Systematics, Biogeography, and Natural History of the Neotropical Moon-gentians (*Macrocarpaea*: Gentianaceae)

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To Mom and Dad, the best parents we kids could ever have.

ABSTRACT

The genus *Macrocarpaea* is comprised of rainforest perennial herbs, epiphytes, treelets, robust rainforest trees to 10 m, and upper páramo shrubs. It occurs in mountainous regions of the neotropics: southeastern Brazil, the Greater Antilles of the Caribbean, Pantepui of the Guayana Shield, Southern Mesoamerica, and the Andes. *Macrocarpaea* is the largest genus in the gentian tribe Helieae, has a high rate of endemic species, and exhibits a wide range of morphological variation. The flowers are generally large (2.0-7.5 cm long); funnelform, white, cream, yellow to light green in color; night blooming; bat- and moth-pollinated nocturnally; and hummingbird- and insect-pollinated diurnally. The genus was last monographed by Ewan (1948) who recognized 31 species based on 98 herbarium specimens from 9 herbaria. In the present study, over 2550 sheets of herbarium specimens from 94 herbaria have been examined. *Macrocarpaea* here is interpreted to comprise 98 species, 63 of which have been identified as new. A complete monographic revision of the genus for *Flora Neotropica* will be the final result of this study. In preparation, a series of papers have been initiated to clarify the nomenclature, typify species, and describe new taxa. Complimentary to the primary studies of gross morphology based on herbarium material, studies on seed anatomy, wood anatomy, palynology, cytology, and molecular data have been conducted or surveyed. The combined studies result in a comprehensive suite of characters from which systematic and taxonomic relationships have been elucidated. Five infrageneric sections are recognized: *Tabacifoliae*, *Caribbigenes*, *Macrocarpaea*, *Magnolifoliae*, and *Choriophylla*. These studies also have given insight into the biogeographic evolution of the genus and may provide broad implications for biogeographical patterns of plants in general in the neotropics.

RÉSUMÉ

Le genre *Macrocarpaea* (Gentianaceae) est composé d'herbes pérennes, d'épiphytes, d'arbustes, ou d'arbres de plus de 10 m dans les forêts ombrophiles, ou de buissons dans les paramos. *Macrocarpaea* est principalement présent dans les régions montagneuses des néotropiques, dans le sud-est du Brésil, les Grandes Antilles (Caraïbes), le plateau Guyanais (Pantepui), le sud Mésoaméricain et les Andes. Ce genre appartenant à la tribu des Helieae, est très variable morphologiquement et comprend un grand nombre d'espèces endémiques. Les fleurs, généralement grandes (2.0 -7.5 cm de long), tubulaires, de couleur blanche, crème, jaune ou vert-clair, s'ouvrent la nuit et sont pollinisées par les chauve-souris ou les phalènes la nuit, et par les colibris ou les insectes le jour. La dernière monographie du genre *Macrocarpaea* (Ewan , 1948) reconnaît 31 espèces sur la base de 98 planches d'herbiers provenant de 9 instituts. La présente révision, reposant sur un échantillonnage plus important (2550 spécimens empruntées à 94 herbiers), comprend 98 espèces, dont 63 nouvelles et encore inédites. Une monographie complète du genre dans « Flora Neotropica » constitue l'objectif ultime de ce travail. Une série de publications est également en cours, afin de clarifier la nomenclature, de typifier les taxons et de décrire les espèces nouvelles. En complément de l'approche morphologique basée principalement sur du matériel d'herbier, d'autres caractères reposant sur l'anatomie fine des graines ou du bois, la palynologie, la cytologie et la biologie moléculaire, ont été utilisés. La combinaison de ces différents résultats a permis une meilleure compréhension de la systématique et de la taxonomie du genre, avec l'établissement de 5 sections: *Tabacifoliae*, *Caribbigenes*, *Macrocarpaea*, *Magnolifoliae*, and *Choriophylla*. Cette étude a également mis en évidence certains mécanismes de l'évolution biogéographique du genre et pourrait, d'une manière plus générale, suggérer certains schémas de spéciation des plantes dans les néotropiques.

RESÚMEN

El género *Macrocarpaea* (Gentianaceae) está compuesto de hierbas perennes, de epífitas, arbustos, o árboles de más de 10 metros. Se encuentran presentes en los bosques ombrófilos, hasta en la vegetación de páramo. El género *Macrocarpaea* ocupa principalmente las regiones montañosas del neotrópico, desde el sureste del Brasil, las grandes Antillas (Caribe), las planicies de Guayana (Pantepui), el sur de Centroamérica, hasta los Andes. Este importante genero perteneciente a la tribu Helieae varía mucho morfológicamente y presenta un gran número de especies endémicas. Las flores generalmente grandes (2.0 - 7.5 cm de longitud), en forma de tubo, de color blanco, crema, amarillo o verde claro se abren en la noche para, entonces, ser polinizadas por murciélagos o mariposas nocturnas; en el día, la polinización la realizan colibríes o insectos. La última monografía sobre el género Macrocarpaea fue realizada por Ewan (1948), quien en esa época reconoció 31 especies en base a 98 testigos de herbarios de 9 instituciones. El presente estudio reposa sobre un muestreo más importante (2550 especímenes prestados por 94 herbarios), en el que revela 98 especies, de las cuales 63 inéditas. Una monografía completa del este género publicada en *Flora Neotropica* constituirá el logro de este trabajo. Una serie de publicaciones están, de igual forma, en proceso, con el fin de clarificar la nomenclatura y realizar la tipificación y descripción de nuevas especies. Como complemento del avance morfológico basado principalmente en material de herbario, otros caracteres anatómicos finos de las semillas o de la madera, la palinología, la citología y la biología molecular han sido tomados en cuenta. La combinación de estos marcadores ha permitido una mejor comprensión de la sistemática y taxonomía de este género, con el establecimiento de 5 secciones : *Tabacifoliae*, *Caribbigenes*, *Macrocarpaea*, *Magnolifoliae*, y *Choriophylla*. Este estudio ha esclarecido de igual manera la evolución biogeográfica del género, y de una forma más general ciertos esquemas de especiación de las plantas del neotrópico.

ZUSAMMENFASSUNG

Die Gattung *Macrocarpaea* (Gentianaceae) beinhaltet mehrjährige Kräuter, Epiphyten, Sträucher, Regenwaldbäume mit einer Höhe bis 10 m, sowie Büsche der oberen Paramo-Region. Das Verbreitungsgebiet umfasst Gebirgsregionen der Neotropis; das südliche Brasilien, die Grossen Antillen, der Guayana-Schild (Pantepui), das südliche Mittelamerika und die Anden. Es handelt sich um die grösste Gattung des Tribus Helieae; verbunden mit einem hohen Anteil an endemischen Arten und starker morphologischer Variation. Die Blüten sind in der Regel gross (2.0-7.5 cm lang), röhrenförmig, weiss, cremefarbig, gelb bis hellgrün gefärbt, nachtblühend und daher fledermaus- oder nachtfalterbestäubt, sowie kolibri- und insektenbestäubt bei Tagblüte. Die Gattung wurde letztmals von Ewan (1948) bearbeitet, welcher 31 Arten basierend auf 98 Herbariumbögen aus 9 Herbarien identifizierte. Für die vorliegende Arbeit wurden über 2550 Bögen aus 94 Herbarien untersucht. Demzufolge umfasst *Macrocarpaea* 98 Arten, von denen 63 neu identifiziert wurden. Eine vollständige monographische Revision der Gattung für die *Flora Neotropica* wird das Ziel der Arbeit sein. Gleichzeitig befindet sich eine Reihe von Publikationen in Bearbeitung, die sich mit der Nomenklatur, der Typifizierung, sowie der Beschreibung neuer Arten befassen. Ergänzend zur Studie morphologischer Kriterien basierend auf Herbarmaterial wurden die Samen- und Holzanatomie, palynologische, zytologische und molekularbiologische Merkmale untersucht. Kombiniert ermöglichen die unterschiedlichen Ansätze einen guten Einblick in die Systematik und Taxonomie der Gattung. So wurden fünf Sektionen beschrieben: *Tabacifoliae*, *Caribbigenes*, *Macrocarpaea*, *Magnolifoliae*, and *Choriophylla*. Diese Studie gibt einen Einblick in die biogeographische Evolution der Gattung, sowie in Artbildungs- und Verbreitungsmechanismen von Pflanzen aus der Neotropis.

RIASSUNTO

Il genere *Macrocarpaea* (Gentianaceae) è composto da perenni erbacee, epifite, arbusti del "paramo" superiore e da robusti alberi delle foreste pluviali alti più di 10 metri. *Macrocarpaea* è presente soprattutto nelle regioni montagnose neotropicali: sud-est del Brasile, le Grandi Antille (Caraibi), l'altopiano della Guyana (Pantepui), il sud mesoamericano e le Ande. Quest'importante genere è il più grande della tribù delle Helieae, possiede una morfologia molto variabile e comporta un gran numero di specie endemiche. I fiori, generalmente grandi (da 2.0 a 7.5 cm di lunghezza) e a forma d'imbuto, si aprono di notte. Il colore è generalmente bianco, crema, giallo o verde chiaro. Di notte, l'impollinazione è effettuata da pipistrelli o falene, mentre di giorno è l'opera di colibrì o insetti vari. L'ultima monografia di questo genere risale al 1948 ed è l'opera di Ewan, il quale riconobbe 31 specie basandosi su 98 campioni provenienti da 9 erbari. Il nostro studio, basandosi su un campionamento più vasto (2550 campioni provenienti da 94 erbari), ha identificato 98 specie, di cui 63 non identificate precedentemente. Una monografia completa del genere in *Flora Neotropica* costituirà il risultato finale di questa parte dello studio. Inoltre, una serie di pubblicazioni è attualmente in corso, al fine di chiarificare la nomenclatura e la descrizione delle specie inedite. In aggiunta alle analisi morfologiche, basate su materiale d'erbario, questo studio ha comportato analisi dettagliate dell'anatomia di semi e legno, analisi palinologiche e citologiche nonché di biologia molecolare. La combinazione di questi differenti marcatori a permesso di comprendere meglio la sistematica e la tassonomia del genere, e a portato ad una classificazione in 5 sezioni: *Tabacifoliae*, *Caribbigenes*, *Macrocarpaea*, *Magnolifoliae* e *Choriophylla*. Questo studio a inoltre fornito importanti indicazioni per la comprensione dell'evoluzione biogeografica del genere, i quali potrebbero servire da spunto per capire meglio la biogeografia generale delle piante neotropicali.

RESUMO

O gênero *Macrocarpaea* inclui ervas perenes da floresta tropical, epífitos, árvores pequenas, árvores de até 10 metros de altura da floresta tropical, ou arbustos dos páramos. Este gênero ocorre nas regiões montanhosas dos neotrópicos, sudeste do Brasil, Grandes Antilhas do Caribe, Pantepui na Guiana, Sul da Mesoamérica, e nos Andes. É o maior gênero da tribo Helieae, tem uma alta incidência de espécies endêmicas e exibe uma ampla gama de variações morfológicas. As flores são geralmente grandes (2.0-7.5 cm de comprimento) em forma de funil, de cores branca, creme, amarelo a verde claro, florescem à noite e são polinizadas por morcegos e mariposas à noite, por beija-flores e insetos durante o dia. Este gênero foi tratado na monografia de Ewan (1948) que reconheceu 31 espécies baseadas em 98 especímenes oriundos de 9 herbários. No presente estudo, mais de 2550 especímenes pertencentes a 94 herbários foram examinados. *Macrocarpaea* é aqui revisado e possui 98 espécies, das quais 63 são por enquanto inéditas. Uma revisão monográfica completa do gênero para « Flora Neotropica » é o objetivo final deste estudo. Duranto o processo, uma série de publicações foi iniciada para especificar a nomenclatura, tipificar os taxons, assim como descrever as espécies. Além dos estudos de macromorfologia baseados no material de herbário, aspectos de anatomia das sementes e da madeira, palinologia, citologia e biologia molecular foram abordados. Os resultados combinados fornecem uma seqüência completa de marcadores que contribuiram a elucidar os relacionamentos sistemáticos e taxinômicos. Cinco seções infragenéricas são reconhecidas: *Tabacifoliae*, *Caribbigenes*, *Macrocarpaea*, *Magnolifoliae*, e *Choriophylla*. Estes estudos também ajudaram a compreender a evolução biogeográfica do gênero e de maneira mais geral, poderiam sugerir implicações mais abrangentes para explicar os padrões biogeográficos das plantas nos neotrópicos.

RESUMÉ

Släktet *Macrocarpaea* består av perenna regnskogsörter, epifyter, småträd, robusta regnskogsträd upp till 10 meters höjd och páramo-buskar. *Macrocarpaea* uppträder i neotropiska bergsområden, sydöstra Brasilien, de större Antillerna i Karibien, Pantepui i Guyana, sydöstra Mellanamerika och i Anderna. Det är det största släktet inom gentianacé-tribusen Helieae, består av ett stort antal endemiska arter och visar upp en stor morfologisk variation. Blommorna är för det mesta stora (2.0-7.5 cm långa), tubulära, vita, gräddfärgade, eller gula till ljusgröna till färgen, nattblommande, fladdermus- och nattfjärilspollinerade nattetid och kolibri- och insektspollinerade dagtid. Släktet reviderades senast av Ewan (1948) som erkände 31 arter baserade på 98 herbarieark från 9 herbarier. I denna föreliggande studien, har mer än 2550 herbarieark från 94 herbarier studerats. *Macrocarpaea* tolkas härmed att bestå av 98 arter, av vilka 63 arter är nya för vetenskapen. En fullständig taxonomisk revision av släktet för Flora Neotropica kommer att bli slutresultatet av denna studie. Under hand har ett antal artiklar påbörjats för att reda ut nomenklaturen, typifiera arter och beskriva nya taxa. Som komplement till de omfattande morfologiska studierna som baseras på herbariematerial, har även studier på fröanatomi, vedanatomi, palynologi, cytologi och molekylärbiologi genomförts. Dessa kombinerade studier har lett till en övergripande svit av karaktärer från vilka systematiska och taxonomiska relationer har kunnat belysas. Fem sektioner inom släktet har kunnat identifieras: *Tabacifoliae*, *Caribbigenes*, *Macrocarpaea*, *Magnolifoliae* och *Choriophylla*. Dessa studier har också påvisat släktets biogeografiska evolution och bör kunna bidra allmänt till studier av biogeografiska mönster för neotropiska växter.

摘要

Macrocarpaea属包括雨林多年生草本，附生植物，小树，高到10米的大树，高原灌木。Macrocarpaea属出现在新热带区的山区，巴西东南部，加勒比海的大安替列斯群岛，中美洲南部和安第斯山脉。它是龙胆Helieae族中最大的一属，有高比例的特有种，并表现出较大的形态学变异。花通常较大，2.0到7.5cm长，漏斗型，白色，奶油色，黄色到浅绿色。晚上开花，蝙蝠和蛾是夜间的传粉者，，蜂鸟和昆虫是白天的传粉者。Ewan1948年写了本属的专著，他从9个蜡叶标本夹中98份样品中辨认了31个种。在本研究中，查阅了来自94个蜡叶标本夹中2550份样品。Macrocarpaea属包含98个种，其中63种被定义为新种。本研究将给新热带区植物志的本属部分i已较完整修正。正在准备中的一系列文章，将阐明系统命名法，典型种和描述新种。我们调查并鉴定了之前的基于蜡叶标本材料的总体形态学，种子解剖学，木材解剖学，孢粉学，细胞学和分子生物学工作。综合各种研究从而得出较为满意的结果，从中可给出系统学的和分类学的解释。五个i遗传下的组清晰辨出，Tabacifoliae,Caribbigenes,Macrocarpaea,Magnolifoliae,Choriophylla.这些研究也给本属的生物地理学进化一些指示，也给新热带区植物的生物地理模式提供了更多的暗示。

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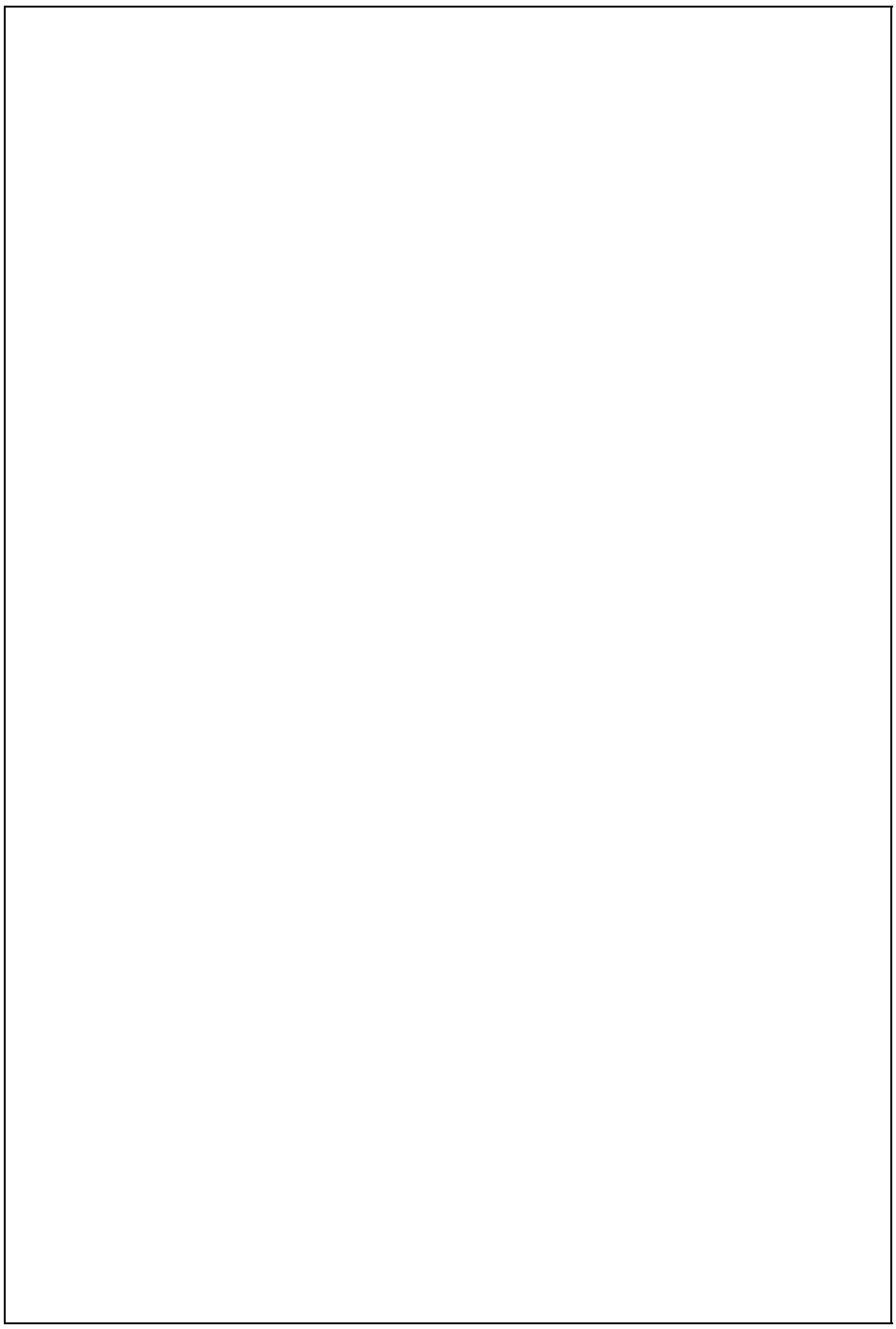

Jason R. Grant with *Macrocarpaea subsessilis*
on Cerro Toledo, Loja, Ecuador, 2001.

PREFACE

This thesis is based on the following published or in-press papers (numbers 1-7), or manuscripts that are in various stages of preparation (numbers 8-12).

1. Grant, J. R. and L. Struwe. 2000. Morphological evolution and neotropical biogeography in *Macrocarpaea* (Gentianaceae: Helieae). Amer. J. Bot. 87 (suppl.): 131.
2. _____ 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(2): 489-498.
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7. _____ *Macrocarpaea* (Gentianaceae) in Catálogo de las Plantas Vasculares de Bolivia. Submitted April 2003.
8. Carlquist, S. and J.R. Grant. Wood anatomy of *Macrocarpaea* (Gentianaceae: Helieae). Syst. Bot. To submit (October 2003)
9. Grant, J. R. De Macrocarpaeae Grisebach (ex Gentianaceis) speciebus novis V: Thirty-four new species of *Macrocarpaea* (Gentianaceae: Helieae) from Colombia, Ecuador, and Peru, and typification of all species in the genus. Harvard Pap. Bot. To submit (November 2003)
10. Grant, J. R. and L. Struwe. Phylogeny of *Macrocarpaea* (Gentianaceae: Helieae): implications for neotropical biogeography. Pl. Syst. Evol. To submit (December 2003)
11. _____ De Macrocarpaeae Grisebach (ex Gentianaceis) speciebus novis V: Nine new species of *Macrocarpaea* (Gentianaceae: Helieae) from Colombia, Ecuador, and Peru. Harvard Pap. Bot. To submit (January 2004).
12. _____ Flora Neotropica Monograph. *Macrocarpaea* (Gentianaceae: Helieae). New York Botanical Garden To submit (summer 2004)

Presentations, Seminars and Posters:

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2001 _____ Morphological evolution and neotropical biogeography in *Macrocarpaea* (Gentianaceae: Helieae). Seminar series, Universität Zurich, Switzerland.

