11 September 1996, (Fl., Fr.), *T. Croat 79247* (CR, MO); Puntarenas, Cóbano, Estacion San Miguel, ca. 2 km S. de Malpais, 18 January 1996, (Infer.), *B. Hammel 20115* (CR); Golfito, Jiménez, Estacion Sirena, al borde del bosque primario, 2 m, 1 October 1990, (Fl.), *J. Saborio 100* (CR); Corredores, Ciudad Neily, Cerro Punta Gorda, 3 km, northwest of Punta de Burica, Mature rainforest, 200 m, 5 March 1973, (Fr.), *P. Busey 777* (MO); Osa, Bahía Ballena, Cerros de playa Dominical, 550 m, 30 Octubre 2016, (Fl.), *M. Cedeño et al., 946* (USJ); Golfito, Puerto Jiménez, Camino a la Estación Biológica Piro, 23 m, 31 Mayo 2016, (Fr.), *M. Cedeño et al., 891* (USJ); Parrita, En una plantació vieja de palma africana, ca. 4 km después de parrita, 10 m, 20 Enero 2001, (Fr.), *C. Morales 1498* (USJ). **San José**. Mora, Colón, Z.P. El Rodeo, Bosque de la Universidad para la Paz, Bosque Premontano Húmedo, Fila Diamante, 850 m, 13 December 1993, (Fl.), *A. Cascante et al., 90* (CR); Mora, Colón, Ciudada Colón, Finca El Rodeo, Camino Universidad para la Paz, 650 m, 27 April 1994, (Infer.), *V. Nilsson & A. Ruiz 441* (CR); Mora, Colón, Z.P. El Rodeo, Reserva de la Universidad para la Paz, Bosque húmedo premontano, 500 m, 2 May 1994, (Fr.), *V. Nilsson 462* (CR); Puriscal, Chires, Santa Rosa de Puriscal, Bosque primario y secundario en las faldas de Fila La Cangreja, 500 m, 6 January 1993, (Fr.), *J. Morales 1019*

(CR); Puriscal, Chires, Mastatal de Puriscal; bosque primario en la Quebrada Grande, por la fila y el rio,200 m, 28 May 1994, (Fr.), *J. Morales 2817* (CR, MO); Puriscal, Chires, Cerro Pelon, charrales y bosque primario remanente en la cima del cerro y cerca del antiguo camino a Quepos, 920 m, 20 April 1995, (Fr.), *J. Morales 3890* (CR).

26. *Monstera pittieri* Engl., *Bot. Jahrb. Syst.* 37: 116. 1905. — Type: COSTA RICA. [Limón:] Matina, Aug. 1895, *H. Pittier 9766* (lectotype, B! seen on-line, photos: BH, SEL!; isolectotypes, BR!, CR!, US! seen on-line; designated by Madison, 1977).

Nomadic vine, appressed-climbing and pendent habit. SEEDLINGS: filiform. JUVENILE PLANTS: root climbers; **stems** light to dark green, flattened; **internodes** 4–6 cm long, 3–5 mm diam.; **petiole** slightly visible, dark green, smooth, 6–12 cm long, sheathed to the base of the geniculum; **petiole sheath** persistent; **blades** lanceolate, subcordate to truncate at the base, acuminate at apex, 7–15 × 5–8 cm, slightly appressed to the phorophyte; **fenestrations** absent. ADULT PLANTS: root climbers; **stems** dark green, cylindrical or dorsoventrally compressed and slightly sulcate on one side; **internodes** 1–3 cm long, 1–3 cm diam.; **anchor roots** dark brown; **feeder roots** corky; **petiole** light or dark-green, smooth, 6–10 cm long, sheathed up to 3 cm before the geniculum or to the base of the geniculum; **petiole sheath** deciduous or slightly persistent with fibrous residues, ligule up to 1 cm long; geniculum smooth, flattened adaxially, convex abaxially, 1.5–2.5 cm long; **blades** broad to narrowly ovate, elliptical or oblong or lanceolate, broadly cuneate to rounded or truncated at the base, obtuse to short-acuminate at apex, sub-coriaceous to coriaceous, drying yellowish, blackish or greenish, 13–18 × 5–10 cm, no decurrent to the geniculum; **midrib** flattened adaxially, convex abaxially, drying yellowish or blackish on both surfaces, wavy distally; **primary lateral veins** 4–7 per side, obscure adaxially, prominent abaxially, departing midrib at 35–45°, drying yellowish or dark brown; **secondary veins** inconspicuous; **collective veins** not visible; **fenestrations** absent or present, one side of the blade more perforated than the other, 1–5 fenestrations per blade; **margins** entire. INFLORESCENCES on pendent stems, 1–9 simultaneously at flowering time, arranged in the axils of the leaves; **peduncle** smooth, 1–4 cm long, 2–6 mm diam.; **spathe** obtuse or mucronate, green externally during development, green externally and white internally at anthesis, tearing longitudinally when fully opened (rarely not tearing), the margins revolute, deciduous after anthesis; 9–12 × 6–8 cm, as long as the spadix; **spadix** white during development, creamy-yellow at anthesis, 4–9 cm long, 1.5–3.5 cm diam., (2.4)3.0–3.6 times longer than wide; **basal sterile flowers** 4–5 mm long, with an orange stigmatic secretion; **fertile flowers** 5–7 mm long; stamens with laminar filaments, 0.5–3.5 mm long; anthers 1.5–2 mm long, the filaments not exceeding the styles at anthesis, the styles slightly separated from adjacent ones, allowing exposure of thecae; ovary ribbed, square in

longitudinal section, 3–4 × 3–4 mm, narrower than style; style quadrangular, cylindrical or hexagonal, 3–5 × 3–4 mm; stigma linear, black post-anthesis; **berries** with a yellowish-green stylar cap during development, mature stylar cap yellow; pulp white; **seeds** oblong, black, 6–9 mm long. (**Figure 45)**.

Distribution and habitat: From Costa Rica to Colombia (Chocó). In Costa Rica it is distributed in the Caribbean watershed of the cordilleras de Tilarán, Volcánica Central, Talamanca, and Llanuras de Tortuguero, in the Pacific watershed from the Parque Nacional Carara to South, at 0–800 m. It lives *Tropical moist forest* and *Tropical wet forest* life zones; primary and secondary forest.

Phenology: Flowering has been recorded in April–May, July–August, November–December, and the fruit in January–December.

Conservation status: *Monstera pittieri* is protected in the Reserva Forestal Golfo Dulce, Reserva Forestal Río Macho, Refugio de Vida Silvestre Barra del Colorado, Refugio de Vida Silvestre Mixto Gandoca-Manzanillo, Estación Biológica La Selva, Reserva Biológica Hitoy Cerere, Parque Nacional Carara, Parque Nacional Corcovado and Parque Nacional Tortuguero.

Comments: The species is a member of section *Marcgraviopsis*. It differs from the other species of the genus in Costa Rica by the thin petiole, deciduous petiolar sheath, entire leaf blade with or without fenestration (when fenestrate, one side of the blade more perforated than the other), the externally pale green spathe tearing longitudinally when fully opened, flowers in the spadix slightly separated, with stamens that stretch to the middle of the pistil, and the infructescence with the stylar layer yellow when ripe.

Monstera pittieri is one of a group of species that only bloom on hanging stems. It could be confused with *Monstera tuberculata*, but that species has the petiolar sheath (also deciduous) with a ligule up to 5 cm in length, the leaf blade basally cordate, the spathe yellow or cream externally, spadix with flowers not separated and the infructescence green when ripe. *Monstera pittieri* is also similar to *M. luteynii*, but the latter differs because it has smooth stems, fenestrated leaves and the petiolar sheath reaching the base of the geniculum or up to 3 cm below it.

Madison (1977) mentioned that *Monstera pittieri* has the styles projecting, giving the spadix a thorny appearance, while *M. luteynii* has the spadix smooth. However, the holotype of *Monstera luteynii* (*Luteyn 3227*, MO) shows a developing infructescence with projected styles, giving the spadix a thorny appearance. On the other hand, notes to a collection of *Monstera luteynii* from the Balsa de San Ramón, at 900 m (*Lent 3889*), describe the spathe opening in irregular pieces and that it is white, features shared with *M. pittieri*. However, *Monstera*

pittieri occurs in lowland moist forests, while *M. luteynii* is found in the cloud forests of the Cordillera Central and Talamanca.

Additional specimens seen: COSTA RICA: **Alajuela**. Alajuela, Carrizal, Forest along Río Sarapiquí downstream and upstream from crossing of road to Colonia Virgen del Socorro, 740 m, 3 July 1985, (Fl.), *M. Grayum 5523* (CR, MO); San Ramón, Peñas Blancas, Peñas Blancas river valley NE of San Carlos; in woods on slopes along river, 350 m, 29 June 1985, (Fl., Fr.), *B. Hammel et al., 14062* (CR, MO); San Carlos, Fortuna, San Carlos, Fortuna, R. B. Arenal Mundo Aventura, 250 m, 30 April 2004, (Fl.), *A. Rodríguez 8767* (CR). **Cartago**. Jiménez, Pejibaye, R. V. S. La Marta, Pejibaye, Turrialba, 700 m, 20 September 2003, (Fr.), *R. Kriebel 3853* (CR). **Heredia**. Sarapiquí, La Virgen, P.N. Braulio Carrillo, Estación Magsasay, Bosque primari, 150 m, 2 June 1990, (Fr.), *G. Carballo 61* (CR, MO); Sarapiquí, Las Horquetas, Some what disturbed primary forest in low, wet area between Río Sucio and railroad tracks, SW of Finca Zona Ocho, Río Frío de Sarapiquí, 110 m, 6 July 1985, (Fl.), *M. Grayum & B. Hammel 5570* (CR, MO); Heredia, Path beyond Río Sucio, 400 m, 4 May 1984, (Fr.), *L. Gómez 21205* (MO). **Limón**. La Concepción, Llanuras de Santa Clara, 250 m, Feb. 1896, *J. Donnell-Smith 6809* (K, US).Talamanca, Sixaola, Headwaters of Quebrada Mata de Limón, central fork, and hills between central and westernmost forks, Finca Anai, Sixaola region, 35 m, 19 November 1984, (Fr.), *M. Grayum et al., 4513* (CR, MO); Pococí, Colorado, P.N. Tortuguero, Lomas de Sierpe, 1.5 km al O del puesto del parque nacional en el río Sierpe, Topografía quebrada conpendientes medianamente pronunciadas, Suelo bien drenado, 100 m, 12 August 1988, (Fl., Fr.), *R. Robles et al., 2026* (CR, MO); Talamanca, Cahuita, R.V.S. Gandoca-Manzanillo, In and around large swamp at Manzanillo, Northwestern end of swamp, 5 m, 2 November 1984, (Fr.), *M. Grayum & W. Burton 4341* (CR, MO); Limón, Valle la Estrella, R.B. Hitoy Cerere, Cerro Bitarkara, Cordillera de Talamanca, 800 m, 28 February 1989, (Fr.), *G. Herrera & M. Solís 2494* (CR, MO); Pococí, Colorado, R. N. F. S. Barra del Colorado, (Refugio Nacional de Vida Silvestre) Fields and pastures between Río Chirripocito and Río Sardina ("Sardinal" Chirripó Atlantico quadrangle), 12 m, 22 April 1990, (Fl., Fr.), *M. Grayum 982*4 (CR, MO); Pococí, Colorado, R.N.F.S. Barra del Colorado, Llanura de Tortuguero, Sardinas, 18 m, 1 March 1995, (Fr.), *F. Araya 755* (CR, MO); Limón, Valle La Estrella, Pasture adjoining Bananito Lodge, Pasture with a few remnant trees and pockets of disturbed vegetation, 100 m, 26 March 2010, (Fr.), *A. Monro 6609* (CR, MO); Talamanca, Cahuita, A orilla de la carretera, 1 Km despues de Cahuita, Ruta a Puerto Viejo, 1 m, 22 October 1997, (Fr.), *A. Rodríguez 2653* (CR, MO); Talamanca, Cahuita, Bosques de Manzanillo, 50 m, 9 January 2017, (Fl., Fr.), *M. Cedeño et al., 1106* (USJ); Limón, Talamanca, Cahuita, Bosques de Manzanillo, 20 m, 30 January 2019, (Fr.), *M. Cedeño & A. Hay 1615* (USJ). **Puntarenas**. Osa, Sierpe, R.F. Golfo Dulce, Península de Osa,

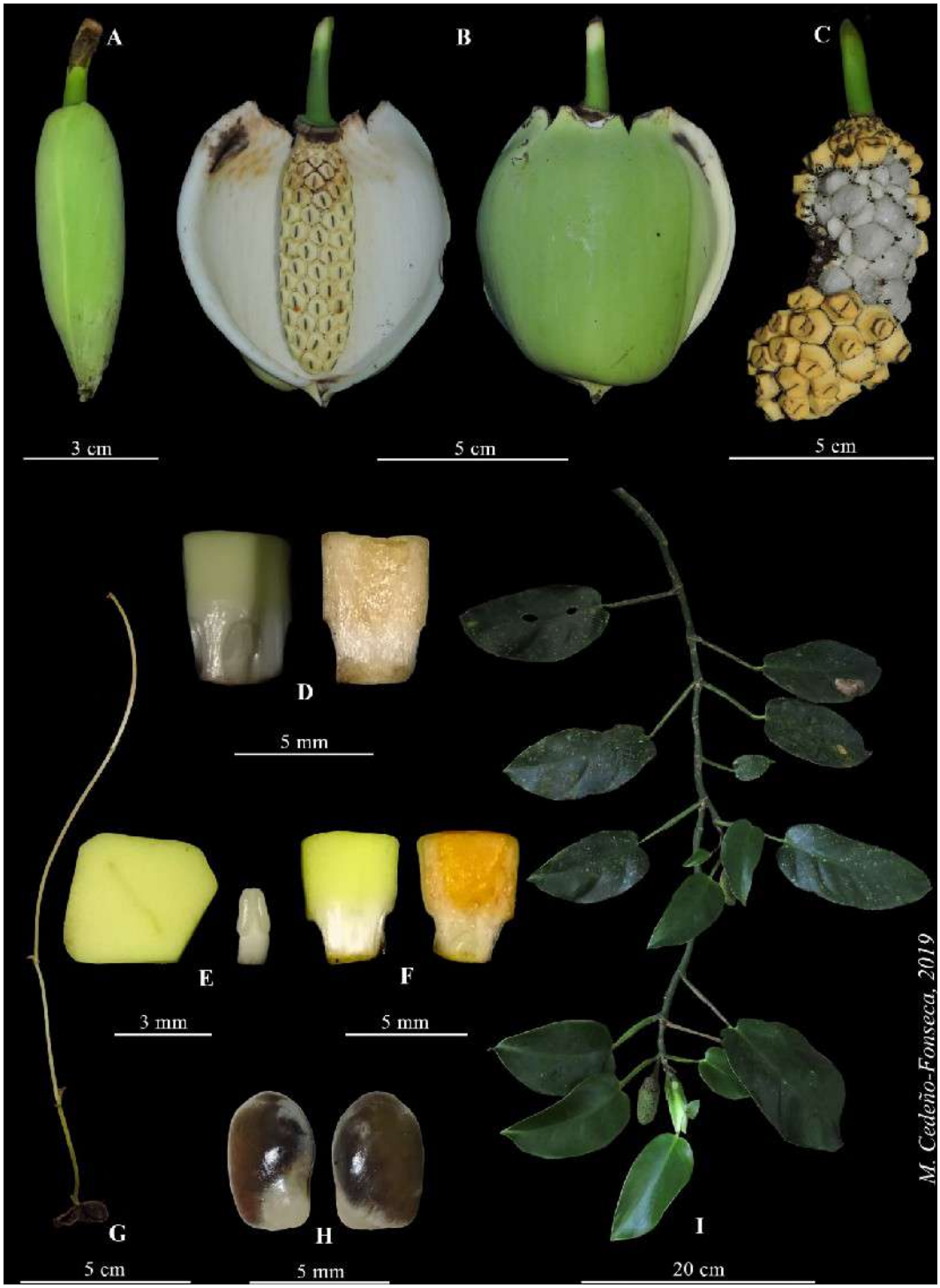

Figure 45. *Monstera pittieri*. (A) Developing inflorescence. (B) Inflorescence with open spathe, front and back views. (C) Mature infructescence, stylar plates detached toward the. (D) Fertile flower in lateral view (left) and in longitudinal section (right). (E) Stylar plate with stigma (left) and one stamen (right). (F) Sterile flower; lateral view (left) and longitudinal section (right). (G) Seedling. (H) Seeds. (I) Adult plant. *M. Cedeño et al. 1106* (USJ).

Aguabuena oeste, cerca de casa de Don Beto, 50 m, 21 November 1992, (Fr.), *R. Aguilar 1501* (CR, MO); Golfito, Puerto Jiménez, P.N. Corcovado, Dos Brazos de Río Tigre, Jiménez, Cuenca superior del Río Madrigal, margen derecha, 600 m, 8 December 1990, (Fr.), *G. Herrera 4740* (CR, MO); Golfito, Puerto Jiménez, P.N. Corcovado, Near estation Sirena, 10 m, 5 December 1989, (Infer.), *Merz 437* (CR); Golfito, Puerto Jiménez, P.N. Corcovado, Lower Lookout Trail, 25 m, 31 July 1988, (Fr.), *C. Kernan 749* (CR); Rancho Quemado, Lote de Orellana, Bosque primario, Rincón, 200 m, 15 May 1991, (Fr.), *J. Quesada 518* (CR); Streams and slopes adjacent to Airfield. Disturbed primary forest, Rincón de Osa, 150 m, 6 February 1974, (Fr.), *R. Liesner 1844* (CR, MO); Garabito, Tárcoles, Saddle between Cerros Quebrada Bonita and Montanas Jamaica, headwaters of Quebrada Bonita, and ridge to N, 420 m, 27 July 1995, (Infer.), *M. Grayum 10759* (CR, MO); Osa, Sierpe, Alrededores de la toma de Agua, Rancho Quemado, Rincon, Bosque primario, 200 m, 15 January 1991, (Fr.), *J. Quesada 324* (CR); Osa, Hillls north of Palmar Norte, 50–700 m, 21 May 1976, (Infer.), *T. Croat 35159* (MO); Osa, Vicinity of Boscosa at Quebrada Aguabuena, 11 September 1996, (Infer.), *T. Croat 79316* (CR, MO). **San José**. Perez Zeledón, Barú, Tinamaste, Finca de los Suizos, 650 m, 3 December 1998, (Fl., Fr.), *A. Estrada et al., 1989* (CR, USJ); Turrubares, San Juan de Mata, P.N. Carara, Cuenca del Río Grande de Tárcoles, Puesto Carara, Río Carara abajo de la unión con Río del Sur, 150 m, 5 April 1993, (Infer.), *B. Hammel & M. Grayum 18939* (CR, MO); Acosta, Sabanillas, Fila San Jeronimo, Colorado, en el camino que conduce a Fila Pital, 600 m, 13 April 1999, (Fr.), *J. Morales 7050* (CR); Acosta, Sabanillas, Acosta, Tiquires, Fila Zoncuano, Falda S., Entre Río Parritilla y Zoncuano, 700 m, 13 May 2001, (Fl.), *J. Morales 8097* (CR).

27. *Monstera punctulata* (Schott) Schott ex Engl. in Martius, *Fl. Bras.* 3(2). 1878. 111. — *Anadendrum ?punctulatum* Schott, *Prodr. Syst. Aroid.* 393. 1860. — Type: Cult. Vienna [most probably originally introduced to Germany from ?Mexico by Warszewicz], *H.W. Schott s.n.* (holotype, W✝ — see Riedl & Riedl-Dorn, 1988: 847). — Schott drawing No. 3281 (neotype, W!, inventory no. NhMW-AfW-HWSB0012, seen as a digital scan; designated by Madison, 1977 (as no. '2281'). — Schott drawings Nos 3276 & 3279 (epitype, W!, inventory nos. NhMW-AfW-HWSB0010 & NhMW-AfW-HWSB0011, seen as digital scans, designated here). — See notes below.

