

DE MACROCARPAEAE GRISEBACH (EX GENTIANACEIS)
SPECIEBUS NOVIS VI: SEED MORPHOLOGY, PALYNOLOGY,
AN INFRAGENERIC CLASSIFICATION, AND ANOTHER
TWENTY-THREE NEW SPECIES LARGELY FROM COLOMBIA

JASON R. GRANT¹

Abstract. A brief survey of seed morphology and palynology in *Macrocarpaea* is discussed and illustrated by Scanning Electron Microscopy (SEM) photographs. An infrageneric classification is presented where four sections are recognized: sect. *Tabacifoliae*, sect. *Macrocarpaea*, sect. *Magnolifoliae*, and sect. *Choriophylla*. Another 23 new species, largely from Colombia, are here described and illustrated: Brazil (1): *M. illecebrosa*; Colombia (14): *M. betancuriana*, *M. callejasii*, *M. gaudialis*, *M. gondoloides*, *M. gravabilis*, *M. gulosa*, *M. hilarula*, *M. jocularis*, *M. lacrossiformis*, *M. laudabilis*, *M. maryae*, *M. silverstonei*, *M. umerulus*, and *M. ypsilo-caule*; Ecuador (4): *M. berryi*, *M. jactans*, *M. neillii*, and *M. voluptuosa*; and Peru (4): *M. chthonotropa*, *M. gran-pajatena*, *M. quechua*, and *M. xerantifulva*.

Keywords: Macrocarpaea, Gentianaceae, seed morphology, palynology, Brazil, Colombia, Ecuador, Peru.

SEED MORPHOLOGY

There is a great diversity of previously unrecognized, taxonomically useful seed morphological characters in *Macrocarpaea*. To date, seed morphology has only been summarized at the generic rank. Bouman et al. (2002) discussed the seed morphology of *Macrocarpaea* in comparison to other members of the family. However, since his sampling was limited, neither all seed types nor the full picture of the evolution of seed morphology was elucidated. What follows here is a brief introduction to seed morphology in the genus, while illus-

trating seeds of new species described below. A more thorough and detailed survey of seed morphology with comparison to pollen types, as well as the molecular phylogeny, is in preparation.

Seeds of *Macrocarpaea* are miniscule in size, 0.2–2.2 × 0.2–1.0(–2.2) mm. Therefore, Scanning Electron Microscopy (SEM) has been used to examine seed characters and determine seed type. Seeds were removed from approved herbarium specimens, placed on double-sided carbon stickers mounted on aluminum sample

This work was funded by two Swiss National Science Foundation grants, No. 3100-052885 and No. 3100-065395, to Philippe K upfer at the Universit e de Neuch atel, Switzerland. The line drawings were prepared by Bobbi Angell and partially funded by William J. and Lyla Grant. Library research was carried out at the Conservatoire et Jardins botaniques de la Ville de Gen ve, Switzerland. Scanning Electron Microscopy (SEM) of seeds and pollen was conducted at the Centre Suisse d'Electronique et de Microtechnique SA (CSEM) in Neuch atel, Switzerland, under the supervision of Mireille Leboeuf. During visits to Bogot , Cali, and Medell n, Colombia, in February 2004, I visited six herbaria (COAH, COL, CUV, HUA, MEDEL, and VALLE) and examined additional material either brought or sent on loan to COL , HUA , or CUV  from nine additional herbaria (AFP , CAUP , CHOCO , FAUC , FMB , HUQ , JAUM , UDBC , and UPTC ). I am appreciative of the help and kindness of numerous individuals in Colombia, including Julio Betancur (COL), Ricardo Callejas (HUA), Dairon C ardenas (COAH), Alvaro Cogollo (JAUM), Jos e Enrique Castillo (FMB), Rocio Cortes (UDBC), Jos e Luis Fern andez-Alonso (COL), Favio Gonz alez (COL), Carlos Parra (COL), Jorge P erez (MEDEL), Nayive Pino (CHOCO), and Philip Silverstone-Sopkin (CUV). I also thank the following herbaria for either the loan of material, photocopies of specimens, data on their collections, or hospitality extended during visits* to examine material of *Macrocarpaea*: AAU, AFP, ALA*, B, BM, BP, BR*, BRIT, BSB, C, CAS, CAUP, CHOCO, CHR*, COAH*, COL*, CR, CUV*, CUZ*, DAV, DUKE, E, EHH, F, FAUC, FI, FLAS, FMB, FR*, G*, GB, GH, GOET, HAC, HAL, HAM, HAO*, HUA*, HUCP, HUQ, HUT*, IAN*, INB, INPA*, JAUM, JBSD, JE, K, L, LD, LINN, LOJA*, LPB, LS, M, MA*, MANCH, MARY*, MBM*, MEDEL*, MER*, MG*, MICH, MIN, MO, MOL*, MSB, MU, MY, NA, NEU*, NO, NSW*, NY*, OXF, P*, PH, PORT*, PR, PRC, Q*, QAP*, QCA*, QCNE*, QPLS*, QUSF*, R*, RB*, S*, SBBG*, SEL*, SP*, SPF*, TEX, U, UC, UCWI, UDBC, UPCB, UPS, UPTC, US*, USM*, VALLE*, VEN*, W*, WIS, WU*, YU, and Z*.

¹Laboratoire de Botanique  volutive, Institut de Botanique, Facult e des Sciences, Universit e de Neuch atel, rue  mile-Argand 11, Case Postale 2, 2007 Neuch atel, Switzerland. E-mail: jason.grant@unine.ch

holders, sputtered with gold, and examined with a Philips XL 30 ESEM-FEG microscope. Seed morphology was studied in 81 species (all the species in the genus that have herbarium specimens with fruits with mature seeds). Four morphological seed types are identified, largely conforming to the sections defined below: “Flattened-type seeds” (sensu Bouman et al., 2002: 533) for sect. *Tabacifoliae*, “perimetrically winged-type seeds” for sect. *Choriophylla* (described here), “rimmed-type seeds” (sensu Bouman, 2002: 531) for sect. *Macrocarpaea*, and “winged-type seeds” (modified from Bouman et al., 2002: 531) for sect. *Magnolifoliae*. Eight representative species illustrate the variation in the genus: *M. ericii* (rimmed type), *M. gaudialis* (rimmed type), *M. gulosa* (perimetrically winged type), *M. illecebrosa* (flattened type), *M. jactans* (winged type), *M. laudabilis* (rimmed type), *M. sodiroana* (perimetrically winged type), and *M. xerantifolva* (perimetrically winged type).

1. *Flattened-type seeds* (Fig. 1A–B) correspond to sect. *Tabacifoliae*. The seeds are gen-

erally triangular in outline, flattened to polygonal, and have no wings. *Macrocarpaea illecebrosa*, *M. glaziovii*, and *M. rubra* have extended chalazal and micropylar ends; however, the chalazal end in *M. obtusifolia* either falls off before seed maturity or is lost during seed development.

2. *Perimetrically winged-type seeds* (Fig. 1C–H) correspond to sect. *Choriophylla*. The seeds are flattened with wings surrounding the perimeter of the seed. They are typically very light in weight, likely an adaptation for wind dispersal.

3. *Rimmed-type seeds* (Fig. 2A–F) correspond to sect. *Macrocarpaea*. The seeds are polygonal to slightly flattened, and rimmed (typically without, yet sometimes with, very short wings).

4. *Winged-type seeds* (Fig. 2G–H) correspond to sect. *Magnolifoliae*. The seeds are flattened and prominently winged at chalazal and micropylar ends, or rarely all around. This seed type is a key character used to define sect. *Magnolifoliae*.

PALYNOLOGY

Pollen of *Macrocarpaea* has been thoroughly discussed in two important papers (Nilsson, 1968; Nilsson, 2002). In the first paper, Nilsson (1968) conducted a sampling of 26 species and related genera. His results led Weaver (1974) to transfer the monotypic genus *Rusbyanthus cinchonifolius* to *Macrocarpaea*, and Maguire and Boom (1989) to remove the species of *Macrocarpaea* with pollen in tetrads to a new genus, *Rogersonanthus*. Nilsson’s second paper (2002) expanded on the first, especially in following Weaver (1974) and Maguire and Boom (1989).

Two morphological types of pollen grains occur in *Macrocarpaea*. The *Glabra*-type (Nilsson, 1968) is present in most species of the genus, whereas the *Corymbosa*-type has been identified in 13 species. According to Nilsson (2002), *Glabra*-type pollen (Fig. 3A–D) is “3–colporate, rarely porate, 23–44 × 26–42 m, spheroidal to subspheroidal, with reticulate to verrucose-gemmate exine, and usually relatively wide muri.” According to Nilsson (2002), *Corymbosa*-type pollen is “3–colporate to colporate, 28–35 × 28–39 m, subspheroidal to spheroidal, and with warty exine (verrucae,

gemmae, pila, and clavae are present).” The *Corymbosa*-type (Fig. 3E–H) (Nilsson, 1968) conforms to *Macrocarpaea* sect. *Magnolifoliae*, and provides an important character to define the section. *Corymbosa*-type pollen was originally described as *Rusbyanthus*-type by Gilg (1895).

In the present study, palynology has been studied in 88 species (all the species in the genus that have herbarium specimens with flowers with pollen). Pollen grains were removed from approved herbarium specimens, dusted onto double-sided carbon stickers mounted on aluminum sample holders, sputtered with gold, and examined with a Philips XL 30 ESEM-FEG microscope. Five representative species illustrate the intergrading variation in the genus (Fig. 3): *Macrocarpaea subcaudata* (*Glabra*-type), *M. kuepferiana* (*Glabra*-type), *M. wurdackii* (*Glabra*-type), *M. revoluta* (*Glabra*-type intergrading to *Corymbosa*-type), and *M. canoëfolia* (*Corymbosa*-type). The study here of pollen by SEM confirms the conclusions of Nilsson and provides the context in which *Corymbosa*-type pollen evolved.

It appears that pollen with reticulate exine (*Glabra* type) is an ancestral character state in *Macrocarpaea* and its close relatives *Tachia* and *Chorisepalum* (Nilsson, 2002). Within *Macrocarpaea*, the group possessing reticulate exine is paraphyletic, since the majority of species in the monophyletic section *Magnolifoliae* (nested within *Macrocarpaea*) have *Corymbosa* type pollen.

There is a gradient in the exine pattern of species of sect. *Magnolifoliae* (sister to sect. *Choriophylla*). This ranges from a rather classic

Glabra-type pattern in basal members, for example, *M. luna-gentiana* J. R. Grant & Struwe, *M. maguirei* Weaver & J. R. Grant, and *M. viscosa* (Ruiz & Pavon) Gilg; to a “*Glabra* type intergrading to *Corymbosa* type” in *M. revoluta* (Ruiz & Pavon) Gilg (Fig. 3E–F); to a complete *Corymbosa* type in derived members, for example, *M. cinchonifolia* (Gilg) Weaver, *M. canoëfolia* J. R. Grant (Fig. 3G–H), and *M. jactans* J. R. Grant. This makes the *Corymbosa*-type pollen derived within a genus where most sections and species have *Glabra*-type pollen.

INFRAGENERIC CLASSIFICATION OF *MACROCARPAEA*

Four sections are here recognized within *Macrocarpaea* on the basis of seed morphology (Fig. 1–2), palynology (Fig. 3), floral morphology, and molecular characters. These include

sect. *Tabacifoliae*, sect. *Macrocarpaea*, sect. *Magnolifoliae*, and sect. *Choriophylla*. Upon completing additional studies, I expect to divide these well-defined sections into subsections.

ARTIFICIAL KEY TO THE SECTIONS OF *MACROCARPAEA*

- 1a. Pollen *Corymbosa* type (Fig. 3E–F) and seeds winged type (Fig. 2 G–H) in most species [though several basal species have *Glabra*-type pollen (Fig. 3 A–D) and perimetrically winged seeds (Fig. 1C–H)], branches of the inflorescence generally sparsely flowered, calyces large (7–)10–20 mm, plants of the Andes of Ecuador, Peru (15 of the 18 placed species), and Bolivia sect. *Magnolifoliae*
- 1b. Pollen *Glabra* type (Fig. 3A–D), seeds otherwise (flattened type, rimmed type, or perimetrically winged type), branches of the inflorescence generally multi-flowered, calyces small (2–)6–14(–22), plants of southeastern Brazil, the Andes, Pantepui of the Guayana Shield, Central America, and the Greater Antilles of the Caribbean 2
- 2a. Seeds flattened type (Fig. 1A–B), plants of southeastern Brazil. sect. *Tabacifoliae*
- 2b. Seeds rimmed type (Fig. 2A–F) or perimetrically winged type (Fig. 1C–H), plants of the Andes, Pantepui of the Guayana Shield, Central America, and the Greater Antilles of the Caribbean 3
- 3a. Seeds rimmed type (Fig. 2A–F) in most species (the five epiphytic members of the genus belong here yet have perimetrically winged seeds), plants of the Andes of Colombia, Venezuela, and Ecuador, Pantepui of the Guayana Shield, Central America, and the Greater Antilles of the Caribbean sect. *Macrocarpaea*
- 3b. Seeds perimetrically winged type (Fig. 1C–H) in most species (though a group of Peruvian species have rimmed-type seeds), plants of the Andes, largely the Huancabamba region of Ecuador and Peru, also extending to Colombia and Bolivia. sect. *Choriophylla*

Macrocarpaea (Griseb.) Gilg in Engl. & Prantl, Nat. Pflanzenfam. 4(2): 94. 1895. Based on: *Lisianthus* sect. *Macrocarpaea* Griseb., Gen. Sp. Gent. 173. 1839. T.: *Lisianthus glaber* L.f., Suppl.: 134. 1781. *Macrocarpaea glabra* (L.f.) Gilg in Engl. & Prantl, Nat. Pflanzenfam. 4(2): 94. 1895.

= *Rusbyanthus* Gilg in Engl. & Prantl, Nat. Pflanzenfam. 4(2): 95. 1895. T.: *Rusbyanthus cinchonifolius* Gilg, in Engl. & Prantl, Nat. Pflanzenfam. 4(2): 95. 1895. *Macrocarpaea cinchonifolia* (Gilg) Weaver, J. Arnold Arbor. 55(2): 300. 1974.

1. Sect. ***Tabacifoliae*** Ewan, Contr. U. S. Natl. Herb. 29: 215. 1948. T.: *Lisianthus obtusifolius* Griseb., Gen et Sp. Gent.: 175. 1839. *Macrocarpaea obtusifolia* (Griseb.) Gilg, in Engl. & Prantl, Nat. Pflanzenfam. 4(2): 94. 1895.

= *Macrocarpaea* subg. *Paranagenes* Ewan, Contr. U. S. Natl. Herb. 29: 215. 1948. T.: *M. rubra* Malme, Arkiv Bot. Stockh. 22A(2): 3. 1928.

Macrocarpaea sect. *Tabacifoliae* comprises the four species that occur in Southeastern Brazil: *M. glaziovii*, *M. illecebrosa*, *M. obtusifolia*, and *M. rubra*.

2. Sect. ***Macrocarpaea***. T.: *Lisianthus glaber* L.f., Suppl.: 134. 1781. *Macrocarpaea glabra* (L.f.) Gilg in Engl. & Prantl, Nat. Pflanzenfam. 4(2): 94. 1895.

Macrocarpaea sect. *Macrocarpaea* comprises 42 species largely of the Northern Andes (Colombia and Venezuela), southern Mesoamerica (Costa Rica and Panama), Pantepui of the Guayana Shield, and the Greater Antilles of the Caribbean (Cuba,

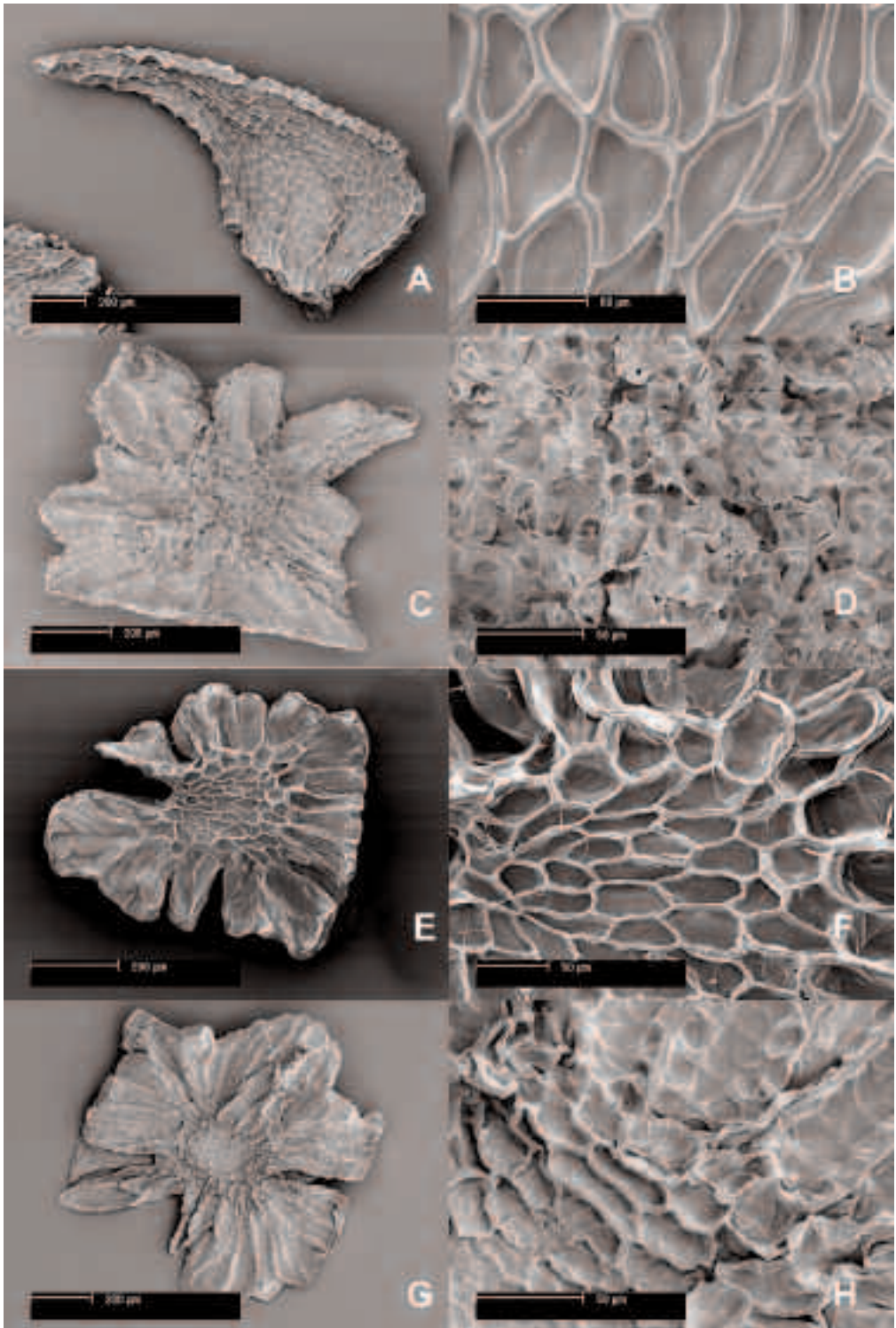


FIGURE 1. Seed morphology in *Macrocarpaea*. A–B, “flattened-type seeds,” *Macrocarpaea illecebrosa*, from Grillo & Conceição 217 (SPF); C–D, “perimetrically winged-type seeds,” *M. xerantifulva*, from Campos & Garcia 3960 (MO); E–F, “perimetrically winged reversal from rimmed-type seeds,” *M. gulosa*, from Ramos 1477A (MO); G–H, “perimetrically winged-type seeds,” *M. sodiroana*, from Rubio 1636 (MO).