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B. 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(2): 489-498

C. Thiv, M. and J.R. Grant. 2002. *Macrocarpaea* (Gentianaceae) in Flora de la República de Cuba Fasc. 6(1): 23-26

D. Grant, J.R. 2003. De Macrocarpaeae Grisebach (ex Gentianaceis) speciebus novis II: Typification of the Ruiz & Pavon Names. Harvard Pap. Bot 7(2): 423-436

E. Grant, J. R. and L. Struwe. 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(1): 61-81

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H. Grant, J.R. De Macrocarpaeae Grisebach (ex Gentianaceis) speciebus novis V: Thirty-four new species of *Macrocarpaea* (Gentianaceae: Helieae) from Colombia, Ecuador, and Peru, and typification of all species in the genus. Harvard Pap. Bot. To submit October 2003

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INTRODUCTION

Macrocarpaea is good candidate to study for several important reasons. Foremost, the taxonomy of the genus has been neglected since the last revision in 1948. In functional terms, since no significant studies have been made for more than 50 years, a large collection of unidentified herbarium specimens have accumulated. This material has come from diverse regions where new species are often found. Therefore, it was a foregone conclusion that a number of new species were available to be described. Secondly, since *Macrocarpaea* is comprised of different life forms, many interesting morphological characters are available for study. Since the genus has such a wide array of morphological variation, it was thought that molecular variation would also exist on which phylogenetic studies could be based. Thirdly, since the genus occurs in all major mountainous regions of the Neotropics, perhaps this genus also could be used as a model for understanding biogeography and dispersal.

Therefore, all herbarium material of *Macrocarpaea* was requested for loan to Neuchâtel. In many cases, material could not be sent on loan, so a number of travels to herbaria all over the world were made to examine material. Basic morphological characters were studied from these specimens, and material for seed anatomy, palynology, and molecular systematic studies were removed. Fieldwork was initiated to collect fresh material for studies of cytology, wood anatomy, and DNA, in addition to the primary interest of amassing a large collection of newly collected herbarium material for morphological studies. Studies on the pollination biology and dispersal of *Macrocarpaea* were initiated to learn what are the vectors of pollination and mode of seed dispersal.

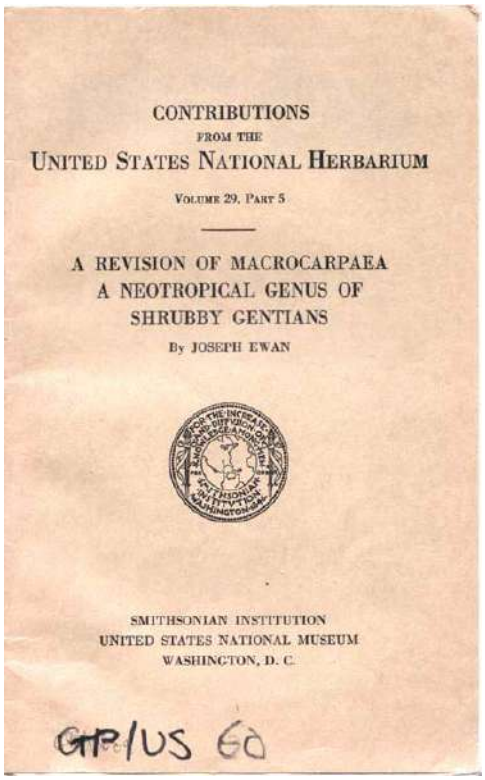
Due to the large number of new species, previously unrecognized biodiversity, and lack of basic scientific studies in *Macrocarpaea*, thorough understanding the genus remains a goal to be reached. New species are still being found and described, leaving in-depth studies such as interspecific relationships, hybridization, etc. for future planned study.

The studies conducted for this thesis present the building blocks on which a thorough understanding of the genus may be based. Traditional alpha-level taxonomy therefore has been the core to this research in order to describe species and provide names. Providing name that are accurate and precise are important for *herbaria* (many even send spontaneous gifts for identification), *botanists* (sending specimens and photographs), *geographers* needing plant names for their evaluation of vegetation types, and *molecular biologists* who may work in concert with the taxonomist.

2. HISTORICAL SURVEY

The Gentianaceae is a worldwide plant family belonging to the order Gentianales comprised of five families: Apocynaceae, Gelsemiaceae, Gentianaceae, Loganiaceae, and Rubiaceae (Struwe et al. 2002). A modern classification of the Gentianaceae was provided by Struwe et al. (2002) who recognized 87 genera and 1615–1688 species in six tribes: Chironieae, Exaceae, Gentianeae, Helieae, Potalieae, and Saccifolieae. *Macrocarpaea* belongs to tribe Helieae that is restricted to the Neotropics and comprises 22 genera and around 194 species (Struwe et al. 2002). *Macrocarpaea* is the most speciose genus in the Helieae (98 species as recognized here; 90 species noted in Struwe et al. (2002)), whereas the large majority of genera are monotypic or are known from less than ten species. In fact, *Macrocarpaea* alone contains more species than are in all the 21 remaining genera of the Helieae combined (194 total species Helieae, minus 90 species of *Macrocarpaea*, equals 94 remaining species in the Helieae [sensu Struwe et al. 2002]).

Macrocarpaea has had a rather brief taxonomic history. In the first major worldwide classification of the Gentianaceae, Grisebach in *Genera et Species Gentianearum* (Grisebach 1839: 173) described *Lisyanthus* sect. *Macrocarpaea* The next comprehensive treatment of the family was published by Gilg in *Die natürlichen Pflanzenfamilien* (Gilg 1895), and stood until that of Struwe et al. (2002). In this work, Gilg (1895: 94) elevated *Macrocarpaea* to the generic rank. Gilg recognized the subfamily Gentianoideae, tribe Gentianeae, subtribe Tachiinae, to comprise eight genera: *Eustoma*, *Hockinia*, *Lisianthus*, *Macrocarpaea*, *Tachia*, *Tachiadenus*, *Zonanthus*, and *Zygostigma*. While most of these genera have been moved to other groups, *Macrocarpaea*, *Tachia* and *Zonanthus* form with *Chorisepalum* the "*Macrocarpaea* clade" of the tribe Helieae (Struwe et al. 2002). Gilg (1895: 95) also described the new tribe Rusbyantheae for a new monotypic genus, *Rusbyanthus*, largely based on its unique warty pollen. However, Weaver (1974) transferred *Rusbyanthus* to *Macrocarpaea* effectively sinking the monotypic tribe Rusbyantheae.


CONTRIBUTIONS
FROM THE
UNITED STATES NATIONAL HERBARIUM
VOLUME 29, PART 5

A REVISION OF MACROCARPAEA
A NEOTROPICAL GENUS OF
SHRUBBY GENTIANS
By JOSEPH EWAN

SMITHSONIAN INSTITUTION
UNITED STATES NATIONAL MUSEUM
WASHINGTON, D. C.

GP/US 60

Fig. 1. Front cover of: A revision of *Macrocarpaea*, a neotropical genus of shrubby gentians (Ewan (1948).

The only revision ever made of *Macrocarpaea* was published by Ewan (1948) (Fig. 1). Ewan recognized 31 species based on 98 herbarium collections. However, his treatment is problematic. Ewan recognized a disparate assemblage of unrelated species within a relatively broad interpretation of the genus. The problems appear to stem from the rather limited number of specimens available to him. Yet, at the time he prepared his revision, the 98 specimens were undoubtedly seen as a large amount of material.

The herbarium material on which Grisebach and Gilg based their treatments came from separate plant expeditions by botanists of

different countries to different regions or countries of South America. Ewan's monograph was prepared just at the time of the major expanse of American plant collecting in South America. Therefore Ewan had at his disposal not only the older collections seen by Grisebach and Gilg, but some recently collected specimens of better quality and label information.

Some of the earliest plant collections of *Macrocarpaea* were made in Ecuador and Peru in the early 1800's during the search for treatments of malaria. *Macrocarpaea* was collected in southern Ecuador when Tafalla traveled to Loja in 1805 in search of material of *Cinchona* (Rubiaceae) from which quinine was extracted (Grant 2003). Coincidently, one of the major developments in the expansion of neotropical plant collecting was during and after the World War II when American botanists were sent to South America in search of high-quinine-yielding *Cinchona* species and other plants that could be used to treat malaria and other tropical diseases. These expeditions by Fosberg (Colombia), Little (Colombia), and Steyermark (Ecuador) brought a large number of collections back to American botanical institutions for study. *Cinchona* is similar morphologically to *Macrocarpaea*, and therefore many fruiting collections were possibly made of *Macrocarpaea* in err of *Cinchona*. In fact, the previously mentioned *Rusbyanthus cinchonifolius* (= *Macrocarpaea cinchonifolia*) was explicitly named for its leaves that resemble that of some species of *Cinchona*. Ewan cited many of these collections in his monograph.

The Neotropics had effectively been opened, and large-scale expeditions were initiated into the Andes and Guayana Shield in search of new plant species. Ewan was perhaps too early in the publication of his monograph. If he had waited a few years as the large number of plant collections were arriving at the major herbaria in the United States, e.g., U.S. National Herbarium of the Smithsonian Institution (US), the Missouri Botanical Garden (MO), the New York Botanical Garden (NY), the Field Museum of Natural History in Chicago (F), and the Gray Herbarium of Harvard University (GH), his treatment could perhaps have been more thorough. Ewan's monograph of *Macrocarpaea* is based on 98 collections from nine herbaria. The monograph was published in 1948, and the most recently collected specimens cited are from 1946. When these dates are compared to the number of herbarium collections of *Macrocarpaea* available from 1780 to the present, Ewan's monograph clearly appeared just as the major expansion in plant collecting in the Neotropics began (see Fig. 3).

Since Ewan (1948) to the beginning of the present monographic studies, 14 species have either been transferred to *Macrocarpaea* or described as new: *M. acuminata* Weaver (Weaver 1972), *M. affinis* Ewan (Ewan 1950), *M. angustifolia* J.S. Pringle (Pringle 2002), *M. autanae* Weaver (Weaver in Maguire 1981), *M. browallioides* (Ewan) Robyns & Nilsson (Robyns & Nilsson 1970), *M. cinchonifolia* (Gilg) Weaver (Weaver 1974), *M. harlingii* J.S. Pringle (Pringle 1995), *M. loranthoides* (Griseb.) Maas (Maas 1993), *M. marahuacae* Struwe & V. Albert (Struwe & Albert 1998), *M. neblinae* Maguire (Maguire 1981), *M. pauciflora* Alain (Alain 1955), *M. pinetorum* Alain (Alain 1955), *M. piresii* Maguire (Maguire 1981), and *M. rugosa* Steyerm. (Steyermark 1963). Additionally, the five species with pollen in tetrads were segregated by Maguire and Boom (1989) as a new genus *Rogersonanthus*: *M. arborea* (Britton) Ewan, *M. cerronis* Ewan, *M. quelchii* (N. E. Brown) Ewan, *M.*

salicifolia Ewan, and *M. tepuiensis* (Gleason) Steyerm. This resulted in the genus *Macrocarpaea* being defined as having pollen only in monads (Nilsson 1968, 1970).

Recent morphological studies on all specimens described or annotated as *Macrocarpaea* have revealed two additional problems. *Macrocarpaea guttifera* Ewan (Ewan 1948) was determined to actually be *Ravenia biramosa* Ducke of the Rutaceae (Grant & Struwe 2001). A specimen annotated as "*Macrocarpaea* sp." and discussed by Ewan (1950) is actually *Tabernaemontana crassa* Benth. of the Apocynaceae (Grant 2003).

Several works have addressed *Macrocarpaea* taxonomy in specific regional areas: Brazil (Reitz 1971), Costa Rica (Standley 1938; Weaver 1972), Ecuador (Pringle 1995), Panama (Sytsma 1987), Peru (MacBride 1959), and the Venezuelan Guayana (Maguire 1981; Maguire & Boom 1989; Struwe et al., 1999). However, no modern comprehensive treatment existed for the genus. Therefore, studies on the entire genus were initiated with the goal of publication of a full monograph for *Flora Neotropica*.

There is a tremendous need for alpha-level taxonomy and the identification of species. Botanists, ecologists, geographers, anatomists, etc, and especially molecular biologists rely on the names provided by plant taxonomists. It is in this spirit that this thesis has been conducted, to provide names for specimens of *Macrocarpaea*, and make the identifications available to other scientists.

2. SOURCES OF TAXONOMIC EVIDENCE

Studies in various fields may be employed to elucidate taxonomy and systematics. The subjects studied here include gross plant morphology (including leaf morphology, inflorescence architecture, and floral morphology), seed anatomy, wood anatomy, palynology, cytology, and molecular data. The studies are in various degrees of completion. Studies of plant morphology resulting in the identification and circumscription of species are the primary focus of this thesis, and the most advanced. Some analyses are far from complete, and data presented here are very preliminary (especially studies of molecular data and wood anatomy).

GROSS MORPHOLOGY

The monographic studies of *Macrocarpaea* presented here have relied upon herbarium material for study. The morphological characters seen on dried herbarium specimens provide the characters for the understanding of the genus. From the herbarium material, pollen, seeds, wood, and leaf material were removed and studied. Seeds have been studied by light microscopy, and project to be soon expanded to include study by SEM. The wood anatomical data has been gathered in collaboration with Sherwin Carlquist, Santa Barbara Botanical Garden, California. The palynological data is surveyed that of Nilsson who studied a broad range of species (1968; 2002). The cytological data are elaborated upon from those of Weaver (1972). Leaf material has been used for studies of DNA sequences in collaboration with Lena Struwe, Rutgers University-Cook College.

Many groups of plants, especially temperate groups, are well-known taxonomically. However, this is not so the case in most tropical groups, e.g., *Macrocarpaea*. The only serious attempt to understand the genus was made by Joseph Ewan more than 50 years ago (Ewan 1948). In his study of 98 specimens from nine herbaria (A, COL, F, GH, MO, NA, NY, PH, US), 31 species were recognized. At the time, this amount of material was likely seen as large and covering a substantial number of species. The Neotropics were still largely unknown then, yet have since been explored and combed for interesting plants. Inventories of many remote areas have led to the amassment of a large amount of unidentified material of *Macrocarpaea*. Since Ewan, only a few regional treatments of *Macrocarpaea* have been attempted. These studies have been based on the collections from rather restricted areas, and largely have had to use the nomenclature of Ewan (1948), e.g., *Flora of Ecuador* (Pringle 1995). Since Ewan to the present time, 14 species have been added to the genus, but no thorough monographic studies of the genus had been attempted.

Once the material was assembled and type specimens aligned to existing species concepts, many new species were apparent. In fact, I have often looked upon this as a giant 2550-piece puzzle where an unknown and seemingly varying number of puzzles were to be solved by matching a continuously enlarging number of specimens to another (by the more loans of specimens I received and institutions I visited to examine material). These solved puzzles or morphological groups would then represent discrete species.

Herbarium material comprising some 2550+ sheets including nearly all type specimens have been examined and databased (Appendix K) either via the loan of

specimens to Neuchâtel, or during visits to herbaria. In some cases, material could only to be examined *in situ*, so numerous trips to herbaria were undertaken to verify type specimens and search for and study unidentified material. As *Macrocarpaea* is a poorly understood and enigmatic genus, specimens are found routinely in folders of "unidentified" Apocynaceae, Gentianaceae, Rubiaceae, or even folders of specimens for material that the family was unknown. Some herbaria sent data on their material via letter or e-mail when loans were not possible. For example, some material is not allowed to be sent on loan, such as Linnaean specimens from the Linnaean Society herbarium in London, or the Herbario Luis Sodiro, Quito. Material from some institutions was not requested on loan once data were collected. Some material was selected for loan and either carried back to Neuchâtel or sent via the postal service.

The following herbaria either loaned material, sent photocopies of specimens or data on their collections, or were visited for examination of material (acronyms following Holmgren et al. 1990): AAU, ALA*, B, BM, BP, BR, BRIT, BSB, C, CAS, CHRB*, COL*, CR, CUVC, CUZ*, DAV, DUKE, E, F, FI, FLAS, FR*, G*, GB, GH, GOET, HAC, HAL HAM, HAO*, HUCP, HUT*, IAC, IAN*, INB, INPA*, JBSD, JE, K, L, LD, LOJA*, LPB, LS, M, MA*, MANCH, MARY*, MBM*, MER*, MG*, MICH, MIN, MO, MOL*, MSB, MY, NA, NEU*, NO, NSW*, NY*, OXF, P*, PH, PORT*, PR, PRC, Q*, QAP*, QCA*, QCNE*, QPLS*, QUSF*, R*, RB*, S*, SBG*, SEL*, SP*, SPF*, TEX, U, UC, UCWI, UPCB, UPS, US*, USM*, VEN*, W*, WIS, WU*, YU, and Z*. For a full list of the names of these institutions, see Tab. 2.

Fig. 2. Herbarium specimen of *Macrocarpaea cf. glaziovii*. Photo by J.R. Grant.

During the work of this thesis, the large majority of herbarium material of *Macrocarpaea* that exists in the world has been examined (e.g., Fig. 2). Specimens from all major institutions in Australia, Central America, Europe, North America and South America have been studied. During travels to South America I have had the opportunity to visit herbaria in Brazil, Colombia, Ecuador, Peru, and Venezuela. I would suggest that the only significant gap in material is from Colombian institutions. For reasons of recent political instability, travel to Colombian herbaria and especially the field has been severely restricted. Peru, Ecuador, and Colombia have the largest number of species of *Macrocarpaea*, and are therefore the most important countries for *Macrocarpaea* diversity . I have visited the major herbaria in Peru (CUZ, HAO, HUT, MOL, USM), and Ecuador (LOJA, Q, QAP, QCA, QCNE, QPLS, and QUSF), yet only one herbarium in Colombia (COL). In Colombia a large number of regional herbaria such as COAH, CUVC, HUA, JAUM, MEDEL TULV, UDBC, and VALLE should be visited prior to completion of the monograph.

There are 2210 herbarium specimens collected between 1780-1999 (Fig. 3). Additionally, there are 340+ collections alone from between 2000-2003 that would show a continued increase at the end of the scale. These collections may be roughly categorized into three periods, I: Discovery (1780-1839), II: Stability (1840-1939), and III: Growth (1940-2002). In Period I comprising the 60 years between 1780-1839, 83 specimens were collected, for an average of 13.6 specimens per decade. In Period II, comprising the 100 years between 1840-1939, 378 specimens were collected, for an average of 37.8 specimens per decade. In Period III comprising the 60 years between 1940-1999, 1750 specimens were collected, for an average of 291.6 specimens per decade. Please note that these figures are based on the *number of herbarium sheets*, not the *number of collections*. For example, a single collection, e.g., *Grant 4002* may be represented by several duplicate specimens. However, overall the number of duplicates seems to be rather constant throughout history.

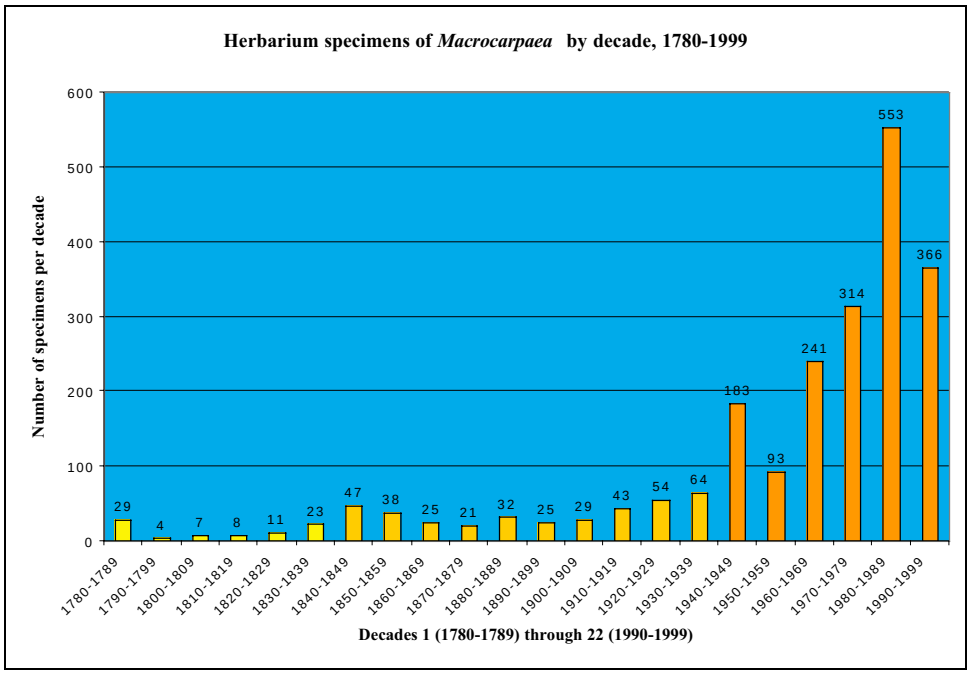


Fig. 3. Number of herbarium specimens arranged by the decade in which they were collected.