Robust nomadic vine, canopy plant, appressed-climbing and pendent habit. SEEDLINGS: filiform. JUVENILE PLANTS: root climbers; **stems** light-brown or beige, warty with brown pustules; **internodes** 3–8 cm long, 0.5–1.5 cm diam.; **petiole** not visible, dark green, smooth, 2–4 cm long; **blades** obovate or orbicular, cordate to subcordate at the base, obtuse to short-acuminate at apex, sometimes white-spotted, sometimes variegated, 5–10 × 4–8 cm, appressed to the phorophyte; **fenestrations** absent. ADULT PLANTS:

root climbers; **stems** yellowish or beige, warty with abundant pustules, dorsoventrally compressed and sulcate on one side; **internodes** 2–20 cm long, 1–3.5 cm diam.; **cataphylls** deciduous, but leaving dry fragments on the peduncle; **anchor roots** dark brown; **feeder roots** beige, warty and corky; **petiole** light-green with white dots, warty and striated at the base, with pustules, 30–65 cm long, sheathed up to 2 cm before the base of the geniculum; **petiole sheath** deciduous with fibrous residues; geniculum striated or smooth, flattened adaxially, convex abaxially, 3–5 cm long; **blades** ovate to broadly elliptical or oblong, cordate at base, overlapping posterior lobes, obtuse or acuminate at apex, subcoriaceous to coriaceous, drying yellowish with blackish dots, light green or light brown, 45–110 × 30–45 cm, 1.3–1.6 times longer than wide, not decurrent on the geniculum; **midrib** flattened adaxially, convex abaxially, drying yellowish or light brown on both surfaces; **primary lateral veins** 11–20 per side, prominent on both surfaces, drying yellowish; **secondary veins** reticulate towards the margin and prominent, wavy throughout its length when dry; **collective veins** not visible; **fenestrations** rounded or oval, arranged throughout the blade; **margins** pinnatilobed, 4–9 lobes per side, occasionally 1-nerved and connected by a filament. INFLORESCENCES on ascending and pendent stems, 3–5 simultaneously at flowering time, arranged in the axils of the leaves or into cataphylls; **peduncle** light-green with pustules generating a warty surface, 6–20 cm long, 1.5–2.5 cm diam.; **spathe** obtuse or mucronate, dark green during development, green suffused with yellowish-green externally and white internally at anthesis, coriaceous, tearing longitudinally when fully opened, deciduous after anthesis, 10–20 × 6–10 cm, as long as the spadix; spadix white during development, creamy-yellow at anthesis, 10–15 cm long, 2.5–3 cm diam., 4–5.6 times longer than wide; **basal sterile flowers** 4–6 mm long, yellowish secretion; **fertile flowers** 5–8 mm long; stamens with laminar filaments, 2–8 mm long; anthers 1.5–3 mm long; ovary rectangular in longitudinal section, ribbed, 5–6 × 3–4 mm; style hexagonal, 3–4 × 4–5 mm; stigma linear, with transparent sticky stigmatic secretion; **berries** with a green stylar cap during development, mature stylar cap moss-green; pulp white; **seeds** dark-brown with white dots, oblong, elongated, 6–9 mm long. (**Figures 46–50**).

Distribution and habitat: From Mexico to Panama. In Costa Rica is distributed from the Caribbean watershed to North of the Talamanca, and in the Pacific watershed in the Cordillera de Talamanca, Montes del Aguacate and the Tablazo, at 600–1800 m. It lives in *Premontane wet rain forest* and *Lower montane rain forest* life zones; primary and secondary forest, and open areas.

Phenology: In Costa Rica, the flowering has been recorded in August–September, and the fruit in January–April, June–July.

Conservation status: *Monstera punctulata* is protected in the Zona Protectora Cerros de La Carpintera, Zona Protectora Las Tablas, Estación Biológica Las Cruces and Parque Internacional de La Amistad.

Comments: The species is a member of sect. *Marcgraviopsis*. It differs from the other species of the genus in Costa Rica in its verrucate stems, the light green petiole with white spots, verrucate and grooved in the base, sheathing to the base of the geniculum, with deciduous wings, the coriaceous very fenestrated leaf blade, inflorescences on ascending stems (and occasionally in hanging stems), the externally pale green and internally white spathe tearing longitudinally when fully opened, and the stylar cap brown at maturity. It is similar to *Monstera dubia*, but the latter species has a smooth petiole, often entire leaves and inflorescences with pink spathe externally.

Monstera punctulata is a robust species of pre-montane and cloud forests. The collections in herbaria do not reflect the abundance of this species, because botanists avoid collecting it because of its tendency to bloom in the canopy and because of the large size of the plants, which require a single collection to be represented by up to five parts. Some *Monstera punctulata* plants develop hanging stems, which can be reproductive. Such plants (which could be considered as a morphotype) have little-fenestrated and often entire leaves; However, the morphology of the inflorescence, the flowers and the way of opening the spathe and the color of the ripe fruits are similar in both morphotypes, so they are considered here as variations of the same species.

When reaching the soil, the hanging stems take up the morphology of the juveniles (growing in creeping form and producing much smaller leaves), but when finding another suitable phorophyte, they restart the ascent and develop leaves with the morphology of adult plants. This pattern of growth occurs in other species such as *Monstera dissecta*, *M. glaucescens*, *M. pinnatipartita* and *M. tenuis*.

Nomenclatural notes: Madison (1977) cited the type (of unspecified kind) of *Anadendrum punctulatum* Schott, currently (see below) taken to be the basionym of *Monstera punctulata*, as three unpublished Schott illustrations, numbered "2281, 3276, and 3279", at W. The number 2281 is an error for 3281: the actual drawing no. 2281 is of *Monstera microstachys* Schott, currently viewed as a synonym of *M. obliqua* Miq., and a plant unmistakably different from *M. punctulata*. Drawing no. 3281 (**Figure 48)** is of the entire-leaved, appressed juvenile shingling stage, annotated "*Anadendrum punctulatum*?", "Mexico!", and "Leipoldt" [the artist Wenzel Leipoldt (M.-D. Riedl, pers. comm.)]. Drawings nos. 3276 and 3279 (**Figures 49 & 50**) are respectively of the mature leaf and the inflorescence with floral parts, each identically annotated "*Monstera punctulata* Klotzsch", and both bearing the initial "L" [for Leipoldt].

Madison's type citation can be viewed as an implicit neotypification of *Anadendrum punctulatum*, given that its presumed holotype at W was destroyed (Riedl & Riedl-Dorn, 1988), and that the first of the Schott illustrations he cited can reasonably be taken to be an illustration of the transient juvenile stage which Schott named — the original plant, if not part of the original material itself as it is undated. [Nadruz Coelho & Mayo (2007) have proposed that in general Schott's undated illustrations of living plants cannot usually be identified with precision as part of the original material, and so should, where they are being considered as types, be treated as neotypes rather than lectotypes]. However, it seems quite impossible, had drawings 3276 and 3279 of the mature vegetative and fertile structures been part of the original material, that Schott would have placed the species in *Anadendrum* (the juvenile foliage does however, somewhat resemble leaves of *Anadendrum*). Indeed, in the protologue, the description consists of merely two words: "*caudex anceps*" [stem two-edged], a feature of the appressed juvenile stem clearly depicted in cross section in drawing 3281 (see **Figure 48)**, but there is no mention at all of any feature of the adult plant. Since Schott (1860: 393) included *Monstera punctulata* Klotzsch [sic] in *Anadendrum punctulatum*, it would seem not unreasonable to infer that Schott had received living material from Germany, to where it seems first to have been introduced, under Klotzsch's name, and then tentatively ascribed it to *Anadendrum* having grown it only to the juvenile stage at the time of publication. We therefore conclude that drawing 3281 is the only element that can be said to accord with the protologue of *Anadendrum punctulatum*, and exclude the other two drawings from Madison's neotypification as they must form a separate, later element.

Nevertheless, the coloured illustrations of the living adult vegetative and fertile stages included by Madison (1977) in his typification are, characteristically of those made under Schott's supervision, of such superb quality and detail that we here designate them, taken together as identically annotated, complementary parts forming a single element, as the interpretive epitype. While it may be preferable in general to use specimens as epitypes, in this case the drawings provide far greater clarity of morphological detail than would any dried specimen. Furthermore, it is extremely likely that the drawings are of a plant from the original introduction by Warscewicz, as no other collection or introduction of this species had ever been cited anywhere, even nearly fifty years later (Engler & Krause, 1908: 110). Lastly, in thus epitypifying *Monstera punctulata*, we maintain continuity with Madison's taxonomic thought by making no more change than a technical adjustment to his typification.

Although the name *Monstera punctulata* is treated as a new combination effected by Engler (loc. cit.) based on Schott's *Anadendrum punctulatum*, Schott, as already noted, had included '*Monstera punctulata* Klotzsch' in it. The name has not so far

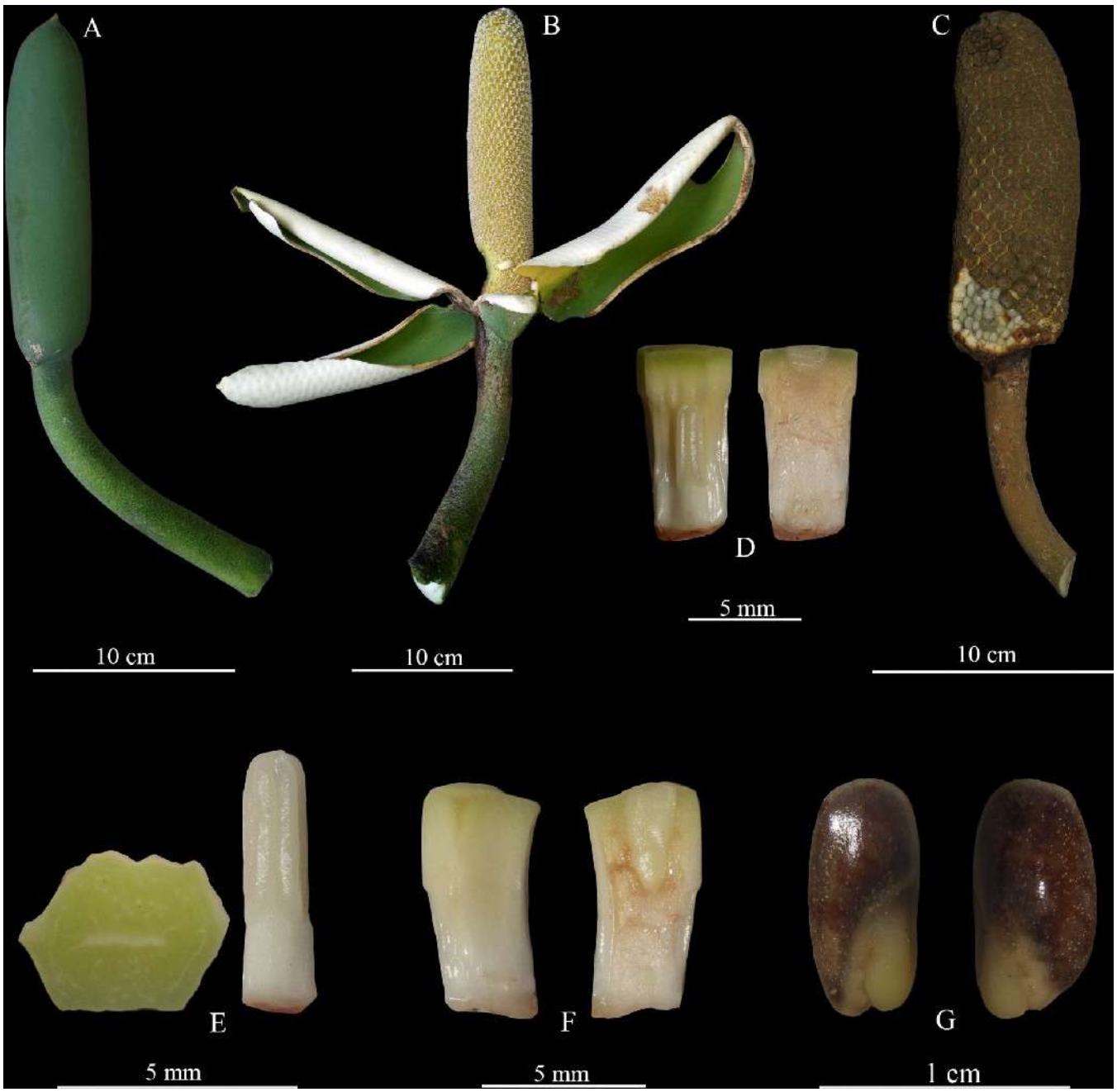

Figure 46. *Monstera punctulata*. (A) Developing inflorescence. (B) Inflorescence with open spathe torn longitudinally into three strips. (C) Mature infructescence, stylar plates detaching. (D) Fertile flower in lateral view (left) and in longitudinal section (right). (E) Stylar plate with stigma (left) and one stamen (right). (F) Sterile flower; lateral view (left) and longitudinal section (right). (G) Seeds. *M. Cedeño et al. 1127* (USJ).

Figure 47. *Monstera punctulata*. (A) Adult individual. (B) Fenestrated leaf blade, with filaments <0.5 cm wide connecting adjacent lobes (arrows). (C) Stem with fibrous cataphylls (arrow), and five inflorescences. (D) Inflorescence with the spathe starting to open (arrow). *M. Cedeño et al. 782* (USJ).

Figure 48. The neotype of *Monstera punctulata* (Schott) Schott ex Engl. — Schott drawing No. 3281, of the shingling juvenile phase. [From the Archive for the History of Sciences, Natural History Museum Vienna (inventory no. NhMW-AfW-HWSB0012); reproduced with permission].

Figure 49. Part 1 of the epitype of *Monstera punctulata* (Schott) Schott ex Engl. — Schott drawing No. 3276, of the adult leaf. [From the Archive for the History of Sciences, Natural History Museum Vienna (inventory no. NhMW-AfW-HWSB0010); reproduced with permission].

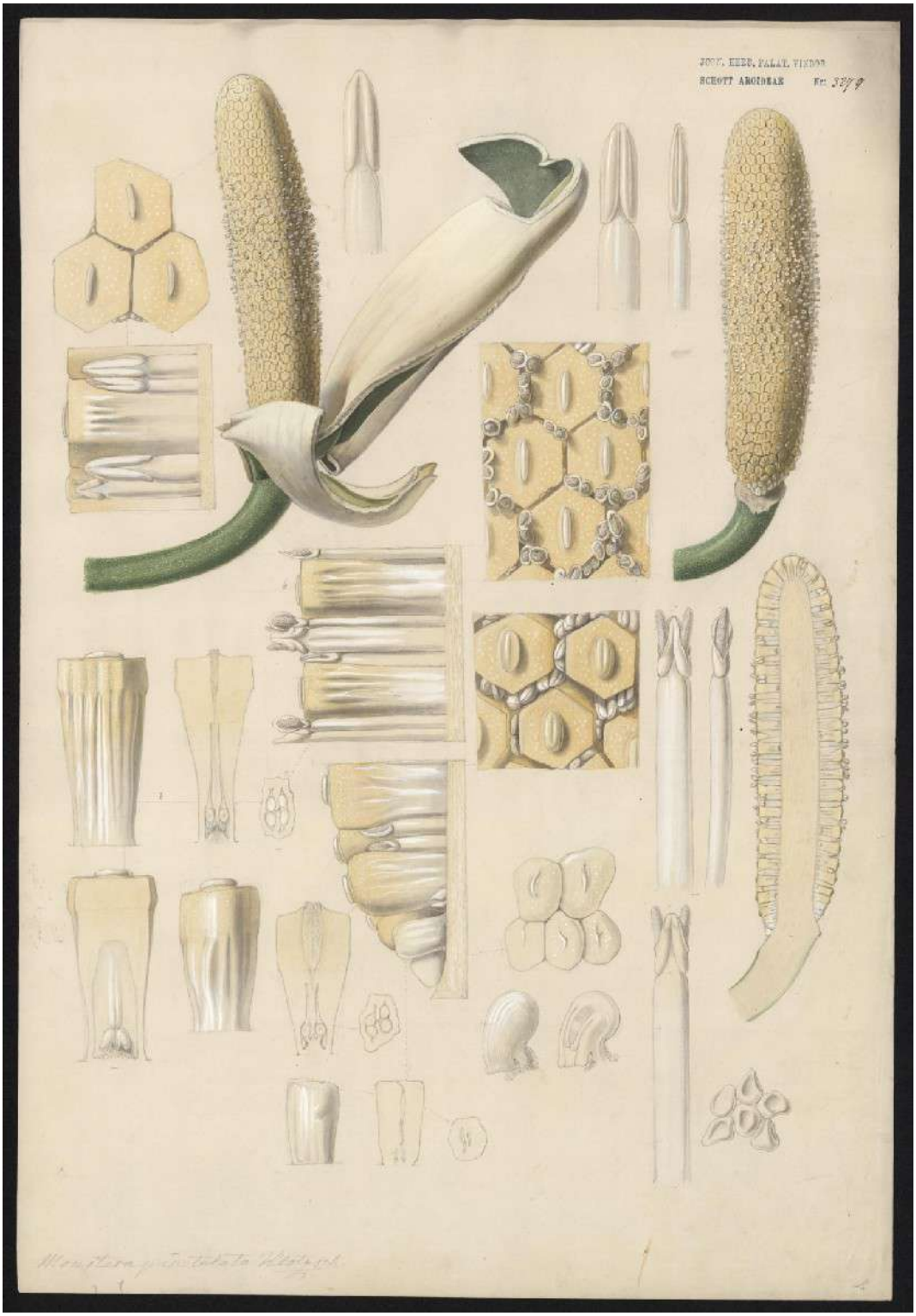

Figure 50. Part 2 of the epitype of *Monstera punctulata* (Schott) Schott ex Engl. — Schott drawing No. 3279, of the inflorescence. [From the Archive for the History of Sciences, Natural History Museum Vienna (inventory no. NhMW-AfW-HWSB0011); reproduced with permission].

been found validated with Klotzsch's authorship, but it had been mentioned in 1854 by E.A. Regel [*Gartenflora* 3: 97], discussing new ornamental introductions from the Berlin nursery of Louis Mathieu (1793–1867), where it is stated (translated from the German) "The rich catalogue of this gentleman [Mathieu] also contains the following new introductions, thanks to Mr. von Warscewicz, namely: ... *Monstera punctulata* Kl. [among others]". If that catalogue, likely from 1853, can be found, and it contains validating descriptive information, then the typification and authority of this name will need to be reconsidered. However, it is not known that any Mathieu catalogues still exist (Clemens Wimmer, pers. comm., 8 July 2021). [Engler (1878: 111) indicated that there was a specimen attributed to Warszewicz at B, which might potentially be the type of Klotzsch's name, but it is apparently no longer extant, and there is no photo of it at F].