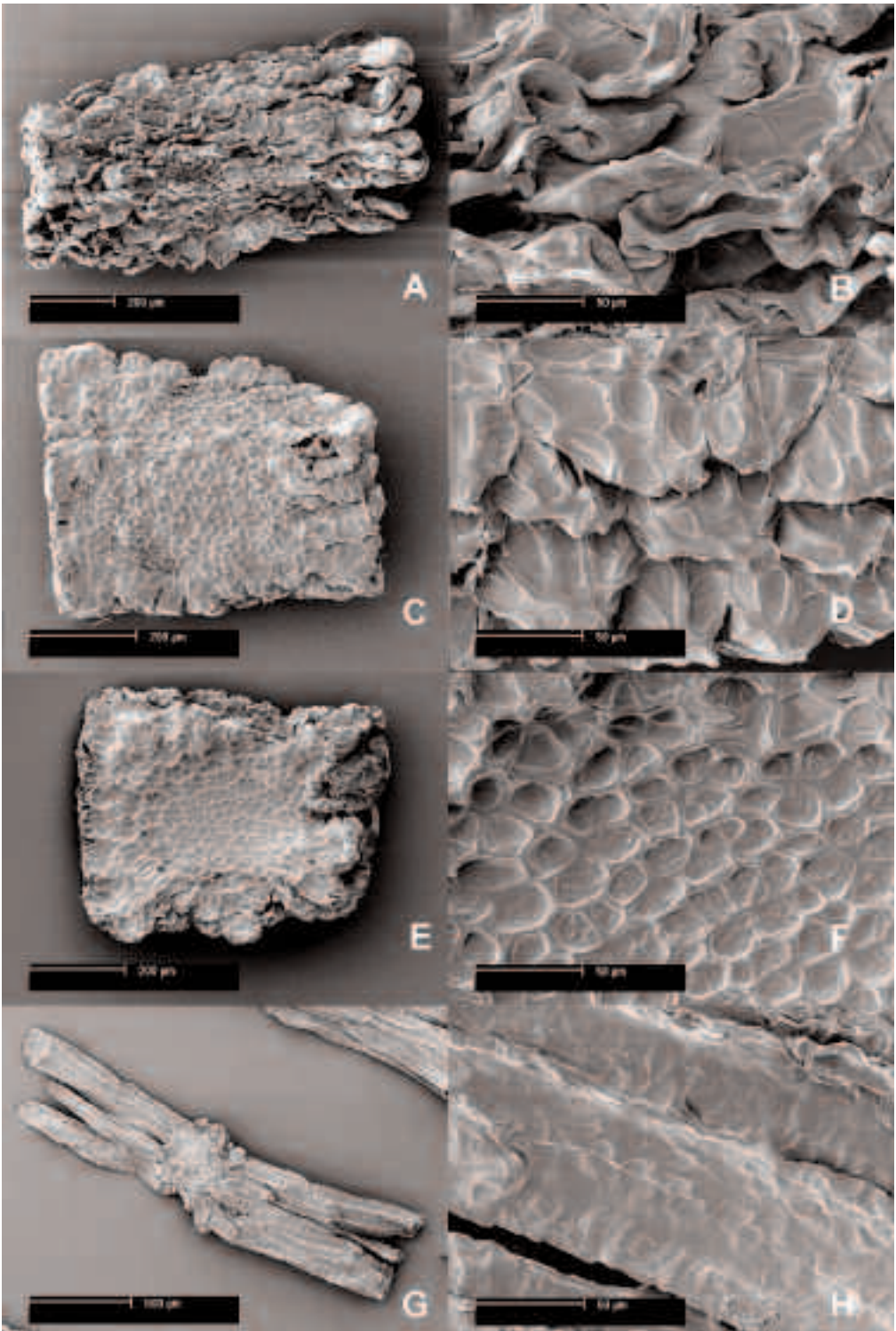


FIGURE 2. Seed morphology in *Macrocarpaea*. A–B, “rimmed-type seeds,” *Macrocarpaea laudabilis*, from Garcia Barriga & Hawkes 12884 (COL); C–D, “rimmed-type seeds,” *M. ericii*, from Campos & Diaz 4410 (U); E–F, “winged-type seeds,” *M. gaudialis*, from Schultes 10415 (NEU); G–H, “winged-type seeds,” *M. jactans*, from Vasquez 20219 (MO).

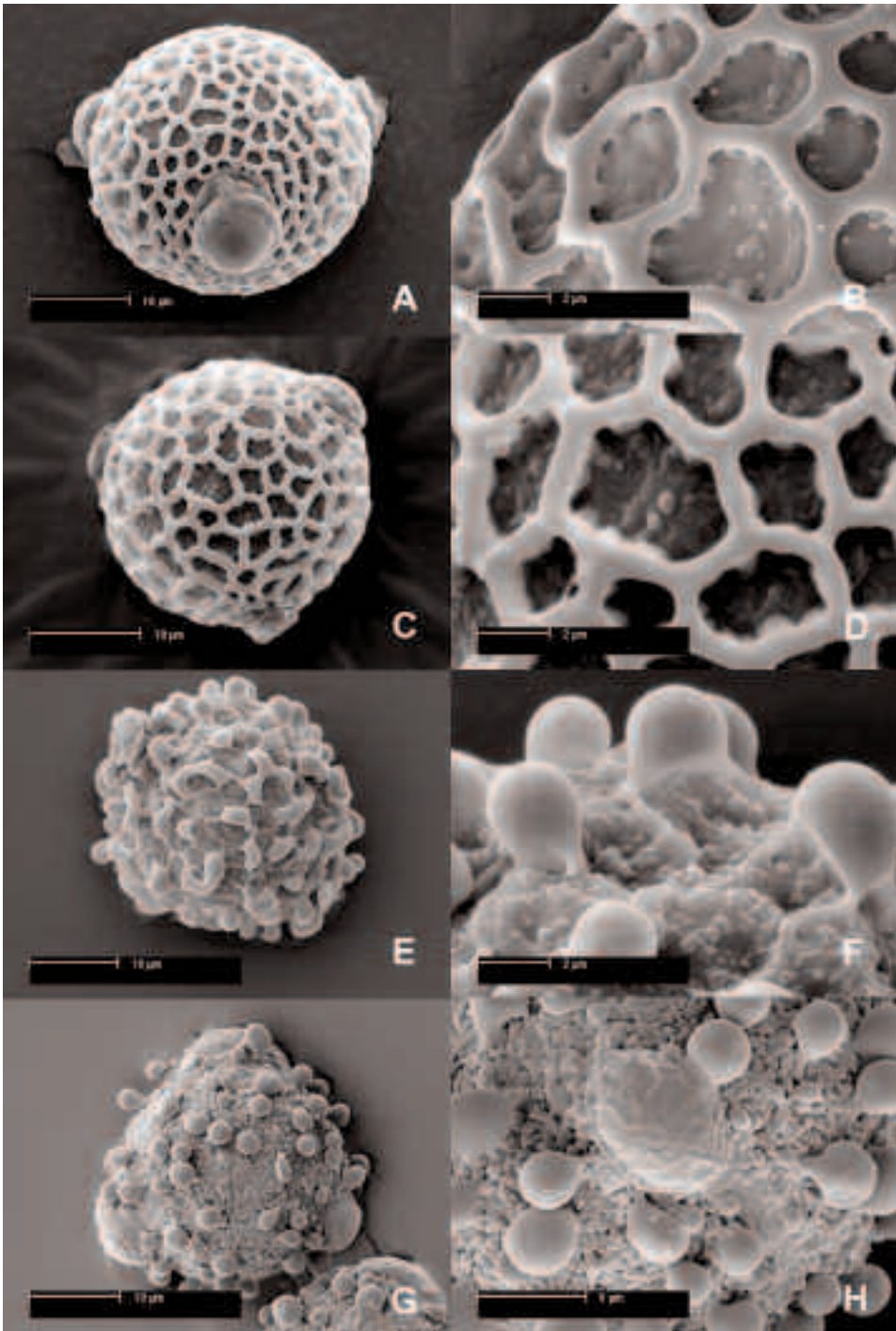


FIGURE 3. Pollen grains of *Macrocarpaea*. A–D, *Glabra* type; E–H, *Corymbosa* type. A, equatorial view of 3-colporate reticulate pollen of *M. subcaudata* from *Luteyn 3918* (NY); B, detail of reticulate exine in pollen of *M. subcaudata*, from *Vargas 18928* (CUZ); C, polar view of 3-colporate reticulate pollen of *M. wurdackii*, from *Smith 4793* (NEU); D, detail of reticulate exine in pollen of *M. wurdackii*, from *Smith 4793* (NEU); E, polar view of 3-colporate verrucose pollen of *M. revoluta*, from *Smith 2748* (NY); F, detail of intergrading reticulate to verrucose warty exine in pollen of *M. revoluta*, from *Smith 2748* (NY); G, polar view of 3-colporate verrucose pollen of *M. canoëfolia*, from *Woytkowski 35417* (F); H, detail of verrucose warty exine and an operculum in pollen of *M. canoëfolia*, from *Woytkowski 35417* (F).

Hispaniola, and Jamaica). These include *Macrocarpaea affinis*, *M. auriculata*, *M. autanae*, *M. ayangannae*, *M. betancuriana*, *M. biremis*, *M. bracteata*, *M. browallioides*, *M. callejasii*, *M. calophylla*, *M. densiflora*, *M. domingensis*, *M. duquei*, *M. ewaniana*, *M. gattaca*, *M. gaudialis*, *M. glabra*, *M. gondoloides*, *M. gulosa*, *M. hilarula*, *M. jocularis*, *M. lacrossiformis*, *M. laudabilis*, *M. luteynii*, *M. macrophylla*, *M. marahuacae*, *M. neblinae*, *M. nicotianifolia*, *M. pachyphylla*, *M. papillosa*, *M. pinetorum*, *M. piresii*, *M. rugosa*, *M. schultesii*, *M. silverstonei*, *M. subcaudata*, *M. thamnoides*, *M. umerulus*, *M. valerii*, *M. voluptuosa*, *M. weaveri*, and *M. ypsilocaule*.

3. Sect. **Magnolifoliae** Ewan, Contr. U. S. Natl. Herb. 29: 215. 1948. T.: *Lisianthus revolutus* Ruiz & Pav., Fl. Peruv. Chil. 2: 14. 1799. *Macrocarpaea revoluta* (Ruiz & Pav.) Gilg in Engl. & Prantl, Nat. Pflanzenfam. 4(2): 94. 1895.

Macrocarpaea sect. *Magnolifoliae* comprises 18 species of the Central Andes (Ecuador, Peru, and Bolivia). These include *Macrocarpaea canoëfolia*, *M. cinchonifolia*, *M. cochabambensis*, *M. fortisiana*, *M. gran-pajatena*, *M. jactans*, *M. luna-gentiana*, *M. maguirei*, *M. normae*, *M. obnubilata*, *M. ostentans*,

M. pachystyla, *M. revoluta*, *M. robin-fosteri*, *M. tahuantinsuyuana*, *M. viscosa*, *M. weigendiorum*, and *M. zophoflora*.

4. Sect. **Choriophylla** (Griseb.) J.R. Grant, comb. nov. Based on: *Lisianthus* sect. *Choriophyllum* Griseb., Gen Sp. Gent. 179. 1839. T.: *Lisianthus loranthoides* Griseb., Gen Sp. Gent. 179. 1839. *Macrocarpaea loranthoides* (Griseb.) Maas. Cat. Fl. Pl. Gymn. Peru (Mon. Syst. Bot. Missouri Bot. Gard. 45): 1256. 1993.

Macrocarpaea sect. *Choriophylla* comprises 37 taxa largely of the Central Andes (western Colombia, Ecuador, Peru, Bolivia), especially the Huancabamba region of Ecuador and Peru. These include *Macrocarpaea angelliae*, *M. angustifolia*, *M. apparata*, *M. arborescens*, *M. bangiana*, *M. berryi*, *M. bubops*, *M. chthonotropa*, *M. dillonii*, *M. elix*, *M. ericii*, *M. gracilis*, *M. gravabilis*, *M. harlingii*, *M. innarrabilis*, *M. jalca*, *M. jensii*, *M. kayakifolia*, *M. kuelap*, *M. kuepferiana*, *M. lenae*, *M. loranthoides*, *M. luya*, *M. maryae*, *M. micrantha*, *M. neillii*, *M. noctiluca*, *M. pajonalis*, *M. pringleana*, *M. quechua*, *M. sodiroana*, *M. stenophylla*, *M. subsessilis*, *M. tabula-fluctivagifolia*, *M. wallnoeferi*, *M. wurdackii*, and *M. xerantifulva*.

NEW SPECIES

Another 23 new species that represent nearly all the remaining new species to be described in *Macrocarpaea* are here described and illustrated. This is the continuation of a series of articles publishing novelties in preparation for a monograph (Grant and Struwe, 2001; Grant and Struwe, 2003; Grant and Weaver, 2003; Grant, 2003; Grant, 2004). These include species from Brazil (1): *M. illecebrosa*; Colombia (14): *M. betancuriana*, *M. callejasii*, *M. gaudialis*, *M. gondoloides*, *M. gravabilis*, *M. gulosa*, *M. hilarula*, *M. jocularis*, *M. lacrossiformis*, *M. laudabilis*, *M. maryae*, *M. silverstonei*, *M. umerulus*, and *M. ypsilocaule*; Ecuador (4): *M. berryi*, *M. jactans*, *M. neillii*, and *M. voluptuosa*; and Peru (4): *M. chthonotropa*, *M. gran-pajatena*, *M. quechua*, and *M. xerantifulva*. The geographic distribution of these species is shown in Fig. 4–5.

During World War II between 1942 and 1946, the United States Department of Agriculture and the Office of Economic Warfare spearheaded the “*Cinchona* Mission” or “*Cinchona*

Project.” At the time, *Cinchona* (Rubiaceae) was the only natural source of quinine, a treatment for malaria. Although tropical American in origin, the majority of the world’s supply came from plantations in Southeast Asia. Once these plantations were captured by the Japanese, the United States lost its major importer of quinine. Therefore, the *Cinchona* Project was initiated to search for wild populations of quinine in Colombia.

Cinchona is morphologically and ecologically similar to *Macrocarpaea*. Both are shrubs to small trees occurring in mid-elevation tropical rainforests in South America. They share opposite entire leaves and are therefore often difficult to identify when sterile. *Macrocarpaea cinchonifolia* (Gilg) Weaver was even named for the resemblance of its leaves to that of *Cinchona*. During the *Cinchona* Mission, eight different species of *Macrocarpaea* (Gentianaceae) were collected in Colombia: *M. affinis*, *M. glabra*, *M. hilarula*, *M. jocularis*, *M. lacrossiformis*, *M. macrophylla*, *M. nicotianifo-*

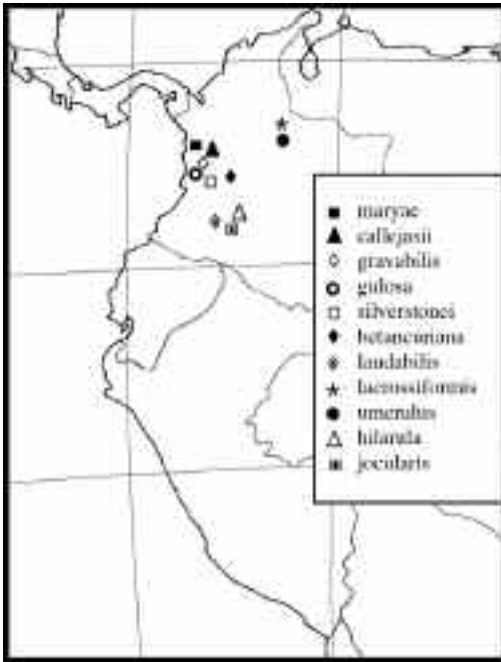


FIGURE 4. Distribution of *Macrocarpaea betancuriana*, *M. callejasii*, *M. gravabilis*, *M. gulosa*, *M. hilarula*, *M. jocularis*, *M. lacrossiformis*, *M. laudabilis*, *M. maryae*, *M. silverstonei*, and *M. umerulus* in Colombia, northwestern South America.

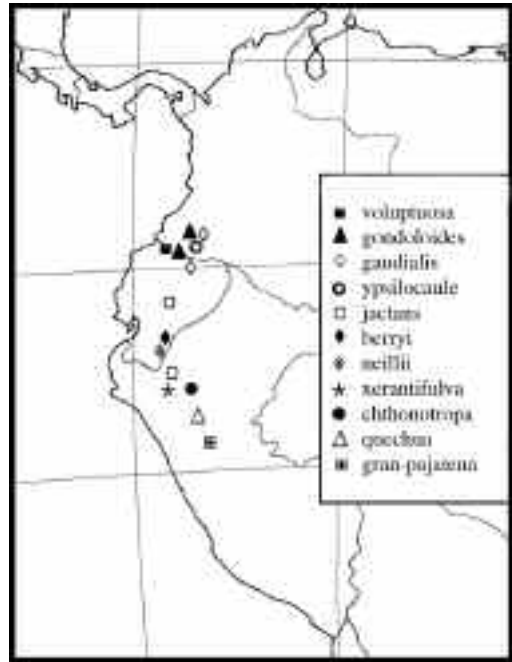


FIGURE 5. Distribution of *Macrocarpaea berryi*, *M. chthonotropa*, *M. gaudialis*, *M. gondolooides*, *M. gran-pajatena*, *M. jactans*, *M. neillii*, *M. quechua*, *M. voluptuosa*, *M. xerantifulva*, and *M. ypsilocaule* in Colombia, Ecuador, and Peru in northwestern South America.

lia, and *M. pachyphylla*. The collectors of these plants, employed by the *Cinchona* Mission, include Joseph Ewan (future monographer of the genus, see Ewan [1948]), Norman C. Fassett, Francis Raymond Fosberg, Martin Lawrence Grant, Walter Henricks Hodge, Ellsworth Paine

Killip, Elbert L. Little, and Harold St. John. Of these eight species, five were new species, including three described in this paper: *M. affinis* (Ewan, 1948), *M. hilarula* (this paper), *M. jocularis* (this paper), *M. lacrossiformis* (this paper), and *M. nicotianifolia* (Grant and Weaver, 2003).

BRAZIL

1. *Macrocarpaea illecebrosa* J. R. Grant, *sp. nov.* TYPE: BRAZIL. Bahia: Município de Palmeiras, Estrada que sai da BR-242 e da acesso ao Morro do Pai Inácio, arbusto ca. 2 m alt., caule e folhas amarelados, frutos amarelo-verdeados, 7 January 1997, A. A. Grillo & A. A. Conceição 217 (Holotype: SPF). Fig. 6A–B.

A *M. obtusifolia* (Griseb.) Gilg *cui affinis sed caule petiolis foliis inflorescentiis pedicellis et calycibus glabris vel spiculatis (vs. hispidis), foliis brevioribus (4.0–8.5 vs. 6.0–20.0 cm), et calycibus brevioribus (8–12 × 8–10 vs. 10–16 × 6–14 mm) differt.*

Shrub, 2 m, glabrous to spiculate on stems, petioles, leaves (especially along veins on lower surface), inflorescences, pedicels, and calyces. Stems terete to slightly quadrangular,

solid to hollow, 3–7 mm in diam. just below the inflorescence. Leaves ovate, sessile to short-petiolate, 4.0–8.5 cm long. Petioles 0–5 mm long, robust with strong open vagination one half the length of the petiole; interpetiolar ridge 1–3 mm high. Blades 4–8 × 3.0–4.5 cm, entire, not revolute, yellowish in fruit, with slightly impressed veins above, and slightly raised veins below, glabrous, leathery- to thin coriaceous; base equilateral to oblique, cuneate to rounded; apex obtuse to rounded. Inflorescence a much-branched open thyrses, 11–20 cm long; branches 7–12 cm long; 2- to 3-flowered per branch. Bracts ovate, sessile, 12–32 × 5–38 mm; base equilateral to oblique, cuneate to rounded; apex obtuse to rounded; bract petioles sessile. Flowers pedicellate, erect; pedicels



FIGURE 6. A–B, *Macrocarpaea illecebrosa*. A, habit of flowering stem; B, fruit. C–G, *M. xerantifulva*. C, habit of flowering stem; D, flower; E, fruiting stem; F, fruit. A–B drawn from Grillo & Conceição 217 (SPF), C–D drawn from Dostert 98/114 (M), E–F drawn from Campos & Garcia 3960 (MO); G drawn from Sánchez 78-80 (MO).

15–23 mm long; bracteoles inconspicuous and scabrous, linear to ovate, 2–8 × 1–7 mm. Calyx campanulate, 8–12 × 8–10 mm, glabrous to spiculate, smooth, ecarinate; calyx lobes ovate, 5–7 × 5–7 mm, apex rounded to obtuse. Corolla, stamens, and pistil unknown. Capsules ovoid, 17–20 × 8–9 mm, smooth to ribbed, chestnut-tan, erect to slightly spreading; style remnant 8–19 mm long. Seeds “flattened type,” 0.4–1.0 × 1.1–1.9 mm, light orange to translucent amber-colored, testa reticulate.

Macrocarpaea illecebrosa belongs to sect. *Tabacifoliae* and is related to its three other members, *M. glaziovii* Gilg, *M. obtusifolia* (Griseb.) Gilg, and *M. rubra* Malme. The section is restricted to southeastern Brazil, and therefore geographically separate from the

Andes-centered majority of the species in the genus. *Macrocarpaea illecebrosa* occurs on the Espinhaço Range in Bahia, disjunct from the remaining members of the section that occur primarily in the Atlantic Forest in coastal Paraná, São Paulo, Rio de Janeiro, Minas Gerais, and Espírito Santo. It appears to be most closely related to *M. obtusifolia* but differs in being glabrous to spiculate on stems, petioles, leaves (especially along veins on the lower surface), inflorescences, pedicels, and calyces (vs. hyaline hispid to spiculate with short simple hairs), as well as having smaller leaves (4.0–8.5 vs. 6.0–20.0) and smaller calyces (8–12 × 8–10 vs. 10–16 × 6–14).