Between 1999-2003 several expeditions to South America were made to study collections in herbaria, but more importantly to study living plants in the field (Tab. 1). Plant collections included dried herbarium specimens, leaves dried in silica gel for molecular analyses, wood samples for wood anatomical studies, fixated floral buds for chromosome studies, and alcohol-formalin (FAA) preserved flowers and leaves for future anatomical studies. Fieldwork for this thesis has been conducted in Brazil, Colombia, Ecuador, Panama, Peru, and Venezuela:

Year	Months	Country(ies)
1999	Mar-May	Argentina, Brazil, Colombia, Paraguay, Venezuela
2000	Feb	Panama
2001	Jan-Feb	Ecuador I, Peru
2002	Feb-Mar	Ecuador II
	Oct-Nov	Ecuador III
2003	Jul	Brazil

Tab. 1. Plant collecting expeditions to South America

Fig. 4. *M. apparata* J.R. Grant & Struwe

Fig. 5. *M. jensii* J.R. Grant & Struwe

Fig. 6. *M. ayangannae* J.R. Grant, Struwe & Boggan

Fig. 7. *M. lenae* J.R. Grant

Fig. 4–7 are examples of *freshly-collected* herbarium specimens of *Macrocarpaea apparata*, *M. jensii*, *M. ayangannae*, and *M. lenae*. Images downloaded from the web site of the New York Botanical Garden: http://www.nybg.org/bsci/hcol/vasc.

Fig. 8. *M. cinchonifolia* (Gilg) Weaver (sheet 1 of 4)

Fig. 9. *M. cinchonifolia* (Gilg) Weaver (sheet 2 of 4)

Fig. 10. *M. cinchonifolia* (Gilg) Weaver (sheet 3 of 4)

Fig. 11. *M. cinchonifolia* (Gilg) Weaver (sheet 4 of 4)

Fig. 8–11 are examples of *historical* herbarium specimens of *Macrocarpaea cinchonifolia*, indicating the poor conditions of older material. Images downloaded from the web site of the New York Botanical Garden: http://www.nybg.org/bsci/hcol/vasc/.

Tab. 2. Herbaria from which material of *Macrocarpaea* has been examined or visited*.

HERBARIUM	INSTITUTION	COUNTRY
AAU	Univ. Aarhus, Aarhus	Denmark
ALA*	Univ. Alaska Museum, Fairbanks, AK	U.S.A.
B	Botanischer Garten und Botanisches Museum Berlin-Dahlem	Germany
BM	British Museum of Natural History, London, England	U.K.
BP	Hungarian Natural History Museum	Germany
BR	Jardin Botanique National de Belgique, Bruxelles	Belgium
BRIT	Botanical Research Institute of Texas, TX	U.S.A.
BSB	Freie Universität Berlin	Germany
C	Univ. Copenhagen	Denmark
CAS	California Academy of Sciences, San Francisco, CA	U.S.A.
CHRB*	Rutgers University – New Brunswick, NJ	U.S.A.
COL*	Univ. Nacional de Colombia, Bogotá	Colombia
CR	Museo Nacional de Costa Rica, San José	Costa Rica
CUVC	Univ. Valle, Cali	Colombia
CUZ*	Univ. Nacional San Antonio Abad de Cusco	Peru
DAV	Univ. California – Davis, CA	U.S.A.
DUKE	Duke University, Durham, NC	U.S.A.
E	Royal Botanic Garden, Edinburgh, Scotland	U.K.
F	Field Museum of Natural History, Chicago, IL	U.S.A.
FI	Univ. Florentinae, Firenze	Italy
FLAS	Univ. Florida – Gainsville, FL	U.S.A.
FR*	Forschungsinstitut Senckenberg, Frankfurt	Germany
G*	Conservatoire et Jardin botaniques de la ville de Genève	Switzerland
GB	Botanical Museum, Göteborg	Sweden
GH*	Harvard University, Cambridge, MA	U.S.A.
GOET	Univ. Göttingen	Germany
HAC	Inst. de Ecología y Sistemática, Habana	Cuba
HAL	Martin-Luther Univ., Halle	Germany
HAM	Royal Botanical Gardens, Hamilton, Ontario	Canada
HAO*	Univ. Privada Antenor Orrego, Trujillo	Peru
HUCP	Pontifica Universidade Católica do Paraná	Brazil
HUT*	Univ. Nacional de Trujillo	Peru
IAC	Inst. Agronômico de Campinas	Brazil
IAN*	Univ. Federal do Pará, Belém, Brazil	Brazil
INB	Inst. Nacional de Biodiversidad, Heredia	Costa Rica
INPA*	Inst. Nacional de Pesquisas da Amazônica, Manaus, Brazil	Brazil
JBSD	Jardím Botánico Nacional Dr. Rafael M. Moscoso, Santo Domingo	Dominican Rep.

JE	Friedrich-Schiller-Universität, Jena	Germany
K	Royal Botanical Gardens, Kew, England	U.K.
L	Rijksherbarium, Leiden	Netherlands
LD	Lunds Universitet, Botaniska Museet	Sweden
LOJA*	Univ. Nacional de Loja, Loja	Ecuador
LPB	Herbario Nacional de Bolivia, La Paz	Bolivia
M	Botanische Staatssammlung, München	Germany
MA*	Real Jardín Botánico, Madrid	Spain
MANCH	Univ. Manchester, Manchester Museum, England	U.K.
MARY*	Univ. Maryland - College Park, MD	U.S.A.
MBM*	Museo Botânico Municipal, Herbário, Curitíba	Brazil
MER*	Univ. Andes, Mérida, Venezuela	Venezuela
MG*	Museu Paraense Emílio Goeldi, Belém, Brazil	Brazil
MICH	Univ. Michigan - Ann Arbor, MI	U.S.A.
MIN	Univ. Minnesota - St. Paul, MN	U.S.A.
MO*	Missouri Botanical Garden, St. Louis, MO	U.S.A.
MOL*	Univ. Nacional Agraria, La Molina, Lima	Peru
MSB	Ludwig-Maximilians-Universität, München	Germany
MY	Univ. Central de Venezuela, Maracay	Venezuela
NA	U.S. National Arboretum, USDA, Washington, D.C.	U.S.A.
NEU*	Univ. Neuchâtel	Switzerland
NO	Tulane University Herbarium, New Orleans, LA	U.S.A.
NSW*	National Herbarium of New South Wales, Sydney	Australia
NY*	New York Botanical Garden, Bronx, NY	U.S.A.
OXF	Univ. Oxford, England	U.K.
P*	Muséum national d'Histoire naturelle, Paris	France
PH	Academy of Natural Sciences, Philadelphia, PA	U.S.A.
PORT*	BioCentro-UNELLEZ, Guanare, Venezuela	Venezuela
PR	National Museum in Prague, Prague	Czech Republic
PRC	Univ. Charles, Prague	Czech Republic
Q*	Univ. Central, Quito, Ecuador	Ecuador
QAP*	Univ. Central, Quito, Ecuador	Ecuador
QCA*	Pontificia Universidad Católica del Ecuador, Quito	Ecuador
QCNE*	Museo Ecuatoriano de Ciencias Naturales, Quito	Ecuador
QPLS*	Herbario Luis Sodiro, Biblioteca Ecuatoriana, Quito	Ecuador
QUSF*	Univ. San Francisco	Ecuador
R*	Museo Nacional do Rio de Janeiro	Brazil
RB*	Jardim Botânico do Rio de Janeiro	Brazil
S*	Swedish Museum of Natural History, Stockholm	Sweden

SBG*	Santa Barbara Botanical Garden, Santa Barbara, CA	U.S.A.
SEL*	Marie Selby Botanical Gardens, Sarasota, FL	U.S.A.
SP*	Inst. de Botânica, São Paulo	Brazil
SPF*	Univ. São Paulo, Brazil	Brazil
TEX	Univ. Texas – Austin, TX	U.S.A.
U	State University of Utrecht	Netherlands
UC	Univ. California – Berkeley, CA	U.S.A.
UCWI	Univ. West Indies, Kingston	Jamaica
UPCB	Univ. Fed. do Paraná, Curitíba	Brazil
UPS	Univ. Uppsala, Botanical Museum	Sweden
US*	Smithsonian Institution, Washington, D.C.	U.S.A.
USM*	Univ. Nacional Mayor de San Marcos	Peru
VEN*	Herbario Nacional de Venezuela, Caracas	Venezuela
W*	Naturhistorisches Museum Wien	Austria
WIS	Univ. Wisconsin – Madison, WI	U.S.A.
WU*	Univ. Wien, Inst. für Botanik	Austria
YU	Peabody Museum of Natural History, Yale University, CT	U.S.A.
Z*	Univ. Zürich	Switzerland

Tab. 2. Herbaria from which material of *Macrocarpaea* has been examined or visited*.

GROSS MORPHOLOGICAL CHARACTERS

Important and taxonomically consistent morphological characters at the species rank that are readily visible on herbarium material include the architecture of the inflorescence (a thyrse, where the primary branching is racemose, and the secondary is cymose), the position of the flowers before and after anthesis (erect, spreading, horizontal, nodding), calyx size, shape (lobes acute, acuminate, cuspidate, obtuse, rounded), and vestiture (glabrous, scabrous, hairy); and leaf size and shape (linear, lanceolate, ovate, elliptical, obovate).

LEAF MORPHOLOGY

Leaves of *Macrocarpaea* display a wide range of morphological variation. They are always entire, and vary from petiolate to sessile; glabrous to pubescent; small thick and coriaceous, to large thin and papery; and linear-lanceolate, lanceolate, oblong, ovate, oval, elliptic, oblanceolate, to obovate in shape (Fig. 14 A-I). The *leaf base* is aequilateral, oblique, attenuate, cuneate, to rounded; the *leaf apex* is acuminate, acute, mucronulate, obtuse to rounded.

The interpetiolar ridge has several taxonomically useful characters, and is defined as the area between paired opposite leaves where the petioles are fused. Leaves are typically petiolate, though sessile leaves are found in a few species e.g., *M. auriculata* (Fig. 14E). Petioles range from unvaginated to having a long scooped out groove or vagination on the upper surface (Fig. 12–13). In some species, the vagination is so short that it gives the false appearance of a "corona". Coronas do not occur in the Gentianaceae. In other species, the vagination extends from the base of the petiole to its apex (Fig. 12).

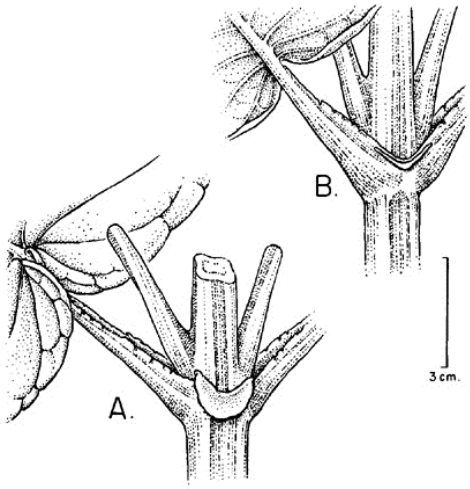


Fig. 12. Interpetiolar ridge of *M. zophoflora* with lunate stipules.

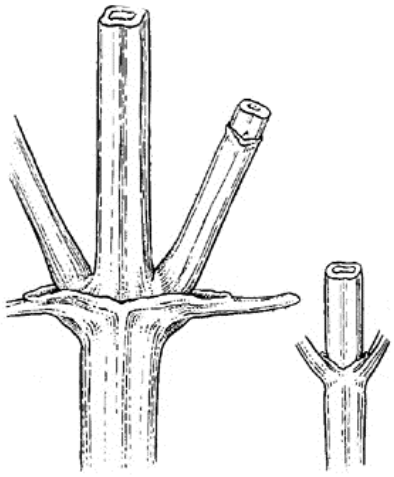
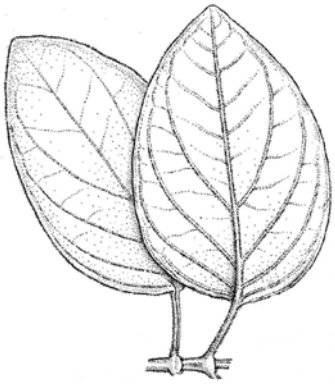


Fig. 13. Interpetiolar ridge of *M. ypsilocaule* with no stipules.

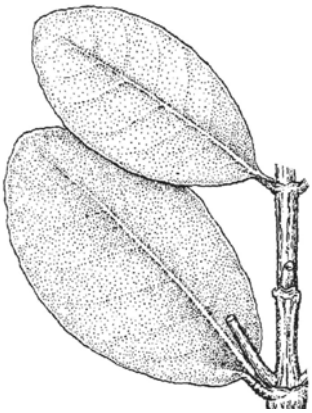
The interpetiolar ridge of one species, *M. zophoflora* possesses a singular feature unknown to any other species of the Gentianaceae, free deciduous interpetiolar stipules (Fig. 12). It is lunate (half-moon or "Pacman" shaped), 7—10 x 11—12 mm, with the convex side facing downward in a flap-like manner, attached in a broad "v" shape to the interpetiolar ridge, about as broad as the stem itself. Even the collector of the material, renowned morphologist John Wurdack, noted on his herbarium labels that the leaves have "stipular flaps at nodes"

A. **Ovate** leaves of *M. luya*.

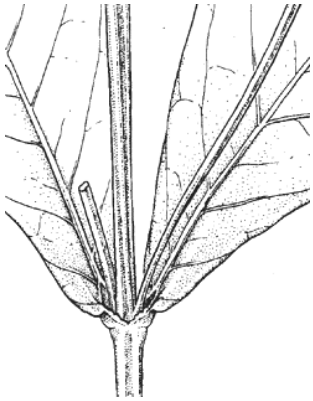


D. **Ovate** leaves of *M. ayangannae*.

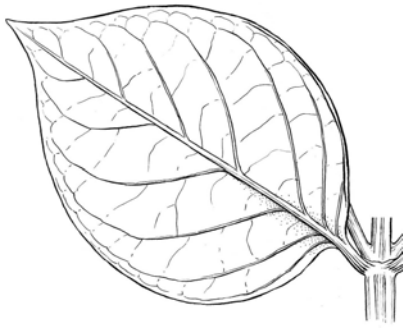
G. **Lanceolate** leaf of *M. kayakifolia*.



B. **Oval** leaves of *M. subsessilis*.

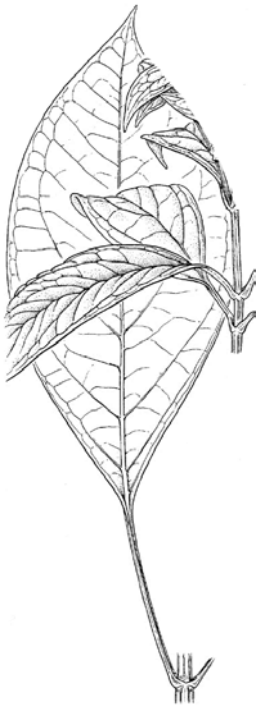


E. **Sessile** leaves of *M. auriculata*.

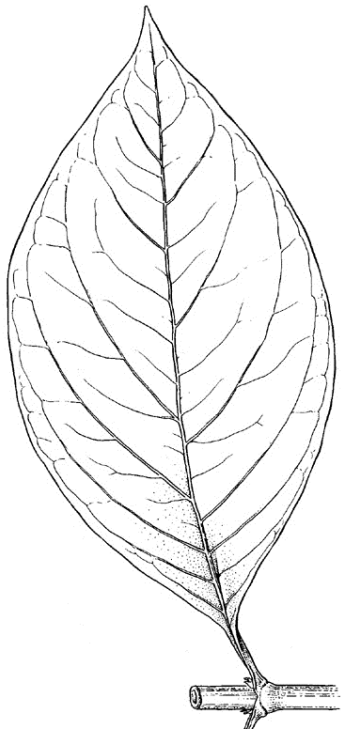


H. **Ovate** leaf of *M. fortisiana*.

C. **Obovate** leaves of *M. lacrossiformis*.



F. **Long-petiolate elliptic** leaves of *M. jensii*.



I. **Elliptic** leaf of *M. papillosa*.

Fig. 14. Range of variation in leaf morphology in *Macrocarpaea*. Illustrations by Bobbi Angell.

Most species of *Macrocarpaea* have glabrous leaves. However, hairs have evolved independently in a few species in different lineages of the genus. For example in the two examples illustrated below, *M. obtusifolia* is positioned in sect. *Tabacifoliae*, and *M. marahuacae* in sect. *Macrocarpaea*: interesting since, in general, hairs are a rare in the Gentianaceae. Only a few genera have hairs, e.g., *Crawfurdia*, *Macrocarpaea*, and *Ornichia* (Struwe et al. 2002). The leaves range from spiculate, puberulent, pubescent, tuberculate, hispid to papillate. Species with large amounts of hairs include *M. ayangannae*, *M. marahuacae* (Fig. 15–17), and *M. obtusifolia* (Fig. 18–20).

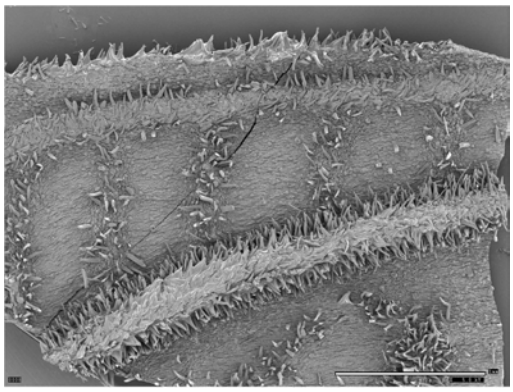


Fig. 15. Lower leaf surface of *M. marahuacae*.

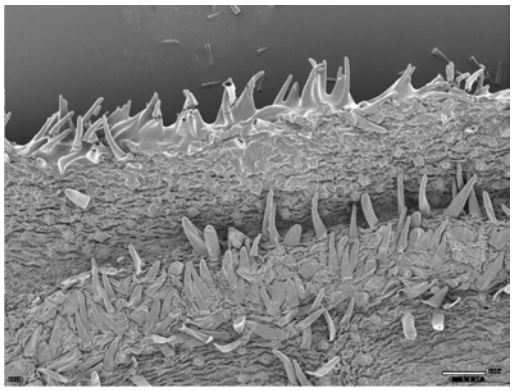


Fig. 16. Lower leaf surface of *M. marahuacae*.

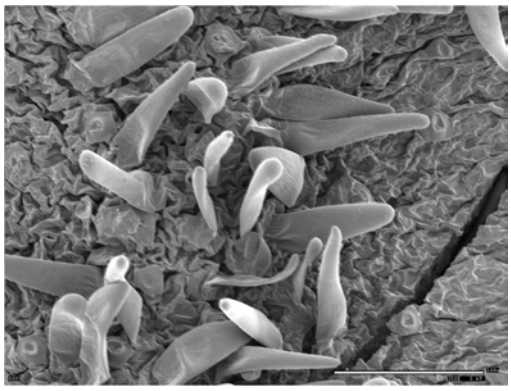


Fig. 17. Lower leaf surface of *M. marahuacae*.

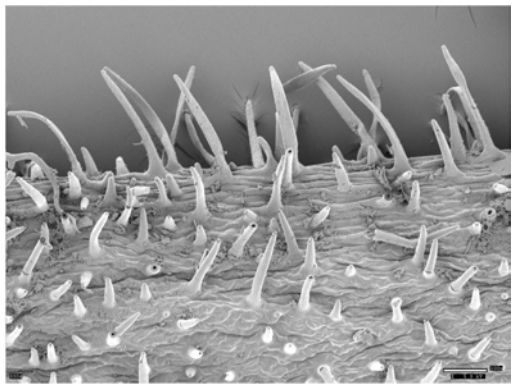


Fig. 18. Upper leaf surface of *M. obtusifolia*.

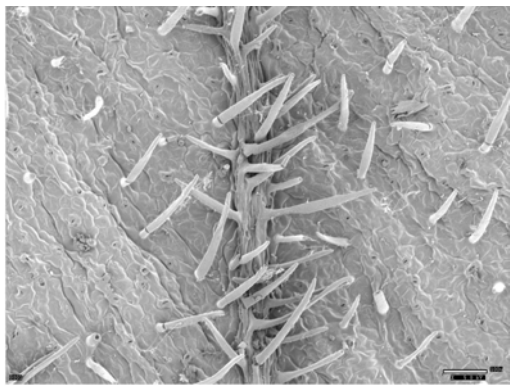


Fig. 19. Lower leaf surface of *M. obtusifolia*.

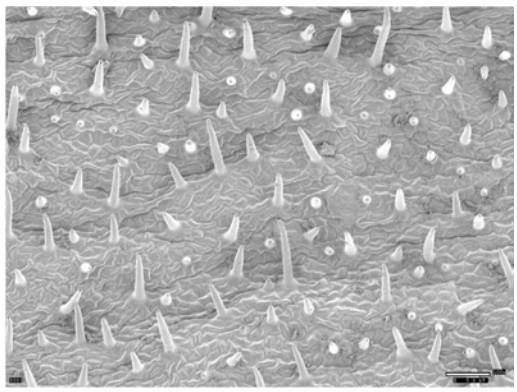


Fig. 20. Lower leaf surface of *M. obtusifolia*.

Fig. 15–20. Lower leaf surfaces of *Macrocarpaea marahuacae* and *M. obtusifolia*. SEM by J.R. Grant & L. Struwe, New York Botanical Garden.

INFLORESCENCE ARCHITECTURE

The inflorescence of *Macrocarpaea* is a thyrse, composed of branches of cymes in a racemose branching pattern (Fig. 21–25. Depending on the species, the inflorescence may consist of 3–7+ cymes per branch. Often in larger species, the only part pressed as herbarium material is a single branch or cyme, causing difficulties when a description is needed. Therefore, in new descriptions by this author, measurements of branch length alone (lateral and terminal branches) are given for all species, and both such branch length and total inflorescence length for species with comparatively small inflorescences when possible. The term "branch" is used as a general term since any branch may comprise several cymes. The term "bract" is defined as all leaves in the inflorescence, except the 1–2 "bracteoles" that subtend each flower. The pair of leaves that subtend the entire inflorescence are recognized as true leaves since their size and shape is more consistent with the leaves below than the bracts above.