Additional specimens seen: COSTA RICA: **Cartago**. La Unión, San Diego, Z.P. La Carpintera, Ladera norte con vista a Tres Ríos, entrando por finca de los Tinoco, 1520 m, 26 March 2008, (Fr.), *A. Cascante et al., 1903* (CR); La Unión, San Rafael, Z.P. Cerros de La Carpintera, Parche boscoso de Campo Istarú, 1712 m, 23 January 2007, (Fr.), *A. Cascante & J. Sánchez 1667* (CR); Cartago, Dulce Nombre, Jardín Botánico Lankester, 1360 m, 10 February 2017, (Fr.), *M. Cedeño 1127* (USJ). **Puntarenas**. Coto Brus, Sabalito, Foothills of the Cordillera de Talamanca, lower montane forest directly N of Las Alturas, 1450 m, 28 August 1983, (Fl.), *G. Davidse 24169* (CR, MO); Coto Brus, Pittier, Forested slopes above the lumber camp at the Río Coton (Las Alturas), 1450 m, 18 January 1967, (Fr.), *W. Burger & G. Matta 4559* (CR); Coto Brus, Sabalito, Along road about halfway between Flor del Roble and Las Alturas de Coto Brus, 1250 m, 13 July 1985, (Fr.), *M. Grayum & B. Hammel 5691* (CR, MO); Coto Brus, San Vito, R.B. Las Cruces, En el camino que va desde La Estación Biológica Las Cruces hasta el Río Jaba, Bosque primario premontano intervenido, 1170 m, 16 June 2003, (Fr.), *R. Moran & M. Mora 6482* (CR); Coto Brus, 10 March 1987, (Fr.), *M. Grayum & J. Affolter 8149* (CR, MO); Coto Brus, Sabalito, Z.P. Las Tablas, Cordillera de Talamanca, Quebrada Pizote, Finca Cafrosa San Vito, 1200 m, 22 September 1990, (Fl.), *M. Ramírez 97* (CR); Coto Brus, Sabalito, 100 m from field station, between fence line and forest edge montane fores, 1600 m, 9 March 1998, (Fr.), *B. Boyle et al.,* 5137 (CR, USJ); Coto Brus, Sabalito, Cerro Pando, ridges above the Río Coton and the Río Negro, Southern Puntarenas, Near La Lucha, Remnants near pastures on Río Coton, edge of road, 1400 m, 19 February 1982, (Fr.), *K. Barringer & L. Gómez 1639* (CR, MO); Coto Brus, Pittier, Santa María, Sobre sendero al Río Canasta, 1700 m, 30 July 2000, (Infer.), *L. Acosta 2346* (CR); Canton of Coto Brus; Las Cruces Tropical Botanical Garden, 1200 m, 6 March 1984, (Fr.), *T. Croat 57263* (MO); Coto Brus, Finca Loma Linda, 1150 m, 26 February 1973, (Fr.), *T. Croat 22289A* (MO); Coto Brus, Finca Loma Linda, 1150 m, 26 February

1973, (Infer.), *T. Croat 22280* (MO); Coto Brus, Sabalito, Zona Protectora Las Tablas, 10 km al noreste de Lucha, camino a la Finca Sandí-Hartmann "El Capricho", 1800 m, 30 Abril 2016, (Fr.), *M. Cedeño et al., 884* (USJ); Coto Brus, San Vito, Estación Biológica Las Cruces, 1200 m, 5 February 2015, (Fr.), *M. Cedeño et al., 782* (USJ); Puntarenas, Coto Brus, Sabalito, Foothills of the Cordillera de Talamanca, lower montane forest directly N of Las Alturas, 1450 m, 28 August 1983, (Fl.), *G. Davidse 24169* (CR, MO). **San José**. Desamparados, San Miguel, Along quebrada El Tablazo and on forested slope above creek, NE part of Altos Tablazo, 1750 m, 23 April 1985, (Fr.), *M. Grayum & G. Schatz 5141* (CR, MO); Perez Zeledon, About 4.5 miles southwest of Canaán along gravel road from Rivas, 900 m, 14 August 1977, (Infer.), *T. Croat 43434* (MO); Curridabat, Granadilla, 18 Octubre 1984, (Fr.), *E. Valerio 112* (USJ).

28. *Monstera spruceana* (Schott) Engl. in Martius, *Fl. Bras.* 3(2): 115. 1878. — *Tornelia spruceana* Schott, *Oesterr. Bot. Z.* 9(2): 40. 1859. — Type: BRAZIL. [Amazonas:] Rio Negro, São Gabriel, [1852?], *R. Spruce 2293* (holotype, K! 2 sheets K000434532 & K000434533, examined on-line).

Robust nomadic vine, appressed-climbing habit. SEEDLINGS: filiform. JUVENILE PLANTS: root climbers; **stems** dark green, smooth, cylindrical; **internodes** 2–8 cm long, 0.5–12 mm diam.; **petiole** not visible, dark green, smooth, 4–6 cm long; **blades** obovate, subcordate at the base, acuminate at apex, coriaceous, 5–15 × 6–12 cm, appressed to the phorophyte; **fenestrations** present, usually 1 that breaks at the margin. ADULT PLANTS: root climbers; **stems** light or dark-green, cylindrical, warty with pustules; **internodes** 3–8 cm long, 2–6 cm diam.; **anchor roots** light brown; **feeder roots** dark brown with white trichomes; **petiole** light-green, smooth or warty, 25–50 cm long, sheathed to the base of the geniculum or to the base of the blade; **petiole sheath** deciduous with fibrous fragments; geniculum smooth or warty, sunken adaxially, convex abaxially, 2–4 cm long; **blades** lanceolate or ovate, obtuse, truncate, subcordate or attenuate at the base, obtuse to slightly acuminate at apex, coriaceous, drying greyish or blackish, 25–60 × 25–30 cm, 1.2–2.2(3.3) times longer than wide, decurrent on the geniculum, decurrent portion 3–4 mm wide; **midrib** ribbed adaxially, convex abaxially, drying black to dark brown on both surfaces; **primary lateral veins** 10–18 per side, sunken adaxially, prominent abaxially, drying blackish or dark brown; **collective veins** not visible; **fenestrations** present in transition to adult plants; **margins** pinnatilobed, 1–6 lobes per side, 2–4 veins per lobe. INFLORESCENCES on ascending stems, 1–2 simultaneously at flowering time, arranged in the axils of the leaves; **peduncle** smooth, 4–10 cm long; **spathe** obtuse to short-acuminate, white internally and light green externally during development, unknown at anthesis; **spadix** white during development, unknown at anthesis, 15–25 cm long, 3–6 cm diam., 8–9 times longer than wide; **basal sterile flowers** 5–7 mm long; **fertile flowers** 6–8

mm long; stamens with laminar filaments, 2–7 mm long; anthers 1.5–2 mm long; ovary rectangular in longitudinal section, ribbed, rectangular, slenderer than style, 3–4 × 2–3 mm; style hexagonal, 3–5 × 3–4 mm, stigma linear; **berries** with a green stylar cap during development, mature stylar cap unknown; pulp unknown; **seeds** unknown. (**Figure 51)**.

Distribution and habitat: From Costa Rica to Bolivia, Brazil and the Guianas. In Costa Rica it is distributed in the Caribbean watershed and Pacific watershed of the Cordillera de Tilarán and the Guanacaste, at 50–1325 m. It lives in *Tropical wet forest*, *Premontane wet forest* and *Premontane rain forest* life zones.

Phenology: In Costa Rica, flowering has not been observed; fruiting was recorded in September and November.

Conservation status: *Monstera spruceana* is protected in the Zona Protectora Arenal-Monteverde and the Reserva Biológica del Bosque Nuboso Monteverde.

Comments: The species is a member of section *Marcgraviopsis*. It is distinguished by its pinnatilobed adult leaf blade, the slightly verrucose or smooth petiole, sheathed up to the base of the geniculum or even up to the base of the blade, the petiolar sheath disintegrating as fibrous residues, short peduncles (<10 cm), long spadices (15–25 cm), and dark green stylar caps after anthesis. It is similar to *Monstera anomala,* but that species is distinguished by its completely entire leaves, by the constricted stylar region, and by its occurrence (at least in Costa Rica and Panama) in lowland humid forests.

Both the description of *Monstera spruceana* by Grayum (2003a), including the specimen cited there, as well as the other Costa Rican specimens previously identified under this name, correspond to the recently described *M. anomala* (q.v.). However, the collections listed below were identified as *Monstera spruceana* during this study.

In Costa Rica, *Monstera spruceana* has been collected in cloud forests at ca. 1200–1300 m and in the lowlands in the Osa Peninsula (50–200 m). However, it has not been found at intermediate elevations, and only the populations in the Osa Peninsula and the Tilarán mountain range are known. Populations in Panama also grow in lowland humid forests and in cloud forests at 1200 m. In Colombia, it grows both in lowlands (Chocó and Amazonian regions) and cloud forests (parts of the Andean Western Cordillera). The populations in Panama and Colombian have some differences with those of Costa Rica; therefore, this species requires more study in the field, to document the morphology of the flowers, and the developing spathe in anthesis.

Additional specimens seen: COSTA RICA: **Alajuela**. Uapala, Slope of cerro Cacao, E to near Río Las Haciendas, 1150 m, 14 August 2007, (Infer.), *M. Grayum*

12713 (MO). **Puntarenas**. Puntarenas, Monteverde, Camino a Tilaran, 1325 m, 21 November 2018, (Fr.), *M. Cedeño & A. Cascante 1501* (USJ); Puntarenas, Osa, Bahía Drake, Camino a Rancho Quemado, 188 m, 3 February 2019, (Infer.), *M. Cedeño, A. Hay 1621* (USJ); Osa, Sierpe, Along road between Rincon and Boscosa, 2 Km W of bridge over Rio Rincon, 50 m, 11 September 1996, (Fr.), *T. Croat 79253* (CR, MO).

29. *Monstera standleyana* G.S.Bunting, *Baileya* 14: 133. 1967 ['1966']. — Type: "Plant cultivated in conservatory, Cornell University, from material of unknown commercial source", Nov 1964, *G.S. Bunting 1543* (holotype, GH!; isotypes, K! seen on-line, NY!, UC, US!).

Robust nomadic vine, appressed-climbing habit. SEEDLINGS: bearing foliage leaves. JUVENILE PLANTS: root climbers; **stems** light to dark green, sometimes white-dotted, smooth, cylindrical; **internodes** 2–6 cm long, 3–5 mm diam.; **petiole** distinct, dark green, smooth, 7–15 cm long, sheathed to the base of the geniculum; **petiole sheath** persistent; **blades** lanceolate, subcordate to truncate at the base, acuminate at apex, coriaceous, 6–15 × 4–10 cm, not appressed to the phorophyte; **fenestrations** absent. ADULT PLANTS: root climbers; **stems** dark green or beige, smooth cylindrical; **internodes** 1–3 cm long, 1–5 cm diam.; **anchor roots** dark-brown; **feeder roots** brown, corky; **petiole** light or dark-green, smooth, 20–80 cm long, sheathed to the base of the blade, less frequent to the base of the geniculum or to 1.5 cm before it; **petiole sheath** persistent with finely wavy margins; geniculum smooth, sunken adaxially, convex abaxially, 2.5–3.5 cm long; **blades** lanceolate-ovate to lanceolate, cuneate to rounded or truncate at the base, obtuse to short-acuminate at apex, coriaceous, drying yellowish green with black dots or blackish with white dots on both surfaces, 30–80 × 10–40 cm, 1.9–2.1 times longer than wide, not decurrent on the geniculum; **midrib** ribbed adaxially, convex abaxially, drying black or yellowish on both surfaces; **primary lateral veins** 12–25 per side, strongly sunken adaxially, prominent abaxially, departing midrib at 45–65°, drying yellowish; **secondary veins** parallel and prominent, reticulate towards the margin; **collective veins** not visible; **fenestrations** rarely present; margins entire, rarely pinnatilobed, 3–6 lobes per side. INFLORESCENCES on ascending stems, 1–2 simultaneously at flowering time, arranged in the axils of the leaves; **peduncle** smooth, 10–35 cm long; **spathe** acuminate to long-acuminate, yellowish green externally during development, creamy yellow with brown dots externally and cream internally at anthesis, persistent after anthesis, light brown when dry, 10–17 × 8–12 cm, up to 5 cm longer than the spadix; **spadix** white during development, creamy-yellow at anthesis, 9–20 cm long, 3.5–5.5 cm diam., 5.4–6.8 times longer than wide; **basal sterile flowers** 4–6 mm long, with a rusty-red stigmatic secretion; **fertile flowers** 5–9 mm long; stamens with laminar filaments, 2–8 mm long; anthers 1.5–2 mm long; ovary rectangular in longitudinal

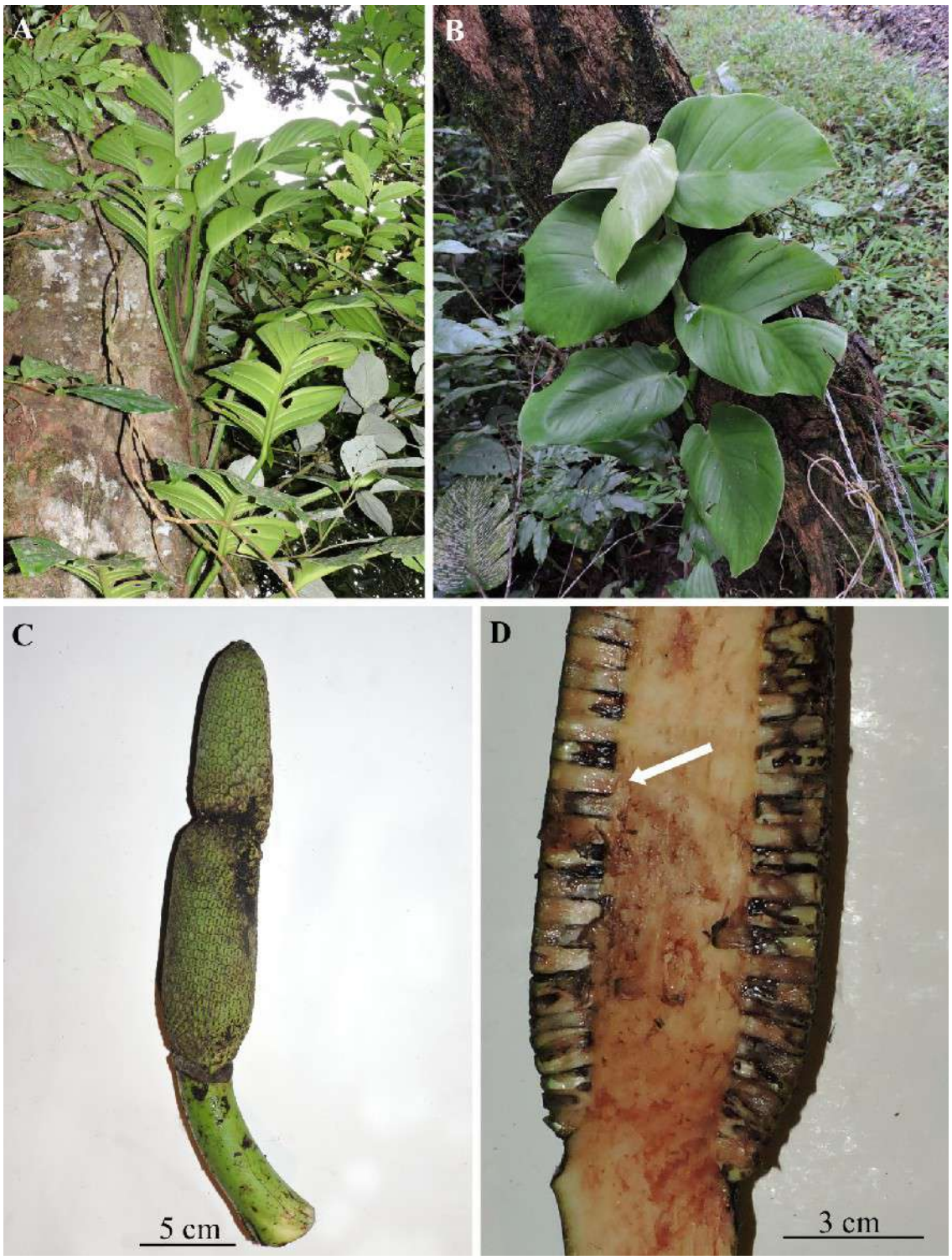

Figure 51. *Monstera spruceana*. (A) Adult plant. (B) Juvenile plant in transition to pre-adult stage. (C) Developing infructescence. (D) Longitudinal section of the spadix to show the shape of the ovary (arrow). *M. Cedeño et al. 1501* (USJ).

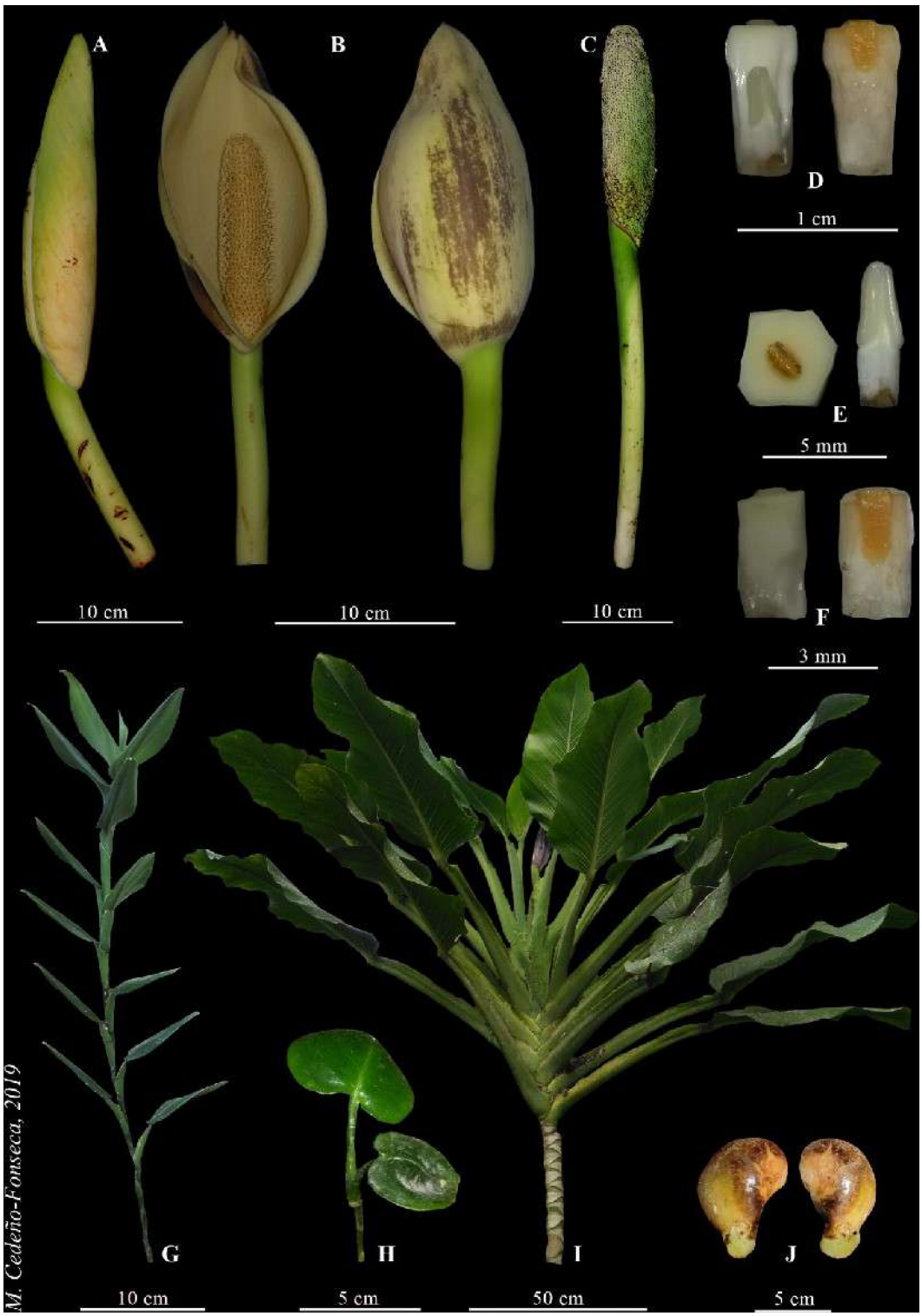

Figure 52. *Monstera standleyana*. (A) Developing inflorescence. (B) Inflorescence with open spathe, front and back views. (C) Immature infructescence. (D) Fertile flower, in lateral view (left), and longitudinal section (right). (E) Stylar plate with stigma (left) and one stamen (right). (F) Sterile flower in lateral view (left) and in longitudinal section (right). (G) Juvenile plant. (H) Seedling. (I) Adult plant. (J) seeds. *M. Cedeño et al. 875* (USJ).