Etymology: from the Latin *illecebrosus*, full of allurements, for its attractive flowers.

COLOMBIA

2. *Macrocarpaea betancuriana* J. R. Grant, *sp. nov.* TYPE: COLOMBIA. Tolima: 16 km west of Fresno on road to Manizales, secondary montane forest, corolla creamy white, the lobes recurved, common shrub to 3 m tall, stems to 3 cm in diam., mostly unbranched and mostly leafless at flowering time, 17 October 1972, R. E. Weaver 2644 (Holotype: GH; Isotypes: MO [2 sheets], NY [2 sheets]). Fig. 7E–H.

A *M. glabra* (L.f.) Gilg *cui affinis sed foliis et inflorescentia molto grandioribus, lobis calycis obtusis vel rotundatis (vs. acutis vel acuminatis) differt.*

Unbranched shrub, 1.2–3.0 m, hyaline hispid to spiculate with short simple hairs on stems, petioles, leaves, inflorescences, bracts, and calyces. Stems terete to quadrangular, hollow to solid, 7–11 mm in diam. just below inflorescence. Leaves elliptic, oval to ovate, petiolate, (13–)26–29 cm long. Petioles 10–20 mm long, robust with strong open vagination one half the length of petiole; interpetiolar ridge 3–4 mm high. Blades (12.0–)24.5–27.0 × (8–)12–14 cm, entire, not revolute, dark above and conspicuously lighter below, with slightly impressed veins above, and slightly raised veins below, glabrous above, hispid to spiculate below most densely so along the principal veins of mature leaves, papery thin, to thin coriaceous; base equilateral to oblique, rounded to cuneate; apex obtuse to rounded. Inflorescence a much-branched open thyrses, 33–49+ cm long; branches 7–23 cm long; 5- to 9-flowered per branch. Bracts ovate to elliptic, petiolate, 19–63 × 9–31 mm; base equilateral to

oblique, rounded to nearly truncate; apex obtuse to acute; bract petioles 2–5 mm long. Flowers pedicellate, erect; pedicels 5–16 mm long; bracteoles ovate to lanceolate, 6–13 × 2–5 mm. Calyx campanulate, 9–12 × 5–7 mm, spiculate to hispid, smooth, ecarinate; calyx lobes ovate to elliptic, 3–4 × 2–4 mm, apex obtuse to rounded. Corolla funnel-shaped, 45–51 mm long, 16–23 mm wide at the apex of the tube, creamy white (Weaver 2644), greenish yellow (Díaz & Jaramillo 2140), smooth; corolla lobes ovate, 9–13 × 7–9 mm, obtuse to rounded. Stamens 20–27 mm long; filaments 25–33 mm long, filiform, flattened; anthers linear to linear-elliptic, 5–6 × 2.0–2.5 mm, sagittate, versatile; pollen *Glabra* type. Pistil 45–52 mm long; ovary 8–9 × 2–3 mm; style 35–40 × 0.75–1.00 mm; stigma lobes spatulate, 2–3 × 1–2 mm. Capsules ovoid, 22–26 × 7–8 mm, smooth to faintly ribbed, greenish brown, tan to light brown, erect to slightly spreading; style remnant 3–8 mm long. Seeds “rimmed type,” 0.7–1.1 × 0.4–0.9 mm, straw-colored, testa rugose-reticulate to wrinkled.

Macrocarpaea betancuriana belongs to sect. *Macrocarpaea* and occurs in the Northern Andes, on the Cordillera Central of Colombia (Fig. 4). It is related to *M. glabra* (L.f.) Gilg of the Cordillera Oriental, Colombia, but differs in generally larger leaves and inflorescences, and calyx lobes that are obtuse to rounded (vs. the distinct sharp acute to acuminate calyx lobes of *M. glabra*).

Etymology: named for Julio C. Betancur (1960–), specialist of Colombian Bromeliaceae



FIGURE 7. A–B, *Macrocarpaea gondoloides*. A, habit of fruiting stem, leaf; B, fruit. C–D, *M. neillii*. C, habit of flowering stem; D, flower. E–H, *M. betancuriana*. E, leaves; F, habit of flowering stem; G, bud; H, fruit. I–J, *M. voluptuosa*. I, habit of flowering stem; J, bud. A–B drawn from Méndez *et al.* 231 (QCNE), C–D drawn from Neill *et al.* 13758 (LOJA, QCNE), E–H drawn from Weaver 2644 (GH, NY), I–J drawn from Boyle 3394 (QCNE).

and Heliconiaceae, Herbario Nacional Colombiano, Universidad Nacional de Colombia, Bogotá (COL).

Paratype: COLOMBIA. Tolima: Cordillera Central, Municipio de Santa Isabel, El Ocheral, bosque de Quercus, 3150 m, planta de 1.20 m, flores amarillo verdosas, 15 February 1980, Díaz P. & Jaramillo M. 2140 (COL).

3. *Macrocarpaea callejasii* J. R. Grant, *sp. nov.*
TYPE: COLOMBIA. Antioquia: Municipio Sonsón, vereda Chaverras, vertiente de la quebrada “El Padre Sanchez,” ascenso al cerro “La Paloma” (3200 m), cerros al NE (2900–3000 m), sitio con gramíneas y vegetación arborea baja (*Brachyotum*, *Weinmannia*, *Cybianthus*, *Ocotea*), 05° 37'N, 75° 16'W, arbusto de 2 m, flores verdes, frutos verdes, ocasional, 10 April 1994, R. Callejas, F. J. Roldán, A. Gómez, A. Uribe, & M. Escobar 11144 (Holotype: HUA). Fig. 8E–G.

A *M. duquei* Gilg-Ben. *cui affinis sed frutex 2–3 m (vs. arbor vel 5 m), foliis brevioribus obovatis vel ellipticis, et corollis molto brevioribus differt.*

Shrub, 2–3 m, generally glabrous throughout, yet sparsely spiculate on stems, petioles, pedicels, bracts, and leaf veins, particularly on lower surfaces. Stems terete to slightly quadrangular above, solid, 4–7 mm in diam. just below the inflorescence. Leaves obovate to elliptic, petiolate, 4–12 cm long. Petioles 5–10 mm long, robust with strong open vagination one half to nearly equaling length of petiole; interpetiolar ridge 2–3 mm high. Blades 3.5–11.0 × 2.0–6.5 cm, entire, slightly revolute, dark above and conspicuously lighter below, with slightly impressed veins above, and slightly raised veins below, glabrous to spiculate above or especially along principal veins, leathery-coriaceous; base equilateral to oblique, cuneate to attenuate; apex obtuse, rounded, to rarely acute. Inflorescence a few-branched open diffuse thyrse, 5–22 cm long; branches 5–12 cm long; 3- to 5-flowered per branch. Bracts obovate to elliptic, petiolate, 12–24 × 4–17 mm; base equilateral to oblique, cuneate to attenuate; apex rounded, obtuse to acute; bract petioles 1–3 mm long. Flowers pedicellate, erect to slightly spreading; pedicels 13–26 mm long; bracteoles lanceolate to oblanceolate, 7–18 × 2–7 mm. Calyx campanulate, 9–14 × 7–10 mm, glabrous, rough to

rugose, ecarinate; calyx lobes ovate to reniform, 3–7 × 4–6 mm, apex rounded to obtuse. Corolla funnel-shaped, 34–36 mm long, 13–14 mm wide at the apex of the tube, pale yellow (*Callejas & Roldán 10660*), green (*Callejas et al. 11114*), smooth; corolla lobes ovate, 7–8 × 6–7 mm, obtuse to rounded. Stamens 22–27 mm long; filaments 18–22 mm long, filiform, flattened; anthers linear to linear-elliptic, 4–5 × 1.5–2.0 mm, sagittate, versatile. Pistil 30–32 mm long; ovary 5–6 × 2–3 mm; style 22–24 × 0.75–1.00 mm; stigma lobes spatulate, 2–3 × 1.0–1.5 mm. Capsules ovoid, 15–20 × 7–8 mm, smooth, faintly verrucose to pustulate, dark brown, spreading to nodding; style remnant 2–4 mm long. Seeds “rimmed type,” 0.6–1.1 × 0.4–0.7 mm, faint orangish-tan, testa rugose-reticulate.

Macrocarpaea callejasii belongs to sect. *Macrocarpaea* and occurs in the Northern Andes, on the Cordillera Occidental, the Chocó of Colombia (Fig. 4). It is related to *M. duquei* Gilg-Ben. and *M. voluptuosa* J. R. Grant of the Cordillera Occidental of Colombia and Ecuador, and *M. densiflora* (Benth.) Ewan and *M. pachyphylla* Gilg of the Cordillera Central of Colombia. It differs from these species in having a much shorter inflorescence (5–22 cm long) that is sometimes nearly sessile within the upper leaves. It differs from *M. duquei* in being a branched shrub to 2–3 m (vs. tree to 5 m), having shorter leaves that are obovate to elliptic, and much shorter corollas.

Etymology: named for Ricardo Callejas Posada (1954–), collector of the type, specialist of the Colombian flora, and curator at the Universidad de Antioquia, Medellín, Colombia (HUA).

Paratypes: COLOMBIA. Antioquia: Municipio Sonsón, vereda Chaverras, vertiente de la quebrada “El Padre Sanchez,” ascenso al cerro “La Paloma” (3200 m), colecciones en cerro (2900–3000 m), al NE de la Paloma, sitio con parches de gramíneas y vegetación arborea baja (*Brachyotum*, *Weinmannia*, *Cybianthus*, *Ocotea*), 05° 37'N, 75° 16'W, arbusto de 2 m, flores amarillo-pálido, frutos verdes, ocasional, 18 August 1992, *Callejas & Roldán 10600* (HUA, NEU); Andes, alrededores de la laguna Santa Rita, 05° 30'N, 76° 05'W, 3450–3750, arbusto de 3 m, frutos verdes, 13 March 1996, *D. Sanchez & N. Parra 2495* (MEDEL).

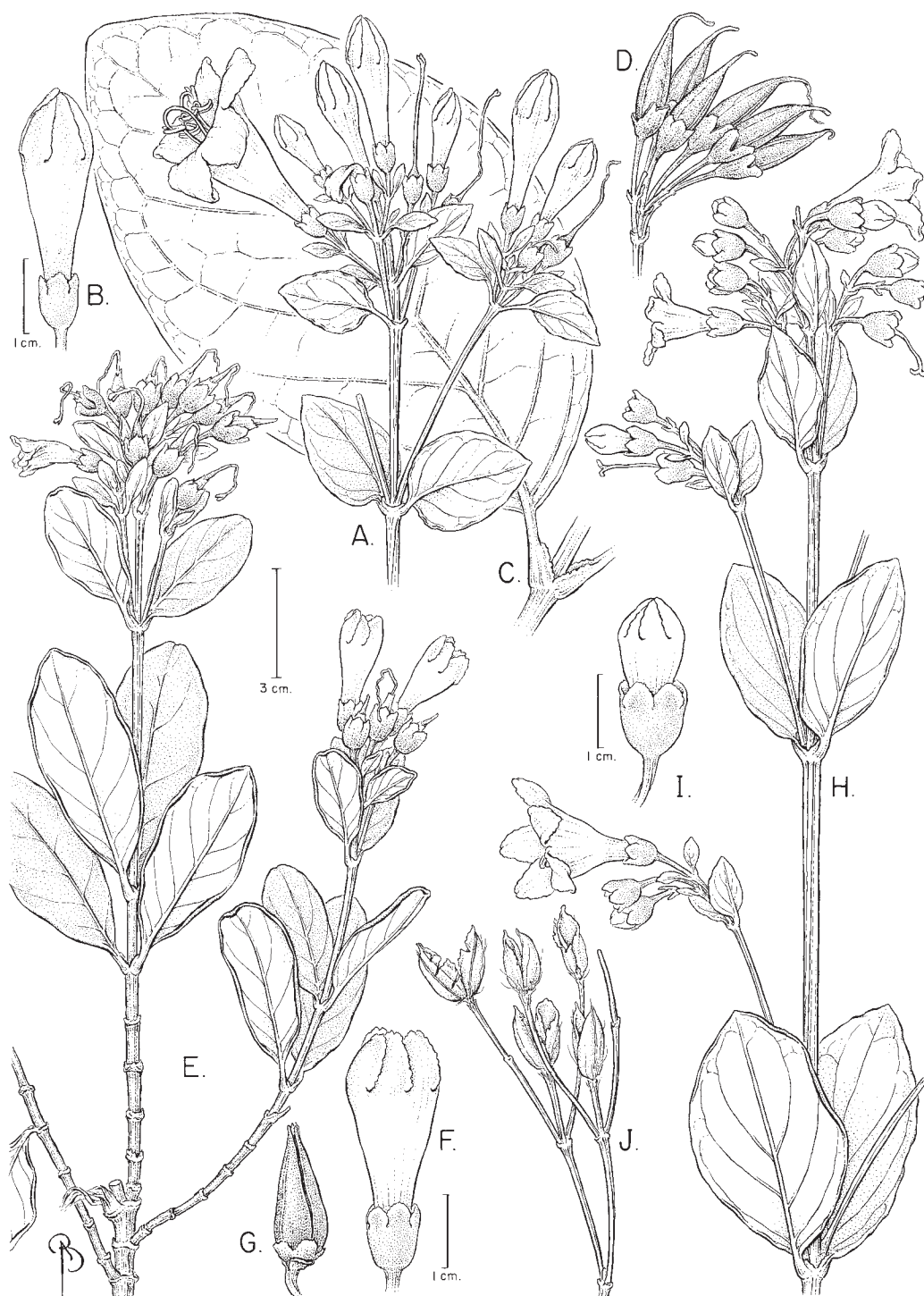


FIGURE 8. A–D, *Macrocarpaea laudabilis*. A, habit of flowering stem; B, bud; C, leaf; D, fruit. E–G, *M. callejasii*. E, habit of flowering stem; F, bud; G, fruit. H–J, *M. silverstonei*. H, habit of flowering stem; I, bud; J, fruits. A–B drawn from Uribe 3871(COL), C–D drawn from Garcia-Barriga 12884 (US), E–F drawn from Callejas 11144 (HUA), G drawn from Callejas & Roldán 10600 (NEU), H–I drawn from Silverstone-Sopkin 4535 (CUVC), J drawn from Ramos et al. 1504 (MO).

4. *Macrocarpaea gaudialis* J. R. Grant, *sp. nov.*

TYPE: COLOMBIA. Nariño: scrubby montane forest near El Encano, 2800 m, common shrub or small tree to 4 m tall, stems 3–4 cm in diam., corolla creamy-yellow, the lobes recurved, 27 October 1972, *R. E. Weaver 2650* (Holotype: GH [2 sheets]; Isotypes: AAU [2 sheets], BM, MO). Fig. 9A–C, 10A–D.

A *M. gattaca* J. R. Grant *cui affinis sed foliis grandioribus, petiolis longioribus*, (5–35 vs. 0–5 mm), *petiolis bracteis longioribus* (2–9 vs. 0–5 mm), *et pedicellis longioribus* (10–32 vs. 7–20 mm).

Shrub or small tree, 1.5–5.0 m, hyaline hispid to spiculate with short simple hairs on stems, petioles, leaves (lower surfaces especially along veins), inflorescences, and calyces. Stems terete to quadrangular, solid to hollow, 5–11 mm in diam. just below the inflorescence. Leaves ovate, oval to obovate, sessile to petiolate, 5.5–33.5 cm long. Petioles 5–35 mm long, robust with strong open vagination one half the length of petiole; interpetiolar ridge 2–4 mm high. Blades 5–30 × 4.5–16.5 cm, entire, slightly revolute, dark green above, lighter below, with slightly impressed veins above and strongly raised veins below, glabrous above, hyaline hispid on all veins below, thick, leathery-coriaceous; base equilateral to oblique, cuneate to rounded; apex acute, obtuse to rounded. Inflorescence a much-branched open thyse, often appearing glaucous on dried herbarium specimens due to minute white crystals covering upper stems, petioles and calyces notably on *Schultes 3223*, 31–50+ cm long; branches 9–50 cm long; 5- to 12-flowered per branch. Bracts ovate to elliptic, petiolate, 15–78 × 4–50 mm; base equilateral to oblique, cuneate to rounded; apex obtuse to acute; bract petioles 2–9 mm long. Flowers pedicellate, erect to slightly spreading; pedicels 10–32 mm long; bracteoles inconspicuous and scabrous, linear, lanceolate to ovate, 2–16 × 0.5–5.0 mm. Calyx narrowly campanulate, 8–12 × 6–7 mm, glabrous to rarely slightly spiculate, green, ecarinate; calyx lobes ovate to reniform, 1.5–2.0 × 2–4 mm, apex obtuse to rounded. Corolla funnel-shaped, 39–60 mm long, 23–28 mm wide at the apex of the tube, white (*Fernández & Knoth 1035-A*), cream-yellow (*Schultes 3223*; *Weaver 2650*), yellow (*López J. 447*), smooth; corolla lobes ovate, 9–18 × 9–15 mm, obtuse to rounded. Stamens 27–35 mm long; filaments 20–26 mm long, filiform, flattened; anthers linear to linear-elliptic, 7–9 × 2.0–3.5 mm, sagit-

tate, versatile; pollen *Glabra* type. Pistil 42–65 mm long; ovary 9–11 × 2–4 mm; style 30–38 × 1.0–1.5 mm; stigma lobes spatulate to suborbicular, 3–6 × 1–3 mm. Capsules ellipsoidal to ovoid, 18–25 × 7–9 mm, shiny and smooth to rugose, ribbed and pustulate, chestnut to dark brown, spreading to nodding; style remnant 4–10 mm long. Seeds “rimmed type,” 0.5–1.0 × 0.4–0.6 mm, straw-colored, testa rugose-reticulate to wrinkled.

Macrocarpaea gaudialis belongs to sect. *Macrocarpaea* and occurs in the Northern Andes, on the Cordillera Central of Colombia (Fig. 5). It is related to *M. pachyphylla* Gilg, also of the Cordillera Central of Colombia, and *M. gattaca* J. R. Grant of the Cordillera Occidental, the Chocó of Ecuador, especially by virtue of inflorescences with large numbers of prominent bracts. It differs from *M. gattaca* in having larger leaves with longer petioles (5–35 vs. 0–5 mm) and bracts of similar shape and size yet with longer petioles (2–9 vs. 0–5) and longer pedicels (10–32 vs. 7–20).

Etymology: from the Latin *gaudialis*, glad, or joyful, for its large panicle of bright, cheerful flowers.

Paratypes: COLOMBIA. Nariño: a lo largo de la carretera de Pasto a Sibundoy, 2600–2800 m, arbusto de 1.5 m, flores blancas, 5 January 1952, *Fernández, A. & Knoth 1035-A* (COL). Putumayo: Región del Valle de Sibundoy, camino desde el Municipio de Colón a la Reserva Natural Privada “La Rejoya,” cuchilla de Bordoncillo, divisoria de aguas entre las cuencas del río Juanambú y del río Putumayo, 2500–2700 m, 13 January 2002, *Gutiérrez O. 225* (COL); Municipio de Santiago al sitio “El Encano,” Valle de Sibundoy, 1–3 April 1993, *Hoyos 18* (HUQ); Mpio. San Francisco, km 83 margen derecha carretera a Mocoa, 2890 m, arbusto 4–5 m, flores de color amarillo claro muy vistoso, 18 November 1971, *López J. 447* (NY); Páramo de San Antonio, entre La Laguna de La Cocha y el Valle de Sibundoy, 3000–3200 m, large shrub, flowers fetid, cream-yellow, 13 February 1942, *Schultes 3223* (Holotype: GH; Isotypes: COL, F); Sibundoy, hill north of valley, 2220–2270 m, February 1949 *Schultes 10415* (GH [2 sheets], MO, NY). ECUADOR. Napo: Valle alto del Río Quijos, 5 km al Sur de Cuyuja, Finca Agroecológica Antisana, bosque primario muy húmedo montano, suelo alluvial, 00°28'S, 78°03'W, 2850 m, arbusto de 3 m, tallos huecos, frutos verdes, 16 June 1998, *Vargas et al*



FIGURE 9. A–C, *Macrocarpaea gaudialis*. A, habit of flowering stem; B, calyx; C, fruits. D–E, *M. jocularis*. D, habit of flowering stem; E, bud. F–H, *M. hilarula*. F, habit of flowering stem; G, interpetiolar ridge and leaves; H, bud. I–K, *M. maryae*. I, habit of flowering stem; J, interpetiolar ridge and leaf; K, bud. A–C drawn from Weaver 2650 (AAU, GH); D–E drawn from Little 8708 (COL); F–H drawn from Fosberg 19285 (US); I–K drawn from Gentry & Fallen 17364 (COL).