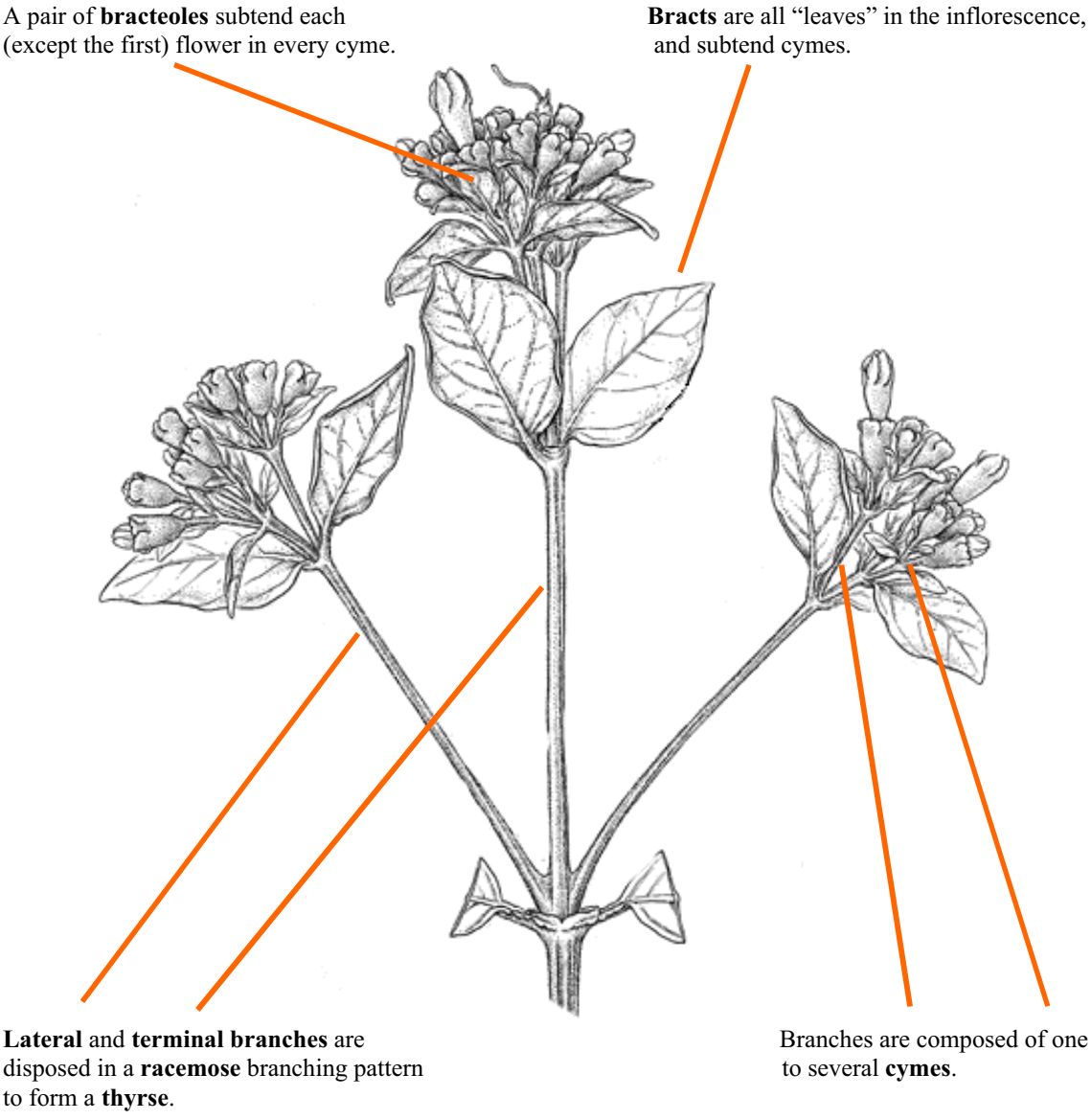


Fig. 21. Inflorescence architecture of a typical species, *Macrocarpaea cochabambensis*.

Fig. 22. Few-flowered inflorescence of *M. jensii*. Photo by J.R. Grant.

Fig. 24. Short compact nearly sessile inflorescence of *M. subsessilis*. Photo by J.R. Grant.

Fig. 23. Large open thyrse of *M. noctiluca*. Photo by J.R. Grant.

Fig. 25. Large candelabriform inflorescence of *M. apparata*. Photo by L. Struwe.

Fig. 21–25 illustrate the different inflorescence forms in *Macrocarpaea* (all of sect. *Choriophylla*).

FLORAL MORPHOLOGY

Flora morphology is the most taxonomically rich character in the genus. A flower consists of a pedicel, bracteoles, calyx, and corolla. The calyx in particular is the most important taxonomically useful character. The androecium and gynoecium do not appear to be taxonomically useful. Comparison of these discrete characters to another provides a suite from which taxonomic judgements may be based.

Pedicel. All flowers of *Macrocarpaea* are pedicellate. However, the length and thickness vary considerably between species. Most species have ecarinate pedicels, but some are strongly carinate, the keels extending down from the carinate calyx (e.g., *M. weigendiorum*, Fig. 30 R).

Bracteoles. The *first flower* to appear in a cyme is subtended by a pair of bracteoles (Fig. 26). When the next flowers (always a simultaneously appearing pair of flowers) arise from within the axils of the bracteoles of the first flower, it then seems that the first flower has no bracteoles (Fig. 27). The bracteoles that subtended the first flower then become known as the *bracts* that subtend the entire cyme. The first flower in any cyme is easy to identify by the "lack" of a subtending pair of bracteoles. Bracteoles vary considerably in size and shape, from small scarious flaps in *M. lenae* (Fig. 26) to sizeable and spathulate in *M. subsessilis* (Fig. 30E).

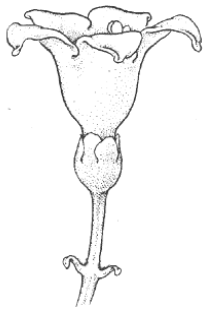


Fig. 26. The first flower to appear in a cyme is subtended by a pair of bracteoles.

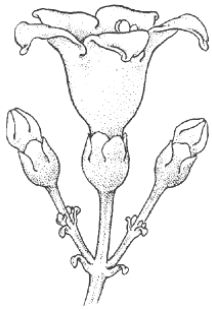


Fig. 27. The first flower, and subsequent simultaneously appearing pair of flowers. In terms of nomenclature, the "bracteoles" of the first flower become bracts.

Calyx. The single-most important morphological feature in terms of taxonomic utility readily visible on all herbarium specimens of *Macrocarpaea* regardless of phenological state (flowering to fruiting), is the calyx. Calyces vary considerably in length and width (e.g., from 2–5 x 3–4 mm in *M. wurdackii* [Fig. 30F], to 15–20 x12–18 mm in *M. zophoflora* [Fig. 30S]). In shape they range from narrowly campanulate (e.g., *M. subsessilis* [Fig. 30E]), to broadly campanulate (e.g., *M. ostentans* [Fig. 30P]); ecarinate (e.g., *M. ostentans* [Fig. 30P]) to strongly carinate (e.g., *M. weigendiorum* [Fig. 30R]); and glabrous, spiculate to pubescent in vestiture (e.g., pubescent in *M. obtusifolia* [Fig. 30C] and *M. schultesii* [Fig. 30H]). *Calyx lobes* vary from scarcely present (e.g., *M. gracilis* [Fig. 30I]) or *M. harlingii* [Fig. 30D]) to dividing the calyx to nearly the base (e.g., *M. glaziovii* [Fig. 30B] and *M. gondoloides* [Fig. 30K]). The lobes range in shape from ovate, oblong, rotund, elliptic, lunate, to small and triangular, with apices that vary from acuminate, acute, obtuse, to rounded (see full variation illustrated in Fig. 30).

Corolla. The corollas of *Macrocarpaea* also display a wide range of morphological diversity (Fig. 30–36). In one species, perhaps the basal-most species in the genus, *M. rubra*, the corolla is urceolate in shape (Fig. 30A). All remaining species of the genus have variations on a funnel-shaped corolla. Despite this, useful characters include length and width, and shape of the corolla lobes. Lobes vary from ovate, elliptic, lanceolate, to lunate, with apices that vary from acute, obtuse, retuse, to rounded. *Macrocarpaea wurdackii* (Fig. 30F) has the smallest corolla in the genus, while *M. zophoflora* has the largest (Fig. 30S). Corolla lobes range in shape from ovate (e.g, *M. lacrossiformis*, Fig. 30L), elliptic, lanceolate, large and lunate (e.g., *M. luna-gentiana*, Fig. 30 S), to small and triangular (e.g., *M. rubra*, Fig. 30A), with apices that vary from acute, obtuse, retuse to rounded.

All flowers of *Macrocarpaea* have an actinomorphic corolla. However, the *ensemble* of corolla and sexual parts indicate that the flower is zygomorphic (Fig. 28–29). Flowers are always positioned with a single petal on top, and two at the base, as in a Star-of-David (Fig. 28). The androecium and gynoecium are positioned at the base of the corolla.

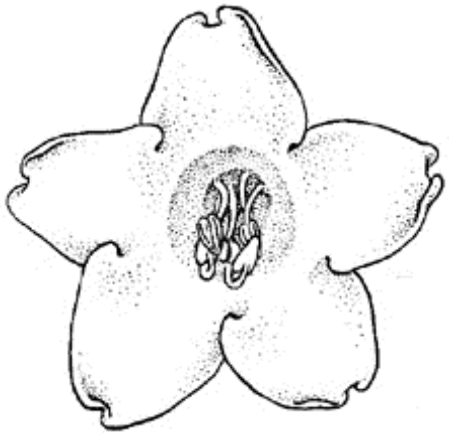


Fig. 28. Face of *M. lenae*. The slightly rotate corolla lobes are reminiscent of Apocynaceae, another family of the order Gentianales.

Fig. 29. Faces of *M. apparata*.

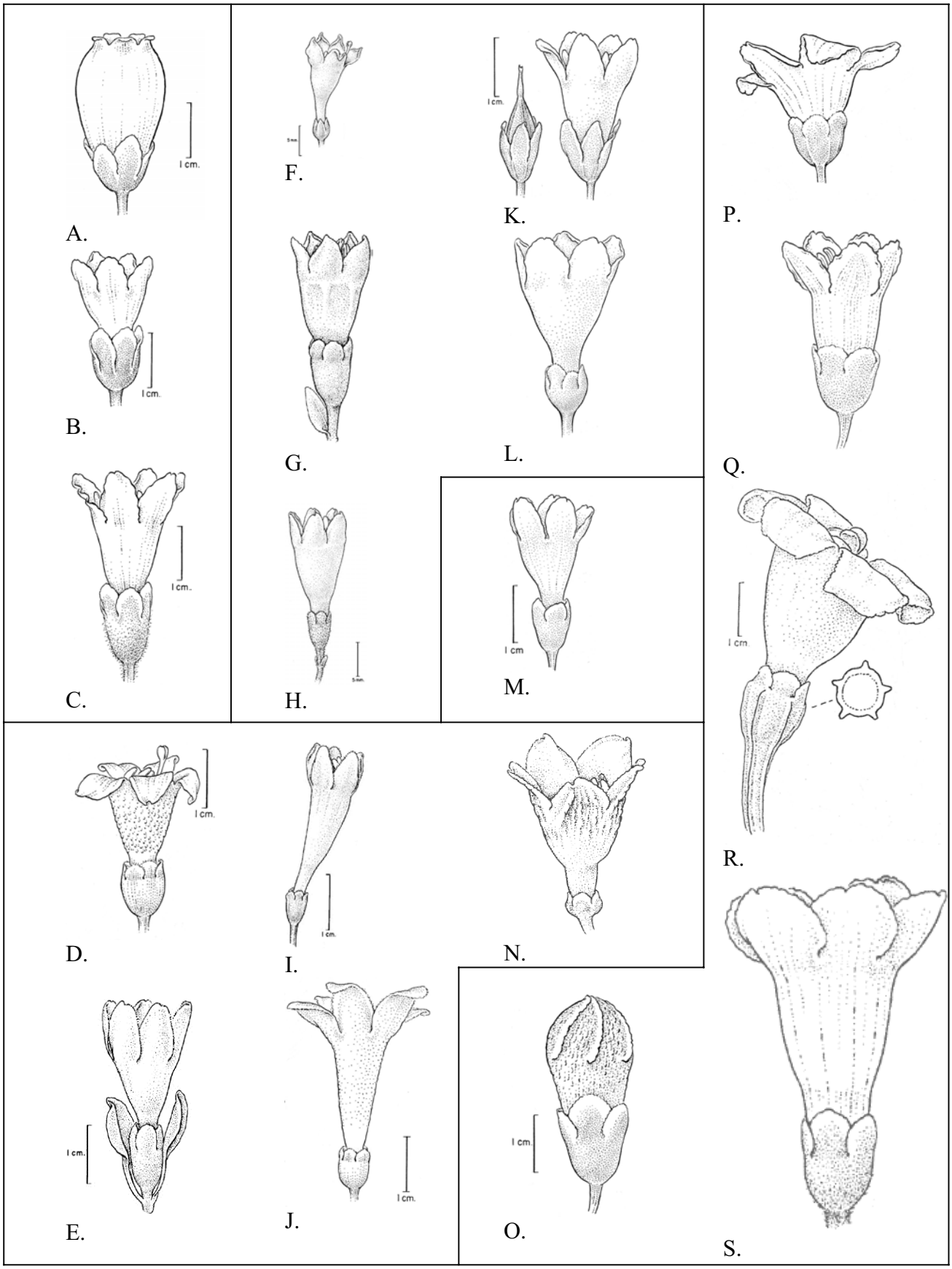


Fig. 30. Floral diversity in *Macrocarpaea*. Sect. ***Tabacifoliae*** A-C; ***Choriophylla*** D-E, I-J, N; ***Macrocarpaea*** F-H, K-L; ***Caribbigenes*** M; ***Magnolifoliae*** O-S. A. *M. rubra*, B. *M. glaziovii*, C. *M. obtusifolia*, D. *M. harlingii*, E. *M. subsessilis*, F. *M. wurdackii*, G, *M. weaveri*, H. *M. schultesii*, I. *M. gracilis*, J. *M. elix*, K. *M. gondoloides*, L. *M. lacrossiformis*, M. *M. thamnoides*, N. *M. jensii*, O. *M. fortisiana*, P. *M. ostentans*, Q. *M. canoëifolia*, R. *M. weigendiorum*, S. *M. luna-gentiana*. Illustrations by Bobbi Angell.

Fig. 31. *M. angelliae* with short-pedicellate erect flowers.

Fig. 32. *M. noctiluca* with long-pedicellate spreading to nodding flowers.

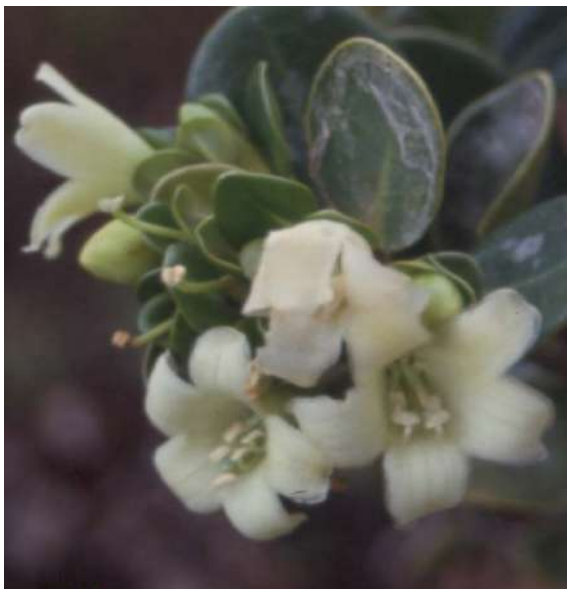


Fig. 33. *M. subsessilis* with short flowers in a nearly sessile inflorescence. Notice the basal position of androecium and gynoecium.

Fig. 34. *M. apparata* with large white night-blooming flower adapted to bat pollination.

Fig. 35. *M. arborescens* with a pendent yellow corolla.

Fig. 36. *M. luna-gentiana* with bright green corolla, and hole indicating the visit of a nectar robber.

Fig. 32–36 illustrate floral diversity in *Macrocarpaea* by color photographs of Ecuadorian species. Photos by J.R. Grant.

SEED ANATOMY

There is a great diversity of previously unrecognized taxonomically useful seed morphological characters in *Macrocarpaea*. To date, seed anatomy has only been summarized at the generic rank for *Macrocarpaea*. Bouman et al. (2002) discussed seed anatomy of *Macrocarpaea* in comparison to other members of the family. But since his sampling was limited, neither all seed types nor the full picture of the evolution of seed anatomy were elucidated.

Here, seed anatomy has been studied in 71 of 98 species in the genus that have capsules with mature seeds. Of these, 24 representative species are illustrated to demonstrate the variation of seed anatomy in the genus (Fig. 42–43). Several morphological types of seeds have been identified, largely conforming to sectional groups within *Macrocarpaea*: **flattened seeds** (sensu Bouman et al. 2002: 533) (Fig. 37), **polygonal seeds** (described here) (Fig. 38); **rimmed seeds** (sensu Bouman 2002: 531) (Fig. 39), **winged seeds** (modified from Bouman et al. 2002: 531) (Fig. 40), and **winged perimetrically seeds** (described here) (Fig. 41).

Seeds are miniscule in size, ca. 0.2–1.6 x 0.2–0.6 mm. Therefore, they have been examined by light microscopy. Photographs were prepared with a Nikon Coolpix 4500 digital camera mounted with adapter onto a Wild Heerbrugg light microscope. Photos were taken in color then transformed to black-and-white for better resolution. The diversity of seed morphology was somewhat unexpected. The photos presented here are preliminary since studies in Autumn 2003 involving Scanning Electron Microscopy (SEM) work will commence here at the Université de Neuchâtel.

Seed types in *Macrocarpaea*

1. **Flattened seeds**, flattened to polygonal, no wings: sect. *Tabacifoliae* (4 sp. in southeastern Brazil)
2. **Polygonal seeds**, no wings: sect. *Caribbigenes* (3 sp. in the Greater Antilles)
3. **Rimmed seeds**, polygonal to flattened, no wings to winged: sect. *Macrocarpaea* (38 sp. in Southern Mesoamerica (Costa Rica and Panama), Pantepui of the Guayana Shield, and Northern Andes, especially Colombia)
   - 3a. polygonal, no rims or wings
   - 3b. polygonal, rimmed
   - 3c. flattened, rimmed to perimetrically winged
4. **Winged seeds**, flattened, wings at base and apex, or all around: sect. *Magnolifoliae* (19 sp. in S Andes, especially C Peruvian Andes)
5. **Perimetrically winged seeds**, flattened with wings all around: sect. *Choriophylla* (34 sp. in S Andes, especially Huancabamba region)

Basal members of *Macrocarpaea* have heavy flattened to polygonal seeds with no wings (sect. *Tabacifoliae*). In the next group, the seeds become entirely polygonal with no wings (sect. *Caribbigenes*). Then, the polygonal seeds become larger, longer, sometimes flat but usually in geometric shapes based on a rectangle (sect. *Macrocarpaea*). The seeds are rimmed with a slight edge, to developing wings in the epiphytic species. Next, the seeds become flattened again, with wings sprouting from both basal and apical ends (sect. *Magnolifoliae*). In the final and most derived group, the light seeds remain flattened but develop wings all along the outer perimeter of the seeds (perimetrically)

(sect. *Choriophylla*). This trend can be seen when the types are mapped on a cladogram based on molecular results (Fig. 43). Generally, heavy flattened seeds with no wings are basal, develop into polygonal seeds, and derive to light winged seeds.

1. **Flattened seeds** (Fig. 37) occur in the four species of sect. *Tabacifoliae* of Southeastern Brazil. The seeds are flattened to polygonal, and have no wings. *Macrocarpaea caatingae*, *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 has been lost during seed development.

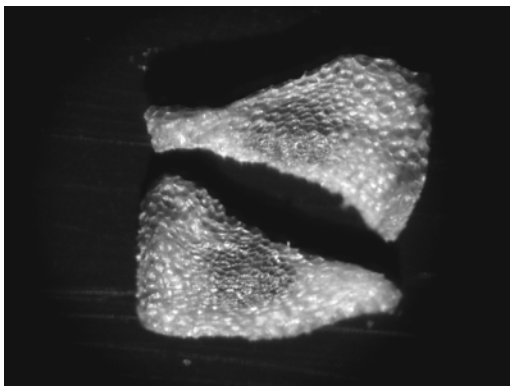


Fig. 37. **Flattened** seed type, *M. rubra*.

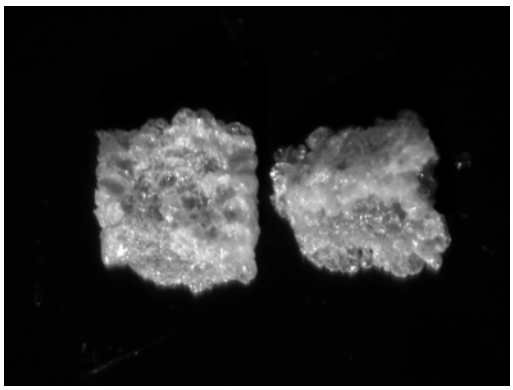


Fig. 38. **Polygonal** seed type, *M. domingensis*.

2. **Polygonal seeds** (Fig. 38) are present in sect. *Caribbigenes* of the Greater Antilles of the Caribbean. These seeds tend to be to short-rectangular seeds with no wings. Two of the three species that comprise the section have been studied, *M. domingensis* and *M. thamnoides*; all material examined of *M. pinetorum* is in flowering state.