Figure 53. *Monstera standleyana*. Adult plant of an atypical form with fenestrate/pinnatifid leaves growing 15m above the ground in the forests around Manzanillo, Limon (not collected).

section, ribbed, 5–7 × 3–4 mm; style hexagonal, 3–4 × 3–4 mm; stigmatophore columnar, 0.5–1 mm long; stigma circular, with a rusty-red stigmatic secretion; **berries** with a green stylar cap during development (covered by cream spathe), mature stylar cap moss-green; pulp grey; **seed** brown with dark dots, oblong, 6–9 mm long. (**Figures 52 & 53**).

Distribution and habitat: From southeast Nicaragua to Panama. In Costa Rica it is distributed in the Caribbean and Pacific watersheds and close to the Continental divide, at 0−1360 m. It lives in *Tropical moist forest* and *Premontane wet forest* life zones.

Phenology: In Costa Rica, flowering has been recorded in April and October, and the fruit in January, March, October and December.

Conservation status: *Monstera standleyana* is protected in the Estación Biológica La Selva, Reserva Indígena Chirripó, Zona Protectora Arenal-Monteverde, Reserva Biológica Alberto Manuel Brenes, Reserva de Vida Silvestre Barra del Colorado, Parque Nacional Braulio Carrillo and Parque Internacional de La Amistad.

Comments: The species is member of sect. *Monstera*. It is distinguished from the other species of the genus in Costa Rica by the dark green petioles sheathing throughout their entire length, with persistent and slightly wavy wings, entire leaf blade usually without fenestrations, externally yellow, coriaceous and marcescent spathe, enveloping the spadix, and the moss green infructescence. It is similar to *Monstera juliusii*, but the latter is distinguished by its fenestrate, sometimes pinnatilobed leaves (but see below), the externally yellowish green spathe, cream-coloured infructescence, and its distribution on both sides of the Cordillera de Talamanca, at elevations of 1800–2200 m.

Monstera standleyana is a common species in lowland moist forests on the Caribbean slope. Adult plants of this species are variable in size, and can become very robust (with leaves up to 160 cm in length). Individuals of this species have been observed in the Gandoca-Manzanillo Mixed Wildlife Refuge (Southern Caribbean slope), with both entire and fenestrate leaves, but have never been observed in the reproductive state (**Figure 53)**.

Additional specimens seen: COSTA RICA: **Alajuela**. San Ramón, Peñas Blancas, R.B. Monteverde, Río Peñas Blancas, 900 m, 16 December 1987, (Fr.), *W. Haber & E. Bello 7955* (CR); San Ramón, Ángeles, Reserva Forestal de San Ramón, 1 km north east of the field station, 1000 m, 2 December 1993, (Fr.), *G. Herrera 6702* (CR); Primary forest, 620 m, 16 September 1972, (Fl.), *R. Lent 2918* (MO); 3 mi N of San Miguel on road between Vara Blanca and Puerto Viejo, 380 m, 26 May 1976, (Fr.), *T. Croat 35667* (MO). **Cartago**. Jiménez, Pejibaye, Selva, Tausito, Estribaciones de cerro que lleva a río Tausito, 1050 m, 20 January 1996, (Fr.), *A. Cascante & M. Blanco*

955 (CR); Turrialba, Chirripó, Along Quebrada Platanillo near confluence of Quebrada Siripi, Platanillo de Chirripó, 1135 m, 2 March 1990, (Fr.), *M. Grayum & D. Hodel 9728* (CR, MO); Paraiso, Valley of Jicotea, 500–700 m, 30 June 1976, (Fr.), *T. Croat 36535* (MO); Cartago, Dulce Nombre, Jardín Botánico Lankester, 1360 m, 14 Junio 2016, (Fr.), *M. Cedeño 901* (USJ); Cartago, Dulce Nombre, Jardín Botánico Lankester, 1360 m, 20 April 2016, (Fl.), M. *Cedeño & M. Blanco 875* (USJ). **Guanacaste**. In forest on slopes of Volcan Tenorio, 1500 m, 25 August 1980, (Fl., Fr.), *B. Hammel 9578* (MO). **Heredia**. Sarapiquí, La Virgen, Pastures between Río Bijagual and Río Peje, Atlantic slope of Volcán Barva, 500 m, 6 April 1986, (Fl.), *M. Grayum & H. Rowell 6810* (CR, MO). **Limón**. Pococí, Guapiles, Guápiles, Bosque Lluvioso, 350 m, 12 October 2005, (Fr.), *L. Acosta 3700* (CR); Pococí, Colorado, Forests and pastures between Rio Chirripocito and Rio Sardina ('Sardinal' on Chirripo Atlantico quadrangle), 12 m, 21 April 1990, (Infer.), *M. Grayum 9806* (CR, MO); Pococí, Guapiles, Finca Bosque Lluvioso, propiedad del INBio, alrededores de la Estación, 400 m, 11 November 1999, (Fr.), *A. Rodríguez 5387* (CR, MO). **Puntarenas**. Coto Brus, San Vito, E.B. Las Alturas, Las Cruces Tropical Botanical Garden, 6 km W of San Vito de Java, Cultivated and native to Costa Rica species, 1200 m, 7 March 1984, (Infer.), *T. Croat 57260* (CR, MO). **San José**. Vázquez de Coronado, Cascajal, Braulio Carrillo National Park, along Hwy. San Jose to Siquirres Hwy., along trail to Rio Sucio, site of the Old Carrillo Station, 600 m, 30 August 1996, (Infer.), *T. Croat 78786* (CR, MO).

30. *Monstera tablasensis* M.Cedeño, **sp. nov.** — Type: COSTA RICA. Puntarenas. Coto Brus. Sabalito. Zona Protectora Las Tablas, Finca Sandí, 2000 m, 30 April 2016, *M. Cedeño, M. Blanco & F. Oviedo 879* (holotype, USJ!; isotype, MO!, PMA!).

Diagnosis: *Monstera tablasensis* differs from the other species of the genus in Costa Rica by having the petiole sheathing in its entire length, deciduous sheath wings with fibrous residues, acute or cuneate leaf base, coriaceous leaf blades, and a marcescent spathe that envelops the spadix. It is a member of sect. *Monstera*.

Robust nomadic vine, appressed-climbing habit. SEEDLINGS: bearing foliage leaves. JUVENILE PLANTS: root climbers; **stems** light green, smooth, cylindrical; **internodes** 2–5 cm long, 3–5 mm diam.; **blades** not appressed to the phorophyte. ADULT PLANTS: root climbers; **stems** dark-green or beige, cylindrical; **internodes** 1–5 cm long, 1–3 cm diam.; **anchor roots** dark brown; **cataphylls** light-green or yellowish, deciduous but leaving dry fragments on the peduncle; **feeder roots** beige; **petiole** light-green, sometimes white-dotted, smooth, 30–60 cm long, sheathed to the base of the geniculum; **petiole sheath** deciduous; geniculum smooth, sunken adaxially, convex abaxially, 2–3 cm long; **blades** lanceolate to ovate, cuneate to rounded or sub-truncate at the base, acuminate at apex, coriaceous, 30–

45 × 20–30 cm, decurrent-wavy on the geniculum with 4–9 undulations of 1–3 mm wide; **midrib** ribbed adaxially, convex abaxially; **primary lateral veins** 15–25 per side, sunken adaxially, prominent abaxially; **secondary veins** inconspicuous; **collective veins** slightly visible; **fenestrations** absent or present, rounded near the midrib, oval towards the margin;; **margins** entire or pinnatilobed, due to tearing of the fenestrations that extend to the margin, 3–6 lobes per side. INFLORESCENCES on ascending stems; 1–3 simultaneously at flowering time, arranged in the axils of the leaves or into cataphylls; **peduncle** smooth, 10–17 cm long, curved at the base of the spadix at an angle of 80°; **spathe** light green during development, yellowish-white externally and white internally at anthesis, marcescent after anthesis, turning dark brown; **spadix** white during development, light-green at anthesis, 12–18 cm long, 2.5–5 cm diam.; **basal sterile flowers** unknown; **fertile flowers** unknown; **berries** with a creamish stylar cap during development, mature stylar cap cream; pulp white; **seeds** black, 3–5 mm long. (**Figure 54)**.

Etymology: This species is named after the Zona Protectora Las Tablas in Coto Brus (in southern part of Puntarenas province), around which the species is especially abundant.

Distribution and habitat: Endemic to Costa Rica, distributed from the South of the Pacific watershed in the Cordillera de Talamanca, at 1900–2300 m. It occurs in *Premontane wet forest* and *Lower montane wet forest* life zones.

Phenology: Flowering has not been observed, fruiting was recorded in April.

Conservation status: *Monstera tablasensis* is protected in the Zona Protectora Las Tablas.

Comments: In Costa Rica, this species is known from a single collection made in the vicinity of the border with Panama. *Monstera tablasensis* is a poorly known species; the documented Costa Rican population had only mature and developing infructescences at the time of collection.

31. *Monstera tacanaensis* Matuda, Anales Inst. Biol. Univ. Nac. Autón, Mexico, Bot. 43(1): 55. 1974 ['1972']. — Type: MEXICO. Chiapas: Unión Juárez, falda del Volcán Tacaná, bosque alto húmedo del Chiquihuite, 850–2000 m, 14 Feb. 1969, *E. Matuda 37584* (holotype, MEXU!).

Terrestrial plants on cliffs or nomadic vine from the canopy, appressed-climbing and pendent habit. SEEDLINGS: bearing foliage leaves. JUVENILE PLANTS: root climbers; **stems** light-green, smooth, cylindrical; **internodes** 10–18 cm long, 1–1.5 cm diam.; **petiole** distinct, 9–20 cm long; **petiole sheath** persistent or

Figure 54. *Monstera tablasensis*. Adult plant with immature infructescence. *M. Cedeño et al. 879* (USJ).

deciduous; **blades** ovate, subcordate to truncate at the base, acuminate at apex, coriaceous, 10–17 × 8–13 cm, not appressed to the phorophyte; fenestrations absent or present. ADULT PLANTS: root climbers; **stems** light-green to dark-green, cylindrical; **internodes** 8–15 cm long, 1.5–2 cm diam.; **cataphylls** light-green or yellowish, deciduous but leaving dry fragments on the peduncle; **anchor roots** slender, black; **feeder roots** greyish, corky; **petiole** dark-green with black dots, smooth, 20–50 cm long, sheathed up to medial part or 6 cm before the base of the geniculum; **petiole sheath** deciduous; **unsheathed portion** slightly terete; geniculum smooth, flattened adaxially, cylindrical convex abaxially, 2–5 cm long; **blades** ovate to sub-orbicular, cordate at the base, acuminate at apex, subcoriaceous to coriaceous, drying brownish, yellowish or greyish, 18–55 × 18–45 cm, not decurrent on geniculum; **midrib** flattened and prominent adaxially, convex abaxially, drying yellowish or brownish on both surfaces; **primary lateral veins** 4–7 per side, prominent on both surfaces, departing midrib at 85–90°, drying yellowish, brownish or blackish; **secondary veins** slightly prominent; **collective veins** not visible; **fenestrations** absent or present, arranged on each side next to the midrib; **margins** entire or pinnatilobed, 2–5 lobes per side, the fenestrations between the lobes break causing a hook-like structure. INFLORESCENCES on ascending or pendent stems, 1–5 simultaneously at flowering time, arranged in the axils of the leaves or subtended by cataphylls; **peduncle** smooth and pruinose from the middle towards the apex, 8–13 cm long; **spathe** obtuse to short-acuminate, light-green or greyish and completely pruinose during development, pale-pink internally and light-green externally and less pruinose at anthesis, the margins revolute, completely open at apex, deciduous or marcescent after anthesis 13–16 × 10–13 cm, up to 2 cm longer than spadix; **spadix** cream-coloured during development and anthesis, 5–15 cm long, 2–3.5 cm diam.; **basal sterile flowers** 4–6 mm long, with a transparent stigmatic secretion; **fertile flowers** 5–9 mm long; stamens with laminar filaments, 0.5–9 mm long; anthers 2–3 mm long; ovary quadrangular in longitudinal section, ribbed, 4–5 × 4–5 mm; style hexagonal, 1.5–2 × 5–7 mm; stigma linear, sunked on style; **berries** with a dark-green stylar cap during development, mature stylar cap moss-green; pulp creamy-white; **seeds** dark green, oblong, 5–10 mm long. (**Figures 55 & 56**).

Distribution and habitat: Southern Mexico (Chiapas), Guatemala, Costa Rica, and Panama. In Costa Rica is distributed in both watersheds of the cordilleras de Guanacaste, Tilarán, Central and Talamanca, close to the Continental divide and South of the fila Costeña, at 550–2400 m. It lives *Tropical wet forest*, *Premontane wet forest*, *Premontane rain forest* and *Lower montane rain forest* life zones.

Phenology: In Costa Rica, flowering has been recorded in October–November, and the fruit throughout the year.

Conservation status: *Monstera tacanaensis* is protected in the Reserva Biológica Las Cruces, Jardín Botánico Wilson, Jardín Botánico Lankester, Parque Nacional Volcán Tenorio, Parque Nacional Braulio Carrillo, Parque Nacional Volcán Arenal, Parque Nacional Tapantí and Parque Internacional de La Amistad.

Comments: The species is a member of sect. *Tornelia*, distinguished from other species in the genus in Costa Rica by its smooth, deep green, pruinose petioles (sometimes with black dots), cylindrical or almost so between the sheath apex and the geniculum, the geniculum lacking wings, shallowly cordate leaf blades with few fenestrations or none (when present, all of similar size, and only one between successive primary lateral veins), the spathe green and pruinose externally and pinkish cream internally, and a relatively short spadix (5–15 cm long) that turns dark bluish-green to dark brown during fruit development.

Until recently (Cedeño-Fonseca et al., 2020c), *Monstera tacanaensis* had been considered a synonym of *M. deliciosa*; however, the latter has usually thicker stems with a lower internode length-to-width ratio, petioles commonly (but not always) verrucose and distally winged, sheath wings with a small apical ligule, leaf blades deeply cordate, that can have up to 15 fenestrations of very different sizes between successive primary lateral veins, the spathe yellowish externally and cream internally, a relatively long spadix (10–23 cm) with many more florets, and low, cupuliform stigmatophores. The developing fruits of *Monstera deliciosa* turn deep green externally, but never as dark as in *M. tacanaensis*. No pruinosity can be seen on the petioles and spathe of *M. deliciosa*.

Additional specimens seen: COSTA RICA: **Alajuela**. Alajuela, Sarapiquí. Along Río Sarapiquí at and upstream from crossing of road to Colonia Virgen del Socorro, 750 m, 18 August 1990, (Fr.), *M. Grayum 9932* (CR, MO); San Ramón, Peñas Blancas, Rio Penas Blancas, Estacion Eladios, 820 m, 14 May 1991, (Fl.), *E. Bello 2683* (CR, MO); San Ramón, Peñas Blancas, Rio Penas Blancas, Refugio Aleman's Quebrada Rojas, 850 m, 29 February 1992, (Fr.), E. *Bello 4441* (CR). **Cartago**. Turrialba, Alvarado, Capellades, Santa Cruz, Linderos del Río Turrialba, 1750 m, 19 June 2015, (Fl., Fr.), *M. Cedeño 795* (USJ); Cartago, Dulce Nombre, Jardín Botánico Lankester, 1360 m, 26 September 2015, (Fl.), *M. Cedeño & M. Blanco 834* (USJ); Cartago, Agua Caliente, Sobre camino rural de Lourdes a Muñeco, ca. 1.5 km del poblado de Muñeco, Fragmentos de bosque sobre ladera hacia Río Navarro, 1300 m, 3 March 2015, (Fr.), *A. Cascante & C. Trejos 2513* (USJ); Along Camino Raiz de Hule, SE of Platanillo (Tsipiri), 1300 m, 1 July 1976, (Fl.), *T. Croat et al., 36722* (CR, MO); Turrialba, Santa Cruz, Monumento Nacional Guayabo, camino arriba de la casa de la administración, 1100 m, 3 September 1992, (Fr.), *G. Rivera 1970* (CR); Turrialba, Valle del Reventazón, Grano de Oro, Moravia de Chirripó, 1110 m, 29 June 1993, (Fr.), *P.*

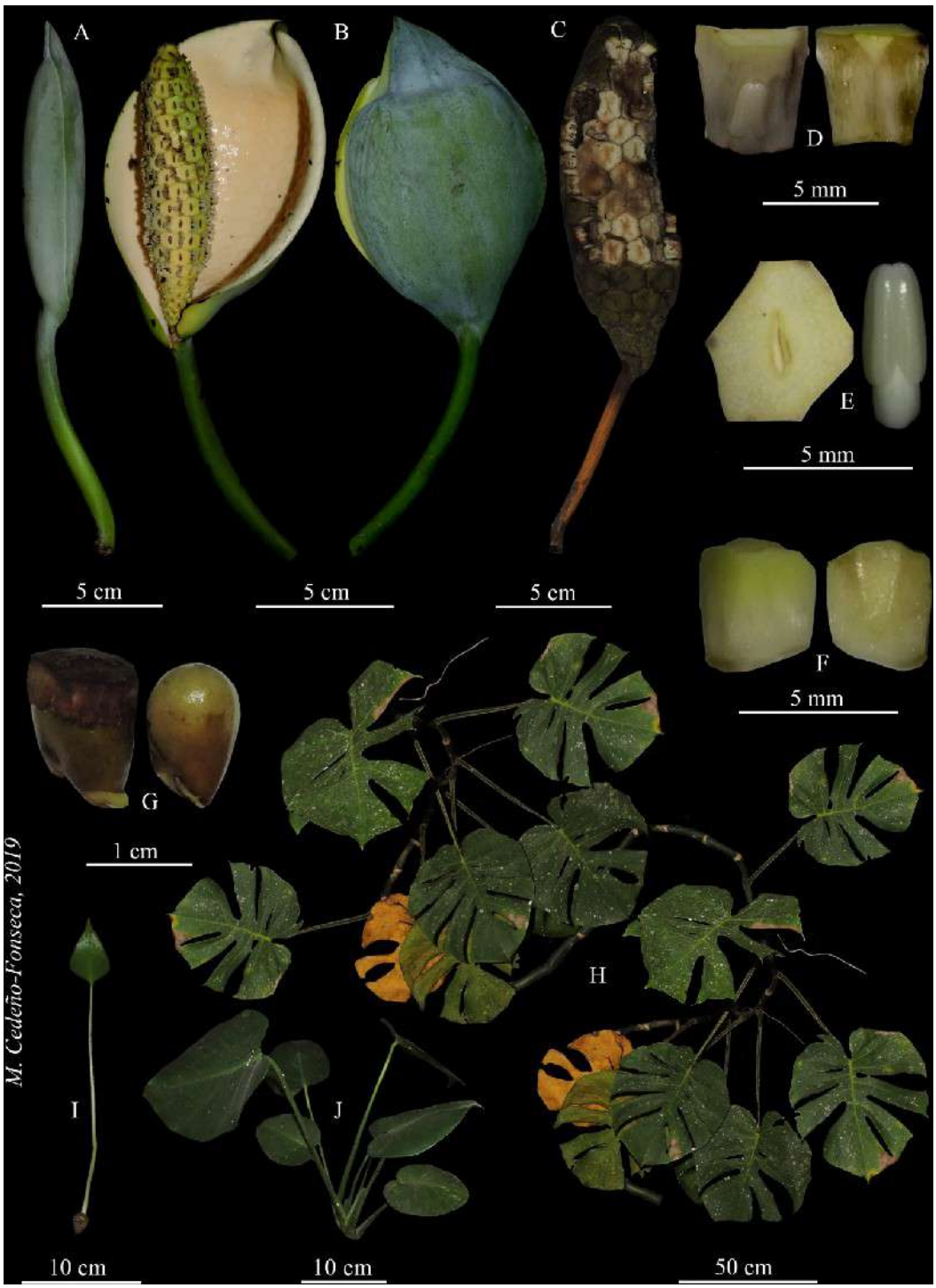

Figure 55. *Monstera tacanaensis*. (A) Developing inflorescence. (B) Inflorescence with open spathe, front and back views. (C) Mature infructescence, stylar plates detached. (D) Fertile flower; lateral view (left) and longitudinal section (right). (E) Stylar plate with stigma (left) and one stamen (right). (F) Sterile floret; lateral view (left) and longitudinal section (right). (G) Seeds; one with persistent stylar plate on top after being extruded from the fruit (left), the other one without stylar plate (right). (H) Portion of adult plant. (I) Seedling. (J) Juvenile plant. *M. Cedeño et al. 834* (USJ).