1851 (MO, NEU, QCNE). Ecuador. Sucumbios: 10 km east of Santa Bárbara de Sucumbios, 1.0–1.5 m high, flowers pale yellow, sometimes +/- greenish, 10–15 February 199, Harling 4120 (S).

5. *Macrocarpaea gondoloides* J. R. Grant, *sp. nov.* TYPE: COLOMBIA. Tulcan, Reserva Indígena Awá, Comunidad San Marcos, 25 km al NW de El Chical, Parroquia Maldonado, bosque pluvial premontano, 01°06'N, 78°14'W, 1500 m, herbácea de 50 cm de altura, en planicie, bajo bosque primario, infrutescencia verde, 16–30 November 1990, D. Rubio, C. Quelal, & J. Pai 1077 (Holotype, MO; Isotype: QCNE). Fig. 7A–B.

A *M. luteynii* J. R. Grant & Struwe *cui affinis sed calycibus longioribus et lobis calycis acuminatis, et a M. gulosa* J. R. Grant *sed calycibus grandioribus striatis verticalis stramineis, lobis calyce rotundatis vel obtusis, et seminibus brevioribus differt.*

Shrub to liana-like shrub, 0.5–3.0 m, glabrous throughout. Stems terete, solid, 2–5 mm in diam. just below the inflorescence. Leaves linear-lanceolate, lanceolate, elliptic to ovate, petiolate, (6.0–)10.5–22.0 cm long. Petioles 2–20 mm long, slender with slight vagination to 1/4 the length of petiole; interpetiolar ridge 1–3 mm high. Blades (5.8–)10.3–20.0 × 3.5–8.0 cm, entire, not revolute, dark above and below, with slightly impressed veins above, and slightly raised veins below, glabrous, papery thin; base equilateral to oblique, cuneate to attenuate and decurrent on the petiole; apex acuminate. Inflorescence a few-branched open thyrse, 9–40 cm long; branches 9–22 cm long; 3- to 9-flowered per branch. Bracts ovate to lanceolate, sessile to short-petiolate, 10–115 × 4–58 mm; base equilateral to oblique, cuneate to rounded; apex

acuminate to acute; bract petioles 0–2 mm long. Flowers pedicellate, erect to slightly spreading, but never nodding; pedicels 8–20 mm long; bracteoles ovate to lanceolate, 5–16 × 1.5–6.0 mm. Calyx campanulate, 11–13 × 5–7 mm, glabrous, vertically striated, straw-colored to tan when dried as herbarium specimen, ecarinate; calyx lobes ligulate to oblong, 6–9 × 3.5–5.0 mm, apex rounded to obtuse. Corolla greenish-white (González & Ramírez 1688), greenish-yellow (Méndez *et al.* 231). Stamens and pistil unknown. Capsules ovoid, 9–14 × 5–10 mm, smooth, ribbed along sutures, straw-colored, erect to slightly spreading but not nodding; style remnant 6–8 mm long, remaining as a strong lignified tube even when capsule below deteriorates to release seeds. Seeds “rimmed-reversal to perimetrically winged type,” 0.4–0.9 × 0.3–0.5 mm, bicolored, testa golden-tan, wings translucent golden, testa reticulate, wings ribbed.

Macrocarpaea gondoloides belongs to sect. *Macrocarpaea* and occurs in the Northern Andes, on the Cordillera Occidental, the Chocó of Colombia and Ecuador (Fig. 5). It is facultatively epiphytic and is closely related to the other four confirmed facultatively epiphytic species in the genus: *M. gulosa* J. R. Grant and *M. luteynii* J. R. Grant & Struwe of the Cordillera Occidental of Colombia, and *M. browalliioides* (Ewan) A. Robyns & Nilsson and *M. subcaudata* Ewan of Costa Rica and Panama. The seeds of these species have the “perimetrically winged” morphology that is more typical of sect. *Choriophylla*. It is possible that the selection pressure for these epiphytic species has resulted in the evolution of winged seeds that better permits dispersal from epiphytic habitats. The following key identifies the principal criteria to discriminate *M. gondoloides* and *M. gulosa*.

- 1a. Calyx 8–10 mm long, smooth, chestnut to dark orange in color when dried as herbarium specimen, the lobes acuminate to acute, dividing the calyx to 3/4, seeds larger (0.5–1.0 × 0.4–0.8 mm) and bicolored (testa orange-tan, wings translucent yellow), plants of Chocó and Antioquia, Colombia *M. gulosa* J. R. Grant
 1b. Calyx 11–13 mm long, vertically striated, straw-colored to tan in color when dried as herbarium specimen, the lobes rounded to obtuse, dividing the calyx to 2/3, seeds smaller (0.4–0.9 × 0.3–0.5) and uniform in color (testa golden-tan, wings translucent golden), plants of Carchi, Ecuador, and Nariño, Colombia *M. gondoloides* J. R. Grant

Etymology: named for the oblique shape of the leaves, similar to the outline of an Italian gondola, a type of boat.

Paratypes: COLOMBIA. Nariño: Mpio. de Ricaurte, Resguardo Indígena Nulpe Medio, Andalucía, camino a Piguantís, 01°4'N,

78°15'W, 780 m, arbusto 2.2 m, flores blanco verdosas, estambres amarillos, 13 January 1996, González, M. S. & Ramírez P. 1688 (QCA). ECUADOR. Carchi: Tulcan, Reserva Étnica Awá, Parroquia El Chical, Centro Gualpi Medio, bosque muy húmedo premontano,

bosque primario, 01°02'N, 78°16'W, 900 m, bejuco trepadora, brácteas verdes, frutos redondos verdes, 18 February 1993, *Aulestia & Grijalva 1122* (MO, QCNE); Tulcan, Reserva Étnica Awá, Parroquia El Chical, Centro San Marcos, bosque muy húmedo premontano, bosque primario alterado, terreno plano inundable, 01°06'N, 78°14'W, 750 m, arbusto de 1.5 m, en bosque secundario, borde de quebrada, botones florales verdes, flores amarillo-verdosas, 20–30 April 1990, *Méndez et al. 231* (AAU, MO, QCNE); Tulcan Canton, Chical, Reserva Étnica Awá-Camumbí, bosque pluvial montaña bajo, bosque primario, suelo pantanoso, 78°16'W, 00°53'N, 1700–1900 m, colectada a 2 m de altura, bosque secundaria, inflorescencia cremosas, nombre común juquillo, 20–29 July 1991, *Quelal et al. 276* (MO, QCNE); Tulcan Cantón, Parroquia Chical, Sector Gualpi medio, Reserva Indígena Awá, Sendero a San Marcos al norte de la casa communal, bosque muy húmedo premontano, bosque primario, 01°02'N, 78°16'W, 3200 m, arbusto de 2 m, en bosque primario, frutos alargados verdes, 23–17 May 1992, *Tipaz et al. 1051* (MO [2 sheets]).

6. *Macrocarpaea gravabilis* J. R. Grant, *sp. nov.* TYPE: COLOMBIA. Caldas: La Selva, Pueblo Rico, 1500 m, 27 January 1946, *K. von Sneider 5434* (Holotype: S). Fig. 10H–J.

A *M. sodiroana* Gilg *cui affinis sed foliis tenuibus molto brevioribus, bracteis longae-acuminatis, et indumentum glauca inflorescentia apprimae calycibus differt.*

Shrub, glabrous throughout. Stems terete to quadrangular, hollow, 6 mm in diam. just below the inflorescence. Leaves elliptic to ovate, petiolate, 21–31 cm long. Petioles 15–30 mm long, robust with strong open vagination 1/4 to 1/3 the length of the petiole; interpetiolar ridge 2–4 mm high. Blades 19.5–27.0 × 6.5–12.5 cm, entire, not revolute, dark above and below, with slightly impressed veins above and slightly raised veins below, glabrous, papery thin; base equilateral to oblique, cuneate to attenuate and decurrent on the petiole; apex acuminate. Inflorescence a much-branched open thyrse, 35+, imperfectly known; branches 7–11 cm long; 3- to 9-flowered per branch. Bracts ovate to lanceolate, sessile to short-petiolate, 17–85 × 3–33 mm; base equilateral to oblique, cuneate; apex acuminate; bract petioles 0–5 mm long. Flowers pedicellate, erect; pedicels 18–21 mm long; bracteoles

inconspicuous and scabrous, to ovate to lanceolate, 3–17 × 0.5–5.5 mm. Calyx campanulate, 8–10 × 8–9 mm, glabrous, smooth, ecarinate, yet with pronounced ridges between calyx lobes from their bases and extending on to pedicels; calyx lobes ovate, 3–5 × 3–4 mm, apex obtuse to rounded. Corolla funnel-shaped, 37–43 mm long, 15–25 mm wide at the apex of the tube, smooth; corolla lobes ovate, 9–12 × 9–12 mm, obtuse to rounded. Stamens 30–35 mm long; filaments 25–30 mm long, filiform, flattened; anthers elliptic to oblong, 5 × 2.0–2.5 mm, sagittate, versatile; pollen unknown. Pistil 35–43 mm long; ovary 10–11 × 3–4 mm; style 23–29 × 1.0–1.5 mm; stigma lobes spatulate, 2–4 × 1.5–2.0 mm. Capsules and seeds unknown.

Macrocarpaea gravabilis belongs to sect. *Choriophylla* and occurs in the Northern Andes, on the Cordillera Occidental, the Chocó of Colombia (Fig. 4). It is related to *M. sodiroana* Gilg, also of the Cordillera Occidental, the Chocó of Colombia and Ecuador, but differs in having much shorter and thinner-textured leaves, long-acuminate bracts, and a glaucous indumentum on the inflorescences, especially the calyces.

Etymology: from the Latin *gravabilis*, troublesome, a species at first particularly difficult to circumscribe.

7. *Macrocarpaea gulosa* J. R. Grant, *sp. nov.* TYPE: COLOMBIA. Chocó: Municipio de Nóvita, ladera norte del Cerro Torrá, filo al oeste del Río Surama, camino al Alto del Oso, 600–900 m, arbusto, 2 m, flores verdosas, 22 February 1977, *E. Forero, A. Gentry, A. Sugden, & D. Daly 3158* (Holotype: COL; Isotype: MO). Fig. 11A–D.

A *M. luteynii* J. R. Grant & Struwe *cui affinis sed calycibus longioribus et lobis calycis acuminatis, et a M. gondoloides* J. R. Grant *sed calycibus brevioribus laevibus castaneis vel atro-aurantiaceis, lobis calycis acuminatis vel acutis, seminibus grandioribus.*

Shrub, 2–3 m, glabrous throughout. Stems terete, solid, 2–4 mm in diam. just below the inflorescence. Leaves linear-lanceolate, lanceolate, elliptic to ovate, petiolate, (5.0–)6.5–22.5 cm long. Petioles 3–25 mm long, slender with slight vagination to 1/4 the length of petiole; interpetiolar ridge 1–3 mm high. Blades 6–20 × 2.5–7.5 cm, entire, not revolute, dark above and below, with slightly impressed veins above and slightly raised veins below, glabrous, papery



FIGURE 10. A–D, *Macroparpea gaudialis*. A, leaf; B, flowers; C, habit of flowering stem; D, bud. E–G, *M. umerulus*. E, mature leaf and detail of interpetiolar ridge; F, habit of flowering stem; G, bud. H–J, *M. gravabilis*. H, leaf; I, habit of flowering stem; J, bud. K–M, *M. umerulus*. K, leaf; L, habit of flowering stem; M, nodding bud. A–B drawn from Lopez 447 (NY); C–D drawn from Schultes 3223 (GH); E–G drawn from Alonso et al. 11794 (COL); H–J drawn from von Sneidern 5434 (S); K–L drawn from Grubb et al. 708 (US); M from Snow 22 (COL).



FIGURE 11. A–D, *Macrocarpaea gulosa*. A, habit of flowering stem; B, interpetiolar ridge; C, flower; D, fruit. E–F, *M. ypsiloaule*. E, habit of flowering stem; F, interpetiolar ridge. A–C drawn from *Forero et al.* 3158 (MO, COL), D drawn from *Forero* 3226 (COL), E–F drawn from *Miguel* 57 (F).

thin; base equilateral to oblique, cuneate to attenuate and decurrent on the petiole; apex acuminate. Inflorescence a few-branched open thyrse, 10–20 cm long; branches 9–13 cm long; 3- to 9-flowered per branch. Bracts ovate, elliptic, to lanceolate, sessile to short-petiolate, 10–65 × 4–34 mm; base equilateral to oblique, cuneate to rounded; apex acuminate to acute; bract petioles 0–3 mm long. Flowers pedicellate, erect to slightly spreading, but never nodding; pedicels 7–24 mm long; bracteoles ovate to lanceolate, 9–13 × 3–6 mm. Calyx campanulate, 8–10 × 5–6 mm, glabrous, smooth, chestnut to dark orange when dried as herbarium specimen, ecarinate; calyx lobes oblong to lanceolate, 6–8 × 2.5–4.0 mm, apex acuminate to acute. Corolla funnel-shaped, 22–24 mm long, 12–13 mm wide at the apex of the tube, green (*Cogollo 3338*, *Forero et al. 3158*), smooth, covered in minute spiculae; corolla lobes ovate, 6–8 × 5–6 mm, obtuse to rounded. Stamens 12.5–16.0 mm long; filaments 10–13 mm long, filiform, flattened; anthers linear to linear-elliptic, 2.5–3.0 × 1.0–1.5 mm, sagittate, versatile; pollen *Glabra* type. Pistil 19–21 mm long; ovary 4–5 × 1.5–2.0 mm; style 12.5–16.0 × 0.5–1.0 mm; stigma lobes spatulate to suborbicular, 1.0–1.5 × 1.0–1.5 mm. Capsules ovoid, 8–14 × 5–8 mm, smooth, ribbed along sutures, straw-colored, erect to slightly spreading but not nodding; style remnant 4–7 mm long, remaining as a strong lignified tube even when the capsule below deteriorates to release seeds. Seeds “rimmed-reversal to perimetrixly winged type,” 0.5–1.0 × 0.4–0.8 mm, bicolored, testa orange-tan, wings translucent yellow, testa reticulate, wings ribbed.

Macroparpaea gulosa belongs to sect. *Macroparpaea* and occurs in the Northern Andes, on the Cordillera Occidental, the Chocó of Colombia and Ecuador (Fig. 4). It is related to *M. gondoloides* J. R. Grant, *M. luteynii* J. R. Grant & Struwe also of the Cordillera Occidental of Colombia, *M. browalliioides* (Ewan) A. Robyns & Nilsson (Costa Rica and Panama), and *M. subcaudata* Ewan (Costa Rica and Panama). The characters differentiating *M. gulosa* from *M. gondoloides* are found in the key above under *M. gondoloides*.

Paratypes: COLOMBIA. Antioquia: Parque Nacional Natural “Las Orquídeas,” camino a San Mateo, margen izquierda de la Quebrada San Mateo, 06° 33'N, 76° 19'W, 1060 m, arbusto de 2.5 m, flor verde, fruto verde, envés

café, 7 June 1988, *Cogollo et al. 3338* (FMB). Chocó: Municipio de Nóvita, ladera norte del Cerro Torrá, filo al oeste del Río Aurama, Alto del Oso, 1000–1150 m, arbusto, 3 m, frutos verdes, bosque, 22 February 1977, *Forero et al. 3226* (COL, MO); Municipio San José del Palmar, Cerro del Torrá, vertiente Occidental, hoyo del Río Negro, vereda de Río Negro, ca 1 hora abajo del helipuerto, 04° 46'N, 76° 29'W, 1800–1900 m, arbusto ca. 3 m, botones florales verde-amarillentos, 23 August 1988, *Ramos et al. 1477A* (COL).

8. *Macroparpaea hilarula* J. R. Grant, *sp. nov.* TYPE: COLOMBIA. Meta: Cordillera Oriental, Hills above ranch house, Finca Balsillas, Upper Río Balsillas (part of old Hacienda Balsillas), 40 km ESE of Neiva, 02° 53'N, 74° 57'W, 2300 m, steep wet densely wooded ravine, shrub with single stem branched only near top, 3 m tall, top composed of decussately arranged inflorescences, corolla campanulate, greenish-white, fruit immature, from a different plant, 7 December 1942, *F. R. Fosberg 19285* (Holotype: US [3 sheets]; Isotypes: NO [3 sheets], S). Fig. 9F–H.

A M. nicotianifolia Weaver & J. R. Grant cui affinis sed petiolis longioribus (10–30 vs. 1–10 mm), bracteis brevioribus (12–80 vs. 10–135 mm), bracteolis brevioribus, (1.5–9.0 vs. 1.0–20.0 mm), lobis calycis brevioribus (1.5–2.0 vs. 4.0–5.0 mm), corollis brevioribus (40–42 vs. 32–60 mm), et antheris brevioribus (6–7 vs. 8–12 mm) differt.

Unbranched shrub, 3 m, hyaline hispid to spiculate with short simple hairs on stems, petioles, leaves, inflorescences, bracts, and calyces, often appearing glaucous on dried herbarium specimens because of minute white crystals covering upper stems, petioles, and calyces. Stems terete to slightly quadrangular above, solid to hollow, 5–6 mm in diam. just below inflorescence. Leaves ovate, broadly oval to obovate, petiolate, 20–31 cm long. Petioles 10–30 mm long, robust with strong open vagination 1/4 to 1/3 the length of petiole; interpetiolar ridge 4–6 mm high. Blades 19–28 × 9.5–17.0 cm, entire, not revolute, dark above and below, with slightly impressed veins above and slightly raised veins below, hyaline hispid to spiculate on veins on lower surface, papery thin, to thin coriaceous; base equilateral to oblique, cuneate to attenuate; apex obtuse to rounded. Inflorescence a much-branched open

thyrses, 26–32+ cm long; branches 7–20 cm long; 5- to 15-flowered per branch. Bracts ovate, petiolate, 12–80 × 5–45 mm; base equilateral to oblique, cuneate to rounded; apex acute; bract petioles 2–5 mm long. Flowers pedicellate, erect to slightly spreading; pedicels 12–27 mm long; bracteoles lanceolate, linear, to ovate, 1.5–9.0 × 1–5 mm. Calyx campanulate, 9–12 × 7–9 mm, glabrous to spiculate, smooth, ecarinate; calyx lobes ovate to reniform, 1.5–2.0 × 3–4 mm, apex rounded to obtuse. Corolla funnel-shaped, 40–42 mm long, 12–18 mm wide at apex of tube, greenish white (Fosberg 19285), smooth; corolla lobes ovate, 6–9 × 5–7 mm, obtuse to rounded, often crisped. Stamens 24–29 mm long; filaments 18–22 mm long, filiform, flattened; anthers linear to linear-elliptic, 6–7 × 2.0–2.5 mm, sagittate, versatile; pollen *Glabra* type. Pistil 35–43 mm long; ovary 7–9 × 2–4 mm; style 26–31 × 1.0 mm; stigma lobes spatulate, 2–3 × 1.0–1.5 mm. Capsules obovoid to ellipsoidal, 18–25 × 7–11 mm, shiny and smooth to rugose, chestnut to brown, erect to slightly spreading; style remnant 6–10 mm long. Seeds “rimmed type,” 0.5–1.0 × 0.4–0.8 mm, faint orangish tan, testa rugose-reticulate to wrinkled.

Macrocarpaea hilarula belongs to sect. *Macrocarpaea* and occurs in the Northern Andes, on the Cordillera Oriental of Colombia (Fig. 4). It is related to *M. nicotianifolia* Weaver & J. R. Grant and *M. jocularis* J. R. Grant of the Cordillera Oriental of Colombia, and *M. laudabilis* J. R. Grant of the Cordillera Central of Colombia. It differs notably from *M. nicotianifolia* in having longer petioles (10–30 vs. 1–10 mm long), shorter bracts (12–80 vs. 10–135 mm), shorter bracteoles, (1.5–9.0 vs. 1–20 mm), similar calyx lengths (9–12 vs. 10–13 mm) yet with calyx lobes less than half as long (1.5–2.0 vs. 4.0–5.0 mm), shorter corollas (40–42 × 32–60 mm), and shorter anthers (6–7 vs. 8–12 mm).

Etymology: from the Latin *hilarulus*, cheerful, for its bright colorful inflorescence. According to the herbarium label, this specimen was collected in 1942 by Ray Fosberg during the “Colombian *Cinchona* Mission.”