3. **Rimmed seeds** (Fig. 39) correspond to sect. *Macrocarpaea* of the Northern Andes, Southern Mesoamerica (Costa Rica and Panama), and Pantepui of the Guayana Shield. The seeds are polygonal to flattened, rimmed, with or without wings. Three subtypes may be identified 3a: “polygonal, no rims or wings”, 3b: “polygonal, rimmed”, and 3c: “flattened, rimmed to perimetrically winged”. Although the seeds vary in morphology, an evolutionary trend can be hypothesized. From the basal members of the section with polygonal with no rims or wings, there is a development of polygonal rimmed seeds, and winged perimetrically seeds. The development of winged seeds in four species (*M. browallioides*, *M. gondoloides*, *M. luteynii*, and *M. subcaudata*) corresponds to their habit as the only known facultatively epiphytic species in the genus. These winged seeds may have evolved to better suit dispersal in an epiphytic habitat.

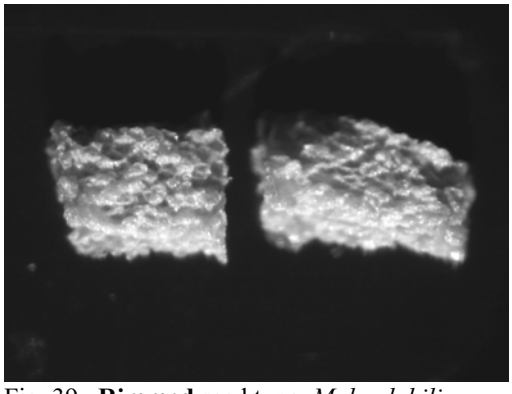


Fig. 39. **Rimmed** seed type, *M. laudabilis*.

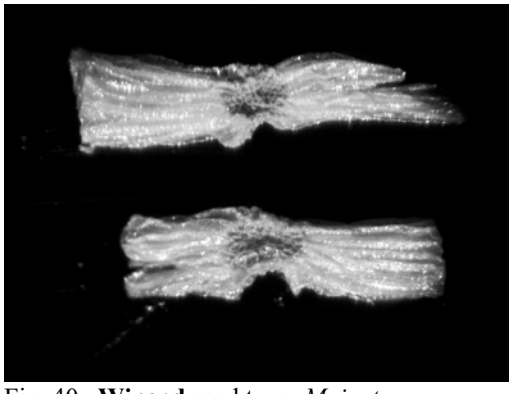


Fig. 40. **Winged** seed type, *M. jactans*.

4. **Winged seeds** (Fig. 40) correspond to sect. *Magnolifoliae* of Peru, Bolivia, and Ecuador. The seeds are flattened, winged at the base and apex, or rarely all around. This seed type is unique within the genus, and is a central character used to define the section. In fact, the combined character of this distinct seed type with the *corymbosa*-type pollen, generally monophyletic clades in the molecular data, and consistenly large flowers, form a suite of characters that define sect. *Magnolifoliae* better than any other.

5. **Perimetrically winged seeds** (Fig. 41) occur in 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. From within the section, at least two separate reversals to polygonal seeds have occurred. A morphologically coherent group including *M. ericii*, *M. loranthoides*, *M. luya*, *M. stenophylla*, and *M. subsessilis* is notable in their high elevation habitat, and particularly large spathulate bracteoles. According to gross morphology and molecular data, these species belong to *M*. sect. *Choriophylla*, yet have classically polygonal seeds. Another group of three closely related species, *M. innarrabilis*, *M. jalca*, and *M. kuelap*, all from Amazonas, Peru have significantly reduced wings.

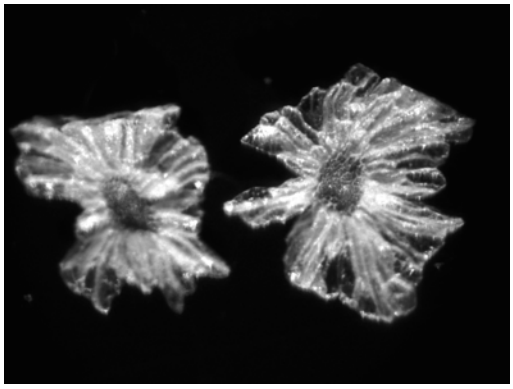


Fig. 41. **Perimetrically winged** seed type, *M. sodiroana.*

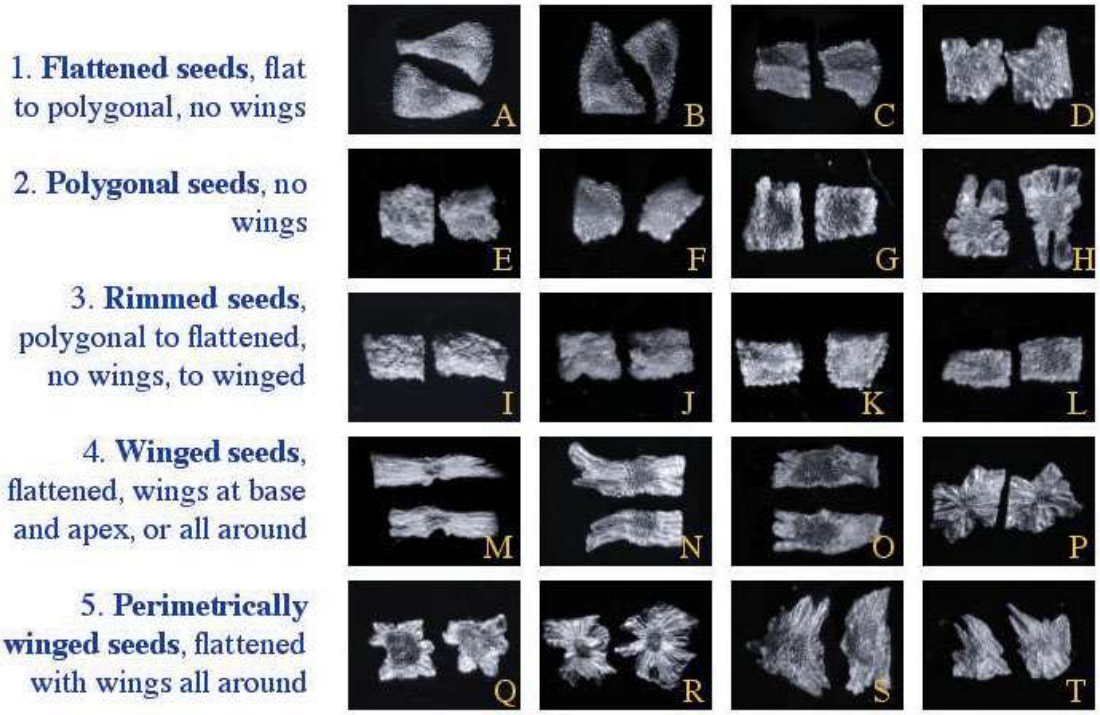


Fig. 42. The five seed types in *Macrocarpaea* are Flattened, Polygonal, Rimmed, Winged, and Perimetrically winged. These are illustrated from left to right. A. *M. rubra*, B. *M. glaziovii*, C. *M. obtusifolia*, D. *M. subcaudata*, E. *M. domingensis*, F. *M. thamnoides*, G. *M. gaudialis*, H. *M. gondoloides*, I. *M. laudabilis*, J. *M. nicotianifolia*, K. *M. rugosa*, L. *M. valerii*, M. *M. jactans*, N. *M. tahuantinsuyuana*, O. *M. maguirei*, P. *M. fosteri*, Q. *M. micrantha*, R. *M. sodiroana*, S. *M. noctiluca*, and T. *M. bangiana*.

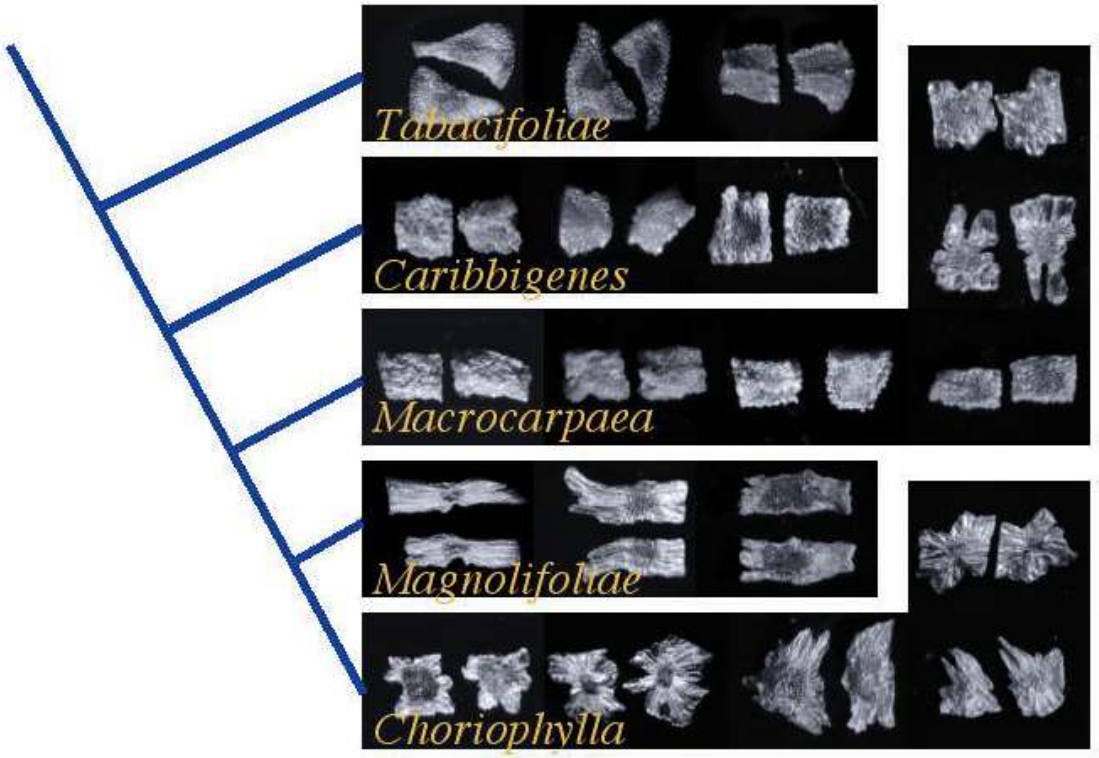
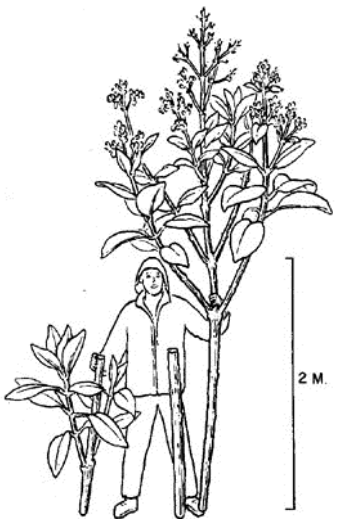


Fig. 43. Seed anatomy is congruent with molecular data that support the recognition of five sections in *Macrocarpaea*: *Tabacifoliae*, *Caribbigenes*, *Macrocarpaea*, *Magnolifoliae*, and *Choriophylla*.

WOOD ANATOMY

Samples of the wood of *Macrocarpaea* and other woody gentians are rare to largely unknown in xylaria (wood collections). Gentians are typically small herbaceous plants, and the tropical woody members of the family have been largely overlooked. While there are 87 genera of Gentianaceae, only 13 have woody species: Chironieae (*Chironia* and *Orphium*), Exaceae (*Gentianothamnus* and *Tachiadenus*), Helieae (*Chorisepalum*, *Macrocarpaea*, *Symbolanthus*, and *Zonanthus*), Potalieae (*Anthocleista*, *Fagraea*, *Lisianthius* and *Potalia*), and Saccifolieae (*Saccifolium*).



Left. Fig. 44. *Macrocarpaea apparata* J.R. Grant & Struwe in Ecuador.

Carlquist (1984) was the first and last to describe wood anatomical characters in Gentianaceae. His sample was limited to three species: *Chelonanthus chelonoides*, *Symbolanthus anomalus*, and *Ixanthus viscosus*. He noted that one would have to wait until a larger sampling of *Macrocarpaea* and *Symbolanthus* (the two most speciose woody gentian genera) could be assembled to conduct more detailed studies on wood anatomy of gentians. Therefore, following this advice during travels in South America, I made wood collections of 14 species of *Macrocarpaea* for studies and began a collaboration to study them with Sherwin Carlquist at the Santa Barbara Botanical Garden, California (Fig. 44–45). Additionally, three more collections of *Macrocarpaea* were located and two "outgroups" were selected, *Symbolanthus macranthus* and *Tachia occidentalis* (Tab. 3). In 2002 I visited his lab to learn techniques used in wood anatomical studies, and began to prepare an article on the wood anatomy of tribe Helieae (Carlquist & Grant MS).

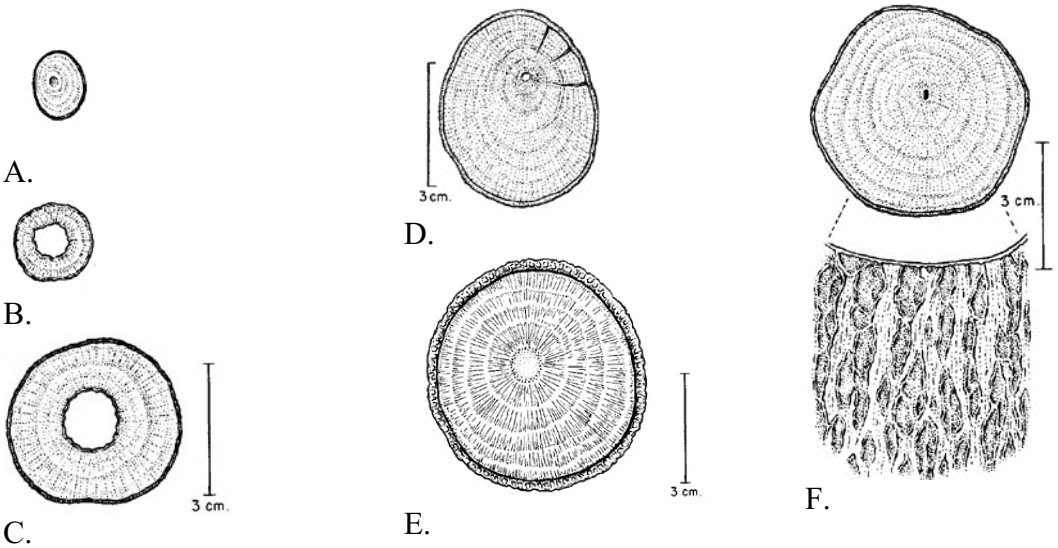


Fig. 45. Wood anatomy of cross-section of main trunk. A. *M. jensii*, B. *M. lenae*, C. *M. apparata*, D. *M. noctiluca*, E. *M. bubops*, and F. *M. luna-gentiana*. Illustrations by Bobbi Angell.

Wood of *Macrocarpaea*, *Symbolanthus*, and *Tachia* as a whole is mesomorphic, but relative low Mesomorphy Ratio values characterize *M. subsessilis*, *M. wurdackii*, and *Symbolanthus macranthus*. Even these values are well above those of shrubs of Mediterranean-type climate. The values of the three genera are typical for cloud-forest shrubs and trees. Only *M. harlingii* rises to a Ratio value characteristic of tropical rain forest levels. The vessels per group ratio also indicates mesomorphic wood structure for all species studied (the highest value, 2.72, is in *M. wurdackii*, the lowest, 1.30, in *M. micrantha*.

Perforation plates of the vessels are all solitary, as is characteristic for all Gentianaceae, and the number of vessels per group ranges from 1.30 (*M. micrantha*) to 2.72 (*M. wurdackii*). Low numbers of vessels per group indicate mesomorphy and high numbers more xeromorphic woods. The average for the species studied as a whole is 1.90. This average indicates that the species are all within a mesomorphic category, because desert shrubs can have vessels-per-group figures that range from 10 to 50 or more. The mean length of vessel elements for the species studied (432 μm), the mean vessel lumen diameter (42 μm) and the mean vessel density (67 per mm^2) are mesomorphic, but the diameter is well below what one would find for vessels of tropical rain forest woody trees (ca. 100 μm) and the density well above what one would find for tropical rain forest woody trees (ca. 10 per mm^2).

Vestured pits occur in vessels of all species, and while there is some variation in vesture appearance from species to species, no clear distinction occurs among species. The imperforate tracheary elements of the wood have much reduced borders, and qualify as fiber-tracheids rather than libriform fibers. Septate fibers occur in the vicinity of vessels in many species. The vestured pits of *Macrocarpaea* are not appreciably different from those of *Symbolanthus* and *Tachia*. The *M. wallnoeferi* is from the outside of the vessel (Fig. 46), the *M. gattaca* from the inside of the vessel (Fig. 47). For *Tachia* and *Symbolanthus*, vestured pits are illustrated as seen from both outside of the vessel (oval outline of pit cavity) and inside the vessel (warty slit, no oval around the pit) (Fig. 48–51). The magnifications are shown at lower right (e.g., × 6.0k for *M. gattaca*) plus a series of dots forming a line the length of which corresponds to the 5μm that is specified.

Rays in wood of all species studied of *Macrocarpaea*, *Symbolanthus*, and *Tachia* show a higher proportion of upright cells than in typical woody dicotyledons, indicative of prolonged juvenilism, and is a feature that suggests increased woodiness, and a likely ancestry consisting of either herbaceous plants or plants less woody than characterize the three genera at present. The wood of *Macrocarpaea* differs in no qualitative features from that of *Symbolanthus*, but *Tachia* has longer strands of axial parenchyma. The axial parenchyma type is vasicentric scanty in all species. Multiseriate rays outnumber or equal uniseriate rays in abundance. The presence of upright cells in rays is quite pervasive; procumbent cells are present in appreciable numbers only in rays of larger-diameter stems, where a more mature ray pattern would be expected. But even in these, proportion of procumbent cells falls well below what one would expect in a typical woody dicotyledon. In all of the species studied, therefore, the rays show paedomorphosis, which is indicative of origin from an herbaceous ancestor or at least a less woody ancestor. Thus the Helieae show secondary woodiness.

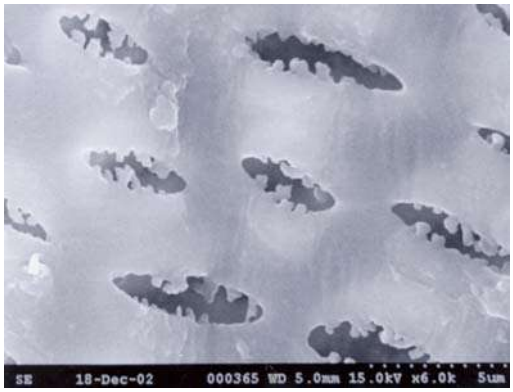


Fig. 46. Vestured pits as seen from outside of the vessel (oval outline of pit cavity) in *Macrocarpaea wallnoeferi.*

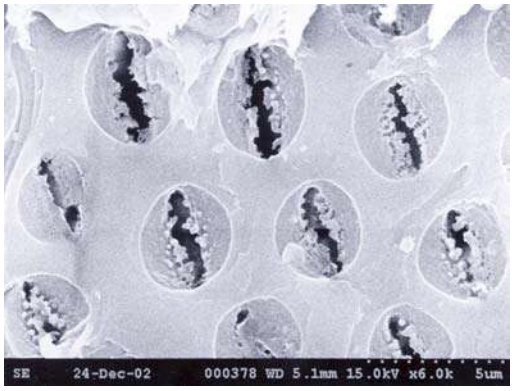


Fig. 47. Vestured pits as seen from inside the vessel (warty slit, no oval around the pit) in *Macrocarpaea gattaca.*

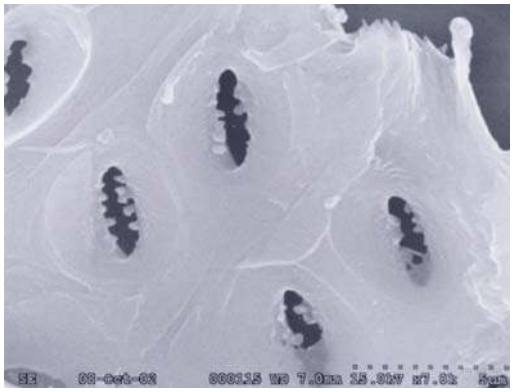


Fig. 48. Vestured pits as seen from outside of the vessel (oval outline of pit cavity) in *Symbolanthus macranthus*.

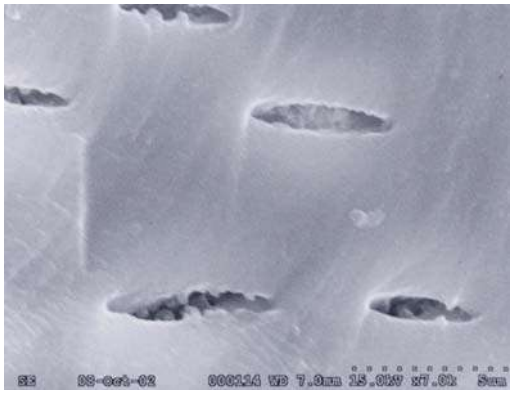


Fig. 49. Vestured pits as seen from inside the vessel (warty slit, no oval around the pit) in *Symbolanthus macranthus*.