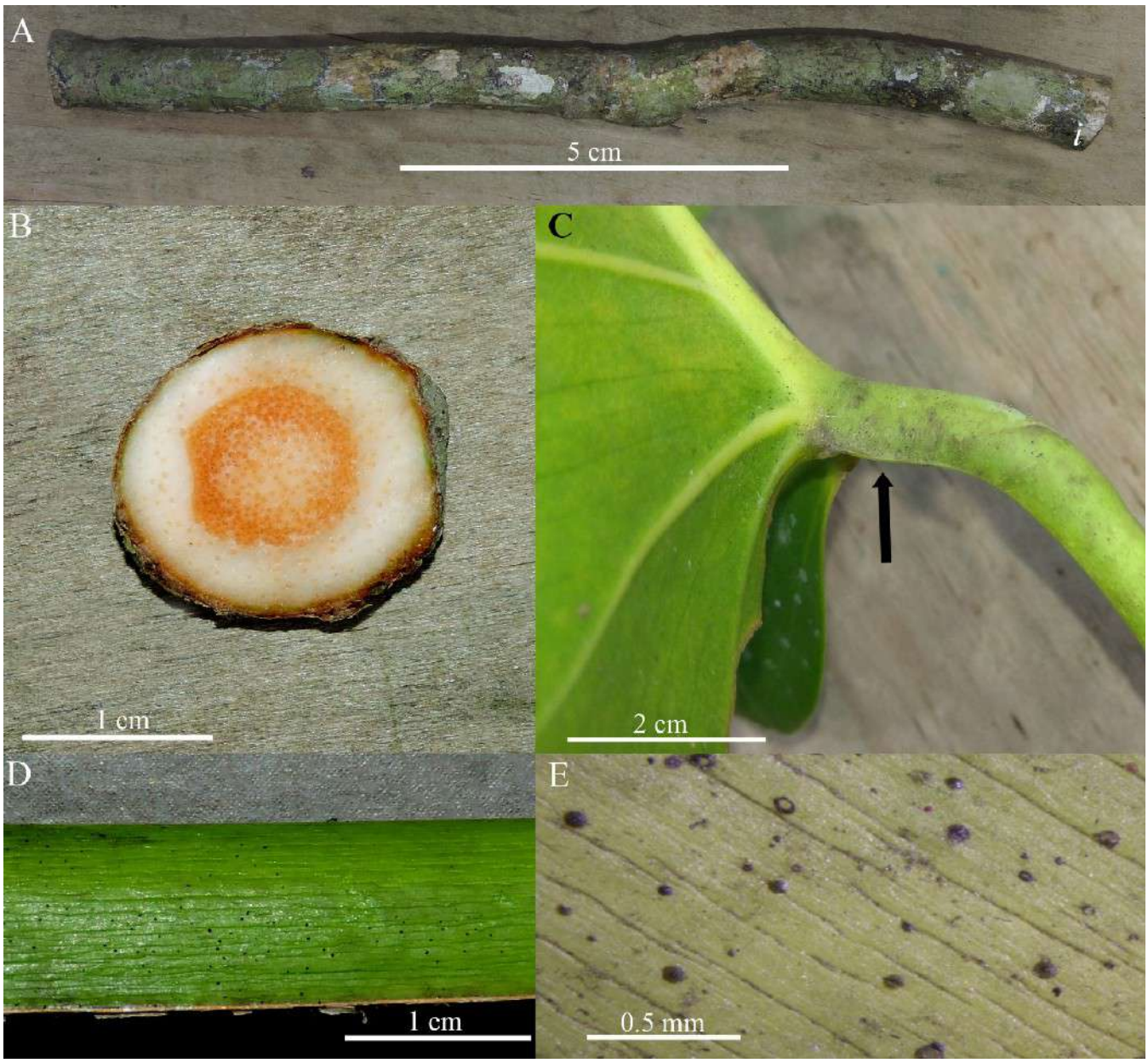

Figure 56. *Monstera tacanaensis*. (A) Older stem. (B) Stem cross sections. (C) Unwinged distal part of petiole and geniculum (arrow). (D) Smooth petiole segment with tiny black dots. (E) Detail of petiole black dots. *M. Cedeño et al. 834* (USJ).

Campos 92 (CR, MO); Pastures in Tapantí, 1200 m, 20 June 1970, (Fr.), *R. Lent et al., 1962* (CR); Paraíso, Orosi, Camino del pueblo de Río Macho al Embalse, Área de cafetales y pequeños bosques alterados, 1480 m, 26 January 2010, (Fl.), *A. Cascante 2175* (CR). **Guanacaste**. Tilarán, Tronadora, Lake Arenal; Hills along south side of lake; from Río Chiquito to Río Caño Negro, 650 m, 9 May 1986, (Infer.), *B. Hammel & G. Hoopen 15139* (CR, MO); Tilarán, Tronadora, Quebrada Grande, Rio Chiquito, Cano Negro, Finca Rodolfo Quesada, 800 m, 10 September 1993, (Infer.), *E. Bello 5400* (CR, MO). **Heredia**. Sarapiquí, La Virgen, Primary forest between Río Peje and Río Sardinalito, Atlantic slope of Río Volcán Barva, 750 m, 3 April 1986, (Infer.), *M. Grayum 6710* (CR, MO). **Limón**. Talamanca, Telire, Gira Transtalamanca, Sendero a la Catarata, 1930 m, 26 Abril 2017, (Fr.), *M. Cedeño et al., 1082* (USJ); Talamanca, Telire, Alto Urén, Cerro Laúbeta entre Río Lorni y Quebrada Chacho, 1190 m, 1 January 1985, (Fr.), *G. Herrera 3383* (CR, USJ, MO); Talamanca, Telire, Alto Lari, Kivut, 1400 m, 1 January 1975, (Fr.), *R. Aguilar & W. Roy 1106* (CR, MO); Pococí, Guápiles, Los Angeles, San Miguel, siguiendo el camino que va al Volcán Irazú, cuenca media del río Blanquillo, margen izquierdo, 1300 m, 26 February 1990, (Fr.), *A. Chacón et al., 790* (CR, MO); Talamanca, Telire, P.N. Cordillera de Talamanca, Cordillera de Talamanca, Siguiendo fila frente unión Queb, Kuisa/ R. Lori, De Ujarrás a San José Cabécar, 1850 m, 21 March 1993, (Fl., Fr.), *G. Herrera et al., 5972* (CR, MO); Limón, Valle la Estrella, Almirante, Fila divisoria entre la Cuenca superior del río Xichiari y la cuenca superior del río Boyei, 1300 m, 13 August 1995, (Fl., Fr.), *G. Herrera 8450* (CR, MO); Pococí, Guapiles, Bosque Lluvioso, 350 m, 14 October 2005, (Fl., Fr.), *L. Acosta 3733* (CR); Talamanca, Bratsi, Rio Coen, 800 m aguas arriba union Queb. Kirigu, De Ujarras a San Jose Cabecar, 1700 m, 28 March 1993, (Fr.), *A. Fernandez 861* (CR); Talamanca, Bratsi, Cima a la derecha union Rios Lori y Coen, Entre Ujarras y San Jose Cabecar, 1600 m, 4 April 1993, (Fr.), *A. Fernandez 1029* (CR); Pococí, Guapiles, Forests mainly to the E of main E branch of Quebrada El Molinete, 480 m, 24 July 1994, (Infer.), *M. Grayum 10677* (CR, MO); Talamanca, Bratsi, Amubri, Alto Lari, Kivut, Afluente innominado del Rio Lari, margen izquierda, 1500 m, 21 March 1992, (Fr.), *G. Herrera 5412* (CR); Talamanca, Bratsi, Bratsi, Parque Internacional La Amistad, sendero Transtalamanca, Entre Ujarrás y San José Cabécar, Entre Quebrada Kuisa y Río Lori, 1809 m, 23 February 2007, (Fr.), *A. Rodríguez 10714* (CR); Talamanca, Bratsi, Bratis, Punto 11 B. Cerca de 1 km NE de Laguna Dabagri, 1571 m, 26 July 2007, (Fr.), *D. Solano 4497* (CR). **Puntarenas**. Coto Brus, San Vito, Estación Biológica Las Cruces, 1200 m, 2 May 2015, (Fr.), *M. Cedeño 778* (USJ); Coto Brus, San Vito, Fila Cruces, 1400 m, 27 Abril 1995, (Fr.), *I. Chacón 14* (USJ); Cloud Forest above Wilson's Finca 6 km s of San Vito de Java. 1523 m, 17 August 1967, (Fr.), *P. Raven & L. Liesner 21860* (CR); Coto Brus, Sabalito, Z.P. Las Tablas, Cordillera de Talamanca, Quijada del Diablo, San Vito, 1200 m, 1

January 1975, (Fr.), *M. Ramírez & H. Schmidt 192* (CR); Región Sur Este del Lago Dabagri, cruzando las filas hacia Telire (Laguna Tiestos y fila de los aguacatillos), 1 January 1985, (Fr.), *L. Gómez & G. Herrera 23205* (CR, MO); Buenos Aires, Buenos Aires, Along ridge between headwaters of Río Chubugra and Río Kuiyé, ca. 12 km NE of Ujarrás, Cordillera de Talamanca, 2100 m, 20 March 1993, (Infer.), *M. Grayum 10387* (CR, MO); Buenos Aires, Potrero Grande, No protegida, Cuenca Térraba-Sierpe, Potrero Grande, Tres Colinas, bajando hacia Helechales, ca. 700 m, Bosque junto al camino, 1700 m, 25 April 2006, (Fl.), *A. Rodríguez & D. Santamaría 10141* (CR, MO); Buenos Aires, Potrero Grande, No protegida, Cuenca Térraba – Sierpe, Sabanas Helechales parte intermedia, Alrededores de la finca del señor Marcial Vidal, 1090 m, 15 June 2006, (Fr.), *F. González & N. Murakami 556* (CR, MO); Coto Brus, Ridge Summit trail on Fila Cruces of Cerro Anguciana, Understory of cloud forest on ridge top, 1535 m, 8 March 1989, (Fr.), *J. Koshear et al., 116* (CR); Coto Brus, Pittier, Sendero a Cerro Gemelo, 1900 m, 31 July 2000, (Fl.), *L. Acosta 2374* (CR, MO); Coto Brus, Sabalito, Zona Protectora Tablas, Cerro Pando, Colecta en bosque y orillas de potreros, 1960 m, 20 November 1996, (Fl.), *E. Alfaro 930* (CR, MO); Coto Brus, Pittier, Estacion Pittier, 1680 m, 8 June 1995, (Fr.), *L. Angulo 334* (CR, MO); Coto Brus, Pittier, Limite Zona Protectora Las Tablas, sendero a Quebrada Gemela, 1650 m, 30 January 1995, (Fl., Fr.), *M. Chinchilla 25* (CR, MO); Coto Brus, Sabalito, Sendero a Cerro Echandi, 1800 m, 10 August 1997, (Fr.), *B. Gamboa 1662* (CR); Coto Brus, Pittier, Estacion Pittier, Sendero Rio Gemelo, 1650 m, 30 January 1995, (Fl.), *E. Navarro 18* (CR); Coto Brus, Pittier, Estacion Pittier, Sendero Pittier, 1680 m, 15 June 1995, (Fr.), *A. Picado 241* (CR); Coto Brus, Pittier, Estacion Pittier, Sendero sobre la Fila hacia el Cerro Pittier, 1640 m, 26 November 1997, (Fr.), *A. Rodríguez 2822* (CR, MO); Buenos Aires, Potrero Grande, Potrero Grande, La Lucha, Cerro Seno, Vegetación achaparrada con predominio de Quercus, Cavendishia, Clusia y helechos, 5–9 m x10–70 cm DAP, 2100 m, 23 February 2008, (Infer.), *D. Santamaría 7118* (CR); Buenos Aires, Potrero Grande, Buenos Aires, Potrero Grande, La Lucha, PILA, Bosque denso de 5–25 m, 1800 m, 25 February 2008, (Fr.), *D. Solano 5164* (CR, MO); Coto Brus, Pittier, Coto Brus, Área de Conservación Amistad Pacífico, Parque Internacional La Amistad, Estación Pittier, Sta. María de Pittier, Sendero Cerro Pittier, 1754 m, 17 May 2015, (Infer.), *N. Zamora 7778* (CR). **San José**. Pérez Zeledón, Rivas, Farmland on steep hills with remnant evergreen forest along streams Río Herradura, tributary of the río Chirripó del Pacífico at 1600 m altitude, northwest of Canán, General Valley, 1600 m, 29 December 1969, (Fr.), *W. Burger & W. Haber 7103* (CR); Vazquez de Coronado, Cascajal, Pastures and forest remnants along the río Cascajal near the waterfalls at 1600 m, 1600 m, 5 November 1978, (Fl.), *M. Thomas et al., 784* (CR); Perez Zeledón, Páramo, R.F. Los Santos, Cerro Lira, 2020 m, 8 March 2001, (Fr.), *A. Quesada 563* (CR); Tarrazú, San Lorenzo, Tarrazú, San

Marcos, between Cerro Toro and Cerro Hormiguero along the road between Basurero and Esquipulas, vicinity of Cerro Hormiguero, 1100 m, 5 September 1996, (Infer.), *T. Croat 78936* (CR, MO); Vázquez de Coronado, Cascajal, Sendero La Montura, entre Estación Quebrada González y Estación Zurquí, 1100 m, 16 February 2000, (Fr.), *A. Rodríguez 5783* (CR); Cartago, La Unión, San Juan, Centro Comercial Auto-Mercado, 1315 m, 18 August 2018, (Fl., Fr.), *M. Cedeño & M. Blanco 1493* (USJ).

32. *Monstera tarrazuensis* Croat & M.Cedeño, *Nordic J. Bot.* 38(12): 5. 2020. — Type: COSTA RICA. San José: Cantón Tarrazú, distrito San Lorenzo, Camino de Tarrazú hacia Quepos, 1386 m, 9 July 2019, (fr.), *M. Cedeño 1686* (holotype, USJ!).

Nomadic vine, appressed-climbing and pendent habit. SEEDLINGS: bearing foliage leaves. JUVENILE PLANTS: root climbers; **stems** light-green with white dots, smooth; **internodes** 3–7 cm long, 3–5 mm diam.; **petiole** distinct, dark or light-green, smooth, 4–10 cm long, sheathed to the base of the geniculum or blade; **petiole sheath** persistent; **blades** lanceolate, cordate at the base, acuminate at apex, coriaceous, 7–14 × 5–9 cm, not appressed to the phorophyte; **fenestrations** absent. ADULT PLANTS: root climbers; **stems** dark green with white dots, smooth, cylindrical; **internodes** 4–11 cm long, 1.2–1.7 cm diam.; **anchor roots** and **feeder roots** light-brown; **petiole** light-green with white dots, smooth, 11–14 cm long, sheathed along its entire length; **petiole sheath** persistent or rarely deciduous; geniculum obscure, 0.5–1 cm long; **blades** ovate to ovate-elliptic, rounded or asymmetrical at the base, short-acuminate at apex, coriaceous, 13–26 × 7.5–13.8 cm, 1.5–2 times longer than wide, not decurrent on the geniculum, drying greyish or brown, faintly glossy; **midrib** ribbed adaxially, convex abaxially, drying dark brown; **primary lateral veins** 5–9 per side, departing midrib at 45–60°, slightly sunken adaxially, prominent abaxially, drying dark brown and wavy; **secondary veins** completely parallel to the primary lateral veins and finely wavy; **collective veins** scarcely visible; **fenestrations** absent; **margins** entire. INFLORESCENCES on pendent stems, arranged in the axils of the leaves; **peduncle** smooth, 13–15 cm long; **spathe** long-acuminate, open at apex and overlapping margins at the medial part, light green during development, white internally and greenish-white or creamy white externally at anthesis, 10–15 × 5–7 cm, up to 5 cm longer that the spadix, falling intact after anthesis; **spadix** oval, white during development, white at anthesis, 5–6 cm long, 2–3 cm diam.; **basal sterile flowers** 2.5–4 mm long, with a transparent stigmatic secretion; **fertile flowers** 3–4 mm long; stamens with laminar filaments, 2–4 mm long; anthers 1.5–2 mm long; ovary rectangular in longitudinal section, 2–3 × 1.5–2 mm; style hexagonal, 1.5–2 × 2–3 mm; stigmatophore absent; stigma linear, with a transparent stigmatic secretion; **berries** with a white stylar cap during development, mature stylar cap white-

cream; pulp white; **seeds** unknown. (**Figures 57 & 58**).

Distribution and habitat: Endemic to Costa Rica in the central Pacific region, on Cerro Hormiguero, at 1100–1400 m elevation. It lives in *Premontane rain forest* life zone.

Phenology: Flowering and fruiting have been recorded in July and September.

Conservation status: *Monstera tarrazuensis* it is not found in any protected areas.

Comments: *Monstera tarrazuensis* belongs to sect. *Monstera*. It differs from the other species of its genus in Costa Rica by its smooth petioles, mottled with light green dots or white dots and with persistent or rarely deciduous sheaths, small (13–26 × 7.5–13.8 cm) coriaceous leaf blades, and inflorescences on hanging stems, with the margins of the spathe overlapping in the lower half. *Monstera tarrazuensis* can be confused with *M. luteynii*, which also has hanging stems, and leaf blades without fenestrations, but it differs because *Monstera luteynii* has stems completely covered with pustules, the leaf blade with tertiary venation strongly prominent on both surfaces, and the terete geniculum. *Monstera tarrazuensis* and *M. luteynii* Madison are both species of hanging habit at elevations greater than 1100 m.

Additional specimens seen: COSTA RICA: **San José**. Tarrazu Cantón, San Marcos de Tarrazu between Cerro Toro and Cerro Hormiguruero along the road between Basuera de Tarrazu and Esquipula, vicinity of Cerro Hormiquero, 1100–1200 m, 5 Septiembre 1996, *T. Croat 78912* (CR, MO); Tarrazu, San Marcos de Tarrazu between Cerro Toro and Cerro Hormiguero along the road between Basuero de Tarrazu and Esquipulas, 1100–1200 m, 5 septiembre 1996, (fr.), *T. Croat 78934* (INB, MO).

33. *Monstera tenuis* K.Koch in A. Braun & C. Bouché, *Index Seminum Hort. Bot. Berol., Appendix*: 4. 1855. — Type: Cultivated at Potsdam, Wildparkstation, *1855, K. Koch s.n.* (holotype, B✝; isotype, K! [fragm.] [barcode K000434515] seen on-line, and here designated as lectotype). — COSTA RICA. Cartago: Tucurrique, 635 m, Jan. 1899, *A. Tonduz 13311* (epitype, B! [barcode B100144968]; isoepitypes: P! 3 sheets [barcodes P00748754, P00748755 & P00748756], US! 2 sheets [barcodes 00087942 & 01095187] all examined on-line, designated here). — See notes below.

Marcgravia paradoxa [W.Bull, *Retail list for 1872*: 7. 1872 & *Gard. Chron*. April 6, 1872: 470. 1872 ('*Marcgraavia paradoxa*'), nom. inval. (provisional)]; W.Bull ex G.W.Johnson & R.Hogg, *J. Hort. Cottage Gard.* n.s. 28: 470. 1875, **syn. nov**. — Type: Cultivated Knowle, Warwickshire, UK, 12 April 1889, *E. Tonks* s.n. (neotype, K!, 3 sheets [barcodes K000626773, K000626774, K000626775], designated here). — See notes below.