9. *Macrocarpaea jocularis* J. R. Grant, sp. nov.
TYPE: COLOMBIA. Huila: Cordillera Oriental, SE side Quebrada de Riolora, 15 km SE of Gigante, dwarf forest type, 3050 m, shrub or small tree 6 m high, 5 cm DBH, bark gray, smooth, large tubular greenish flowers, 20

September 1944, *E.L. Little Jr.* 8708 (Holotype: US; Isotypes: COL, NO). Fig. 9D–E.

A. M. nicotianifolia Weaver & J. R. Grant *cui affinis sed petiolis longioribus* (5–15 vs. 1–10 mm), *lobis calycis brevioribus* (1.5–3.0 vs. 4.0–5.0 mm), *et antheris brevioribus* (6–7 vs. 8–12 mm) *differt*.

Shrub or small tree, 2.5–6.0 m, hyaline hispid to spiculate with short simple hairs on stems, petioles, leaves, inflorescences, bracts, and calyces, often appearing glaucous on dried herbarium specimens because of minute white crystals covering upper stems and petioles; trunk 5 cm in diameter at breast height (DBH) (*Little* 8708). Stems terete to slightly quadrangular above, solid to hollow, 5–8 mm in diam. just below the inflorescence. Leaves ovate, oval to obovate, petiolate, 12–25 cm long. Petioles 5–15 mm long, robust with strong open vagination 1/4–1/3 the length of petiole; interpetiolar ridge 2–5 mm high. Blades 11.5–23.5 × 6.0–11.5 cm, entire, not revolute, dark above and conspicuously lighter below, with slightly impressed veins above and slightly raised veins below, glabrous above, hyaline hispid to spiculate below, especially along veins, papery thin, to thin coriaceous; base equilateral to oblique, cuneate to attenuate; apex obtuse to acute. Inflorescence a much-branched open thyrses, 30–36 cm long; branches 8–30 cm long; 5- to 15-flowered per branch. Bracts ovate, petiolate, 10–165 × 5–85 mm; base equilateral to oblique, cuneate to rounded; apex acute; bract petioles 2–7 mm long. Flowers pedicellate, erect to spreading; pedicels 8–30 mm long; bracteoles lanceolate, linear, to ovate, 1–10 × 0.5–5.0 mm. Calyx campanulate, 8–11 × 6–8 mm, glabrous, smooth, ecarinate; calyx lobes ovate to reniform, 1.5–3.0 × 2.5–4.0 mm, apex obtuse, rounded to truncate. Corolla funnel-shaped, 38–50 mm long, 15–25 mm wide at the apex of the tube, yellowish green (*Llanos et al.* 3322, *Llanos & Botache* 2443), greenish (*Little* 8708), greenish yellow (*Orozco et al.* 2801), smooth; corolla lobes ovate, 6–15 × 6–11 mm, obtuse to rounded. Stamens 26–40 mm long; filaments 20–33 mm long, filiform, flattened; anthers linear to linear-elliptic, 6–7 × 2.0–2.5 mm, sagittate, versatile; pollen *Glabra* type. Pistil 35–52 mm long; ovary 6–9 × 2–4 mm; style 37–39 × 1.0 mm; stigma lobes spatulate, 2–4 × 1.5–2.0 mm. Capsules and seeds unknown.

Macrocarpaea jocularis belongs to sect. *Macrocarpaea* and occurs in the Northern

Andes, on the Cordillera Oriental of Colombia (Fig. 4). It is related to *M. nicotianifolia* Weaver & J. R. Grant and *M. hilarula* J. R. Grant of the Cordillera Oriental of Colombia, and *M. laudabilis* J. R. Grant of the Cordillera Central of Colombia. It differs notably from *M. nicotianifolia* in having longer petioles (5–15 vs. 1–10 mm long), similar calyx lengths (8–11 vs. 10–13 mm) yet with calyx lobes about half as long (1.5–3.0 vs. 4.0–5.0 mm), and shorter anthers (6–7 vs. 8–12 mm).

Etymology: from the Latin *jocularis*, laughable, jocular. Named for collector of the type, American Elbert L. Little (1907–2004), dendrologist and author of many books on North American trees. It was collected in 1944 by Little when he worked at the “Cinchona Division, Foreign Economic Administration, United States Government.” In 1989, I arrived at the Smithsonian Institution from the University of Alaska for a summer internship to study Neotropical Bromeliaceae. I soon introduced myself to Dr. Little, as I was familiar his book “Trees and Shrubs of Alaska.” Then, and on occasions for years afterward, he would joke with me wondering whether I had yet found any bromeliads in Alaska (obviously impossible since the Bromeliaceae is largely tropical).

Paratypes: COLOMBIA. Huila: Municipio de Campoalegre, Vereda Alto El Roble, 2200 m, subarbusto +/- 4 m, flores verde-amarillentas, 29 September 2001, *Llanos et al.* 3322 (COL); Municipio de Campoalegre, Vereda Alto El Roble, 2330 m, subarbusto 4 m, hojas simples, opuestas, flores amarillas-verdosas, 13 October 2001, *Llanos et al.* 3360 (CUVC); Campo Alegre, vereda El Roble, 2170 m, subarbusto 2 m, hojas simples, opuestas, flores verdes-amarillentas, gamopétalas, estambres epipétalos, anteras curvadas, 29 August 1992, *Llanos & Botache* 2443 (COL); Municipio Algeciras, Alto El Roble, via hacia Altamira, 2000–2400 m, arbolito de 5 m, hojas discolores, flores amarillo verdosas, 13 October 1993, *Orozco et al.* 2801 (COL).

10. *Macrocarpaea lacrossiformis* J. R. Grant, *sp. nov.* TYPE: COLOMBIA. Santander: Municipio de Gambita, Corregimiento Talandro, 2200 m, arbol 7 m, haz verde oscuro, semilustroso, nervadura central amarillento, cáliz verde amarillento, corola amarillo verdoso, filamentos amarillo verdoso, estigma verde, 14 February 1983, *C.I. Orozco 1060*

(Holotype: COL [2 sheets]). Fig. 12.

A *M. weaveri* J. R. Grant *cui affinis sed foliis late-obovatis apice rotundata basi longecuneata vel attenuata, et a M. schultesii* Weaver & J. R. Grant *cui affinis sed trichomatibus brevioribus, et calycibus brevioribus et latibus (8–10 × 7–9 mm vs. 9–14 × 5–7 mm) differt.*

Shrub or small tree, 4–8 m, hyaline hispid to spiculate with short simple hairs on stems, inflorescences, bracts, and calyces. Stems terete to slightly quadrangular, solid, 5–13 mm in diam. just below inflorescence. Leaves obovate, varying to slightly elliptic, petiolate, (5.5)12.0–25.0 cm long. Petioles 5–30 mm long, slender with slight vagination to 1/4 the length of petiole; interpetiolar ridge 3–5 mm high. Blades 5–22 × (3.0–)5.5–11.0 cm, entire, slightly revolute, dark green to olive green above, lighter below, with slightly impressed veins above and strongly raised veins below, glabrous above and below, lustrous (*Orozco 1060*), thick, leathery-coriaceous; base equilateral to oblique, cuneate to attenuate and decurrent on the petiole; apex rounded to obtuse. Inflorescence a much-branched open thyrse, 23–50 cm long; branches 8–37 cm long; 5- to 15-flowered per branch. Bracts elliptic, ovate, to oval, petiolate, 11–60 × 5–30 mm; base equilateral to oblique, cuneate to rounded; apex acute, obtuse to rounded; bract petioles 1–8 mm long. Flowers pedicellate, erect to nodding; pedicels 10–30 mm long; bracteoles inconspicuous and scabrous, linear to ovate, 2–11 × 0.5–5.0 mm. Calyx campanulate, 8–10 × 7–9 mm, glabrous to spiculate, rugose, yellowish-green (*Orozco 1060*, *Lozano C. 3731*), pale green (*Lozano C. 3931*), ecarinate; calyx lobes ovate to rotund, 3–5 × 3–5 mm, apex rounded. Corolla funnel-shaped, 34–37 mm long, 15–20 mm wide at the apex of the tube, greenish yellow (*Orozco 1060*), yellowish white (*Castro et al. 1011*), pale yellow (*Torres R. 2637*), cream (*Lozano C. 3721*; *Lozano C. 3931*), smooth; corolla lobes ovate, 8–9 × 5–9 mm, obtuse to rounded. Stamens 18–21 mm long; filaments 15–17 mm long, filiform, flattened; anthers elliptic to oblong, 3–4 × 1.0–2.5 mm, sagittate, versatile; pollen *Glabra* type. Pistil 27–34 mm long; ovary 8–9 × 2–3 mm; style 16–20 × 0.75–1.00 mm; stigma lobes spatulate to suborbicular, 2–3 × 1.5–2.0 mm. Capsules ovoid, obovoid to ellipsoidal, 15–24 × 6–9 mm, smooth to faintly rugose, chestnut-tan, erect to slightly nodding; style remnant 4–9

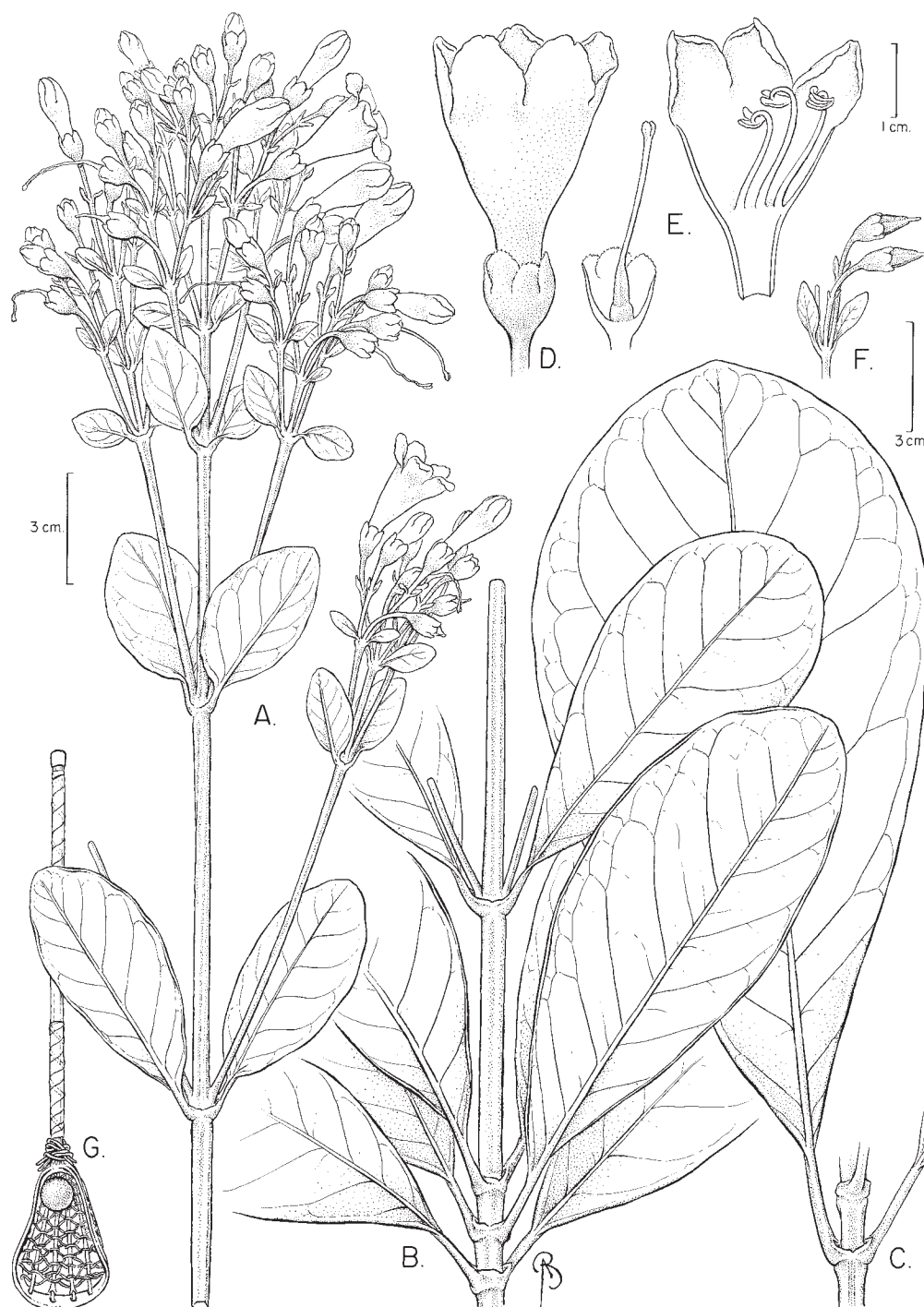


FIGURE 12. *Macrocarpaea lacrossiformis*. A, habit of flowering stem; B, leaves; C, mature leaf and detail of interpetiolar ridge; D, flower; E, dissected flower; F, fruits; G, lacrosse stick. A–B drawn from Orozco 1060 (COL), D–F drawn from Lozano ca. 393 (COL).

mm long. Seeds “rimmed type,” 0.5–0.9 × 0.4–0.6 mm, faint orangish tan, testa rugose.

Macrocarpaea lacrossiformis belongs to sect. *Macrocarpaea* and occurs in the Northern Andes, on the Cordillera Oriental of Colombia (Fig. 4). It is related to *M. weaveri* J. R. Grant and *M. schultesii* Weaver & J. R. Grant also of Cordillera Oriental of Colombia. As mentioned in Grant and Weaver (2003: 108) as an undescribed species, *M. lacrossiformis* differs from *M. weaveri* in having broadly-obovate leaves with rounded apices, long-cuneate to attenuate bases that are dull on the upper surface (vs. elliptic, obovate to oblanceolate leaves with short-attenuate to rounded bases that are shiny on the upper surface. It also differs from *M. schultesii* in having shorter hairs and shorter broader calyces (8–10 × 7–9 vs. 9–14 × 5–7 mm).

Etymology: named for the obovate shape of its leaves, which resemble the outline of the netted racquet of the curved stick used in the originally Native American stickball sport lacrosse.

Paratypes: COLOMBIA. Boyacá: Municipio de Gámbita, Vereda el Taladro, 2100 m, arbolito 8 m, haz verde oliva, envés verde claro, cáliz verde pálido, corola crema, 19 October 1983, *Lozano ca. 3931* (COL [2 sheets]); Municipio de Arcabuco, La Cumbre, Bosque de Robles, 2300 m, arbol +/- de 5 m, haz verde citrino, envés verde amarillento, cáliz verde amarillento, corola crema, estambres blancos, 8 October 1980, *Lozano ca. & Díaz 3721* (COL); Río Pomera, 12 km NW of Arcabuco, thicket on steep slopes, 2805 m, 4 m shrub, corolla greenish yellow, fragrant, 20 August 1944, *St. John 20678* (NO, US); Tota, 3200 m, de 2 m, December 1951, *Yepes-Agreto 3374* (COL). Santander: Municipio de Charalá, Vereda Santa Helena, predio la Sierra, Margen izquierdo aguas abajo del río la Rusia, Santuario de Fauna y Flora Guanentá Alto río Fonce, 06°01'N, 73°09'W, 2700 m, arbol de 4 m, tallos angulosos, hojas apergamizadas, frutos con cáliz persistente, fruto verde, 16 December 1998, *Cadena-M. et al. 243* (COL); Municipio Charalá, Corregimiento de Virolín, camino de quebrada desde la carretera Virolín-Duitama a la Chorrera en la Cuchilla “El Venado,” 2000 m, arbolito de 5–6 m, flor blanco amarillento, 17 October 1985, *Castro & Rodriguez 1011* (COL); Municipio de Charalá,

Corregimiento de Virolín, Sitio Cañaverales, 2170 m, arbusto, haz verde oliva, envés más claro, pétalos amarillo-pálido, filamento verde claro con estigma anteras blanca, 19 October 1983, *Torres R. 2637* (COL).

11. *Macrocarpaea laudabilis* J. R. Grant, *sp. nov.* TYPE: COLOMBIA. Caquetá: Comisaría del Caquetá, Cordillera Oriental sobre el filo divisoria, en Gabinete, 2300–2450 m, 21 March 1940, *J. Cuatrecasas 8435* (Holotype: US; Isotype: COL). Fig. 8A–D.

A *M. nicotianifolia* Weaver & J. R. Grant *cui affinis sed petiolis longioribus (10–20 vs. 1–10 mm long), bracteis brevioribus (10–70 vs. 10–135 mm), petiolis longioribus (3–13 vs. 0–5 mm), et antheris brevioribus (5–6 vs. 8–12 mm) differt.*

Shrub, 2–5 m, hyaline hispid to spiculate with short simple hairs on stems, petioles, leaves, inflorescences, bracts, and calyces. Stems terete to slightly quadrangular above, solid to hollow, 5–7 mm in diam. just below the inflorescence. Leaves ovate, oval to obovate, petiolate, 11.5–24.0 cm long. Petioles 10–20 mm long, robust with strong open vagination 1/3–1/2 the length of petiole; interpetiolar ridge 2–4 mm high. Blades 10.5–22.0 × 6.5–11.0 cm, entire, not revolute, dark above and conspicuously lighter below, with slightly impressed veins above and slightly raised veins below, glabrous above, hispid to spiculate below most densely so along the principal veins of mature leaves, papery thin, to thin coriaceous; base equilateral to oblique, cuneate to rounded; apex obtuse, rounded, to rarely acute. Inflorescence a much-branched open thyrses, 18–35 cm long; branches 10–22 cm long; 3- to 12-flowered per branch. Bracts ovate, petiolate, 10–70 × 4–56 mm; base equilateral to oblique, cuneate to rounded; apex obtuse to acute; bract petioles 3–13 mm long. Flowers pedicellate, erect to slightly spreading; pedicels 4–22 mm long; bracteoles lanceolate, linear, to ovate, 7–15 × 2–7 mm. Calyx campanulate, 7–10 × 6–8 mm, glabrous to spiculate, smooth, ecarinate; calyx lobes ovate to reniform, 2–3 × 3–4 mm, apex rounded to obtuse. Corolla funnel-shaped, 52–61 mm long, 22–26 mm wide at the apex of the tube, greenish cream (*Uribe Uribe 3871*), smooth; corolla lobes ovate, 12–17 × 10–16 mm, obtuse to rounded. Stamens 30–46 mm long; filaments 25–40 mm long, filiform, flat-

tened; anthers linear to linear-elliptic, 5–6 × 2.0–2.5 mm, sagittate, versatile; pollen *Glabra* type. Pistil 50–55 mm long; ovary 7–9 × 2–4 mm; style 40–42 × 0.75–1.00 mm; stigma lobes spatulate, 3–4 × 1–2 mm. Capsules ellipsoidal to ovoid, 25–34 × 7–9 mm, shiny and smooth to rugose, chestnut to light brown, erect to slightly nodding; style remnant 5–15 mm long. Seeds “rimmed type,” 0.6–1.0 × 0.5–0.7 mm, straw-colored, testa rugose-reticulate to wrinkled.

Macrocarpaea laudabilis belongs to sect. *Macrocarpaea* and occurs in the Northern Andes, on the Cordillera Central of Colombia (Fig. 4). It is related to *M. nicotianifolia* Weaver & J. R. Grant, *M. hilarula* J. R. Grant, and *M. jocularis* J. R. Grant, all of the Cordillera Oriental of Colombia. It differs from *M. nicotianifolia* in having longer petioles (10–20 vs. 1–10 mm long), shorter bracts (10–70 vs. 10–135 mm) with longer bract petioles (3–13 vs. 0–5 mm), and shorter anthers (5–6 vs. 8–12 mm).

There is an annotation label in Joseph Ewan’s handwriting on *García-Barriga & Hawkes 12884* (US) that reads “Capsule not as in *M. m.* [*Macrocarpaea macrophylla*] and though leaves here from sterile shoot quite different from that sp. May prove to be new sp.”

Etymology: from the Latin *laudabilis*, laudable or praiseworthy, for the handsome inflorescence.

Paratypes: COLOMBIA. Cauca-Huila: región de Moscopán, adelante de Santa Leticia, 2400–2600 m, arbusto de más de 2 m, flores de color crema verdoso, 8 September 1961, *L. Uribe Uribe 3871* (COL). Huila: Carr. a la Plata, región de Moscopán, Santa Leticia, 2230 m, 21 June 1948, *García-Barriga & Hawkes 12884* (COL, US).

12. *Macrocarpaea maryae* J. R. Grant, *sp. nov.* TYPE: COLOMBIA. Chocó: North ridge of Alto de Buey, premontane wet forest, east-southwest of El Valle, 500–1150, shrub 3 m, flowers greenish yellow, 8 August 1976, *A. Gentry & M. Fallen 17369* (Holotype: COL [2 sheets]; Isotype: U [2 sheets]). Fig. 9I–K.