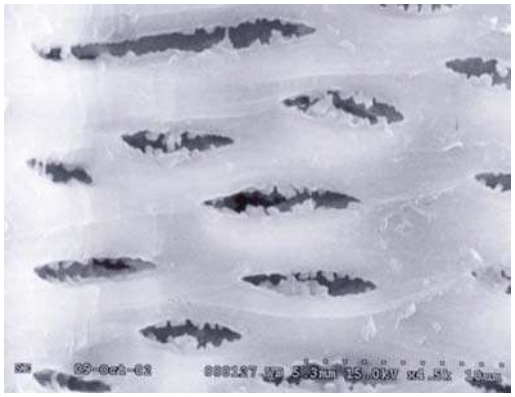


Fig. 50. Vestured pits as seen from outside of the vessel (oval outline of pit cavity) in *Tachia occidentalis*.

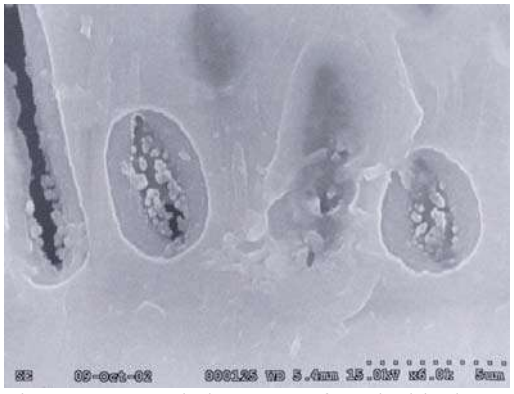


Fig. 51. Vestured pits as seen from inside the vessel (warty slit, no oval around the pit) in *Tachia occidentalis.*

Fig. 46–51 are examples of anatomical characters in *Macrocarpaea*, *Symbolanthus*, and *Tachia*. Scale bar at bottom right hand side consists of a series of eleven small squares, the length of the series equaling 5 or 10 µm. SEM by S. Carlquist.

Genus and Species	Collection number	Country	Herb	Shrub >3m	Tree <3 m
Macrocarpaea angelliae J.R. Grant & Struwe	*Grant 4289*	Ecuador		X	
Macrocarpaea apparata J.R. Grant & Struwe	*Grant 3999, 4002*	Ecuador			X
Macrocarpaea arborescens Gilg	*Grant 4084*	Ecuador			X
Macrocarpaea bubops J.R. Grant & Struwe	*Grant 4046*	Ecuador			X
Macrocarpaea gattaca J.R. Grant	*Grant 4209*	Ecuador		X	
Macrocarpaea harlingii J.S. Pringle	*Grant 4048*	Ecuador		X	
Macrocarpaea jensii J.R. Grant & Struwe	*Grant 4047*	Ecuador		X	
Macrocarpaea lenae J.R. Grant	*Grant 4013*	Ecuador		X	
Macrocarpaea luna-gentiana J.R. Grant & Struwe	*Grant 4027, 4028*	Ecuador			X
Macrocarpaea micrantha Gilg	*Grant 3966*	Peru		X	
Macrocarpaea noctiluca J.R. Grant & Struwe	*Grant 3977, 3994*	Ecuador			X
Macrocarpaea pachystyla Gilg	*Schunke 5298*	Peru			
Macrocarpaea rubra Malme	*Grant 3449*	Brazil	X		
Macrocarpaea sodiroana Gilg	*Grant 4209*	Ecuador		X	
Macrocarpaea subsessilis Weaver & J.R. Grant	*Grant 4020*	Ecuador		X	
Macrocarpaea wallnoeferi J.R. Grant	*Wolfe 12269A*	Peru		X	
Macrocarpaea wurdackii Weaver & J.R. Grant	*Wurdack 1071*	Peru		X	
Symbolanthus macranthus (Benth.) Moldenke	*Grant 3973*	Ecuador			X
Tachia occidentalis Maguire & Weaver	*Woytkowski 5348*	Peru		X	

Tab. 3. Species of *Macrocarpaea* used in Wood Anatomy studies

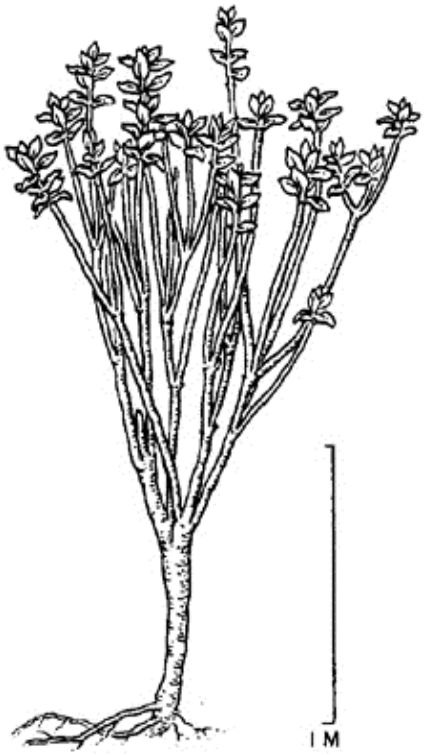


Fig. 52. Subpáramo tree *M. luna-gentiana* J.R. Grant & Struwe
Illustration by Bobbi Angell.

PALYNOLOGY

Pollen of *Macrocarpaea* has been thoroughly discussed in two important papers (Nilsson 1968; 2002). Therefore, below is a survey of Nilsson's results seen in this taxonomic context. In the first paper, Nilsson (1968) conducted a sampling of 26 species and some related genera. His results led Weaver (1972) to transfer the monotypic genus *Rusbyanthus cinchonifolius* to *Macrocarpaea*, and Maguire & Boom (1984) to remove the species with pollen in tetrads to a new genus, *Rogersonanthus*. Nilsson's second paper (2002) expanded on the first, especially in following Weaver (1972) and Maguire & Boom (1984). In Appendix I below, Nilsson's 1968 and 2002 data are modified to exclude the species that were transferred to *Rogersonanthus*, and include four recent counts, for a total of 53 samples from 35 species when aligned to species concepts espoused in this thesis.

Two morphological types of pollen grains occur in *Macrocarpaea*. The *glabra*-type (Nilsson 1968) is present in most species of the genus, while the *corymbosa*-type is identified for a small group of species. According to Nilsson (2002), *glabra*-type pollen is "3–colporate, rarely porate, 23–44 x 26–42 μm, spheroidal to subspheroidal, with reticulate to verrucose-gemmate exine, and usually relatively wide muri" (Fig 53A). The two samples of *longifolius*-type are probably variants on the *glabra*-type, as *M. loranthoides*, the species from which they were identified does in fact belong to genus *Macrocarpaea*.

The *corymbosa*-type (= *Rusbyanthus*-type' of Gilg 1895) (Nilsson 1968) is reported in five species (species names following this thesis): *M. cinchonifolia*, *M. gentryi*, *M. normae*, *M. pachystyla*, and *M. revoluta*. This group conforms to *Macrocarpaea* sect. *Magnolifoliae*, and provides an important character to define the section. According to Nilsson (2002), *corymbosa*-type pollen is "3–colporate to colporate, 28–35 x 28–39 μm, subspheroidal to spheroidal, and with warty exine (verrucae, gemmae, pila, and clavae are present)" (Fig. 53B).

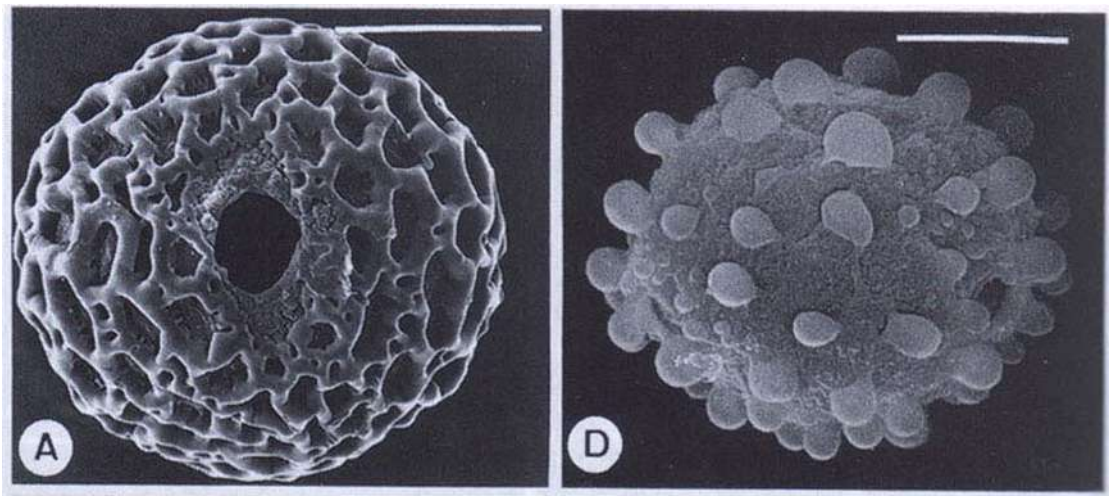


Fig. 53. Pollen grains of *Macrocarpaea* (*glabra*-type and *corymbosa* -type). Fig. 4.20 from Nilsson (2002: 438). A. *M. bracteata* (*glabra*-type; *Dorr 4940*), 3–colporate, reticulate pollen in equatorial, apertural view. D. *M. cinchonifolia* (*corymbosa*-type; *Rusby 1173*), 3–colporate, verrucose pollen in equatorial view. Scale bars: A, D – 10 μm.

CYTOLOGY

In the Gentianaceae, chromosome number has been a useful character to help support taxonomic groups in tribe Chironieae (*Centaurium* s.l., *Sabatia*), and tribe Gentianeae (*Gentiana*, *Gentianella*, *Gentianopsis*, *Swertia* s.l.) (Mészáros et al. 2002). Sections within *Gentiana* for example are supported by different chromosome numbers (Ting-nong & Shang-Wu 2001; Yuan et al. 1998). However, in all genera in tribe Helieae so far examined the chromosome number is consistent; *Chelonanthus* (n = 20), *Macrocarpaea* (n = 21), and *Symbolanthus* (n = 40) (Weaver 1969; 1972a; Weaver & Rüdenberg 1975).

Chromosome counts are reported for eight species of *Macrocarpaea*, each with a consistent number of n=21 (Tab. 4). In addition to the six counts published by Weaver (1969; 1972b; 1975), two new counts are reported here, for *M. arborescens* and *M. sodiroana*. Unlike many other genera of gentians where numerous differences in chromosome number are found, *Macrocarpaea* has proven so far to be invariable, even between sections. The counts are for four of the five sections, largely covering the morphological diversity in the genus. Based on these studies, a wider sampling of species is unlikely to show a differing count. The only section missing is *Tabacifoliae*. Due to its basal position in the genus, and its member *M. rubra* that has an herbaceous habit, chromosome studies should be conducted.

Species	Section	Country	Collector, #	n =	Citation
Macrocarpaea arborescens	*Magnolifoliae*	Ecuador	Chassot 00-15	21	here
Macrocarpaea densiflora	*Macrocarpaea*	Colombia	Weaver 2644	21	Weaver 1975
Macrocarpaea gaudialis	*Macrocarpaea*	Colombia	Weaver 2050	21	Weaver 1975
Macrocarpaea glabra	*Macrocarpaea*	Colombia	Weaver 2636	21	Weaver 1975
Macrocarpaea nicotianifolia	*Macrocarpaea*	Colombia	Weaver 2634	21	Weaver 1975
Macrocarpaea sodiroana	*Choriophylla*	Ecuador	Grant 4210	21	here
Macrocarpaea thamnoides	*Caribbigenes*	Jamaica	Weaver 952	21	Weaver 1969
Macrocarpaea valerii	*Macrocarpaea*	Costa Rica	Weaver 1405	21	Weaver 1972b

Tab. 4. Table of chromosome counts in *Macrocarpaea.*

For chromosome counts, floral buds were opened and fixed in 20 ml of fixating solution prepared with 75 ml absolute ethanol, 23 ml glacial acetic acid, ≈25 drops of acetocarmine, and ≈3–4 drops of acetate de fer. After 2–5 weeks of fixation, anthers were removed and dissected, stained and heated in acetocarmine, then squashed and prepared on slides.

Macrocarpaea is related to three other genera, *Chorisepalum*, *Tachia*, and *Zonanthus*. However, there are no chromosome counts for these genera precluding any theories on chromosomal evolution in the clade. Such counts could provide insight into evolution within the tribe Helieae, and more specifically to *Macrocarpaea*. Since these genera are from relatively remote regions in the Neotropics, we will have to wait until fieldwork aimed specifically at cytology can be performed to understand chromosomal evolution in the tribe.

Cytology has not played a significant role in the understanding of taxonomic relationships within the gentian tribe Helieae. With more chromosome counts made in other genera throughout the tribe, interesting results pertinent to evolutionary relationships may be obtained. Molecular data have shown that *Symbolanthus* (n=40) is the most derived genus within the *Symbolanthus* clade of the Helieae (Struwe 2002). *Symbolanthus* with n=40 is sister to *Chelonanthus* (n=20), and therefore *Symbolanthus* may be an example of ancient polyploidy.

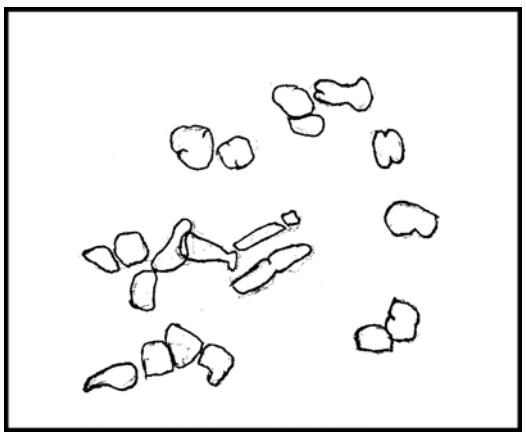


Fig. 54. Chromosomes of *M. sodiroana*, *Grant 4210*. n=21. Illustration by Olivier Stauffer.

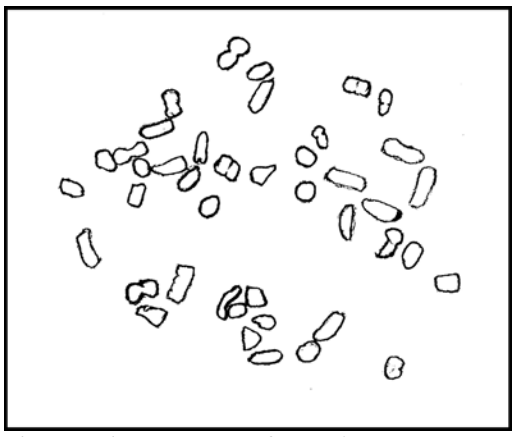


Fig. 55. Chromosomes of *M. arborescens*, *Chassot 00-15*. 2n=42. Illustration by Olivier Stauffer.

3. PHYLOGENY AND CLASSIFICATION

In this study of *Macrocarpaea*, observations of all species have been based on herbarium specimens (as well as many populations in the field). Therefore, the classical *Morphological Species Concept* of Linnaeus is followed. This concept is based on the theory that a species is the "smallest unit with consistent and clearly recognizable characteristics" (Stuessy 1990). A number of modern species concepts exist, but do not fill the need of a traditional plant taxonomist. Concepts such as Autapomorphy, Biological, Diagnostibility, Evolutionary, Genealogical, Phenetic, and Recognition (Judd et al 1999), have their place, but can not be used when one principally studies herbarium specimens or even populations in the field.

That so many new species occur in *Macrocarpaea* is not surprising (63 of 98 species recognized here). The genus has simply not been studied on a genus-wide scale for over 50 years. A tremendous amount of unidentified herbarium material existed to be studied from remote areas where many new species are found. It is not as simple to say that the species concept employed here is that of a taxonomic splitter, dividing species into smaller and smaller groups. In fact, in my estimation, I have actually defined rather broad species. Explaining a species concept is difficult since some decisions may be made on gut feeling or gestalt.

Generalized Species concept in *Macrocarpaea*

A species consists of a group of morphologically similar individuals (herbarium specimens). Secondarily, these individuals typically originate from the same biogeographical area and habitat.

A suite of characters has been used to circumscribe species, species groups, and to formulate an infrageneric classification within *Macrocarpaea*. The most important characters are those of gross plant morphology of herbarium specimens (especially leaf morphology, inflorescence architecture, and floral morphology). Additional sources of taxonomically useful information come from seed anatomy, pollen morphology and molecular data.

A morphological data matrix has been prepared and is constantly updated as descriptions of new species are composed. 83 characters per species are entered into an Excel database. This ensures both parallel descriptions of all new species, and captures data that will eventually be scored and combined with molecular data. Eventually, characters of all 98 species will be catalogued.

The following is the provisional infrageneric classification:

Infrageneric Classification of *Macrocarpaea*

sect. ***Tabacifoliae*** (4 sp.)
Distribution: Southeastern Brazil
Main characters: *glabra*-type pollen; Flattened seeds, flat to polygonal, no wings.

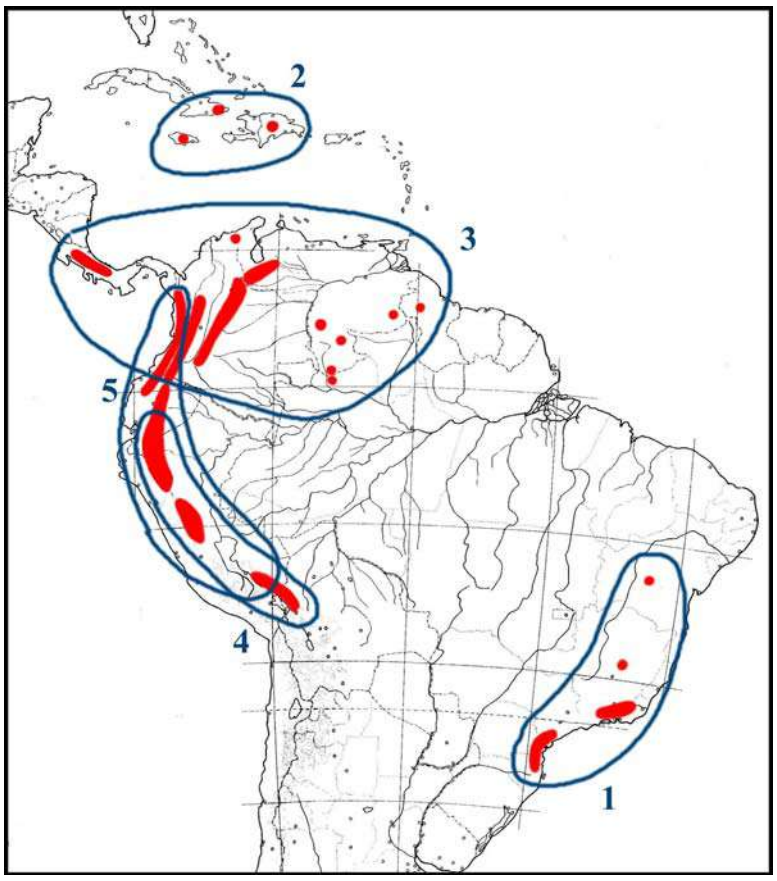
sect. ***Caribbigenes*** (3 sp.)
Distribution: Greater Antilles of the Caribbean
Main characters: *glabra*-type pollen; Polygonal seeds with no wings.

sect. ***Macrocarpaea*** (38 sp.)
Distribution: Northern Andes (especially Colombia), Southern Mesoamerica (Costa Rica and Panama), and Pantepui of the Guayana Shield
Main characters: *glabra*-type pollen; Rimmed seeds, polygonal to flattened, no wings to winged.

sect. ***Magnolifoliae*** (19 sp.)
Distribution: Central Andes (especially Central Peruvian Andes)
Main characters: *corymbosa*-type pollen; Winged seeds, flattened, wings at base and apex, or all around; generally large flowers (broad calyx and corolla).

sect. ***Choriophylla*** (34 sp.)
Distribution: Central Andes (especially Huancabamba region)
Main characters: *glabra*-type pollen; Perimetrically winged seeds, flattened with wings all around.

The sections are based on distribution, pollen morphology, seed morphology, and molecular data. Although trends exist, providing broad definitions of the gross morphology of each group is problematic. Each group has odd or unique members that complicate general characterization, e.g., *Macrocarpaea rubra* of sect *Tabacifoliae* is a perennial herb with an urceolate corolla; *M. zophoflora* of sect. *Magnolifoliae* has interpetiolar stipules.



Map 6. Distributions of the five sections of *Macrocarpaea*: 1.*Tabacifoliae*, 2.*Caribbigenes*, 3. *Macrocarpaea*, 4. *Magnolifoliae*, and 5. *Choriophylla*.