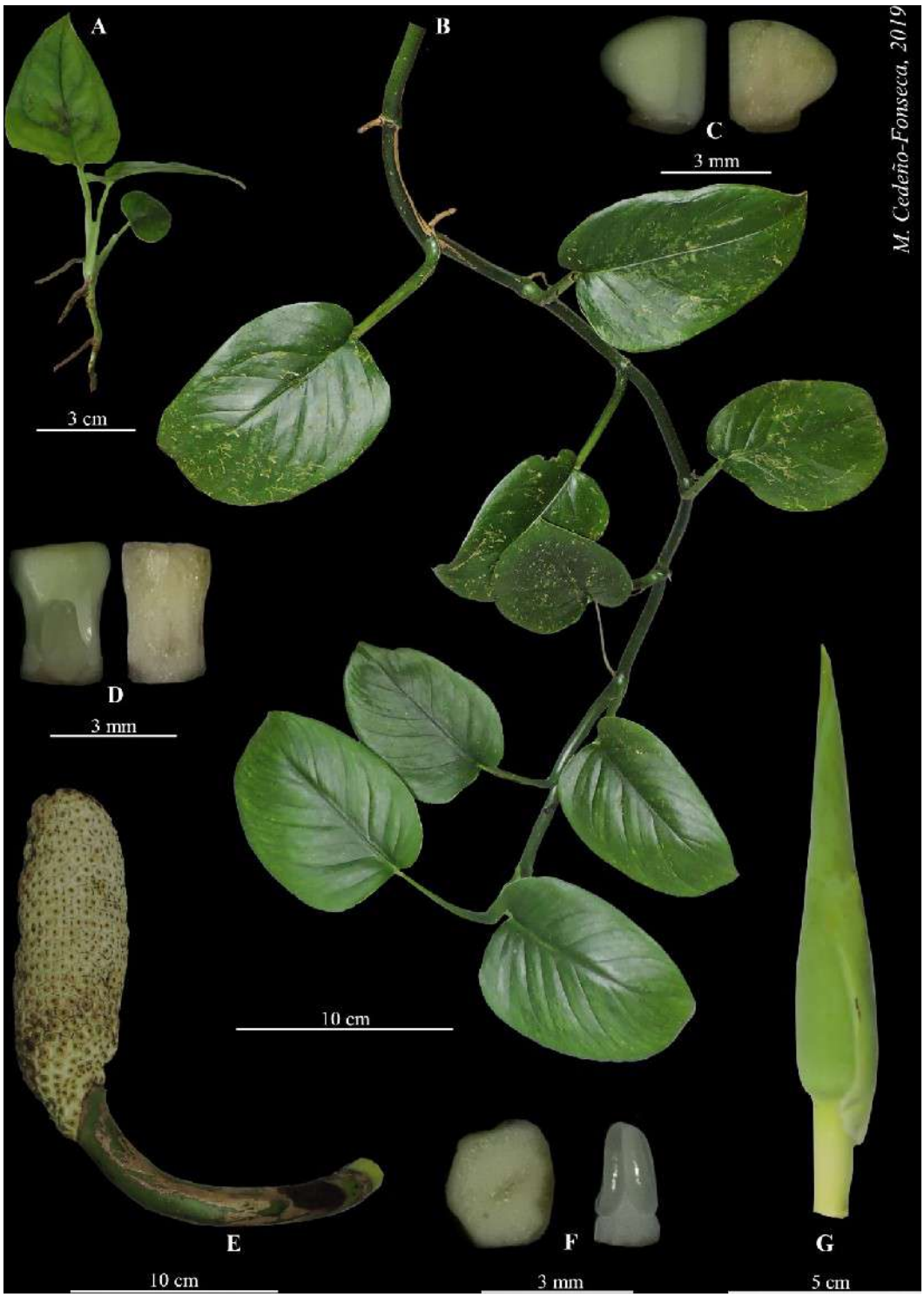

Figure 57. *Monstera tarrazuensis.* (A) Juvenile plant. (B) Adult plant. (C) Sterile flower, in lateral view (left), and longitudinal section (right). (D) Fertile flower, in lateral view (left), and longitudinal section (right). (E) Immature infructescence. (F) Stylar plate with stigma (left) and one stamen (right). (G) Developing inflorescence. *M. Cedeño 1686* (USJ).

Figure 58. *Monstera tarrazuensis*. (A, B) adult plants in their natural habitat, with hanging stems at the edge of the forest, (C) hanging stem with erect inflorescence (arrow), (D) hanging stem with erect infructescence (arrow). *M. Cedeño 1686* (USJ).

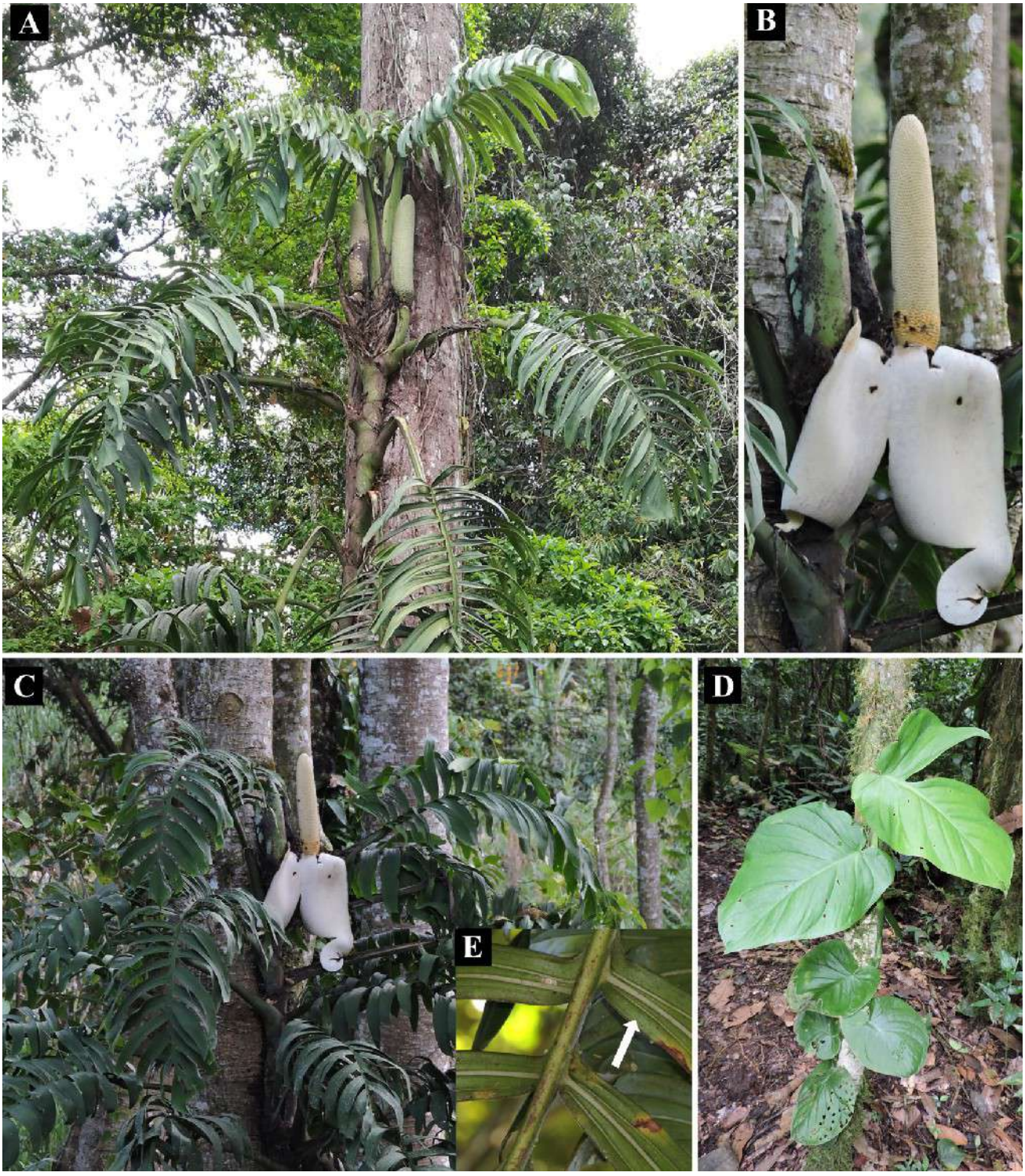

Figure 59. *Monstera tenuis*. (A) Adult individual. (B) Inflorescence in male phase with the spathe opening by longitudinal tearing. (C) Adult plant with inflorescence. (D) Juvenile plant. (E) Abaxial side of lobes of the adult lamina each with a prominent central primary vein and a basally converging secondary vein on each side. Turrialba, Cartago (not collected).

Monstera gigantea Engl., *Bot. Jahrb. Syst.* 37: 118. 1905, [*nom. illeg.*, non *M. gigantea* (Roxb.) Schott, Wiener Z. Kunst 1830(4): 1028. 1830, i.e. *Epipremnum giganteum* (Roxb.) Schott]. — Type: COSTA RICA. Cartago: Tucurrique, 635 m, Jan. 1899, *A. Tonduz 13311* (holotype, B!; isotypes, P!, US! all examined on-line).

Robust to massive nomadic vine, appressed-climbing habit. SEEDLINGS: filiform. JUVENILE PLANTS: root climbers; **stems** light-brown or green, smooth, flattened or cylindrical; **internodes** 2–10 cm long, 5–10 mm diam.; **petiole** not visible (covered by blade), dark green, smooth, 2–4 cm long; **blades** obovate, subcordate at the base, acuminate at apex, coriaceous, 5–15 × 4–10 cm, appressed to the phorophyte; **fenestrations** absent. ADULT PLANTS: root climbers; **stems** light-brown or green, cylindrical, warty with pustules; **internodes** 3–8 cm long, 3–14 cm diam.; **anchor roots** light brown; **feeder roots** dark-brown; petiole light-green, smooth, 25–70 cm long, sheathed to the base of the geniculum; **petiole sheath** deciduous with fibrous remains; geniculum smooth, flattened adaxially, convex abaxially, 2–5 cm long; **blades** lanceolate to ovate to lanceolate-oblong, obtuse, truncate, sub-cordate or attenuate at the base, obtuse to slightly acuminate at apex, coriaceous, drying yellowish, blackish, brownish or reddish, 45–90 × 35–50 cm, 1.5– 2 times longer than wide, decurrent on the geniculum, decurrent portion 1–2 mm wide; **midrib** ribbed adaxially, convex abaxially, drying black to dark brown on both surfaces; **primary lateral veins** 5–60 per side, slightly sunken adaxially, prominent abaxially, drying blackish or dark brown; **collective veins** not visible; **fenestrations** present only in the transition to adult leaves; **margins** deeply pinnatifid, 5–30 lobes per side, often somewhat drooping, with 3–5 veins per lobe (the middle one the most prominent). INFLORESCENCES on ascending stems, 1–5 simultaneously at flowering time, arranged in the leaf axils; **peduncle** smooth, 4–10 cm long, 3–4(6) cm diam.; **spathe** obtuse to short-acuminate, green-yellowish externally and white-cream externally during development, completely open or tearing in fragments, deciduous after anthesis, 15–40 × 10–20 cm, as long as the spadix; **spadix** white-cream during development, yellow at anthesis, 13–40 cm long, 2–6 cm diam.; **basal sterile flowers** 5–8 mm long, with a yellowish stigmatic secretion; **fertile flowers** 0.9–1.5 cm long; stamens with laminar filaments, 2–10 mm long; anthers 1.5–2 mm long; ovary rectangular in longitudinal section, ribbed, 7–11 × 2–3 mm; style hexagonal, 4–6 × 2–3 mm; stigmatophore semi-columnar; stigma linear, with a yellow stigmatic secretion; **berries** with a pale-green stylar cap during development, mature stylar cap moss-green; pulp grey; **seeds** black with light brown dots, elongated, 6–10 mm long. (**Figure 59)**.

Distribution and habitat: from Nicaragua to Costa Rica and Panama. In Costa Rica it is distributed throughout the country (both watersheds), at 0–1766 m. It lives in *Tropical moist* forest, *Tropical wet forest*, *Premontane wet*

forest and *Premontane rain forest* life zones; in primary and secondary forest, and open areas.

Phenology: In Costa Rica, flowering has been recorded in February, May, November–December, and fruit in January–March, and May–September.

Conservation status: *Monstera tenuis* is protected in the Jardín Botánico Wilson, Jardín Botánico Lankester, Reserva Biológica Monteverde, Estación Biológica La Selva, Estación Biológica La Tirimbina, Parque Nacional Guanacaste, Parque Nacional Rincón de la Vieja, Parque Nacional Volcán Arenal, Parque Nacional Braulio Carrillo, Parque Nacional Tortuguero, Parque Nacional Tapantí, Parque Internacional de La Amistad (parte baja caribe y pacífico), Parque Nacional Corcovado, Zona Protectora Volcán Miravalles and Reserva Forestal Golfo Dulce.

Comments: The species is a member of section *Marcgraviopsis*. It is different from the other species of the genus in Costa Rica by the light green petiole, sheathing to the base of the geniculum, with deciduous wings leaving fibrous residues, leaf blades deeply pinnatífid and never fenestrate, inflorescences with the spathe white-cream externally, spadices up to 40 cm long with short peduncles (<10 cm), and the infructescence moss green at maturity. It could be confused with *M. pinnatipartita*, but that species has the petioles speckled, with wings of the leaf sheath persistent and involute, and it lacks the shingling juvenile phase.

Monstera tenuis is among the most robust species of the genus, only rivalled in the size of the leaves by *M. deliciosa* and the recently described Panamanian *M. gigas* Croat et al., the latter with leaves which can reach 3 m long (Cedeño-Fonseca et al., 2021b). *Monstera tenuis* also has the largest spadix of any species, though overall inflorescence size is eclipsed by *M. titanum* Croat et al., also from Panama, whose combined peduncle and spathe length can approach 1 m (Cedeño-Fonseca et al., 2021b).

The morphology of the flowers and fruits of *Monstera tenuis* could not be properly documented for this study because the plants bloom at >10 m above ground, which has made it difficult to collect at different reproductive stages. This species is frequent in humid lowland forests on the Caribbean slope, mainly in open areas and forest edges. Plants that grow within primary and secondary forests are difficult to see in the reproductive state, perhaps because they only bloom very high in the canopy. Plants of this species may develop hanging stems when they cannot continue to ascend on the phorophyte, but inflorescences appear to occur only on ascending shoots.

Nomenclatural notes: *Monstera tenuis* was based by Koch on a juvenile plant in the shingling stage cultivated at Berlin from live

material of unrecorded provenance introduced by Warszewicz, and grown first by the Berlin nurseryman Louis Mathieu (Koch, loc. cit.). The holotype specimen is apparently no longer at Berlin (and there is no photograph of it at F), but two fragments from it, taken and annotated by N.E. Brown, are preserved at K (sheet K000434515) and are to be considered an isotype [see Turland et al. (2018): Art. 8.3, Ex. 8], here further designated as the lectotype. Madison (1977) attributed the type to Warszewicz directly, but a note on the Kew fragments indicates they are taken from "C. Koch's Type specimen" and that the plant was growing at "Wildparkstation" — which may allude to the Prussian royal horticultural school founded and directed by Lenné at Wildpark near Potsdam (N. Köster, pers. comm.), so the type is here attributed to Koch. It is doubtful that the species widely known as *Monstera tenuis* can be unequivocally recognised from these extremely juvenile fragments alone, and therefore an epitype is designated here which accords with Madison's application of the name, itself guided by N.E. Brown's (see below), and widely followed ever since.

Marcgravia paradoxa first appeared in a William Bull retail list for 1872, and, in the same year, in an advertisement from his business in Gardeners' Chronicle (loc. cit.). In both instances it is stated that "This name is provisionally applied to a very remarkable stove creeping-stemmed perennial sent from Nicaragua, by the late Dr. Seemann [Berthold Carl Seemann (1825–1871)], as a species of *Marcgraavia* [sic], but which, under cultivation, has very much more the aspect of a *Pothos*, and may possibly prove to be an entirely new genus", a statement he repeated again and again in later catalogues until 1877. Given the name is explicitly stated to be provisional, it is invalid [see Turland et al. (2018): Art. 36.1, see Ex. 5 & 6] despite the presence of otherwise validating descriptive information. However, the name appeared in 1875 without any qualification about being provisional and with validating descriptive information ("green begonia-like leaves, clinging as closely to a board, as if they were gummed") in *J. Hort. & Cottage Gardener*, (new series) 28: 470. June 17 1875, in a report of its having been exhibited by Bull on June 16th that year at the Royal Botanic Society's summer exhibition at Regent's Park, London. This is the earliest place of valid publication we have found. As the report is anonymous, we attribute the validation of the name to the periodical's then editors George Johnson (1802–1886) & Robert Hogg (1818–1897).

Concerning the application of the name *Marcgravia paradoxa*, there is no known original material, and no illustration or specimen until five years after it first appeared, when Bull's plant was figured by Masters (1877: Figure 2). It is clearly a shingling aroid, though a vague but disconcerting description of a (true) *Marcgravia* inflorescence was included in the text, apparently added for colour. Next, N.E. Brown preserved material at Kew [two un-numbered sheets] taken from Bull's nursery on 20th September 1878 and

annotated "*Monstera tenuis* C.Koch [the epithet and author added in pencil in Brown's hand], Central America (Chontales? [Nicaragua]) Seeman [sic]. Hort. Bull Sept. 20th 1878. N.B. This specimen is from the identical plant described by Dr. Masters in Gard. Chron. 1877 vol 8 p. 13 as ***Marcgraavia paradoxa*** Bull. Cat. 1872, p.7. All these [pieces] are from *one plant*! the bit of stem with the entire leaves is a side shoot of the stem which bore the pinnatifid leaves. *Teste* N.E. Brown" [emphasis original]. They comprise the juvenile leaf phase, an adult pinnatifid leaf, and an almost entire leaf (with one division) from the transition zone between the shingling and adult stages, and accord with *Monstera tenuis* in the current sense. Lastly, a rather later specimen at Kew (mounted on three sheets clearly identified as parts of one element and thus not duplicates) had been sent in 1889 to N.E. Brown by Edmund Tonks of Knowle, Warwickshire, who had obtained the plant as *Marcgravia paradoxa* and grown it to flowering. [Edmund Tonks (1824–1898), barrister and brass founder, whose grounds at Packwood Grange boasted ". . . various hot-houses and conservatories, which were filled with a splendid collection of choice plants." (*Birmingham Daily Post*, Tuesday Sept. 9 1884: 5).]. The specimen includes a juvenile shingling leaf, a pinnatifid adult leaf (with petiole) with the lobes each with one primary vein and basally convergent secondary veins, and a post-anthesis spadix. In addition, it includes a habit sketch of the plant showing the characteristic somewhat drooping lobes of the leaf blade. Brown had identified it as *Monstera tenuis*, and it too accords exactly with *Monstera tenuis* in the current (i.e. Madison's) sense. We therefore here designate the Tonks specimen the neotype of *Marcgravia paradoxa*, given that it is fertile. Madison (1977) indicated he had used the above-mentioned N.E. Brown specimen from Bull's nursery (though he did not explicitly cite it) to guide his interpretation of the name *Monstera tenuis*, since Brown had identified that material as *M. tenuis* after studying Koch's juvenile type. He (Madison) seems to have overlooked that this material was of Bull's *Marcgravia paradoxa*, and consequently did not include it as a synonym.

It is curious that it took some six and more years after the plant's introduction for it to be found to be a *Monstera*, first by Brown in the above-mentioned specimen annotation, and then later by Hemsley (1885: 427) who noted that *Marcgravia paradoxa* ". . .is a barren or juvenile state of some species of [*Monstera*]". That it appears to have remained in cultivation in a persistently juvenile state is possibly related to the practice at the time of growing it on pieces of wood without soil contact (e.g. Masters, 1877: Figure 2).