A *M. sodiroana* Gilg *cui affinis sed foliis tenuibus late-ovatis vel subdeltoideis, inflorescentia diffusis, calycibus brevioribus* (6–8 × 5–7 × vs. 5–10 × 8–10 mm), *et lobis calycis brevioribus* (2–3 vs. 4–7 mm) *differt.*

Shrub, 1–3 m, glabrous throughout. Stems terete to slightly quadrangular, hollow, 7–12 mm in diam. just below the inflorescence. Leaves broadly ovate to subdeltoid, petiolate, 19–32 cm long. Petioles 5–30 mm long, robust with strong open vagination 1/2 to nearly equaling the length of petiole; interpetiolar ridge 2–3 mm high. Blades 18.5–29.0 × 13–19 cm, entire, not revolute, light green to dark green, with slightly impressed veins above and slightly raised veins below, glabrous above and below, papery thin; base equilateral to oblique, rounded to nearly truncate to slightly attenuate and decurrent on the petiole; apex acuminate to acute. Inflorescence a much-branched open thyrs, 41+, imperfectly known; branches 14–41 cm long; 3- to 15-flowered per branch. Bracts ovate to lanceolate, sessile to petiolate, 15–87 × 7–36 mm; base equilateral to oblique, cuneate to rounded; apex acuminate; bract petioles 0–9 mm long. Flowers pedicellate, erect to slightly spreading; pedicels 10–24 mm long; bracteoles inconspicuous and scabrous, linear, lanceolate to ovate, 0.5–13.0 × 0.5–3.0 mm. Calyx campanulate, 6–8 × 5–7 mm, glabrous, smooth, ecarinate; calyx lobes ovate, suborbicular to reniform, 2–3 × 2–4 mm, apex acute, obtuse to rounded. Corolla funnel-shaped, 32–38 mm long, 12–15 mm wide at the apex of the tube, greenish yellow (*Gentry & Fallen 17369*), smooth; corolla lobes ovate to elliptic, 8–12 × 5–10 mm, obtuse to rounded. Stamens 17–22 mm long; filaments 14–18 mm long, filiform, flattened; anthers elliptic to oblong, 3–4 × 1–2 mm, sagittate, versatile; pollen *Glabra* type. Pistil 25–30 mm long; ovary 5–7 × 2–3 mm; style 18–20 × 0.5–1.0 mm; stigma lobes spatulate, 2–3 × 1–2 mm. Capsules and seeds unknown.

Macrocarpaea maryae belongs to sect. *Choriophylla* and occurs in the Northern Andes, on the Cordillera Occidental, the Chocó of Colombia (Fig. 4). It is related to *M. sodiroana* Gilg, also of the Cordillera Occidental, the Chocó of Colombia and Ecuador, but differs in having thin broadly ovate to subdeltoid leaves (vs. broadly elliptic to oblanceolate below, varying to ovate to lanceolate toward the inflorescence), a more open diffuse inflorescence, and smaller calyces (6–8 × 5–7 vs. 5–10 × 8–10 mm) with shorter calyx lobes (2–3 vs. 4–7 mm).

Etymology: named for co-collector of the type, Mary E. Fallen (1949–), now Mary E.

Endress, specialist of the Apocynaceae, Institute of Systematic Botany, Universität Zürich, Switzerland (Z).

Paratype: Antioquia: Trail from Encarnación to Parque Nacional de los Orquídeas, western slope of the Cordillera, 1600–1800 m, herbaceous shrub 1 m, flowers light yellow, 27 January 1979, *Gentry & Renteria 24569* (COL, MO).

13. *Macroparanea silverstonei* J. R. Grant, *sp. nov.* TYPE: COLOMBIA. Chocó: Mun. de San José del Palmar, Cerro del Torrá, vertiente oriental, 2450 m, falda empinada, vegetación herbácea y arbustiva, hierba ca. 1 m, corolla amarillo claro, filamentos blancos, anteras blancuzco-amarillentas, estilo y estigma verdes, 12 August 1988, *P. A. Silverstone-Sopkin, N. Paz, R. T. González, J. E. Ramos, L. H. Ramos & A. Henao 4335* (Holotype: CUVC; Isotype: U). Fig. 8H–J.

A M. macrophylla (Kunth) Gilg cui affinis sed plantis omnino glabris, margo foliis hyalina 1 mm, et calycibus glabris pusticulatis, et lobis patentibus differt.

Shrub, 1.0–1.5 m, glabrous throughout. Stems terete to slightly quadrangular above, solid to hollow, 4–6 mm in diam. just below the inflorescence. Leaves elliptic to elliptic-obovate, petiolate, 7.0–9.5 cm long. Petioles 4–5 mm long, robust with strong open vagination 1/4–1/3 the length of the petiole; interpetiolar ridge 2–4 mm high. Blades 6.6–9.0 × 4.0–5.3 cm, entire, not revolute, with a thin (to 1 mm wide) margin or wing around the entire leaf, dark above and conspicuously lighter below, with slightly impressed veins above and slightly raised veins below, glabrous above and below, papery thin, to thin coriaceous; base equilateral to oblique, cuneate; apex obtuse to rounded, to rarely slightly mucronulate on the thin margin wing. Inflorescence a much-branched open thyrse, 10–31 cm long; branches 6–18 cm long; 3- to 7-flowered per branch. Bracts ovate, sessile to short-petiolate, 12–55 × 8–27 mm; base equilateral to oblique, cuneate to rounded; apex obtuse to acute (almost appearing zigzagged); bract petioles 0–3 mm long. Flowers pedicellate, erect to spreading; pedicels 13–20 mm long; bracteoles lanceolate to ovate, 4–9 × 2–3 mm. Calyx campanulate, 10–12 × 8–11 mm, glabrous, faintly rugose to pusticulate, ecarinate; calyx lobes ovate to elliptic, 3–6 × 4–5 mm, apex obtuse,

rounded to acute. Corolla funnel-shaped, 44–50 mm long, 25–32 mm wide at the apex of the tube, yellow (*Silverstone-Sopkin 4335*), white (*Silverstone-Sopkin 4535*), smooth; corolla lobes ovate, 13–15 × 11–16 mm, obtuse to rounded. Stamens 24–28 mm long; filaments 20–23 mm long, filiform, flattened; anthers elliptic to oblong, 4–5 × 2.0–2.5 mm, sagittate, versatile; pollen *Glabra* type. Pistil 36–39 mm long; ovary 8–10 × 3–4 mm; style 25–26 × 0.75–1.00 mm; stigma lobes spatulate, 2–4 × 1.5–2.0 mm. Capsules and seeds unknown.

Macroparanea silverstonei belongs to sect. *Macroparanea* and occurs in the Northern Andes, on the Cordillera Occidental, the Chocó of Colombia and Ecuador (Fig. 4). It is related to *M. macrophylla* (Kunth) Gilg of the Cordillera Central of Colombia but differs in being glabrous throughout, having a hyaline margin around each leaf to 1 mm wide, and having a glabrous pusticulate calyx with flared lobes.

Etymology: named for Philip Silverstone-Sopkin (1939–), collector of the type and specialist of Colombian floristics, Universidad del Valle–Calí, Colombia (CUVC).

Paratypes: COLOMBIA. Chocó: Mun. San José del Palmar, Cerro Panamá (adyacente al Cerro del Torrá, Cordillera de San Miguel), 2470–2510 m, cumbre, vegetación abierta arbustiva y herbácea, arbusto ca. 1.5 m altura, hojas subcoriáceas, corola y anteras blancas, filamentos, estilo y estigma verdes, 18 August 1988, *P. A. Silverstone-Sopkin et al. 4535* (CUVC).

14. *Macroparanea umerulus* J. R. Grant, *sp. nov.* TYPE: COLOMBIA. Boyacá: Sierra Nevada del Cocuy, in cloud forest near Bocota, by path to Bachira, 2200 m, woody herb to 2.5 m, flowers bright green, anthers greenish, 25 August 1957, *P. J. Grubb, B. A. B. Curry, & A. Fernandez-Perez 708* (Holotype: US; Isotypes: COL, K). Fig. 10E–G, K–M.

A M. nicotianifolia Weaver & J. R. Grant cui affinis sed foliis brevioribus (14–24 vs. [3.5–]9–39 cm), petiolis longioribus (10–20 vs. 1–10 mm long), pedicellis longioribus (15–40 vs. 7–35 mm), calycibus brevioribus (6–11 vs. 10–13 mm) et lobis calycis brevioribus (3–4 vs. 4–5 mm) differt.

Shrub or small tree, 1.5–4.0 m, hyaline hispid to spiculate with short simple hairs on stems, petioles, leaves, inflorescences, and bracts. Stems terete to slightly quadrangular above,

solid to hollow, 4–14 mm in diam. just below the inflorescence. Leaves ovate to ovate-elliptic, petiolate, 14–24 cm long. Petioles 10–20 mm long, robust with strong open vagination 1/2 the length of petiole; interpetiolar ridge 2–3 mm high. Blades 13.5–22.0 × 8–12 cm, entire, not revolute, dark green, with slightly impressed veins above and slightly raised veins below, hyaline hispid to spiculate on veins on lower surface, papery thin, to thin coriaceous; base equilateral to oblique, cuneate to rounded; apex acute. Inflorescence a much-branched open thyrse, 22–46+ cm long; branches 6–46 cm long; 3- to 12-flowered per branch. Bracts ovate to lanceolate, sessile to short-petiolate, 12–75 × 3–32 mm; base equilateral to oblique, cuneate to rounded; apex acuminate to acute; bract petioles 0–4 mm long. Flowers pedicellate, erect to spreading during anthesis to characteristically nodding toward fruiting; pedicels 15–40 mm long; bracteoles inconspicuous and scabrous, linear, triangular to ovate, 1–14 × 0.5–7.0 mm. Calyx campanulate, 6–11 × 6–7 mm, glabrous, smooth, ecarinate; calyx lobes ovate, 3–4 × 3–4 mm, apex obtuse to rounded. Corolla funnel-shaped, 37–45 mm long, 20–25 mm wide at apex of tube, bright green (*Grubb et al.* 708), green (*Fernández Alonso* 11794), yellowish green (*Guarín & Villarreal-V.* 1733), smooth; corolla lobes ovate, 7–13 × 9–14 mm, obtuse to rounded. Stamens 20–25 mm long; filaments 16–20 mm long, filiform, flattened; anthers linear to linear-elliptic, 4–5 × 2–3 mm, sagittate, versatile; pollen *Glabra* type. Pistil 27–35 mm long; ovary 6–9 × 2–3 mm; style 18–22 × 1.0–1.5 mm; stigma lobes spatulate, 3–4 × 1–2 mm. Capsules and seeds unknown.

Macrocarpaea umerulus belongs to sect. *Macrocarpaea* and occurs in the Northern Andes, on the Cordillera Oriental of Colombia (Fig. 4). It is related to *M. affinis* Ewan, *M. nicotianifolia* Weaver & J. R. Grant, and *M. glabra* (L.f.) Gilg, all also of the Cordillera Oriental of Colombia. It differs from *M. nicotianifolia* in having shorter leaves (14–24 vs. [3.5]9–39 cm) with longer petioles (10–20 vs. 1–10 mm long), longer pedicels (15–40 vs. 7–35 mm), and shorter calyces (6–11 vs. 10–13 mm) with shorter calyx lobes (3–4 vs. 4–5 mm). *Macrocarpaea umerulus* is distinctive in having long, slender, straight pedicels during anthesis that characteristically become nodding in maturity.

Etymology: from the Latin *umerulus*, a little shoulder. The name derives from the nodding

(or shoulder-shaped) nature of the pedicel in fruit, coined after I broke my right shoulder in a rollerblading crash in Avenches, Switzerland, on September 1, 2001. The epithet is based on a word used in apposition and is therefore to be maintained according to Article 23.1 of the ICBN (Greuter et al., 2000).

Paratypes: COLOMBIA. Boyacá: Municipio Ramiriquí, San Antonio Alto de Mesetas, hierba bejucosa con tallos verde morado, hojas cactáceas con haz verde opaco y envés amarillento, flores con corolla blanco cremoso, 29 December 1994, *Barrera* 45 (FMB); Ventaquemada, bosques a orillas de la carretera, planta arbustiva de 1.5 m, de alto, corola verde amarillenta, estambres y anteras blanco-amarillentas, 18 May 1973, *Guarín M. & Villarreal-V.* 1733 (UPTC); Municipio de Arcabuco, Cañon del río Pomeca, 05° 48' 80" N, 73° 28' 97" W, 2400 m, arbusto, 15 April 1997, *Mendoza* 3142 (FMB); Arcabuco, La Cumbre, planta arbustiva, flores con corola amarillenta, 9 February 1983, *Ortiz M. & Villarreal-V.* s.n. (UPTC); Vereda El Carare, arbusto de 4 m, flores verde pálido, 3 August 1978, *Snow* 22 (COL). Norte de Santander: Municipio de Toledo, 28.8 km de San Bernardo de Bata en la vía a Saravena, 1 km antes del parador, Alto de Santa Ines, 2300–2400 m, flores verdes, 1 November 1994, *Fernández-Alonso et al.* 11794 (COL).

15. *Macrocarpaea ypsilocaule* J. R. Grant, *sp. nov.* TYPE: COLOMBIA. Putumayo: Páramo de San Francisco (la Depresión), en el camino carretera de San Francisco a Mocoa, 3000–3100 m, January 1942, *P. Fray Miguel* 57 (Holotype: F). Fig. 11E–F.

A *M. biremis* *J. R. Grant* cui *affinis sed petiolis brevioribus* (4–10 vs. 10–15 mm), *bracteis breve-petiolatis* (0–5 vs. 8–12 mm), *et bracteolis linearis vel lanceolatis* 6–14 × 2–3 mm (vs. *obovatis vel spatulatis* 10–22 × 4–8 mm) *differt*.

Shrub, 2 m, glabrous throughout except hispid along veins on the lower surface. Stems terete to slightly quadrangular, solid, 2–5 mm in diam. just below the inflorescence. Leaves elliptic, oval to ovate, petiolate, 5.5–15.5 cm long. Petioles 4–10 mm long, robust with strong open vagination 1/4–1/3 the length of petiole; interpetiolar ridge 1–4 mm high. Blades 5.0–14.5 × 2.5–6.0 cm, entire, not revolute, dark green above, lighter below, with slightly impressed veins above and strongly raised veins

below, glabrous above, hyaline hispid on all veins below, thin to leathery coriaceous; base equilateral to oblique, cuneate; apex acuminate to acute. Inflorescence a few-branched open thyrse, 6–22 cm long; branches 5–15 cm long; 1(–3)-flowered per branch. Bracts ovate to lanceolate, sessile to short-petiolate, 20–70 × 7–15 mm; base equilateral to oblique, cuneate, to short-attenuate; apex acuminate; bract petioles 0–5 mm long. Flowers pedicellate, spreading; pedicels 8–45 mm long; bracteoles linear to lanceolate, 6–14 × 2–3 mm. Calyx campanulate, 15–22 × 8–18 mm, glabrous, faintly rugose to pustulate, ecarinate; calyx lobes ovate to elliptic, 9–13 × 8–11 mm, apex rounded to obtuse. Corolla funnel-shaped, 42–45 mm long, 15–20 mm wide at the apex of the tube, green (Stancik 2807), smooth; corolla lobes ovate, 10–12 × 9–11 mm, obtuse to rounded. Stamens 24–30 mm long; filaments 20–24 mm long, filiform, flattened; anthers elliptic to oblong, 4–6 × 2–3 mm, sagittate, versatile; pollen *Glabra* type. Pistil 40–42 mm long; ovary 8–10 × 2–4 mm; style 29–30 × 0.75–1.00 mm; stigma lobes spatulate, 2–3 × 1.5–2.0 mm. Capsules ovoid, 14–17 × 11–13 mm, smooth, tan, erect to nodding; style remnant 1–3 mm long. Seeds “rimmed type,” 0.8–0.9 × 0.4–0.5 mm, straw-colored, testa rugose-reticulate.

Macrocarpaea ypsilocaule belongs to sect. *Macrocarpaea* and occurs in the Northern Andes, on the Cordillera Central of Colombia (Fig. 5). It is related to *M. biremis* J. R. Grant of the Cordillera Occidental, the Chocó of Colombia, on the basis of few-flowered inflorescences, and flowers with large calyces. It differs in having leaves with shorter petioles (4–10 vs. 10–15 mm), bracts with shorter petioles (0–5 vs. 8–12 mm), bracteoles that are linear to lanceolate and 6–14 × 2–3 mm (vs. obovate to spatulate and 10–22 × 4–8 mm in *M. biremis*). Often the basal branches of the inflorescence of *Macrocarpaea ypsilocaule* only have a single flower. The entire length of the branch is not

measured as a petiole, since a pair of bracts subtends the real petiole on which a pair of bracteoles appears. Nevertheless, this species does have some of the longest petioles in the genus and is unique in having branches composed of very few flowers, typically only 1(–3).

Etymology: from the Greek *ypsilon* (or *upsilon*), the 20th letter of the Greek alphabet, often transliterated as the letter Y in English, and *caulis* (stem) for the unique “Y-shaped” bifurcated branching pattern of the inflorescence.

Paratypes: COLOMBIA. Huila: Vía a la quebrada Cascajal del Conudo, Parque Nacional Natural Cueva de Los Guácharos, 01° 35' N, 76° 00' W, fruto seco, 30 August 1993, *Barbosa 15567* (FMB [2 sheets]); Vía a la quebrada Cascajal del Conudo, Parque Nacional Natural Cueva de Los Guácharos, 01° 35' N, 76° 00' W, fruto verde, 30 August 1993, *Barbosa 15592* (FMB); De la Quebrada Negra al primer cerro vía a Cerro Punta, Parque Nacional Natural Cueva de Los Guácharos, 01° 35' N, 76° 00' W, arbusto, frutos marrón, 2 September 1993, *Barbosa 15625* (FMB). Putumayo: Municipio de Mocoa, Carretera entre Sibundoy y Mocoa, localidad el Mirador, 01° 04' 11" N, 76° 44' 41" W, 2000 m, 7 September 1998, arbusto, flor verde, *Mendoza et al. 6034* (COAH, FMB); Municipio Colon, Reserva Natural “La Rejoja,” forest “bosque altoandino muy húmedo” with *Weinmannia* sp., *Clusia* sp., *Cecropia* sp., Ericaceae sp. div., *Ilex pernervata*, etc., and patches of the páramo with *Espeletia schultesiana*, *Calamagrostis effusa*, etc., 2750 m, shrub 2 m, flowers green, 12 March 1999, *Stancik 2807* (COL, PSO [not seen]). ECUADOR. Carchi: Cerro Golondrinas area, access via Chamorro property above El Carmen, which is above Hualchán, flat hilltop before steep ridge crest approach to peak 1840, stunted upper montane forest, heavily festooned with moss, 00° 50' N, 78° 12' W, 2690 m, shrub, in fruit only, 24 July 1993, *Boyle & Hibbs 2333* (MO, QCNE).

ECUADOR

16. *Macrocarpaea berryi* J. R. Grant, *sp. nov.* TYPE: ECUADOR. Zamora-Chinchi: Elfin forest and semi-open areas along sandstone escarpment above and west of Tikimints, valley of Río Coangas (on topo maps and known locally as “Ijiach Naimt” in Shuar, meaning “Ridge of the Grubs,” 03° 15' 49" S, 078° 10' 12" W, 2000 m, shrub 1.5 m, flowers white, 20 March

2001, *P. Berry & D. Neill 7665* (Holotype: QCNE; Isotypes: MO [not seen], NY). Fig. 13E–G.

A *M. bubops* J. R. Grant & Struwe *cui affinis sed frutex 1–2 m (vs. arbor 1–10 m), ramis inflorescentiis brevioribus (8–19 vs. 14–36 cm), et calycibus brevioribus (7–9 × 6–8 vs. 7–11 × 7–10 mm) differt.*



FIGURE 13. A–D, *Macrocarpaea jactans*. A, leaves; B, inflorescence; C, flower; D, bud. E–G, *M. berryi*. E, habit of flowering stem; F, flower; G, fruit. A–C drawn from Alvarez 1726 (MO), D drawn from Harling & Andersson 21370 (GB), E–G drawn from Berry & Neill 7665 (NY).