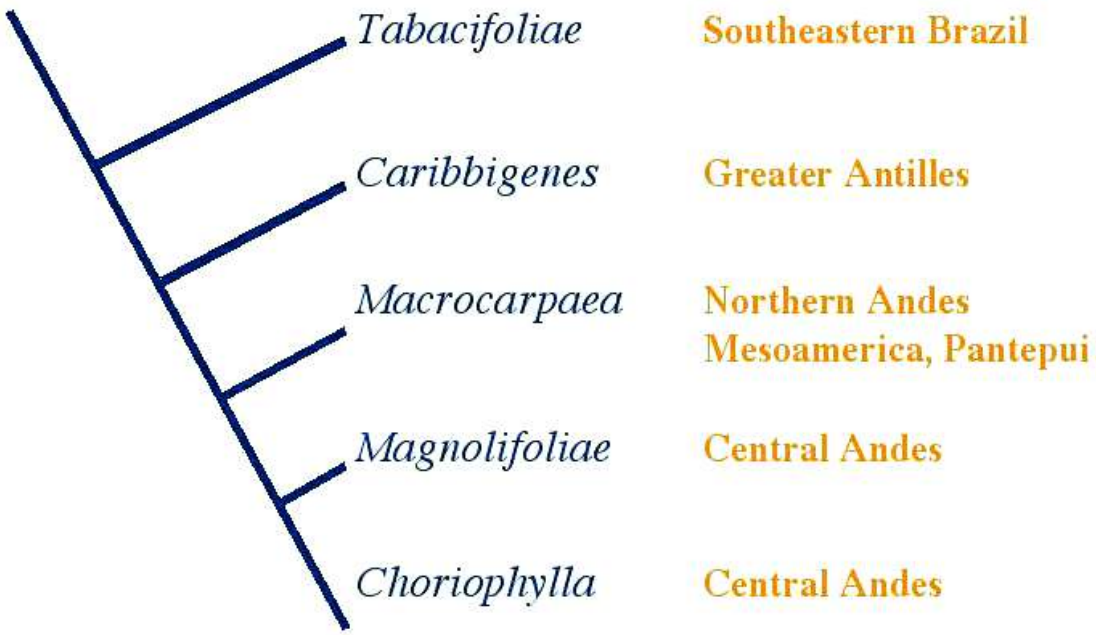
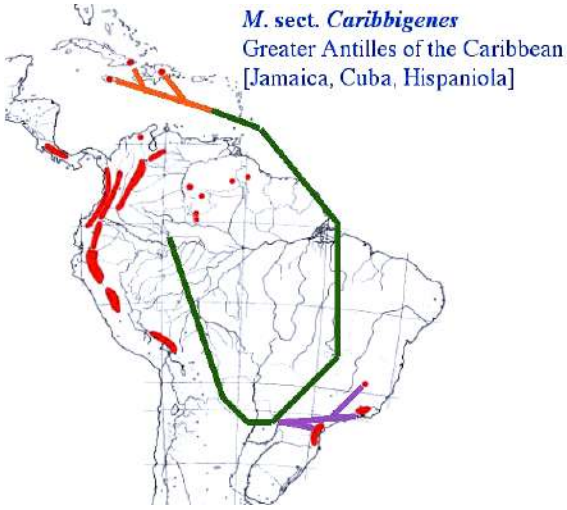
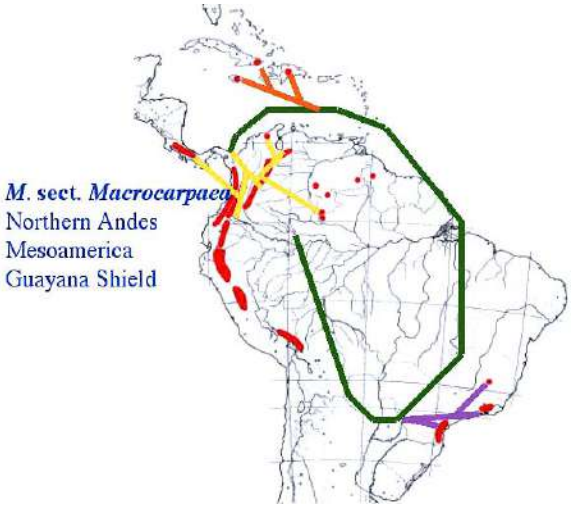


Fig. 56. The relationship between the sections of *Macrocarpaea* and their geographical distributions.

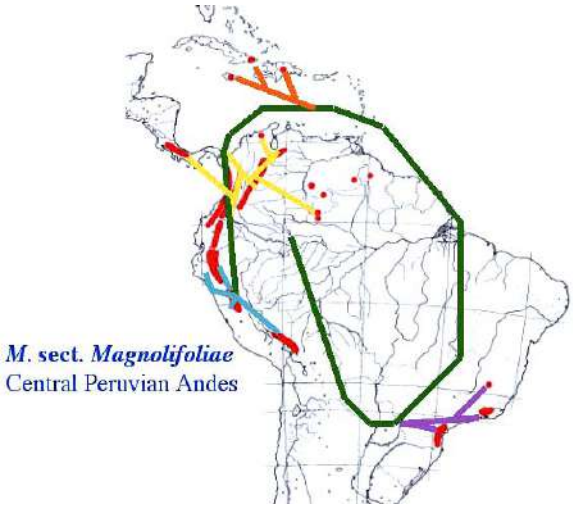
Map. 1. *Macrocarpaea* sect. *Tabacifoliae* is the basal and most ancestral group in *Macrocarpaea*.



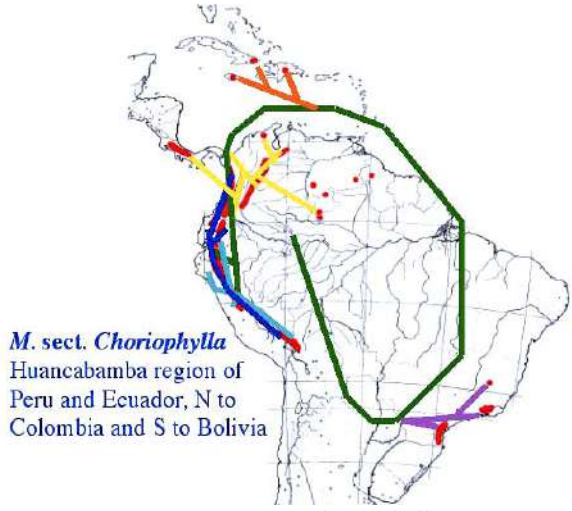
Map. 2. *Macrocarpaea* sect. *Caribbigenes*. Possible long-distance dispersal spread the genus to the Greater Antilles of the Caribbean.



Left. Map. 3. *Macrocarpaea* sect. *Macrocarpaea*. Dispersal may account for the next three, and most speciose lineages. The genus appears to have arrived first in the Northern Andes, and has then spread in a generally southerly direction to the Guayana Shield, Southern Mesoamerica, and the Central Andes.



Map. 4. *Macrocarpaea* sect. *Magnolifoliae*. From the Northern Andes, *Macrocarpaea* dispersed to the Cordillera Central and Oriental of Peru and Bolivia.

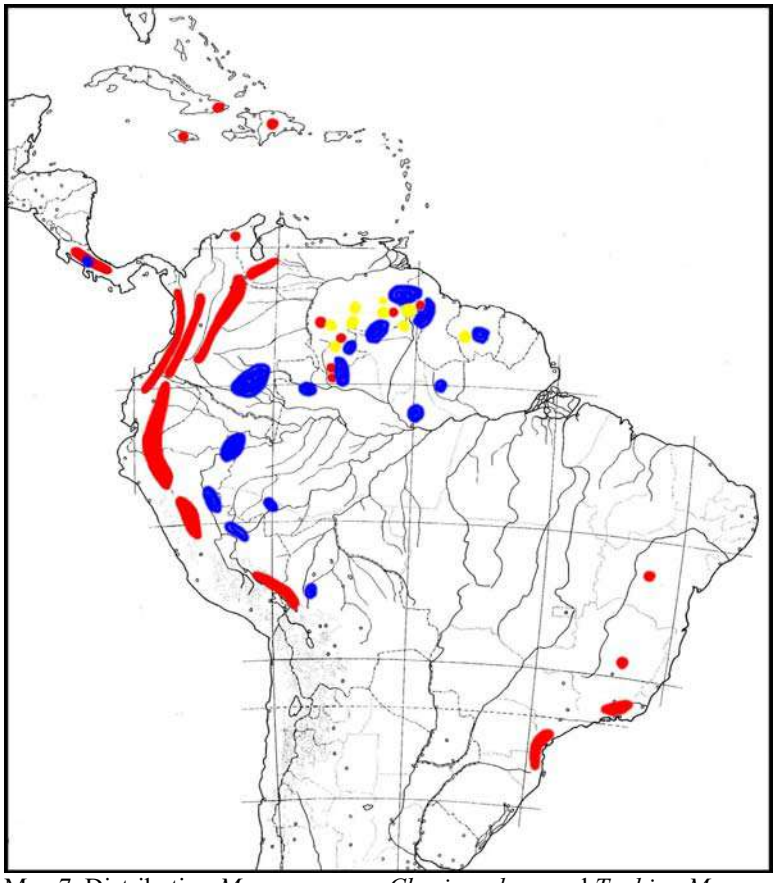


Map. 5. *Macrocarpaea* sect. *Choriophylla*. From the most southerly extend of its range in the Andes, *Macrocarpaea* then began a northward movement from Peru to Ecuador and Colombia.

Maps 1–5 show the hypothesized dispersal of *Macrocarpaea* in the Neotropics based on preliminary 5S-NTS and ITS molecular data.

Relationships of *Macrocarpaea* to other genera

According to molecular data of genera so far analyzed in the Gentianaceae, *Macrocarpaea* is the namesake of the *Macrocarpaea* clade comprising three genera: *Macrocarpaea* (97 sp.), *Tachia* (10 sp.) and *Chorisepalum* (5 sp.) (Struwe et al. 2002). Several woody to woody-herbaceous genera have not been sequenced, yet could potentially join this group including *Rogersonanthus* (3 sp.) and *Zonanthus* (1 sp.). *Zonanthus* is a monotypic genus endemic to Cuba.



Map 7. Distribution *Macrocarpaea*, *Chorisepalum*, and *Tachia*. *Macrocarpaea* in red, *Tachia* in blue, and *Chorisepalum* in yellow. *Macrocarpaea* is mountainous (especially the Andes), *Tachia* is largely lowland Amazonian, and *Chorisepalum* is restricted to Pantepui of the Guayana Shield. Distribution of *Tachia* is modified from Maguire & Weaver (1975) and González (1998).

Fig. 57. *Tachia guianensis* Aubl. *Mori 23439* Photographer C. Gracie.

Fig. 58. *Tachia schomburgkiana* Benth. *Maas 3989* Photographer Paul Maas.

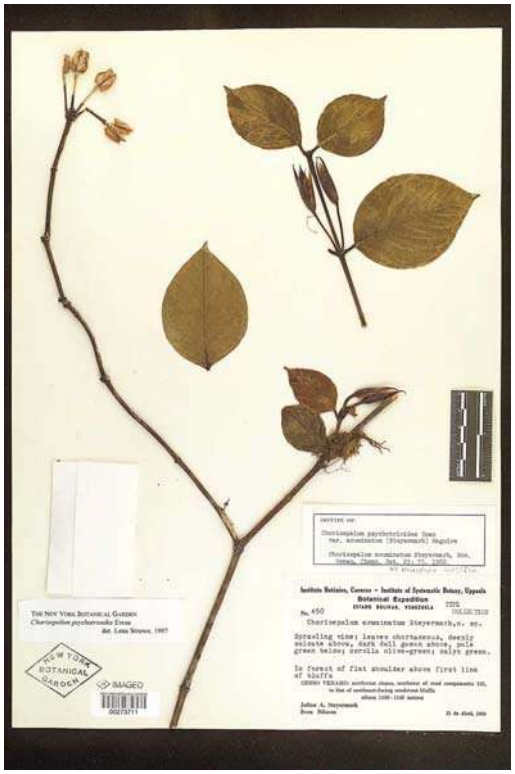


Fig. 59. *Chorisepalum psychotrioides* Ewan.

Fig. 60. *Tachia grandifolia* Maguire & Weaver

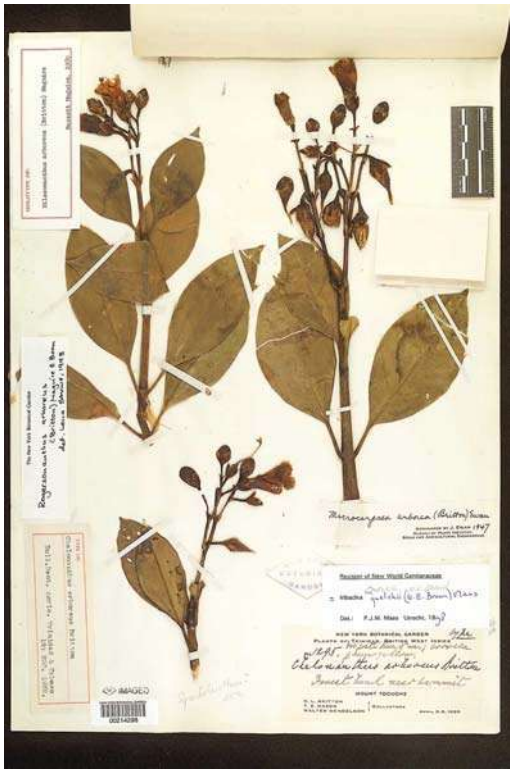


Fig. 61. *Rogersonanthus arboreus* (Britton) Maguire & Boom.

Fig. 62. *Zonanthus cubensis* Grisebach.

Fig. 59–62 represent herbarium specimens of genera related to *Macrocarpaea*: *Chorisepalum*, *Rogersonanthus*, *Tachia*, and *Zonanthus*. Images in Fig. 59–61 were downloaded from the web site of the New York Botanical Garden: http://www.nybg.org/bsci/hcol/vasc/.

4. SYSTEMATIC TREATMENT

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.

Plants branched to unbranched; treelets, robust trees to 10 m, facultative epiphytes (*M. browallioides*, *M. gondoloides*, *M. luteynii*, and *M. subcaudata*), upper páramo shrubs, rarely perennial herbs to 1 m (*M. rubra*); glabrous to pubescent. **Trunk** 0.5–9.5 cm in diameter, wood solid to hollow, typically narrower in trunk and wider in younger branches, growth rings faint to prominent, bark papery thin, to thick and pithy to 4 mm wide. **Stems** terete to quadrangular, solid to hollow. **Leaves** entire, petiolate to sessile; glabrous to pubescent; small thick and coriaceous, to large thin and papery; linear-lanceolate, lanceolate, oblong, ovate, oval, elliptic, oblanceolate, to obovate in shape; **leaf base** is aequilateral, oblique, attenuate, cuneate, to rounded; **leaf apex** acuminate, acute, mucronulate, obtuse to rounded. **Petioles** short to long and slender; unvaginated to having a long scooped out groove or vagination on the upper surface; **interpetiolar ridge** prominent, exstipulate to stipulate (*M. zophoflora*). **Inflorescence** a thyrse, composed of branches of cymes in a racemose branching pattern; short and compact in páramo species from 3 cm (e.g., *M. subsessilis*), to towering and candelabriform over 2 m (e.g., *M. apparata*). **Bracts** leaf-like and found throughout the inflorescence. **Bracteoles** scarious to bract-like. **Flowers** pedicellate, remaining erect or becoming nodding in maturity. **Calyx** narrowly to broadly campanulate; ecarinate to strongly carinate; and glabrous, spiculate to pubescent (Fig. C, H) in vestiture; **calyx lobes** ovate, oblong, rotund, elliptic, to lunate in shape, with apices that vary from acuminate, acute, obtuse, to rounded; persistent in fruit. **Corolla** 5–merous, funnel-shaped and actinomorphic, rarely urceolate (*M. rubra*), yet when androecium and gynoecium are included, the overall flower is zygomorphic; leathery to fleshy; white, cream, yellow to light green in color; **corolla lobes** ovate, elliptic, lanceolate, to lunate, with apices that vary from acute, obtuse, retuse to rounded. **Stamens** of unequal length, originating from about halfway up the corolla tube, displaced such as to aggregate together on the *lower* part of the corolla mouth; **anthers** linear to elliptical, versatile, sagittate; **pollen** in monads with either *glabra*-type (3-colporate, rarely porate, 23-44 x 26-42 μm, spheroidal to subspheroidal, with reticulate to verrucose-gemmate exine, and usually relatively wide muri), or *corymbosa*-type (3–colporate to colporate, 28–35 x 28–39 μm, subspheroidal to spheroidal, and with warty exine [verrucae, gemmae, pila, and clavae are present]). **Ovary** sessile, bilocular, placentation axile or parietal with strongly inrolled placentas; **style** persistent in fruit; **stigma** bilamellate with broad lobes. **Capsule** dry, woody, 2–carpelled, bilocular and dehiscing medially; **seeds** flattened, polygonal, rimmed, winged or winged perimetrically, miniscule, ca. 0.2–1.6 x 0.2–0.6 mm.

Five sections are recognized here within *Macrocarpaea*: *Tabacifoliae*, *Caribbigenes*, *Macrocarpaea*, *Magnolifoliae*, and *Choriophylla*.

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.
2. Sect. ***Caribbigenes*** J.R. Grant, sect. nov. T.: *Macrocarpaea domingensis* Urb. & Ekman, Arkiv Bot. Stockh. 23A(11): 30. 1931.
3. Sect. ***Macrocarpaea***. T.: *Lisianthus glaber* L.f., Suppl.: 134. 1781. *Macrocarpaea glabra* (L.f.) Gilg in Engl. & Prantl, Nat. Pflanzenfam. 4(2): 94. 1895.
4. 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.
5. 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.

Reg.	Biogeographical Area	Sections of *Macrocarpaea*					# sp.
		Taba	Cari	Macr	Magn	Chor	
1	Southeastern Brazil	0	0	0	0	0	[4]
1.1	Southeastern Brazil: Atlantic Forest	2					2
1.2	Southeastern Brazil: Espinhaço Range	2					2
2	Greater Antilles of the Caribbean	0	3	0	0	0	3
3	Pantepui of the Guayana Shield	0	0	6	0	0	6
4	Southern Mesoamerica (Costa Rica and Panama)	0	0	4	0	0	4
5	Andes	0	0	0	0	0	[81]
5.1	Northern Andes: Sierra Nevada de Santa Marta, Colombia	0	0	1	0	0	1
5.2	Northern Andes: Cordillera de Mérida, Venezuela	0	0	3	0	0	3
5.3	Northern Andes: Cordillera Oriental, Colombia	0	0	10	0	1	11
5.4	Northern Andes: Cordillera Central, Colombia	0	0	8	0	0	8
5.5	Northern Andes: Cordillera Occidental, Colombia and Ecuador	0	0	5	0	3	8
5.6	Central Andes: Huancabamba region, Ecuador and Peru	0	0	[1]	[5]	[23]	[29]
5.6.1	Huancabamba of Ecuador	0	0	0	2	6	8
5.6.2	Huancabamba of the Cordillera de Condor, Ecuador/Peru	0	0	0	1	6	7
5.6.3	Huancabamba of Peru	0	0	1	2	11	14
5.7	Central Andes: Cordillera Central, Peru	0	0	0	9	5	14
5.8	Central Andes: Cordillera Oriental, Peru and Bolivia	0	0	0	5	2	7
		4	3	38	19	34	98

Tab. 5. Sections of *Macrocarpaea* and their Biogeographical Areas. This table shows for each of the five sections of *Macrocarpaea*, the number of **endemic** species that occur in each of 17 different geographic regions. It shows that sect. *Tabacifoliae* is restricted to southeastern Brazil, and sect. *Caribbigenes* to the Greater Antilles. Likewise, sect. *Macrocarpaea* occurs predominantly in the Northern Andes (especially Colombia), whereas sects. *Magnolifoliae* and *Choriophylla* occur primarily in the Central Andes (especially Peru).

MACROCARPAEA SECT. TABACIFOLIAE

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. caatingae*, *M. glaziovii*, *M. obtusifolia*, and *M. rubra*. *Macrocarpaea rubra* and *M. glaziovii* occur in the Mata Atlântica, and *M. caatingae* and *M. obtusifolia* occur on the Brazilian Plateau.

1. ***M. caatingae*** J.R. Grant, Harvard Pap. Bot. 2004. **INED**. TYPE: Brazil. Bahia: Mun. de Palmeiras, Estrada que sai da BR-242 e da acesso ao Morro do Pai Inácio, 7 January 1997, *Grillo & Conceição 217* (Holotype SPF).

2. ***M. glaziovii*** Gilg, Bot. Jahrb. Syst. 22: 335. 1896. TYPE: Brazil. Rio de Janeiro: *Glaziou 4939* (type B? [destroyed]; Lectotype: K; isolectotypes: C, P, selected by Grant [Mac V 2003]).
= *Lisianthus obtusifolius* var. *constrictus* Griseb., Gen. et Sp. Gent.: 175. 1839. *Macrocarpaea glaziovii* Gilg subsp. *constricta* (Griseb.) Ewan, Proc. Biolog. Soc. Washington 65: 189. 1952. TYPE: Brazil. Minas Gerais, 1000', *Langsdorff s.n*. (lectotype K (herb. Hooker); isolectotype BR, selected by Grant [Mac V 2003]).

3. ***M. obtusifolia*** (Griseb.) Gilg in Engl. & Prantl, Nat. Pflanzenfam. 4(2): 94. 1895. Based on: *Lisianthus obtusifolius* Griseb., Gen et Sp. Gent.: 175. 1839. *Helia obtusifolia* (Griseb.) Kuntze, Rev. Gen. 428. 1891. TYPE: Brazil. Rio de Janeiro: *Sellow s.n*. (Lectotype: K; isolectotype: P), designated by Weaver (1972: 305).

4. ***M. rubra*** Malme, Ark. Bot. 22A(2): 3. 1928. TYPE: Brazil. Paraná: *Dusén s.n*. (Lectotype: S; isolectotypes: GH, LD, selected by Grant [Mac V 2003]).