Additional specimens seen: COSTA RICA: **Alajuela**. San Ramón, Peñas Blancas, R.B. Monteverde, Río Peñas blancas, Laguna, 850 m, 27 May 1988, (Fr.), *E. Bello 413* (CR); Primary forest and perimeter, Finca Los Ensayos ca 11 miles NE of Zarcero, 850 m, 15 August 1977, (Infer.), *T. Croat 43594* (CR, MO); Along road between Cañas and Upala, 400 m, 24 June 1976,

(Infer.), *T. Croat 36322* (MO); San Isidro de San Ramón, 1259 m, 21 Octubre 1986, (Fr.), *G. Herrera 57* (MO); 3 miles north of San Miguel, 380 m, 26 Mayo 1976, (Infer.), *T. Croat 35644* (MO). **Cartago**. Paraíso, Cachí, Remnant trees near Río Naranjo, 3 km E of Cachí, 1300 m, 20 April 1969, (Fr.), *R. Lent 1589* (CR); Turrialba. Peralta. (Tres Equis), 450 m, 15 April 1935, (Fr.), *F. Solís 237* (CR); Turrialba, La Suiza, Jardín Botánico Carlos Lankester, 6 km al este de la ciudad de Cartago, 1370 m, 22 October 1994, (Infer.), *A. Quesada 21* (CR); Turrialba, Santa Cruz, Sobre ríos Guayabo, Lajitas y monumento, Crece a orillas de las quebradas, 1100 m, 27 June 1992, (Fr.), *G. Rivera et al., 1888* (CR); Turrialba, Turrialba, CATIE, Confluencia del Rìo Tuis y el Rìo Reventazòn, 580 m, 15 June 1994, (Fr.), *G. Herrera 7157* (CR); Turrialba, Along road between Juan Viñas and Turrialba, 1 July 1976, (Fr.), *T. Croat 36838* (MO); Cartago, Wooded slope along the Río Sombrero just outside of El Muñeco, 1300 m, 25 June 1972, (Fr.), *J. Luteyn 3240* (MO); Cartago, Dulce Nombre, Jardín Botánico Lankester, 1360 m, 26 September 2015, (Fr.), *M. Cedeño & M. Blanco 835* (USJ). **Guanacaste**. Liberia, Mayorga, P.N. Guanacaste, Estación Mengo, Sendero al potrero, lado sur, 1100 m, 15 July 1989, (Fr.), *INBio 185* (CR, MO); Bagaces, Mogote, P.N. Rincón de la Vieja, Sendero a San Jorge, límite este, Cabecera de Quebrada Tapezco, 770 m, 12 June 1991, (Fr.), *G. Rivera 1365* (CR); Bagaces, La Fortuna, Z. P. Miravalles, Cuenca del Tempisque, Zona Protectora Volcan Miravalles, 900 m, 24 May 1997, (Fr.), *F. Alvarado et al., 187* (CR); Liberia, Mayorga, Sector Cacao hacia la Estación 2.5 Km después del río Góngora, en bosque remanente, 900 m, 1 May 2000, (Fl.), *L. Acosta 1100* (CR); Liberia, Mayorga, Estacion Cacao, Sendero Pedregal, Bosque primario, 1100 m, 10 February 1995, (Fl.), *B. Gamboa 63* (CR, MO); Parque Nacional Rincón de la Vieja, 900–1200 m, 27 January 1983, (Fl.), *G. Davidse 23387* (MO). **Heredia**. Sarapiquí, Near Puerto Viejo along road near the Río Sucio, 20 m, 27 May 1976, (Infer.), *T. Croat 35712* (MO); Sarapiquí, La Selva Field Station, 100 m, 3 January 1978, (Infer.), *T. Croat 44229* (MO); La Selva Biological Station, 100 m, 16 June 1984, (Fr.), *B. Jacobs 2370* (MO); Along road between San Jose and Puerto Viejo, 100 m, 1 October 1987, (Infer.), *T. Croat 68380* (MO); La Selva Biological Station, 100 m, 9 July 1984, (Fr.), *B. Jacobs 2770* (MO). **Limón**. Pacuarito, Banana and cacao plantations on level areas between Siquirres and the Río Pacuare, and remnant forest on steep hills south of the railroad bridge over the río Pacuare, 80 m, 20 December 1969, (Fl.), *W. Burger & R. Liesner 6955* (CR, MO); Along highway 32 near Río Madre, ca.1 miles southwest of Limón, 10 m, 13 August 1977, (Fr.), *T. Croat 43306* (CR, MO); Pococí, Colorado, P.N. Tortuguero, Estación Agua Fría, 4 km al Norte siguiendo el cauce del Río Agua Fría hasta la unión con el Río Tortuguero, Bosque perturbado, 40 m, 15 March 1988, (Infer.), *R. Robles 1733* (CR, MO); Pococí, Guapiles, Bosque Lluvioso, alrededores de la casa, bordes de bosque, 350 m, 18 August 2005, (Infer.), *L. Acosta 3566* (CR); Talamanca, 7 km SW of Bribrí, 100–250 m, 4 May 1983, (Fl.), *L. Gómez*

20317 (CR, MO); 20 mi SE of Limón on road to Punta Cahuita, 0 m, 11 August 1977, (Infer.), *T. Croat 43171* (MO); Siquirres, 2 miles NW of Río Siquirres on Highway 32 from Limón to Turrialba, 200 m, 11 August 1977, (Infer.), *T. Croat 43160* (MO); Along road from Río Frio to Limón, 360 m, 2 October 1987, (Infer.), *T. Croat 68425* (MO); 20 mi SE of Limón on road to Punta Cahuita, 0 m, 11 August 1977, (Infer.), *T. Croat 43173* (MO). **Puntarenas**. Buenos Aires, Biolley, P.I. La Amistad, Cordillera de Talamanca, area around Río Canasta, 9.5 airline km NW of Agua Caliente, between Cerro Frantzius and Cerro Pittier, 1550 m, 6 September 1984, (Fr.), *G. Davidse et al., 28393* (CR, MO); Buenos Aires, Biolley, P.I. La Amistad, Estación Altamira, cerro Biollley, Cuenca Térraba-Sierpe, 1766 m, 1 June 1996, (Fr.), *J. Quesada 1623* (CR, MO); Coto Brus, Pittier, Pittier, Santa María, Sobre sendero al Río Canasta, 1700 m, 30 July 2000, (Fr.), *L. Acosta 2352* (CR); Coto Brus, Pittier, Estacion Pittier, Sendero Altamira, 1650 m, 28 January 1995, (Fr.), *M. Chinchilla 7* (CR); Buenos Aires, Potrero Grande, Buenos Aires, Potrero Grande, La Lucha, Punto 8, Bosque denso 5–25 m DAP 30–90 cm; Predominio de Hampea appendiculata, Cecropia sp, Ruagea glabra, Lauraceae y helechos arborescentes, 1400 m, 20 February 2008, (Fr.), *D. Santamaría 7027* (CR); Vicinity of San Vito de Java, Disturbed primary forest, 4000 f, 28 February 1976, (Fr.), *T. Croat 32902* (MO); Corredores, En el camino que va desde La Estación Biolgógica Las Cruces hasta el Río Jaba, 1170 m, 16 June 2003, (Infer.), *R. Moran 6481* (MO); Coto Brus. Finca Las Cruces, 5000 f, 17 March 1969, (Fr.), *W. Stevens 233* (MO); Coto Brus, San Vito, Estación Biológica Las Cruces, 1200 m, 2 May 2015, (Infer.), *M. Cedeño 781* (USJ); Comunidad de Monteverde, En arbol en potrero abierto, 1450 m, 26 June 1977, (Fl.), *V. Dryer 1535* (CR). **San José**. Turrubares, Carara, P.N. Carara, Cuenca del Río Grande de Tárcoles, Ridges W of Río del Sur (E foothills of Montañas Jamaica), bet. Carara and El Sur, 280 m, 3 April 1993, (Infer.), *M. Grayum 10446* (CR, MO); Perez Zeledon, About 1 mile beyond divide between San Isidro del General and coastal town of Dominical, 900 m, 22 May 1976, (Infr.), *T. Croat 35320* (MO).

34. *Monstera tuberculata* Lundell, *Lloydia* 2: 78, t. 1. 1939. — Type: BELIZE. El Cayo District, Valentin, June 1936, *C.L. Lundell 6238* (holotype, MICH! sheet MICH1115586, seen on-line; isotype, GH!).

Nomadic vine, appressed-climbing and pendent habit. SEEDLINGS: filiform. JUVENILE PLANTS: root climbers; **stems** light-green to dark, smooth, flattened; **internodes** 3–6 cm long, 3–5 mm diam.; **petiole** not visible, dark green, smooth, 3–6 cm long; **blades** obovate or orbicular, subcordate to truncate at the base, acuminate at apex, coriaceous, variegated, 5–10 × 4–9 cm, appressed to the phorophyte; **fenestrations** absent. ADULT PLANTS: root climbers; **stems** dark-green to light-green, smooth, cylindrical or dorsoventrally compressed and slightly sulcate on one side, with caducous

epidermis; **internodes** 5–15 cm long, 1–2 cm diam.; **anchor roots** dark-brown; **feeder roots** corky; **petiole** light or dark-green, smooth, 2–6 cm long, sheathed to the base of the geniculum, the sheath apically prolonged in a free ligule, 3–6 cm long; **petiole sheath** dry-persistent for several days, leaving fibrous residues; geniculum smooth, flattened adaxially, convex abaxially, 5–10 mm long; **blades** ovate, cordulate to cordate at the base, obtuse to short-acuminate at apex, coriaceous, drying blackish, yellowish or greyish, 5.5–20 × 4–12 cm, 1.4–1.9 times longer than wide, not decurrent on the geniculum; **midrib** convex on both surfaces, drying blackish abaxially, **primary lateral veins** 4–7 per side, obscure adaxially, prominent abaxially, drying yellowish or blackish; **secondary veins** reticulate and prominent, wavy throughout its length when dry; **collective veins** slightly visible; **fenestrations** absent; **margins** entire. INFLORESCENCES on pendent stems, 1–10 simultaneously at flowering time, arranged in the leaf axils; **peduncle** smooth, 2–5 cm long, 2–6 mm diam.; **spathe** acuminate to long-acuminate, green externally during development, yellowish green or creamy white externally and white internally at anthesis, marcescent or deciduous after anthesis, 7–10 × 6–8 cm, up to 3 cm longer than the spadix; **spadix** white during development, yellow at anthesis, 4–7 cm long, 1.5–3.5 cm diam.; **basal sterile flowers** 4–6 mm long, with a yellowish stigmatic secretion; **fertile flowers** 5–9 mm long; stamens with laminar filaments, 1–5 mm long; anthers 1.5–2 mm long; ovary acute at the base, ribbed, 3–5 × 2–3 mm; style pentagonal or hexagonal, 5–6 × 3.5–5 mm; stigmaphore thickly conical and recurved, 3–6 mm long; stigma linear, with a rusty red stigmatic secretion; **berries** with a yellowish-green stylar cap during development, mature stylar cap dark-green; pulp white; **seeds** brown with white dots, oblong, 6–9 mm long. (**Figure 60)**.

Distribution and habitat: From Mexico (Oaxaca) to western Panama. In Costa Rica it is distributed in the Caribbean watershed, at 0−1100 m. It lives in *Tropical rain forest*, *Tropical wet forest* and *Premontane rain forest* life zones; primary and secondary forest.

Phenology: In Costa Rica, flowering has been recorded in February, April, June–July and November, and the fruit in May–August.

Conservation status: *Monstera tuberculata* is protected in the Estación Biológica La Selva, Estación Biológica La Tirimbina, Refugio de Vida Silvestre Mixto Gandoca-Manzanillo and Parque Nacional Braulio Carrillo.

Comments: The species is a member of section *Echinospadix*. It differs from the other species of the genus in Costa Rica by the petiole sheathing up to the base of the geniculum, with the sheath apically prolonged in a free ligule of 3–6 cm, wings of the petiole that dry and persist for several days, eventually leaving fibrous residues, the leaf blade basally cordate, entire and without fenestrations,

inflorescences produced only in hanging stems, and the linear stigma raised by an abruptly conical and curved stigmatophore. This species grows as a canopy vine, similar to *Monstera pittieri,* but the latter is differentiated by its not cordate leaves, flowers without stigmatophores, and the yellow stylar layer.

In Costa Rica there are five species of *Monstera* that produce inflorescences only on hanging stems: *M. luteynii*, *M. molinae*, *M. pittieri*, *M. tuberculata* and *M. tarrazuensis*, the most frequent being *M. tuberculata*, which sometimes grows sympatrically with *M. pittieri* in the southern Caribbean (Gandoca-Manzanillo Mixed Wildlife Refuge). *Monstera molinae* is mainly found in cloud forests of the Cordillera de Tilarán and less frequently in the humid forests of the lowlands, and it has the leaves lobed (rarely entire). Juvenile plants of *Monstera tuberculata* have variegated leaves, and retain this pattern in the pre-adult ascending stems in the canopy. The hanging stems (adult) produce completely green or variegated leaves. *Monstera punctulata* and *M. dubia* show light variegation in the leaves of juveniles, but these species are not sympatric with *M. tuberculata*. *Monstera dubia* is distributed in the lowlands of the Pacific slope and *M. punctulata* grows at elevations above 600 m, in cloud forests.

Costa Rican material of *Monstera tuberculata* corresponds to var. *brevinoda* (Standl. & L.O.Williams) Madison, which is distinguished by having a stigmatophore that originates at the top of the style. In *Monstera tuberculata* var. *tuberculata*, there is no clear demarcation between the style and projection of the stigmatophore. Some populations of *Monstera tuberculata* var. *tuberculata* in Belize (*Brewer 7635,* MO), have adult leaf blades with abundant impressed glands on the underside, and in Mexico, in the region of Veracruz (*Ceja et al. 1881*, XAL) they present leaves with a few fenestrations, a characteristic never observed in the populations of Costa Rica and Panama.

Additional specimens seen: COSTA RICA: **Alajuela**. San Carlos, Pocosol, Azucena, Concho de Cutris, 80 m, 4 April 1991, (Fl., Fr.), *Q. Jiménez et al., 962* (CR, MO); Upala, Aguas Claras, P.N. Rincón de la Vieja, Cordillera de Guanacaste, Colonia Blanca, Finca Los Moras, junto a Quebrada Mora, 770 m, 13 June 1991, (Fr.), *G. Rivera 1393* (CR, MO); Upala, San José o Pizote, San José, 4 km al Noroeste del pueblo, Laguna Las Camelias, 20 m, 19 April 1988, (Fl.), *G. Herrera 1848* (CR, MO); Upala, Aguas Claras, Sector de Rio Aguas Verdes, 2 Km aguas arriba del puente, falda NE del volcan Santa Maria, 600 m, 12 February 1991, (Fl.), *G. Rivera 1052* (CR); Upala, Prov., Guanacaste-Alajuela, lower montane rainforest, 1500 m, 1 November 1982, (Infer.), *L. Gómez 19175* (MO). **Cartago**. Turrialba, Along road from Río Pacuare to Grano de Oro on road from Turrialba to Moravia, 600–1200 m, 30 June 1976, (Fr.), *T. Croat 36574* (MO). **Heredia**. Sarapiquí, Las Horquetas, Along Starkey Road", 50 m, 7 August 1979, (Fr.), *W. Stevens 13475* (CR, MO); Sarapiquí, La Virgen, S base of

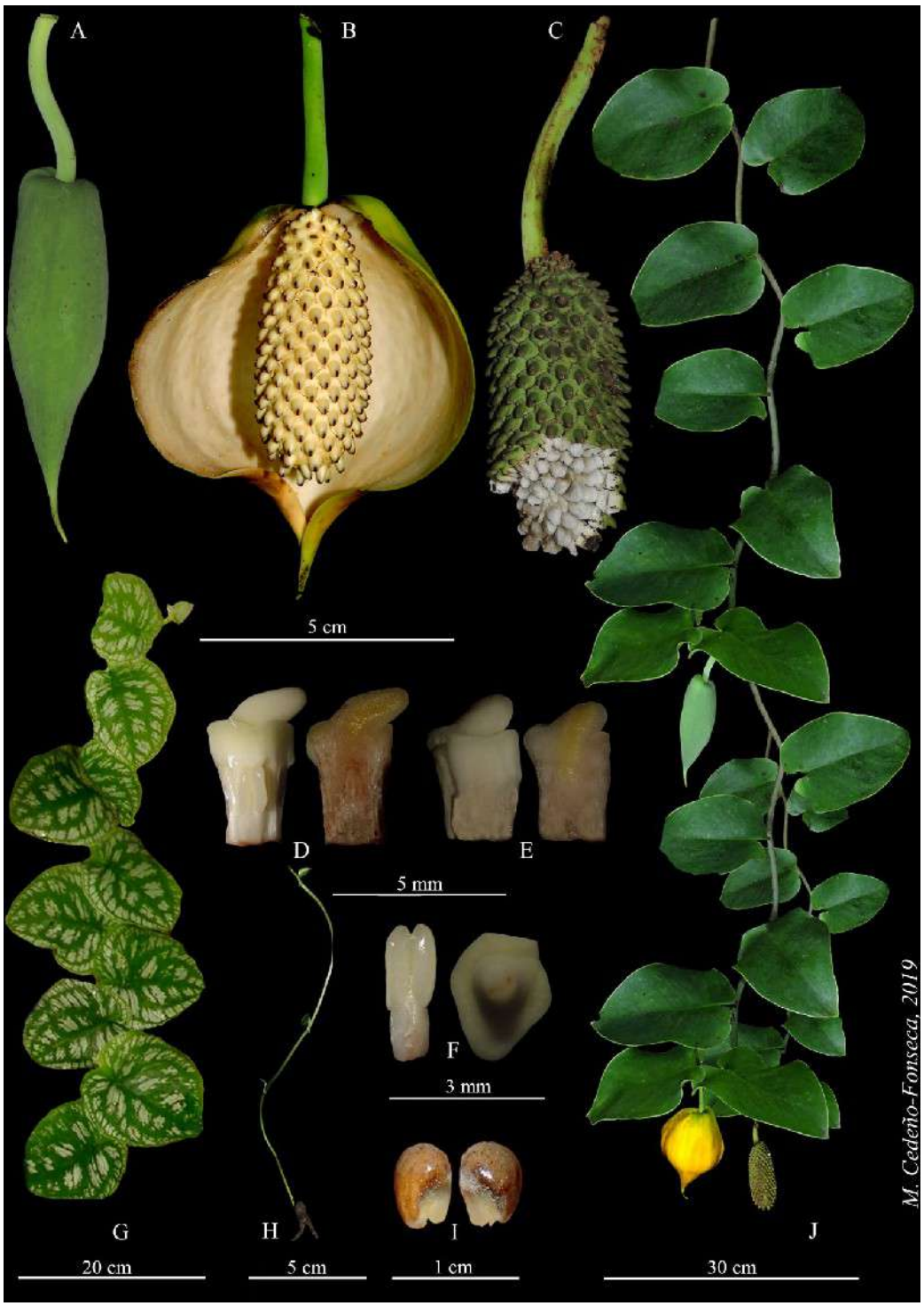

Figure 60. *Monstera tuberculata*. (A) Developing inflorescence. (B) Inflorescence with open spathe, front view. (C) Mature infructescence, stylar plates detaching. (D) Fertile flower, in lateral view (left), and longitudinal section (right). (E) Sterile flower in lateral view (left) and in longitudinal section (right). (F) Stylar plate with stigma (left) and one stamen (right). (G) Juvenile plant. (H) Seedling. (I) Seeds. (J) Adult plant. *M. Cedeño et al. 874* (USJ).