Shrub, 1–2 m, glabrous, spiculate to scabrous (generally rough-textured throughout) on stems, petioles, leaves (especially veins on the lower surface), inflorescences, and pedicels. Stems terete, solid, 3–7 mm in diam. just below the inflorescence. Leaves elliptic, oval to ovate, petiolate, 5.5–13.0 cm long. Petioles 5–20 mm long, robust with strong open vagination 1/2 to nearly equaling the length of petiole; interpetiolar ridge 2–4 mm high. Blades 5–11 × 2.5–5.0 cm, entire, slightly revolute, dark above and conspicuously lighter below, with slightly impressed veins above, and slightly raised veins below, glabrous above, hispid to spiculate below, leathery-coriaceous; base equilateral to oblique, cuneate; apex acute, obtuse to rounded. Inflorescence a much-branched open thyrse, 9–20 cm long; branches 8–19 cm long; 5- to 15-flowered per branch. Bracts ovate, elliptic to obovate, petiolate, 7–83 × 3–22 mm; base equilateral to oblique, cuneate, to short-attenuate and decurrent on petiole; apex obtuse to rounded; bract petioles 1–12 mm long. Flowers pedicellate, erect to slightly spreading, but never nodding; pedicels 5–24 mm long; bracteoles ovate to obovate, 3–10 × 2–4 mm. Calyx campanulate, 7–9 × 6–8 mm, glabrous, rough to rugose, ecarinate; calyx lobes ovate, suborbicular to reniform, 2.0–3.5 × 3–4 mm, apex rounded to obtuse. Corolla funnel-shaped, 33–42 mm long, 12–22 mm wide at the apex of the tube, pale yellow (Neill *et al.* 13102), white (Berry & Neill 7640, Berry & Neill 7665), smooth; corolla lobes ovate, 7–10 × 5–9 mm, obtuse to rounded. Stamens 18–24 mm long; filaments 14–19 mm long, filiform, flattened; anthers linear to linear-elliptic, 4–5 × 1.5–2.0 mm, sagittate, versatile; pollen *Glabra* type. Pistil 31–33 mm long; ovary 6–8 × 1.5–2.0 mm; style 21.5–22.0 × 0.5–1.0 mm; stigma lobes spatulate to suborbicular, 3.0–3.5 × 1.5–2.0 mm. Capsules ovoid, 16–20 × 5–7 mm, smooth, faintly verrucose to pustulate, greenish to tan, erect, not nodding; style remnant 3–12 mm long. Seeds “perimetrically winged type,” 0.5–1.1 × 0.5–0.8 mm, straw-colored, testa reticulate, wings ribbed.

Macrocarpaea berryi belongs to sect. *Choriophylla* and occurs in the Central Andes, in the Huancabamba region of Ecuador (Fig. 5). It is related to *M. bubops* J. R. Grant & Struwe and *M. noctiluca* J. R. Grant & Struwe, also of the Huancabamba region of Ecuador, especially because of the two “dots” on either side of the

petiole of the base of the lower leaf side. It differs from *M. bubops* in being a shrub to 1–2 m (vs. a tree to 1–10 m) and having shorter branches of the inflorescence (8–19 vs. 14–36 cm) and smaller calyces (7–9 × 6–8 vs. 7–11 × 7–10 mm).

Etymology: named for Paul E. Berry (1952–), collector of the type and specialist of Euphorbiaceae and Onagraceae, University of Wisconsin–Madison (WIS).

Paratypes: ECUADOR. Morona-Santiago: Limon Indanza Cantón, Cordillera de Huaracayo, east of Cordillera del Cóndor and Río Coangos, Cerro Ijiach Naimt, flat-topped sandstone mountain, east of Shuar village of Tinkimints, low dense montane forest and shrubby vegetation on summit, 03° 15' 49" S, 78° 10' 13" W, 2000 m, shrub 2 m tall, corolla pale yellow, 21 March 2001, Neill *et al.* 13102 (QCNE). Zamora-Chinchiipe: Elfin forest and semi-open areas along sandstone escarpment above and west of Tikimints, valley of Río Coangos (on topo maps and known locally as “Ijiach Naimt” in Shuar, meaning “Ridge of the Grubs,” 03° 15' 49" S, 078° 10' 12" W, 2000 m, shrub 1.5 m, fruits green, 20 March 2001, Berry & Neill 7630 (MO, QCNE); Elfin forest and semi-open areas along sandstone escarpment above and west of Tikimints, valley of Río Coangos (on topo maps and known locally as “Ijiach Naimt” in Shuar, meaning “Ridge of the Grubs,” 03° 15' 49" S, 078° 10' 12" W, 2000 m, shrub 1.5 m, flowers white, 20 March 2001, Berry & Neill 7640 (MO, QCNE).

17. *Macrocarpaea jactans* J. R. Grant, *sp. nov.*
TYPE: ECUADOR. Napo: Parque Nacional Napo-Galeras, Cordillera de Galeras, Sendero hacia el Río Pucuno, bosque primario, Bosque Pluvial Pre-Montano, 00° 39' S, 077° 32' W, 1550–1650 m, hierba de 3 m, flores crema-verdosas, 20 March 1997, A. Alvarez, P. Cerda, & B. Shiguango 1726 (Holotype: MO; Isotype: QCNE). Fig. 13A–D.

A *M. ostentans* J. R. Grant *cui affinis sed calycibus brevioribus* (12–16 × 10–16 vs. 16–20 × 15–20 mm), *calycibus porcatibus inter lobis calycis, et lobis calycis rotundatis vel ellipticis cum apice rotundatis obtusis vel acutis differt.*

Shrub or small tree, 1.5–5.0 m, glabrous throughout. Stems terete to slightly quadrangular, solid to hollow, 10–15 mm in diam. just below the inflorescence. Leaves oval, elliptic to

ovate, sessile to short-petiolate, 20.5–35.5 cm long. Petioles 0–25 mm long, robust with strong open vagination 1/4–1/3 the length of petiole; interpetiolar ridge 5–8 mm high. Blades 20.5–33.5 × 12.0–16.5 cm, entire, not revolute, dark above and conspicuously lighter below, with slightly impressed veins above, and slightly raised veins below, papery thin, to thin coriaceous; base equilateral to attenuate and decurrent on the petiole; apex rounded, obtuse to acute. Inflorescence a much-branched open thyrse, 24–38+ cm long; branches 5–38 cm long; 2- to 5-flowered per branch. Bracts ovate to elliptic, sessile to short-petiolate, 45–96 × 32–50 mm; base equilateral to oblique, cuneate, rounded to short-attenuate; apex acute to obtuse; bract petioles 0–3 mm long. Flowers pedicellate, erect to spreading; pedicels 10–34 mm long; bracteoles inconspicuous and scabrous, linear to triangular, 1–13 × 0.5–6.0 mm. Calyx campanulate, 12–16 × 10–16 mm, glabrous, smooth, faintly rugose to pustulate, ecarinate, yet with pronounced ridges between calyx lobes from their bases and extending to the base of the calyx; calyx lobes rotund, ovate to elliptic, 5–9 × 7–10 mm, apex rounded, obtuse to acute. Corolla funnel-shaped, 45–55 mm long, 20–30 mm wide at the apex of the tube, crema-verdosa (*Alvarez et al. 1726*), yellow (*Tillett 673-278*, *Tirado & Gray 887*), smooth; corolla lobes ovate, 14–22 × 14–19 mm, obtuse to rounded. Stamens 18–30 mm long; filaments 13–25 mm long, filiform, flattened; anthers elliptic to oblong, 5–9 × 2–4 mm, sagittate, versatile; pollen *Corymbosa* type. Pistil 40–43 mm long; ovary 7–10 × 2–4 mm; style 33–37 × 1.0 mm; stigma lobes spatulate, 3–7 × 2–4 mm. Capsules ellipsoidal to oblong, 30–45 × 12–16 mm, shiny smooth to pustulate, tan to light brown, spreading to slightly nodding; style remnant 7–14 mm long. Seeds “winged type,” 1.2–2.2 × 0.3–0.5 mm, straw-colored, testa reticulate, wings ribbed.

Macrocarpaea jactans belongs to sect. *Magnolifoliae* and occurs in the Central Andes, in the Huancabamba region of Ecuador and Peru (Fig. 5). It is related to *M. ostentans* J. R. Grant, *M. robin-fosteri* J. R. Grant, and *M. tahuantinsuyuana* J. R. Grant of the Cordillera Central of Peru, and *M. cinchonifolia* (Gilg) Weaver of the Cordillera Oriental of Peru and Bolivia. The unique characters that particularly unite these species are *Corymbosa*-type pollen morphology and winged-type seeds. It differs

from *M. ostentans* in having a smaller calyx (12–16 × 10–16 vs. 16–20 × 15–20 mm, with pronounced ridges between calyx lobes from their bases and extending to the base of the calyx, and rotund ovate to elliptic calyx lobes that are rounded obtuse to acute at the apex.

Etymology: from the Latin *jactans*, boastful, or vainglorious, for its large showy inflorescences.

Paratypes: ECUADOR. Zamora-Chinchipe: Above Valladolid on road to Yangana, 2300m, montane rain forest, tree ca. 5 m, corolla yellow, 1 February 1985, *Harling & Andersson 21370* (GB); Cordillera del Cóndor, Destacamento military Cóndor Mirador, Ruta hacia el hito limítrofe Perú-Ecuador, 03°38'29" S, 78°23'14" W, 1770 m, arbolito de ca. m de alto, hojas muy reticuladas, botones florales verdes, frutos secos, 8 September 2003, *Rodríguez R. et al. 2669* (NY); Cordillera del Cóndor, Campamento Militar Pachicutza, camino al hito, Bosque muy húmedo Montano-Bajo, bosque primario, bosque con dosel de 25–30 m de altura, 04°07'17" S, 28°54'17" W, 1849 m, arbusto de 2–3 m, flores amarillas tubulares, 22 February 1994, *Tirado & Gray 887* (MO, NEU, QCNE, U). Peru. Amazonas: Bagua, 12 km E of La Peca (by trail), humid cloud forest, 1775 m, herb to 1.5 m, 4 July 1978, *Barbour 2635* (MO); Near O'Neill base camp, ca. 12 trail km E of La Peca in Serranía de Bagua, 1650–1800 m, lower montane rain forest, tree 4 m, buds light yellow, 13 June 1978, *Gentry et al. 23030* (NY); Prov. Bongará, Distr. Yambrasbamba, across R. Chiriaco from Yambrasbamba, and some 40 km N of Jumbilla, and along partially completed carretera past Cpto. Esperanza, around the ridge at K (3)57, Bosque Húmedo Montano Bajo, infrequent, wand-like with few short, crowded branches at top, and overgrown herb, taller and more branched in forest, left standing in cutover right-of-way of carretera, ca. K 60, stem straight erect ribbed green becoming light brown toward base, brittle, hollow internodes and mostly perforated nodes, some not, and internodes with water within, no latex, leaves fleshy, brittle, upper leaf surface lustrous dark olive green, lower surface matte medium olive green, flowers without fragrance, sepals medium green, petals fleshy open flaring-campanulate, with tips reflexed, yellow (Munsell 7.5 Y 9/8) without, within (2.5 Y 9/9), filaments greenish yellow, anthers with white pollen,

style and stigma green, stamens and style deflexed along lower side of corolla, 1860–2000 m, 2 March 1967, *Tillett 673-278* (US, USM); Cajamarca: San Ignacio, San José de Lourdes, camino al Cerro Picorana, bosque primario, 05°01'40"S, 78°54'30"W, 2100–2200 m, hierba 2 m, frutos verdes (en borde de camino), 15 August 1998, *Campos et al. 5519* (MO); San José de Lourdes, Selva Andina, base del Cerro Picorana, bosque primario, 1900–2010 m, arbusto 1.8 m, frutos verdes, 26 August 1999, *Díaz, C. et al. 10764* (MO [not seen], NEU); San Ignacio, San José de Lourdes, Santo Tomas, bosque primario, 04°55'S, 78°50'W, 2200 m, arbusto 2 m, frutos verdes, 15 June 1995, *Vasquez et al. 20219* (MO, NY).

18. *Macrocarpaea neillii* J. R. Grant, *sp. nov.* TYPE: ECUADOR. Zamora-Chinchi: Nangaritza Cantón, Cordillera de Nanguipa, Cerro Colorado, about 8 km SSE of Nambija, 20 km ESE of Zamora, montane forest and dense shrubby vegetation on exposed ridges, 04°07'29"S, 78°46'25"W, 2700 m, shrub to 2 m, in open areas, sub-páramo and páramo, inflorescences terminal on erect stems, plant with few branches, corolla greenish yellow, 18 February 2002, *D. Neill, W. Quizhpe, J. Manzanares, A. Hirtz, T. DeLinks, & C. Cole 13758* (Holotype: QCNE; Isotypes: AAU, LOJA, NY, MO [not seen], US [not seen]. Fig. 7C–D.

A *M. wurdackii* Weaver & J. R. Grant *cui affinis sed inflorescentiis brevioribus* (4–10 vs. 3–19 cm), *bracteis sessilibus* (vs. *breve-petiolatis*), *bracteolis brevioribus* (1–3 × 0.5–1.0 vs. 1–10 × 0.5–3.0 mm), *ok et calycibus grandioribus* (7–8 × 5–6 vs. 2–5 × 3–4 mm) *differt*.

Unbranched shrub, 2 m, glabrous throughout. Stems terete, solid, 3–4 mm in diam. just below the inflorescence. Leaves obovate varying to elliptic, petiolate to nearly sessile in upper leaves, 4–8 cm long. Petioles 0–10 mm long, slender with very slight vagination; interpetiolar ridge 1–4 mm high. Blades 4–7 × 2.0–3.5 cm, entire, slightly revolute, dark above and conspicuously lighter below, with slightly impressed veins above and slightly raised veins below, leathery-coriaceous; base equilateral to oblique, cuneate to attenuate and decurrent on the petiole; apex acute, obtuse to rounded. Inflorescence a few-branched open thyrse,

4–10 cm long; branches 3–4 cm long; 3- to 9-flowered per branch. Bracts obovate nearing on spatulate, sessile, 11–21 × 4–17 mm; base equilateral to oblique, cuneate; apex acute to obtuse; bract petioles sessile. Flowers pedicellate, erect to slightly spreading, but never nodding; pedicels 9–15 mm long; bracteoles inconspicuous and scabrous, to ovate to obovate, 1–3 × 0.5–1.0 mm. Calyx campanulate, 7–8 × 5–6 mm, glabrous, faintly rugose to pustulate, ecarinate; calyx lobes ovate to rotund, 2–3 × 2.5–3.0 mm, apex rounded to obtuse. Corolla funnel-shaped, 21–27 mm long, 7–10 mm wide at the apex of the tube, greenish yellow (*Neill et al. 13758*), smooth; corolla lobes ovate, 5–6 × 4–5 mm, obtuse to rounded. Stamens 13.0–15.5 mm long; filaments 10–12 mm long, filiform, flattened; anthers elliptic to oblong, 3.0–3.5 × 1.5–2.0 mm, sagittate, versatile; pollen *Glabra* type. Pistil 22–29 mm long; ovary 5–6 × 2.0–2.5 mm; style 15.0–20.5 × 0.5 mm; stigma lobes spatulate, 2.0–2.5 × 1.0–1.5 mm. Capsules and seeds unknown.

Macrocarpaea neillii belongs to sect. *Choriophylla* and occurs in the Central Andes, in the Huancabamba region of Ecuador (Fig. 5). It is related to *M. wurdackii* Weaver & J. R. Grant and *M. stenophylla* Gilg, both of the Huancabamba region of Peru. It differs from *M. wurdackii* in having a shorter inflorescence (4–10 vs. 3–19 cm), sessile (vs. short-petiolate) bracts, smaller bracteoles (1–3 × 0.5–1.0 vs. 1–10 × 0.5–3.0 mm), and larger calyces (7–8 × 5–6 vs. 2–5 × 3–4 mm).

Etymology: named for David A. Neill (1953–), collector of the type, specialist of the flora of Ecuador, and curator at the Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador (QCNE).

19. *Macrocarpaea voluptuosa* J. R. Grant, *sp. nov.* TYPE: ECUADOR. Carchi: Cresta del Cerro Golondrinas Hembra, bosque húmedo montaña bajo, vegetación arbustiva en la cresta de la montaña, 00°51'N, 078°08'W, 3000 m, arbusto de 1–2 m, flores vistosas amarillas, 21 August 1994, *W. Palacios 12515* (Holotype: MO; Isotypes: QCNE, U). Fig. 7I–J.

A *M. pachyphylla* Gilg *cui affinis sed caule, petiolis, foliis, inflorescentiis, bracteis et calycibus breve-spiculatis vel hispidis* (vs. *longe-hispidis*), *et trichomatibus sparsis et molto brevioribus differt*.

Shrub, 1–3 m, hyaline hispid to spiculate with short simple hairs on stems, petioles, leaves, inflorescences, bracts, and calyces. Stems terete to slightly quadrangular, solid to hollow, 9–15 mm in diam. just below the inflorescence. Leaves ovate to subdeltoid, petiolate, 9.5.0–16.5(–25) cm long. Petioles 5–10 mm long, robust with strong open vagination 1/2 the length of petiole; interpetiolar ridge 2–3 mm high. Blades 9.0–17.5 × 9.5–11.0 cm, entire, not revolute, dark green, with slightly impressed veins above and slightly raised veins below, hyaline hispid to spiculate on veins on lower surface, papery thin, to thin coriaceous; base equilateral to oblique, cuneate to rounded; apex acute, obtuse to rounded. Inflorescence a much-branched open thyrses, 36+ cm long; branches 6–36 cm long; 3- to 15-flowered per branch. Bracts ovate, elliptic, to lanceolate, petiolate, 16–78 × 8–52 mm; base equilateral to oblique, cuneate; apex acute to acuminate; bract petioles 1–6 mm long. Flowers pedicellate, erect to spreading; pedicels 5–21 mm long; bracteoles ovate, lanceolate to oblanceolate, 6–16 × 2–8 mm. Calyx campanulate, 9–13 × 8–10 mm, glabrous, smooth, green (Boyle *et al.* 3394), ecarinate; calyx lobes ovate, suborbicular to reniform, 2–3 × 3–5 mm, apex rounded to obtuse. Corolla funnel-shaped, 41–55 mm long, 18–26 mm wide at the apex of the tube, white (Boyle *et al.* 3394), yellow (Palacios & Clark 12515), smooth; corolla lobes ovate to elliptic, 9–17 × 9–14 mm, obtuse to rounded. Stamens 30–35 mm long; filaments 24–28 mm long, filiform, flattened; anthers linear to linear-elliptic, 6–7 × 2–3 mm, sagittate,

versatile; pollen *Glabra* type. Pistil 40–51 mm long; ovary 8–9 × 2–4 mm; style 36–38 × 1.0–1.5 mm; stigma lobes spatulate, 3–4 × 1.5–2.0 mm. Capsules and seeds unknown.

Macrocarpaea voluptuosa belongs to sect. *Macrocarpaea* and occurs in the Northern Andes, on the Cordillera Occidental, the Chocó of Ecuador (Fig. 5). It is related to *M. duquei* Gilg-Ben. and *M. callejasii* J. R. Grant of the Cordillera Occidental Colombia, and *M. densiflora* (Benth.) Ewan and *M. pachyphylla* Gilg of the Cordillera Central Colombia. It differs from *M. pachyphylla* in being short-spiculate to hispid on stems, petioles, leaves, inflorescences, bracts, and calyces vs. long-hispid (i.e., the hairs of *M. voluptuosa* are much shorter and less densely arranged than in *M. pachyphylla*). Likewise, where the distinct leaves of *M. pachyphylla* have strongly raised veins below and strongly impressed veins above, giving the leaves a quilted appearance, the leaves of *M. voluptuosa* have only slightly raised veins below and slightly impressed veins above, like most species in the genus.

Etymology: from the Latin *voluptuosus*, pleasant or delightful, for its large showy inflorescences.

Paratypes: ECUADOR. Carchi: Cerro Golondrinas, on crest of N ridge, just below peak, low elfin forest–páramo ecotone scrub, 00°51'15"N, 78°08'21"W, 3000–3060 m, robust herb to 3 m, basal leaves much larger, to 25 cm long, calyx green, corolla and stamens white, stigma and style green, flowers smell like inner pulp of pumpkin, 24 July 1994, Boyle *et al.* 3394 (MO, QCNE, U).

PERU

20. *Macrocarpaea chthonotropa* J. R. Grant, *sp. nov.* TYPE: PERU. San Martín: Huallaga, Saposá, alrededores de Monumentos Históricos de Buenos Aires (Zarumilla), 1440 m, 11 August 2000, V. Quipuscoa, S. Leiva, Y. Díaz, & M. Strarup 2044 (Holotype: F, Isotype: HUT). Fig. 14F–H.

A *M. dillonii* J. R. Grant *cui affinis sed frutex 2–3 m (vs. arbor vel frutex 3–9 m), trichomatibus longioribus (appime super calycibus), bracteis grandioribus (10–140 × 8–76 vs. 9–32 × 1–16 mm), calycibus grandioribus (9–13 × 8–10 vs. 7–9 × 6–8 mm, lobis calycis grandioribus (3–6 × 5–7 vs. 3–4 × 4–5 mm),*

capsulis nutantibus longioribus (35–45 vs. 33–37 mm), et seminibus parvis differt.

Tree or shrub, 3–9 m, glabrous throughout except petioles, bracteoles, and calyces, which are hyaline hispid to spiculate with short simple hairs. Stems terete to slightly quadrangular above, hollow, 8–13 mm in diam. just below the inflorescence. Leaves broadly ovate, petiolate, (21.0–)26.5–39.0 cm long. Petioles 25–50 mm long, robust with strong open vagination 1/4–1/3 the length of petiole; interpetiolar ridge 2–4 mm high. Blades (17.5–)24.0–34.0 × (9–)13–20 cm, entire, not revolute, dark above and conspicuously lighter below, with slightly

impressed veins above and slightly raised veins below, glabrous above and below, papery thin; base equilateral to oblique, cuneate to attenuate and decurrent on the petiole; apex acute to acuminate. Inflorescence a much-branched open thyrse, 28–53+ cm long; branches 12–53 cm long; 3- to 12-flowered per branch. Bracts ovate, lanceolate to obovate, petiolate, 10–140 × 8–76 mm; base equilateral to oblique, cuneate, to short-attenuate and decurrent on the petiole; apex acuminate to acute; bract petioles 2–11 mm long. Flowers pedicellate, erect to nodding; pedicels 17–37 mm long; bracteoles inconspicuous and scabrous, linear, triangular to ovate, 2–10 × 0.5–1.0 mm. Calyx campanulate, 9–13 × 8–10 mm, hyaline hispid to spiculate with short simple hairs, ecarinate; calyx lobes ovate to reniform, 3–6 × 5–7 mm, apex rounded to obtuse. Corolla, stamens, and pistil unknown. Capsules linear-long to ellipsoid, 35–45 × 7–9 mm, smooth to faintly ribbed, greenish brown, tan to light brown, erect to slightly nodding; style remnant 5–9 mm long. Seeds “perimetrically winged type,” 0.6–1.1 × 0.5–1.0 mm, straw-colored, testa reticulate, wings ribbed.

Macrocarpaea chthonotropa belongs to sect. *Choriophylla* and occurs in the Central Andes, in the Huancabamba region of Peru (Fig. 5). It is related to *M. dillonii* J. R. Grant, *M. gracilis* Weaver & J. R. Grant, *M. quechua* J. R. Grant, and *M. xerantifolva* J. R. Grant, all also of the Huancabamba region of Peru. It differs from *M. dillonii* in being a shrub to 2–3 m (vs. tree or shrub 3–9 m), having longer hairs especially on its calyces, larger bracts (10–140 × 8–76 vs. 9–32 × 1–16 mm), larger calyces (9–13 × 8–10 vs. 7–9 × 6–8 mm), larger calyx lobes (3–6 × 5–7 vs. 3–4 × 4–5 mm), fruits that nod in maturity, longer fruits (35–45 vs. 33–37 mm), and smaller seeds.

Etymology: from the Greek *chthonos*, earth, and *tropus*, turn, for the capsules that are nodding to pendent in fruit.

Paratypes: PERU. Amazonas: Luya, Camporredondo, Tullany, Pajaro Tigre, 2200 m, 4 December 1996, *Campos & Campos 3103* (MO [not seen], NEU, U); Luya, Camporredondo, Localidad Condorpuñuna–Las Aguas, 1800–1950 m, 28 March 1997, *Campos et al. 3685* (MO [not seen], NEU, U [2 sheets]); Mendoza, 1600 m, 29 July 1963, *Woytkowski 8071* (GH, MO, US).

21. *Macrocarpaea gran-pajatena* J. R. Grant, *sp. nov.* TYPE: PERU. San Martín: Prov. Mariscal Cáceres, trail between La Playa Camp and Papayas camp, Río Abiseo National Park, tropical wet forest, 7° S, 77° W, 2650–2750 m, tree 5 m, fruits green, 25 July 1987, *K. Young & B. León 4977* (Holotype: U; Isotype: HUT). Fig. 14I–K.

A *M. fortisiana* J. R. Grant *cui affinis sed bracteolis brevioribus* (2–6 × 1–2 vs. 2–13 × 0.75–5.0 mm), *calycibus brevioribus* (8–11 × 8–10 vs. 14–19 × 13–18 mm), *et lobis calycis ovatis vel reniformibus* (vs. *rotundatis vel ovatis*) 2–3 × 4–6 mm (vs. 6–12 × 6–10 mm) *differt*.

Tree, 2–5 m, glabrous throughout. Stems terete to slightly quadrangular above, hollow to solid, 7–9 mm in diam. just below the inflorescence. Leaves ovate to elliptic, petiolate, 20–29 cm long. Petioles 25–40 mm long, robust with strong open vagination 1/4–1/3 the length of petiole; interpetiolar ridge 2–4 mm high. Blades 17.5–25 × 11–14 cm, entire, not revolute, with slightly impressed veins above and slightly raised veins below, glabrous above and below, papery thin; base equilateral to oblique, cuneate, rounded to short-attenuate; apex acute to acuminate. Inflorescence a much-branched open thyrse, 31+ cm, the total inflorescence unknown as has been cut into various segments for separate herbarium sheets; branches 15–28 cm long; 5- to 9-flowered per branch. Bracts unknown. Flowers pedicellate, erect to slightly spreading; pedicels 12–28 mm long; bracteoles inconspicuous and scabrous, linear to triangular, 2–6 × 1–2 mm. Calyx campanulate, 8–11 × 8–10 mm, glabrous, smooth, faintly rugose to pustulate, ecarinate; calyx lobes ovate to reniform, 2–3 × 4–6 mm, apex rounded to obtuse. Corolla, stamens, and pistil unknown. Capsules ellipsoidal to ovoid, 30–35 × 6–10 mm, smooth to faintly rugose, tan to light brown, erect to slightly spreading; style remnant 3–7 mm long. Seeds “winged type,” 0.8–1.3 × 0.5–1.1 mm, straw-colored, testa reticulate, wings ribbed.

Macrocarpaea gran-pajatena belongs to sect. *Magnolifoliae* and occurs in the Central Andes, in the Huancabamba region of Peru (Fig. 5). It is related to *M. pachystyla* Gilg of the Cordillera Central of Peru, and *M. fortisiana* J. R. Grant of the Cordillera Oriental of Peru. It differs from *M. fortisiana* in having shorter bracteoles (2–6 × 1–2 vs. 2–13 × 0.75–5.0 mm) and shorter calyces (8–11 × 8–10

vs. 14–19 × 13–18 mm) with calyx lobes that are ovate to reniform (vs. rotund to ovate) and 2–3 × 4–6 mm (vs. 6–12 × 6–10 mm). There is a slight gradient in the seed type of *M. granpajatena*, with winged-type and some perimetrically winged-type seeds found in the same capsule. This may indicate the continued evolution of seed characters in *Macrocarpaea*.

Etymology: named after the pre-Columbian fortress Gran Pajatén, situated within the distribution of this species.

Paratypes: PERU. San Martín: Prov. Mariscal Cáceres, Parque Nacional Río Abiseo, arbolillo estéril, raro en al sotobosque, 5 July 1988, *León & Young 2075* (HUT); Prov. Mariscal Cáceres, Río Abiseo National Park, trail between Las Papayas and La Playa Camps, montane rain forest, 7° S, 77° W, 2600 m, 3 m tree, green fruit, 27 July 1985, *Young 1340* (HUT); Prov. Mariscal Cáceres, approx. 7° S, 77° W, hill past Las Palmas, 2–10 m tall vegetation on ridge top, 2650–2750 m, shrub 2 m, 16 August 1986, *Young 4024* (HUT).

22. *Macrocarpaea quechua* J. R. Grant, *sp. nov.* TYPE: PERU. San Martín: Prov. Lamas, Alonso de Alvarado, Cerro Blanco, carretera a Moyobamba, al borde de la quebrada, en bosque alto, terreno húmedo, 900–1000 m, arbusto de 1–2 m, frutos verde amarillenta, sépalos verde amarillenta, las hojas son brillosas de color verde intenso, en el envés con nervaduras prominentes, 14 May 1973, *J. Schunke-Vigo 6280* (Holotype: NY; Isotypes: GH [2 sheets], MG, U). Fig. 14A–E.

A. M. dillonii J. R. Grant *cui affinis sed foliis late-ovatis vel ellipticis vel late-lanceolatis (vs. ovatis vel ovate-ellipticis), basi foliis rotundata vel truncata vel attenuatis (vs. cuneatis et attenuatis), calycibus glabris, et capsulis molto brevioribus (17–25 vs. 33–37 mm long) differt.*

Herb to shrub, 0.5–3.0 m, glabrous throughout except along the veins of lower leaf surfaces that are spiculate. Stems terete, hollow, 4–9 mm in diam. just below the inflorescence. Leaves broadly ovate to elliptic to broadly lanceolate, petiolate, (9–)24–40 cm long. Petioles (5–)30–70 mm long, robust with strong open vagination 1/4–1/3 the length of petiole; interpetiolar ridge 1–3 mm high. Blades (8.5–)21.0–33.0 × (5–)11–19 cm, entire, not revolute, dark green, with slightly impressed veins above, and raised veins below,

glabrous to spiculate on veins on lower surface, papery thin; base equilateral to oblique, rounded to nearly truncate to slightly attenuate and decurrent on the petiole; apex acuminate. Inflorescence a much-branched open thyrses, 8–35 cm long; branches 5–30 cm long; 5- to 9-flowered per branch. Bracts lanceolate, sessile to petiolate, 12–55 × 5–22 mm; base equilateral to oblique, cuneate, rounded to short-attenuate; apex acuminate; bract petioles 0–5 mm long. Flowers pedicellate, erect to slightly spreading; pedicels 9–28 mm long; bracteoles lanceolate to linear, 4–16 × 0.5–5.0 mm. Calyx campanulate, 7–9 × 8–10 mm, glabrous, smooth, ecarinate; calyx lobes rotund to ovate, 3–7 × 4–6 mm, apex rounded, obtuse to acute. Corolla, stamens, and pistil unknown. Capsules linear-long to ellipsoid, 17–25 × 6–9 mm, smooth to faintly ribbed, straw-colored to dark brown, erect to slightly spreading; style remnant 2–7 mm long. Seeds “perimetrically winged type,” 0.6–1.2 × 0.6–0.9 mm, straw-colored to bicolored (testa brown, wings straw-colored), testa reticulate, wings ribbed.

Macrocarpaea quechua belongs to sect. *Choriophylla* and occurs in the Central Andes, in the Huancabamba region of Peru (Fig. 5). It is related to *M. chthonotropa* J. R. Grant, *M. dillonii* J. R. Grant, and *M. xerantifulva* J. R. Grant, all also of the Huancabamba region of Peru. It differs from *M. dillonii* in having broadly ovate to elliptic to broadly lanceolate leaves (vs. ovate to ovate-elliptic), with leaf bases that are rounded to nearly truncate to slightly attenuate and decurrent on the petiole (vs. cuneate to attenuate and decurrent on the petiole), glabrous calyces, and much shorter fruits (17–25 vs. 33–37 mm long).

Etymology: from the name of the language of the descendants of the Inca, Quichua. The epithet is based on a word used in apposition, and therefore to be maintained according to Article 23.1 of the ICBN (Greuter et al., 2000).

Paratypes: PERU. San Martín: Serranía NE of Tarapoto on road to Yurimaguas, scrubby forest on sandy soil, ca. 16 km NE of Tarapoto, 6°30'S, 76°25'W, 800 m, herb 0.5 m, fruits green, 19 July 1982, *Gentry et al. 37783* (MO, NY, USM); Tarapoto-Yurimaguas, 1100 m, 12 July 1981, *Halton & Besse 40* (SEL); Ríoja, 100 km from Ríoja on road to Pomacocha (Florida), km 384 of carretera marginal, 5°45'S, 77°35'W, 1900 m, shrub ca. 3 m tall, leaves and



FIGURE 14. A–E, *Macrocarpaea quechua*. A, habit of flowering stem; B, bud; C, habit of fruiting stem; D, fruit; E, leaf. F–H, *M. chthonotropa*. F, habit of fruiting stem; G, fruit; H, leaf. I–K, *M. gran-pajatena*. I, habit of fruiting stem; J, fruits; K, leaves. A–B drawn from Stein & Todzia 218 (USM), C–D drawn from Schunke 6280 (NY), E drawn from Gentry et al. 37783 (USM), F–G drawn from Quipuscoa et al. 2044 (F), H drawn from Campos et al. 3685 (NEU), I–J drawn from Young 1340 (HUT), K drawn from Young 4977 (U).

inflorescence clustered at tip, on forest edge, buds greenish, whorled, 16 February 1985, *Stein & Todzia 2187* (NY, U, USM).

23. *Macrocarpaea xerantifulva* J. R. Grant, *sp. nov.* TYPE: PERU. Cajamarca: San Ignacio, La Coipa, vista Florida-La Laguna, bosque primario, 05°26'00"S, 78°56'30"W, 2000–2100 m, arbusto 3 m, frutos verdes, 11 June 1997, *J. Campos & Z. García 3960* (Holotype: MO; Isotype: U). Fig. 6C–G.

A. M. dillonii J. R. Grant *cui affinis sed bracteis longioribus* (17–62 × 8–32 vs. 9–32 × 1–16 mm), *et calycibus glabris vel hispidis differt.*

Shrub or small tree, 1.5–3.0 m, glabrous throughout. Stems terete to slightly quadrangular, hollow, 5–8 mm in diam. just below the inflorescence. Leaves ovate to ovate-elliptic, petiolate, 7.5–32.0 cm long. Petioles 5–40 mm long, robust with strong open vagination 1/2 the length of petiole; interpetiolar ridge 1–4 mm high. Blades 7–28 × 5–16 cm, entire, not revolute, green, with slightly impressed veins above and slightly raised veins below, glabrous above and below, papery thin; base equilateral to attenuate and decurrent on the petiole; apex acuminate to apiculate. Inflorescence a much-branched open thyrses, 18–31+ cm long; branches 11–31 cm long; 5- to 15-flowered per branch. Bracts ovate to elliptic, sessile to short-petiolate, 17–62 × 8–32 mm; base equilateral to oblique, cuneate to rounded; apex acuminate; bract petioles 0–5 mm long. Flowers pedicellate, erect; pedicels 13–26 mm long; bracteoles inconspicuous and scabrous, triangular, linear to ovate, 0.5–12.0 × 0.5–3.0 mm. Calyx campanulate, 5–9 × 5–10 mm, typically glabrous to hispid (*Sánchez Vega 73-80*), ecarinate; calyx lobes ovate to reniform, 2.5–3.5 × 3–4 mm, apex rounded to obtuse. Corolla funnel-shaped, 23–31 mm long, 15–20 mm wide at the apex of the tube, green/yellow (*Dostert 98/114*), greenish yellow (*Sánchez Vega 73-80*), greenish (*Friedberg 696*), smooth; corolla lobes ovate,

6–9 × 7–9 mm, obtuse to rounded. Stamens 12–20 mm long; filaments 9–15 mm long, filaments filiform/flattened; anthers ovate-elliptic, 4–5 × 2.00–2.25 mm, sagittate, versatile; pollen *Glabra* type. Pistil 20–27 mm long; ovary 4–8 × 2–3 mm; style 14.0–16.5 × 1.0 mm; stigma lobes spatulate, 2.0–2.5 × 1.0–1.5 mm. Capsules ellipsoidal to fusiform, 25–35 × 5–7 mm, smooth varying to faintly striated, rugose or ribbed, greenish brown, tan to light brown, erect to slightly nodding; style remnant 2–7 mm long. Seeds “perimetrically winged type,” 0.8–1.0 × 0.4–1.0 mm, bicolored, testa tannish, wings straw-colored, testa reticulate, wings ribbed.

Macrocarpaea xerantifulva belongs to sect. *Choriophylla* and occurs in the Central Andes, in the Huancabamba region of Peru (Fig. 5). It is related to *M. chthonotropa* J. R. Grant, *M. dillonii* J. R. Grant, and *M. quechua* J. R. Grant, all also of the Huancabamba region of Peru. It differs from *M. dillonii* in having larger bracts (17–62 × 8–32 vs. 9–32 × 1–16 mm), and glabrous to hispid calyces. Only two species are known from Piura Province Peru, *M. ericii* and *M. xerantifulva*.

Etymology: from the Greek *xeros*, dry, and the Latin *fulvus*, yellowish, for the stems and inflorescence that dry rather yellowish gold in color.

Paratypes: PERU. Cajamarca: Prov. Jaén, Colosay, above the village, between fields and forest remnants, 1800–2300 m, flower green/yellow, ca. 1.5 m, 7 March 1998, *Dostert 98/114* (MSB); Prov. Cutervo, Dist. San Andrés, km 1.5 nor-oriente de San Andrés, 2250 m, ladera boscosa, poco pedregosa, arbusto, hojas grandes, simples opuestas, decurrentes, inflorescencias racimos axilares, flores amarillo verdosas, 18 June 1980, *Sánchez Vega 73-80* (MO); Piura: Huancabamba, Cordillera de San José, 1700 m, hierba, flores verdosas, 23 September 1961, *Friedberg 696* (NY). Peru. Casapi, *Matthews 2097* (E, K, OXF).

LITERATURE CITED

- BOUMAN, F., L. COBB, N. DEVENTE, V. GOETHALS, P. J. M. MAAS, AND E. SMETS. 2002. The seeds of Gentianaceae. Pages 498–572 in L. STRUWE AND V. A. ALBERT, EDs., *Gentianaceae: Systematics and Natural History*. Cambridge University Press, Cambridge.
- EWAN, J. 1948. A revision of *Macrocarpaea*, a Neotropical genus of shrubby gentians. *Contr. U.S. Natl. Herb.* 29(5): 209–250.
- GILG, E. 1895. Gentianaceae. Pages 50–108 in A. ENGLER AND K. PRANTL, EDs., *Die Natürlichen Pflanzenfamilien*. Vol. 4(2). Verlag von Wilhelm Engelmann, Leipzig.
- GRANT, J. R. 2003. De *Macrocarpaea* Griseb. (ex *Gentianaceae*) speciebus novis II: Typification of the Ruiz & Pavon names. *Harvard Pap. Bot.* 7: 423–436.

- . 2004. De Macrocarpaeae Grisebach (ex Gentianaceis) speciebus novis V: Twenty-three new species largely from Peru, and typification of all species in the genus. *Harvard Pap. Bot.* 9: 11–49.
- GRANT, J. R., AND L. STRUWE. 2001. De Macrocarpaeae Grisebach (ex Gentianaceis) speciebus novis I: An introduction to the genus *Macrocarpaea* and three new species from Colombia, Ecuador, and Guyana. *Harvard Pap. Bot.* 5: 489–498.
- . 2003. De Macrocarpaeae Grisebach (ex Gentianaceis) speciebus novis III: Six new species of moon-gentians (*Macrocarpaea*, Gentianaceae: Helieae) from Parque Nacional Podocarpus, Ecuador. *Harvard Pap. Bot.* 8: 61–81.
- GRANT, J. R., AND R. E. WEAVER. 2003. De Macrocarpaeae Grisebach (ex Gentianaceis) speciebus novis IV: Twelve new species of *Macrocarpaea* (Gentianaceae: Helieae) from Central and South America, and the first report of the presence of a stipule in the family. *Harvard Pap. Bot.* 8: 83–109.
- GREUTER, W., ET AL. 2000. *International Code of Botanical Nomenclature*. (Saint Louis Code) Adopted by the Sixteenth International Botanical Congress, St. Louis, Missouri, July–August 1999. *Regnum Veg.* 138. Koeltz Scientific Books, Königstein, Germany.
- MAGUIRE, B., AND B. M. BOOM. 1989. Gentianaceae. Part 3. In B. MAGUIRE AND COLL., *The Botany of the Guayana Highland*. Part 13. *Mem. New York Bot. Gard.* 51: 2–56.
- NILSSON, S. 1968. Pollen morphology in the genus *Macrocarpaea* (Gentianaceae) and its taxonomical significance. *Svensk Bot. Tidskr.* 62: 338–364.
- . 2002. Gentianaceae: A review of palynology. Pages 377–497 in L. STRUWE AND V. A. ALBERT, EDS., *Gentianaceae: Systematics and Natural History*. Cambridge University Press, Cambridge.
- WEAVER, R. E. 1974. The reduction of *Rusbyanthus* and the tribe *Rusbyanthae* (Gentianaceae). *J. Arnold Arb.* 55: 300–302.