Cerros Sardinal, Chilamate de Sarapiquí (N side of Río Sarapiquí), 90 m, 4 July 1985, (Fr.), *M. Grayum & B. Hammel 5544* (CR, MO); Sarapiquí, La Virgen, E.B. La Selva, Estación Biológico, La Selva, Along road leading to the reserve, 100 m, 16 August 1987, (Fr.), *J.F. Smith 475* (CR); Sarapiquí, Las Horquetas, La Esperanza, orillas de río San José, Finca propiedad de José Rufino Chaves, 168 m, 31 July 2010, (Fr.), *A. Estrada 4624* (CR); Sarapiquí, La Virgen, P.N. Braulio Carrillo, Estación Biológica Magsasay, Bosque primario y orillas de potreros, Sotobosque, 200 m, 23 June 1990, (Fr.), *E. Alcázar 102* (CR); Sarapiquí, La Virgen, Estacion Magsasay, Bosque primario y orillas de potreros, 200 m, 23 June 1990, (Fr.), *E. Alcázar 118* (CR, MO); Sarapiquí, Puerto Viejo, Sendero Tres ríos y lindero el Peje, 0 m, 11 July 2003, (Fl., Fr.), *R. Kriebel 3618* (CR); Sarapiquí, Horquetas, Estación Biológica La Selva, 50 m, 24 Junio 2016, (Fr.), *M. Cedeño & M. Blanco 907* (USJ); Sarapiquí, La Virgen, Reserva Biológica La Tirimbina, 150 m, 16 April 2016, (Fr.), *M. Cedeño & J. Ley 874* (USJ). **Limón**. Talamanca, Cocles, 12 June 1981, (Infer.), *R. Alfaro & R. Ocampo 27* (CR); Pococí, Rita, Cariari de Pococí, Palmitas, El Triángulo, Las Brisas, finca de Guillemo Acosta, 30 m, 18 April 1997, (Fl.), *A. Estrada et al., 743* (CR); Talamanca, Cahuita, Punta de Riel, 4 June 1985, (Infer.), *R. Soto 2128* (CR); NW 0982, 5 km rd Cahuita Bribri, Sea level, flat land periodically flooded, pasture with shade tres, 1 February 1984, (Infer.), *T. Pennington 11459* (CR); Talamanca; R.V.S. Gandoca-Manzanillo, Trail between the town of Manzanillo and Punta Mona, Old secondary growth with old cocoa crops by the coast, 10 m, 3 August 1994, (Fr.), *W. Alverson & V. Stilio 2580* (CR); Siquirres, Pacuarito, Carretera a Siquirres, Entre Siquirres y río Pacuarito, 100 m, 17 November 1994, (Fl.), *V. Nilsson et al., 572* (CR); Talamanca, Cocles, 12 June 1981, (Fl.), *R. Alfaro & R. Ocampo 26* (CR); Limón, Río Blanco, Camino a Veragua Rainforest, entre Río Quito y las Brisas, Árboles en potreros, finca de Sr. Antonio Calderón, 118 m, 26 May 2011, (Fr.), *A. Cascante et al., 2295* (CR); Talamanca, Cahuita, R.V.S. Gandoca-Manzanillo, Sendero entre Manzanillo y Gandoca, Aprox. 1,4 km de la entrada al sendero por el sector de Manzanillo, 10 m, 10 April 2012, (Fl.), *A. Estrada et al., 5324* (CR); Pococí, Rita, Finca La Suerte, 50 m, 10 July 1995, (Fl.), *R. Aguilar 4206* (CR, MO); Talamanca, Sixaola, Cerro Manzanillo, sobre la fila, 100 m, 5 December 1992, (Infer.), *A. Fernandez 477* (CR); Talamanca, Sixaola, Punta Uva, peñón innominado adyacente a la Quebrada Ernesto, 0 m, 4 May 2001, (Fr.), *J. Morales 7972* (CR); Talamanca, Sixaola, Sendero a Punta Mona, 74 m, 4 April 2011, (Fr.), *L. Vargas 4350* (CR); Talamanca, Along the road S of Limón from the corner at the road to Bomba, 0–50 m, 26 February 1985, (Fr.), *C. Taylor 4442* (MO); Region between Hone Creek and ca. 4–5 km NW on a trail roughly paralleling the Río Carbon (Río Hone), Collection from Cacao and second growth, 60–100 m, 17 January 1974, (Fr.), *J. Utley 659* (MO); Talamanca, Road between Cahuita and Punto [Puerto] Vargas, 0–5 m, 7 July 1980, (Fr.), *B. Hammel 9152* (MO); Talamanca,

Puerto Viejo, 500 m del cruce de Bribri, 40 m, 5 December 2012, (Fl., Fr.), *J. Gómez et al., 15783* (USJ); Talamanca, Cahuita, Camino detrás de la carretera, Finca La Montaña, 10 m, 11 July 1999, (Fl.), *M. Blanco et al., 997* (USJ); Talamanca, Cahuita, Bosques de Manzanillo, 50 m, 9 January 2017, (Fl.), *M. Cedeño et al., 1104* (USJ); Limón, Talamanca, Bribri, Proyecto ARA, 4 m, 30 September 2018, (Fl.), *M. Cedeño et al.,, 1480* (USJ).

35. *Monstera wilsoniensis* M.Cedeño & Grayum, *Nordic J. Bot.* 38(12): 1–13. 2020. — Type: COSTA RICA. Puntarenas: Coto Brus, San Vito, Jardín Botánico Wilson, Reserva de bosque primario, 1353 m, 10 Oct 2018 (fr.), *M. Cedeño, M. Blanco, M. Mata & O. Alvarado 1484* (holotype, USJ! [two sheets]; isotypes, MO!, PMA!).

Nomadic vine, appressed-climbing or pendent habit. SEEDLINGS: bearing foliage leaves. JUVENILE PLANTS: root climbers; **stems** light green with black pustules; **internodes** 3–5 cm long, 4–6 mm diam.; **petiole** distinct, dark or light-green, smooth, 5–10 cm long, sheathed to the base of the geniculum; **petiole sheath** deciduous; **blades** ovate, lanceolate, attenuate or truncate at the base, acuminate at apex, sub-coriaceous, 8–15 × 2–6 cm, not appressed to the phorophyte; **fenestrations** absent. ADULT PLANTS: root climbers; **stems** light-green to dark with black pustules, cylindrical; **internodes** 2–10 cm long, 1–1.5 cm diam.; **cataphylls** light-green, deciduous but leaving dry fragments on the peduncle; **anchor roots** dark brown; **feeder roots** brown; **petiole** dark green, sometimes white-spotted, smooth, 13–20 cm long, sheathed to the base of the geniculum; **petiole sheath** deciduous; geniculum smooth, sunken adaxially, convex abaxially, 1–2.5 cm long; **blades** lanceolate or oblique, cordate, subcordate to obtuse at the base, acuminate at apex, sub-coriaceous, drying greenish, yellowish or blackish, 15–25 × 13–15 cm, slightly decurrent to the medial part of the geniculum; **midrib** ribbed adaxially, convex abaxially, drying yellowish or blackish on both surfaces; **primary lateral veins** 15–25 per side, forked, slightly sunken adaxially, prominent abaxially, departing midrib at 55–65°, drying yellowish or blackish; **secondary veins** reticulate; **collective veins** visible; **fenestrations** absent or infrequently present; **margins** entire. INFLORESCENCES on ascending or pendent stems, 1–3 simultaneously at flowering time, arranged in the axils of the leaves or into cataphylls; **peduncle** smooth, 10–15 cm long; **spathe** long-acuminate or mucronate, light green during development, yellowish green externally and white internally at apex, thin, completely open, deciduous after anthesis, 13–18 × 9–13 cm, up to 4 cm longer than spadix; **spadix** creamy during development, yellowish-cream at anthesis, 7–13 cm long, 1.5–2 cm diam.; **basal sterile flowers** 3–5 mm long, with a transparent stigmatic secretion; **fertile flowers** 4–6 mm long; stamens with laminar filaments, 2–6 mm long; anthers 1–2 mm long; ovary quadrangular in longitudinal section, ribbed, 3–4 × 3–4 mm; style hexagonal, 1–2 × 3–4 mm; stigma

linear, with a transparent stigmatic secretion; **berries** with a green stylar cap during development, mature stylar cap white-cream; pulp white; **seeds** black, 3–5 mm long. (**Figures 61 & 62**).

Distribution and habitat: Endemic to Costa Rica on the Pacific slope of the Cordillera of Talamanca, as well as the Cerros de La Carpintera, Cerros de Escazú, and Fila Costeña, from 900 to 2200 m. It lives in *Tropical wet forest*, *Premontane wet forest* and *Lower montane wet forest* life zones

Phenology: Flowering has been recorded from March to October, fruiting throughout the year.

Conservation status: *Monstera wilsoniensis* is protected at the Estación Biológica Las Cruces, on the Pacific versant of Parque Internacional La Amistad, and in the Zona Protectora Cerros de La Carpintera.

Comments: *Monstera wilsoniensis* is a member of sect. *Monstera*. It differs from the other species of its genus in Costa Rica by having petioles sheathed along their entire length, and the sheath deciduous, leaf blades cordate at the base, scarcely fenestrate, and with numerous primary lateral veins, and inflorescences on both ascending and hanging stems. This species has been confused with the lowland morphotype on the Pacific slope of *Monstera adansonii*, but differs from that by having shorter petioles 13–20 (vs. 35–55 cm) and smaller leaf blades (15–25 × 13–15 cm, vs. 25–65 × 25–45 cm) that are cordate or subcordate to obtuse (vs. cuneate or attenuate) at the base. *Monstera wilsoniensis* grows mainly in *Premontane moist forests* life zones of the Las Cruces Biological Station and the Pacific slope of the Cordillera de Talamanca, at elevations of 900–2200 m, while the *M. adansonii* morphotypes that could be confused with it grow in Tropical dry forest and Tropical moist forest at elevations of 0–900 m and have fenestrate leaf blades.

Additional specimens seen: COSTA RICA: **Cartago**. La Unión, San Diego, Z.P. Cerros de La Carpintera, 1800 m, 28 September 2006, (Fr.), *J. Sanchéz 1586* (CR); Cartago, La Unión, San Diego, Z.P. La Carpintera, Ladera norte con vista a Tres Ríos, entrando por finca de los Tinoco, 1520 m, 26 March 2008, (Fr.), *A. Cascante et al., 1905* (CR); Cartago, San Nicolás, Z.P. Cerros de La Carpintera, 1689 m, 21 March 2006, (Fr.), *A. Quesada 1604* (CR); Cartago, La Unión, San Diego, Cerro La Carpintera, bosque sobre ladera hacia Tres Ríos, 1700 m, 28 February 2013, (Fr.), *A. Cascate & C. Trejos 2387* (USJ); Cartago, Cartago, San Nicolas, Cerros La Carpintera, 1700 m, 22 April 2016, (Fr.), *A. Cascate & C. Trejos 2593* (USJ); Cartago, Cartago, San Nicolas, Cerros de la Carpintera, Bosques remanentes en la parte alta, 1750 m, 3 September 2013, (Fr.), *A. Cascate & C. Trejos 2409* (USJ). **Puntarenas**. Coto Brus, San Vito, E.B. Las Cruces, Estación Biológica Las Cruces, Java, Reserva Forestal, 1150 m, 4 July 1994, (Fl.), *W. Kress & S. Martén 94–4360* (CR); Las Cruces, 1300 m, 11 January 1978, (Fr.), *T.*

Croat 44388 (MO); Coto Brus, San Vito, E.B. Las Cruces, Las Cruces Tropical Botanical Garden, 6 km W of San Vito de Java, Cultivated and native species, 1200 m, 6 March 1984, (Infer.), *T. Croat 57235* (CR, MO); Buenos Aires, Biolley, P.I. La Amistad, Cordillera de Talamanca, area around Río Canasta, 9.5 airline km NW of Agua Caliente, between Cerro Frantzius and Cerro Pittier, Lower montane wet forest with a few pasture clearings, 1550 m, 6 September 1984, (Fr.), *G. Davidse et al., 28424* (CR, MO); Coto Brus, San Vito, E.B. Las Cruces, Along trail between Las Cruces Botanical Garden and Río Jaba, ca. 3.5 km SE of San Vito de Coto Brus, 1180 m, 12 September 1985, (Fr.), *M. Grayum et al., 5974* (CR, MO); Coto Brus, San Vito, E.B. Las Cruces, Jardín Botánico Wilson, Las Cruces, San Vito de Coto Brus, Sobre sendero Este hacia Río Java, 1100 m, 3 September 1993, (Fr.), *G. Rivera 2151* (CR); Coto Brus, San Vito, E.B. Las Cruces, Forest below Las Cruces Biological Station along trail to Rìo Java, San Vito de Java, 1275 m, 29 June 1994, (Fl.), *W. Kress & W. Alverson 94–3773* (CR); Coto Brus, San Vito, E.B. Las Cruces, Estación Biológica Las Cruces, Java, Reserva Forestal, 1275 m, 8 April 1994, (Fl., Fr.), *W. Kress & J. Runk 94–4654* (USJ); Coto Brus, Pittier, Colecta en bosque en el límite oeste de la estación, 1700 m, 2 August 2000, (Fr.), *L. Acosta 2425* (CR); Coto Brus, San Vito, Jardín Botánico Wilson, Las Cruces, Sobre sendero Este hacia Río Java, 1100 m, 30 September 1993, (Fr.), *G. Rivera 2163* (CR). **San José**. Pérez Zeledón, San Pedro, Las Nubes, Santa Elena, Colecta en bosque secundario y potrero, 1210 m, 4 August 1995, (Fr.), *E. Alfaro 324* (CR); San José, Dota, Copey, Providencia, Montaña fría, 1850 m, 11 October 2002, (Fr.), *J.Sánchez 1344* (CR); San José, Acosta, Sabanillas, Bajo Vanegas, por Quebrada Delicias, 1500 m, 17 December 1996, (Fr.), *B. Hammel 20604* (CR); San José, Pérez Zeledón, Páramo, Páramo, Providencia, Cruce sitio Pierdas, 4.7 SO de Providencia, 1854 m, 21 March 2001, (Fl.), *A. Rodríguez 7276* (CR, MO); San José, Dota, Manglar on estero between Río Paquita and Río Viejo, 1146 m, 14 August 1936, (Fr.), *C. Dodge 9825* (MO); San José, Dota, Copey, Dota, Providencia, Zapotal, Finca propiedad de Joyce Zurcher, 1800 m, 20 August 2003, (Fr.), *A. Rodríguez 8262* (CR, MO); San José, Pérez Zeledón, El General, Reserva Universidad de York, 1200 m, 28 November 2017, (Fr.), *M. Cedeño & M. Mejía 1138* (USJ); San José, Mora, Tabarcia, Zona Protectora Cerros de Escazú, cuenca del río Negro, 2 km en línea recta al noreste de la plaza de Palmichal en remanentes de bosque a la orilla del río, 1283 m, 19 August 2010, (Fr.), *J. Sánchez & R. Chacón 2166* (CR); San José, Alajuelita, San Antonio, Z.P. Cerros de Escazú, Alrededores de Cerro Rabo de Mico, 2200 m, 22 September 1989, (Infer.), *G. Vargas & J. Sanchéz 765* (CR); San José, Acosta, Palmichal, Z.P. Cerros de Escazú, Cuenca superior del Río Negro, Finca de señor Jericó Vindas, 1825 m, 8 July 2010, (Fl., Fr.), *A. Cascante et al., 2229* (CR); Desamparados, San Miguel, Camino rural entre pequeños fragmentos de bosque y potreros arbolados a 4.5 km E de Tobosi, siguiendo la carretera 228, 1850 m, 4 August 2015, (Fr.), *A.*

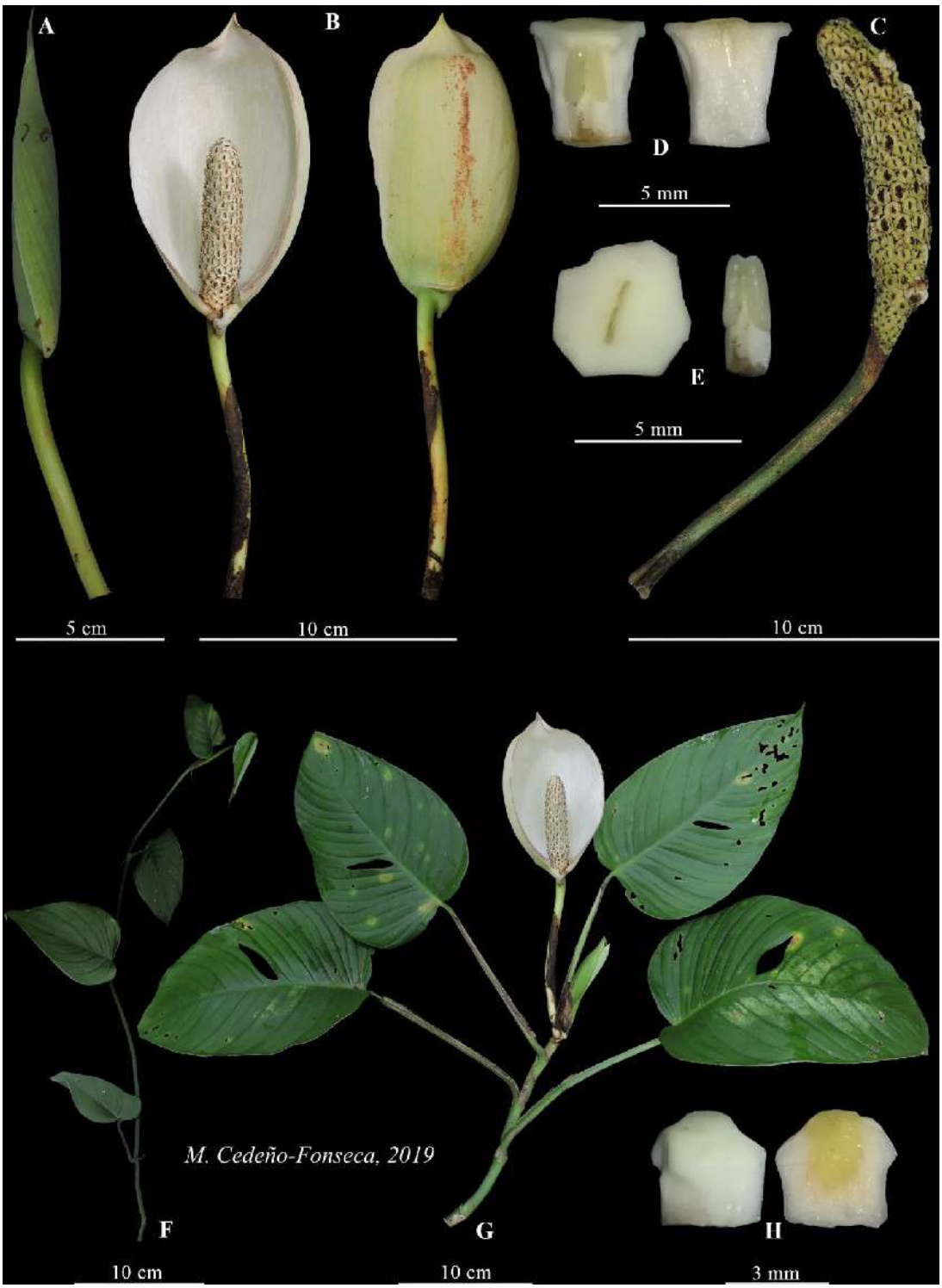

Figure 61. *Monstera wilsoniensis*. (A) Developing inflorescence. (B) Frontal (left) and back (right) views of opened inflorescence. (C) Infructescence. (D) Fertile flower, in lateral view (left), and longitudinal section (right). (E) Stylar plate with stigma (left) and one stamen (right). (F) Portion of juvenile plant. (G) Portion of adult plant. (H) Sterile flower, in lateral view (left), and longitudinal section (right). *M. Cedeño et al. 1484* (USJ).

Figure 62. *Monstera wilsoniensis*. (A, B) adult plants in their natural habitat, (C) hanging stems with pendulous or sub-erect infructescences (arrow). *M. Cedeño et al. 1484* (USJ).

Cascate & C. Trejos 2546 (USJ); San José, Perez Zeledón, Páramo, Providencia, Zapotal, Bosque secundario detrás de la casa, 1805 m, 20 August 2003, (Fr.), *A. Ruíz & S. Lobo 743* (CR); San José. Aserrí. Vuelta de Jorco, Tarbaca; Bajos de Praga; b. secundario en la union de los rios Tarbaca y Cedral, 1475 m, 29 January 1994, (Fr.), *J. Morales 2299* (CR).

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