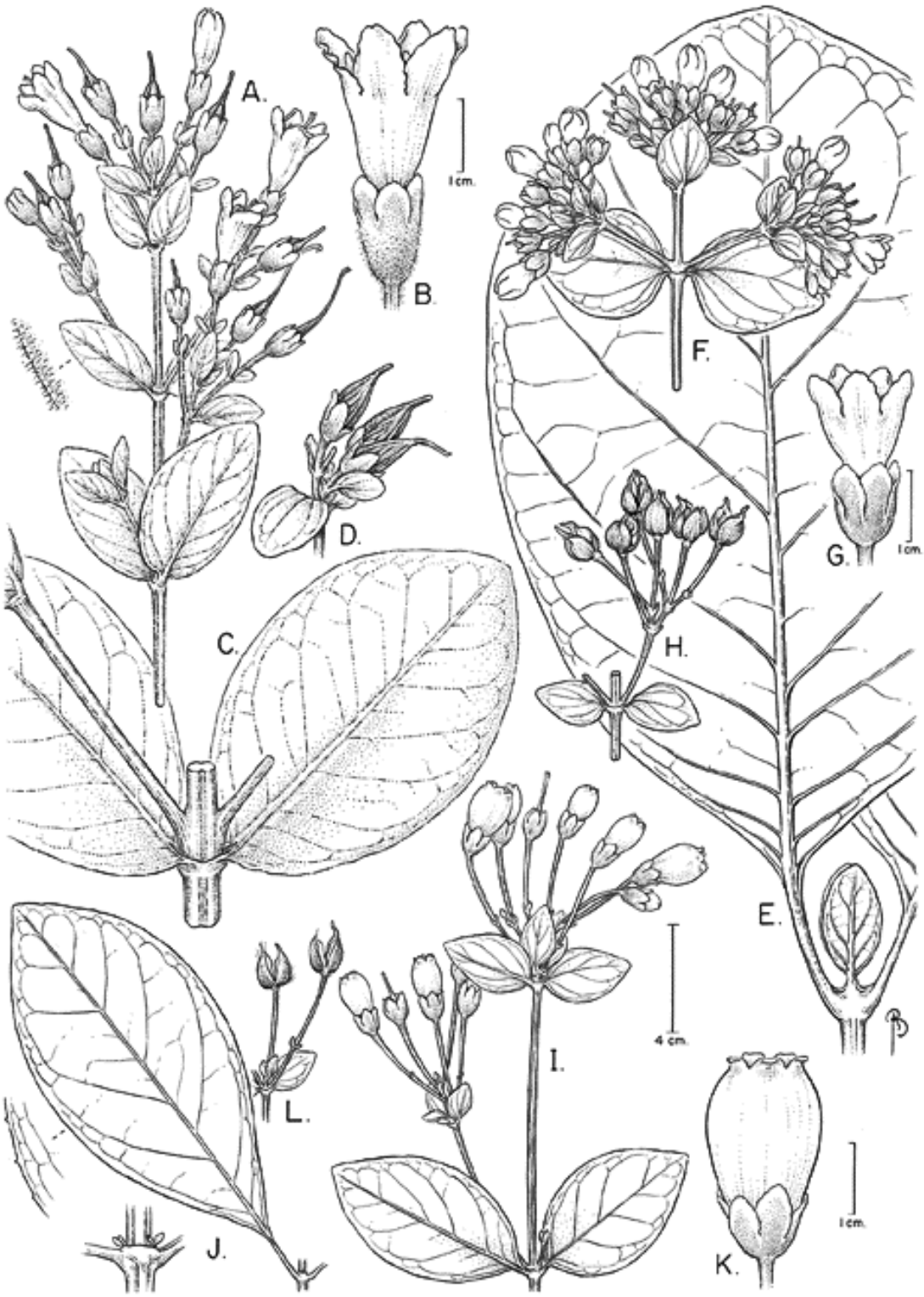


Fig. 63. Representatives of *Macrocarpaea* sect. *Tabacifoliae*. A–D *Macrocarpaea obtusifolia.* A, habit of flowering stem; B, flower; C, leaves; D, fruits. E–H *M. glaziovii.* E, leaves; F, habit of flowering stem; G, flower; H, fruits. I–L *M. rubra.* I, habit of flowering stem; J, interpetiolar ridge, and leaf; K, flower; L, fruits. A drawn from *Irwin et al. 22249* (NY); B–C drawn from *Duarte 2280* (RB); D drawn from *Farney 1207* (RB); E–G drawn from *Glaziou 4939* (P); H drawn from *Pereira 229* (RB); I–K drawn from *Oliveira 686* (MBM); L. drawn from *Kummrow 2385* (MBM).

MACROCARPAEA SECT. CARIBBIGENES

2. Sect. ***Caribbigenes*** J.R. Grant, sect. nov. **INED** T.: *Macrocarpaea domingensis* Urb. & Ekman, Arkiv Bot. Stockh. 23A(11): 30. 1931.

Macrocarpaea sect. *Caribbigenes* comprises the three species that occur in the Greater Antilles of the Caribbean: *M. domingensis* (Hispaniola: Dominican Republic), *M. pinetorum* (Cuba), and *M. thamnoides* (Jamaica). Species 5–7.

5. ***M. domingensis*** Urb. & Ekman, Ark. Bot. 23A(11): 30. 1931. TYPE: Dominican Republic. Santo Domingo: *Ekman H11504* (Holotype: S; isotypes: K, US).

6. ***M. pinetorum*** Alain Mem. Soc. Cubana Hist. Nat. 22: 114. 1955. TYPE: Cuba, Oriente: *Clemente 4401* (Holotype: LS [not seen]; isotypes: GH, US).

= *Macrocarpaea pauciflora* Alain, Mem. Soc. Cubana Hist. Nat. 22: 115. 1955. TYPE: Cuba, Oriente: *Alain 3855* (Holotype: LS [not seen]; isotype: NY).

7. ***M. thamnoides*** (Griseb.) Gilg in Engl. & Prantl, Nat. Pflanzenfam. 4(2): 94. 1895. Based on: *Lisianthus thamnoides* Griseb., Fl. Brit. W. Ind.: 424. 1864. *Helia thamnoides* (Griseb.) Kuntze, Rev. Gen. 428. 1891. TYPE: Jamaica. *Macfayden s.n*. (Holotype: K).

= *Macrocarpaea hartii* Krug & Urb., Notizbl. Bot. Gart. Berlin 1: 80. 1895. TYPE: Jamaica. *Hart 1417* (Lectotype: S; isolectotype: US, selected by Grant [Mac V 2003]).

Fig. 64. Representatives of *Macrocarpaea* sect. *Caribbigenes*. A–D *Macrocarpaea thamnoides.* A, leaf; B, habit of flowering stem; C, flower; D, fruits. E–G *M. pinetorum.* E, leaf; F, habit of flowering stem; G, bud and flower. H–K. *M. domingensis.* H, leaves; I, habit of flowering stem; J, bud; K, fruits. A–B drawn from *Proctor 19665* (BM); C drawn from *Acevedo 9700* (NY); D drawn from *Proctor 23868* (BM); E drawn from *Clement 4401* (US); F–G drawn from *Wright 1347* (BM); H drawn from *Zanoni et al. 41117* (NY); I–J drawn from *Zanoni et al. 44171* (NY); K drawn from *García & Peláez 1030* (NY).

MACROCARPAEA SECT. MACROCARPAEA

3. 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 38 species largely of the northern Andes (Colombia and Venezuela), Southern Mesoamerica (Costa Rica and Panama), and Pantepui of the Guayana Shield. Species 8–45.

8. ***M. affinis*** Ewan, Proc. Biol. Soc. Wash. 63: 163. 1950. TYPE: Colombia. Santander: *Uribe 1991* (Holotype: US).

9. ***M. auriculata*** Weaver & J.R. Grant, Harvard Pap. Bot. 8(1): 88. 2003. TYPE: Costa Rica. Heredia: forests of Rio Vueltas, 23 May 1969, *L.D. Gomez 2265* (Holotype: GH; isotypes: F [2 sheets], MO, NY).

10. ***M. autanae*** Weaver, Mem. New York Bot. Gard. 32: 336. 1981. TYPE: Venezuela. Amazonas: *Steyermark 105191* (Holotype: VEN; isotype: NY).

11. ***M. ayangannae*** J.R. Grant, Struwe & Boggan, Harvard Pap. Bot. 5(2): 493. 2001. TYPE: Guyana. *Pipoly 11103* (Holotype: US [2 sheets], isotype: NY)

12. ***M. biremis*** J.R. Grant, Harvard Pap. Bot. 8(2): 2003. **INED.** TYPE: Colombia. Cauca: "La Gallera", Micay Valley, 1 July 1922, *Killip 8000* (Holotype: GH).

13. ***M. bracteata*** Ewan, Contr. U. S. Natl. Herb. 29: 236. 1948. TYPE: Venezuela. Lara: *Steyermark 55224* (Holotype: F; isotype: US).

14. ***M. browallioides*** (Ewan) A. Robyns & S. Nilsson, Bull. Jard. Bot. Natl. Belg. 40: 14. 1970. Based on: *Lisianthus browallioides* Ewan, Proc. Biol. Soc. Washington 64: 132. 1951. TYPE: Panama. Bocas del Toro: *Allen 4932* (Holotype: MO; isotype: G).

15. ***M. calophylla*** Gilg, Bot. Jahrb. Syst. 22: 339. 1896. TYPE: Colombia. Magdalena: *Funcke 530* (type B? [destroyed]; Lectotype: G; isolectotypes: BM, K, LD, OXF, W, selected by Grant [Mac V 2003]).

16. ***M. densiflora*** (Benth.) Ewan, Contr. U. S. Natl. Herb. 29: 232. 1948. Based on: *Lisianthus densiflorus* Benth., Pl. Hartw. 227. 1846. TYPE: Colombia. Cauca: *Hartweg 1241* (Holotype: K).

17. ***M. duquei*** Gilg-Ben., Notizbl. Bot. Gart. Berlin 13: 382. 1936. TYPE: Colombia. Cauca: *Duque-Jaramillo 2* (Holotype: B? [destroyed]; neotype: Colombia. Cauca: *Cuatrecasas 21824* (US); isoneotypes COL, F, selected by Grant [Mac V 2003]).

18. ***M. ewaniana*** Weaver & J.R. Grant, Harvard Pap. Bot. 8(1): 103. 2003. TYPE: Venezuela. Trujillo: Dto. Urdaneta, Guirigay, hacia Peña Blanca, August 1958, *Aristeguieta & Medina 3590* (Holotype: VEN; isotypes: NO, NY, US).

19. ***M. gattaca*** J.R. Grant, Harvard Pap. Bot. 8(2): 2003. **INED**. TYPE: Ecuador. Pichincha: Vía San Juan-Chiriboga-Empalme, 10 September 1977, *Jaramillo 22* (Holotype: NY; isotypes: AAU, QCA).

20. ***M. gaudialis*** J.R. Grant, Harvard Pap. Bot. 8(2): 2003. **INED**. TYPE: Colombia. Nariño: scrubby montane forest near El Encano, 27 October 1972, *Weaver 2650* (Holotype: GH [2 sheets]; isotypes: AAU [2 sheets], BM, MO).

21. ***M. glabra*** (L.f.) Gilg in Engl. & Prantl, Nat. Pflanzenfam. 4(2): 94. 1895. Based on: *Lisianthus glaber* L.f., Suppl.: 134. 1781. TYPE: Colombia. *Mutis* specimen 213.2 (Lectotype: LINN), designated by Weaver (1972a: 304).

= *Macrocarpaea bogotana* Gilg, Bot. Jahrb. Syst. 22: 337. 1896. TYPE: Colombia. Cundinamarca: *Holton 470* (type B? [destroyed]; Lectotype: G; isolectotypes: G, GH, K, NY, selected by Grant [Mac V 2003]).

= *Macrocarpaea polyantha* Gilg, Bot. Jahrb. Syst. 22: 336. 1896. TYPE: Colombia. Cundinamarca: *Goudot 1* (type B? [destroyed]; Lectotype: G; isolectotypes: G, GOET, K, P, selected by Grant [Mac V 2003]).

22. ***M. gondoloides*** J.R. Grant, Harvard Pap. Bot. 8(2): 2003. **INED**. TYPE: Colombia. Chocó: Municipio de Nóvita, ladera norte del Cerro Torrá, filo al oeste del Río Surama, camino al Alto del Oso, 22 February 1977, *Forero et al. 3158* (Holotype: MO; isotype: COL).

23. ***M. gulosa*** J.R. Grant, Harvard Pap. Bot. 8(2): 2003. **INED**. TYPE: Colombia. N de Santander: Municipio de Toledo, 28.8 km de San Bernardo de Bata en la via a Saravena, 1 km antes del parador, Alto de Santa Ines, 1 November 1994, *Fernández Alonso et al. 11794* (COL).

24. ***M. hilarula*** J.R. Grant, Harvard Pap. Bot. 8(2): 2003. **INED**. TYPE: Colombia. Meta: Hillsa above ranch house, Finca Balsillas, Upper Río Balsillas (part of old Hacienda Balsillas), 40 km ESE of Neiva, 7 December 1942, *Fosberg 19285* (Holotype: US [3 sheets]; isotypes: NO [3 sheets], S).

25. ***M. illecebrosa*** J.R. Grant, Harvard Pap. Bot. 8(2): 2003. **INED**. TYPE: Colombia. Putumayo: Páramo de San Antonio, entre La Laguna de La Cocha y el Valle de Sibundoy, 13 February 1942, *Schultes 3223* (Holotype: GH; isotypes COL, F).

26. ***M. jocularis*** J.R. Grant, Harvard Pap. Bot. 8(2): 2003. **INED**. TYPE: Colombia. Huila: Cordillera Oriental, SE side Quebrada de Riolora, 15 km SE of Gigante, 20 September 1944, *Little 8708* (Holotype: US; isotypes: COL, NO).

27. ***M. lacrossiformis*** J.R. Grant, Harvard Pap. Bot. 8(2): 2003. **INED**. TYPE: Colombia. Santander: Municipio de Gambita, Corregimiento Talandro, 14 February 1983, *Orozco 1060* (holotype COL [2 sheets]).

28. ***M. laudabilis*** J.R. Grant, Harvard Pap. Bot. 9(1): 2004. **INED**. TYPE: Colombia. Cauca-Huila: región de Moscopán, adelante de Santa Leticia, 8 September 1961, *Uribe Uribe 3871* (holotype COL).

29. ***M. luctans*** J.R. Grant, Harvard Pap. Bot. 9(1): 2004. **INED**. TYPE: Colombia. Chocó: Mun. de San José del Palmar, Cerro del Torrá, vertiente oriental, 12 August 1988, *Silverstone-Sopkin et al*. *4335* (holotype CUVC; isotype U).

30. ***M. luteynii*** J.R. Grant & Struwe, Harvard Pap. Bot. 5(2): 495. 2001. TYPE: Colombia. Cauca: *Luteyn 7466* (Holotype: NY; isotypes: COL, F, HAM, MO, U, US).

31. ***M. macrophylla*** (Kunth) Gilg in Engl. & Prantl, Nat. Pflanzenfam. 4(2): 94. 1895. Based on: *Lisianthus macrophyllus* Kunth, Nov. Gen et Sp. 3: 183. (9 July) 1819. TYPE Colombia. crescit locis subfrigidus in declivitate Parami de Almaguer, inter Pansitarra et flumen, *Humbolt & Bonpland s.n*. (Lectotype: P [P-Herbarium Humboldt, Bonpland & Kunth, microfiche, IDC 6209. 72: III. 6], designated by Weaver [1972a: 305]; isolectotype *Humboldt 3561* [B-Willd, microfiche 7440, No. 246, 3561], determined here).

32. ***M. marahuacae*** Struwe & V.A. Albert, Harvard Pap. Bot. 3(2): 182. 1998. TYPE: Venezuela. Amazonas: *Liesner 24651* (Holotype: MO).

33. ***M. neblinae*** Maguire & Steyerm., Mem. New York Bot. Gard. 32: 332. 1981. TYPE: Venezuela. Amazonas: *Maguire 37103* (Holotype: NY; isotype: US).

34. ***M. nicotianifolia*** Weaver & J.R. Grant, Harvard Pap. Bot. 8(1): 83. 2003. TYPE: Colombia. Cundinamarca: montes abajo de Salto de Tequendama, cerca a la planada de La Vencedora, March 1966, *Uribe Uribe 5577* (Holotype: US).

35. ***M. pachyphylla*** Gilg, Bot. Jahrb. Syst. 22: 338. 1896. TYPE: Colombia. Nariño: *Jameson 467* (type B? [destroyed]; Lectotype: G; isolectotypes: BM, G [2 sheets], K, OXF, US, selected by Grant [Mac V 2003]).

36. ***M. papillosa*** Weaver & J.R. Grant, Harvard Pap. Bot. 8(1): 104. 2003. TYPE: Venezuela. Mérida: Road to La Carbonera, 10-19 km from the guard station, 25 September 1972, *Weaver 2611* (Holotype: GH; isotypes: BM, G, MO, WIS).

37. ***M. piresii*** Maguire, Mem. New York Bot. Gard. 32: 338. 1981. TYPE: Brazil. Amazonas: *Maguire 60453* (Holotype: NY; isotypes: MG, NY, US, VEN).

38. ***M. rugosa*** Steyerm., Bol. Soc. Venez. Cienc. 25: 83. 1963. TYPE: Venezuela. Bolivar: *Steyermark & Wurdack 861* (Holotype: VEN; isotypes: F, NY).

39. ***M. schultesii*** Weaver & J.R. Grant, Harvard Pap. Bot. 8(1): 86. 2003. TYPE: Colombia. Norte de Santander: Cordillera Oriental, Páramo de Fontibón, 15 October 1941, *J. Cuatrecasas, R.E. Schultes & E. Smith 12271* (Holotype: GH; isotypes: BM, COL, F, MO, U, US).

40. ***M. subcaudata*** Ewan Contr. U. S. Natl. Herb. 29: 224. 1948. TYPE: Costa Rica. San José: *Wercklé 16492* (Holotype: US; isotype: NY).

41. ***M. umerulus*** J.R. Grant, Harvard Pap. Bot. 8(2): 2003. **INED**. TYPE: Colombia. Boyacá: Sierra Nevada del Cocuy, in cloud forest near Bocota, by path to Bachira, 15 August 1957, *Grubb et al. 708* (holotype: US; isotype K).

42. ***M. valerii*** Standl., Publ. Field Mus. Nat. Hist. Chicago Bot. Ser. 18: 928. 1938. TYPE: Costa Rica. San José: *Valerio 692* (Holotype: F).

43. ***M. weaveri*** Weaver & J.R. Grant, Harvard Pap. Bot. 8(1): 106. 2003. TYPE: Venezuela. Táchira: Base of Páramo de Tamá, above the settlement of Betania, 27 September 1972, *Weaver 2613* (Holotype: GH; isotypes: BM, G, MO, WIS).

44. ***M. wurdackii*** Weaver & J.R. Grant, Harvard Pap. Bot. 8(1): 98. 2003. TYPE: Peru. Amazonas: Bongará, *jalca* zone along Yambrasbamba-Pomacocha trail between Yanayacu and Pomacocha, 26 June 1962, *J.J. Wurdack 1071* (Holotype: US; isotypes: NY, USM).

45. ***M. ypsilocaule*** J.R. Grant, Harvard Pap. Bot. 8(2): 2003. **INED**. TYPE: Colombia. Putumayo: Páramo de San Francisco (la Depresion), en el camino carretero de San Francisco a Mocoa, January 1942, *P. Fray Miguel 57* (Holotype: F).

Fig. 65. Representatives of *Macrocarpaea* sect. *Macrocarpaea*. 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).

MACROCARPAEA SECT. MAGNOLIFOLIAE

4. 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* is comprised of 19 species largely of the Puno of Peru and Bolivia, and Eastern slopes of the central Peruvian Andes. Species 46–64.

46. ***M. arborescens*** Gilg, Bot. Jahrb. Syst. Beibl. 111: 50. 1913. TYPE: Colombia. Cauca: *Lehmann 5450* (type B? [destroyed]; Lectotype: GH; isolectotypes: F, K, US), selected by Grant (2002).

47. ***M. canoëifolia*** J.R. Grant, Harvard Pap. Bot. 8(2): 2003. **INED**. TYPE: Peru. Junín: Tarma, Agua Dulce, 5 March 1948, *Woytkowski 35417* (holotype F; isotype UC).

48. ***M. cinchonifolia*** (Gilg) Weaver, J. Arnold Arbor. 55(2): 300. 1974. Based on: *Rusbyanthus cinchonifolius* Gilg, in Engl. & Prantl, Nat. Pflanzenfam. 4(2): 95. 1895. TYPE: Bolivia. La Paz: *Rusby 1173* (type B? [destroyed]; Lectotype: NY; isolectotypes: BM, E, G, P, PH, S, US, WIS, selected by Weaver 1974: 300).

49. ***M. cochabambensis*** Gilg-Ben., Notizbl. Bot. Gart. Berlin 13: 381. 1936. TYPE: Bolivia. Cochabamba: *Steinbach 8992* (type B? [destroyed]; Lectotype: NY; isolectotypes: BM, E, G, K, MO, S, U, Z, selected by Grant [Mac V 2003]).

50. ***M. fortisiana*** J.R. Grant, Harvard Pap. Bot. 8(2): 2003. **INED**. TYPE: Peru. Puno: Sandia, near Sagrario, on trail, 26 May 1942, *Metcalf 30629* (G, GH, MO, UC, US).

51. ***M. fosteri*** J.R. Grant, Harvard Pap. Bot. 8(2): 2003. **INED**. TYPE: PERU. Pasco: Oxapampa, road in construction between Oxapampa and Villa Rica, km 7 SE from Miraflores crest, 11 October 1982, *Foster, R. 9114* (holotype MO; isotypes HAM, USM).

52. ***M. gran-pajatena*** J.R. Grant, Harvard Pap. Bot. 9(1): 2004. **INED**. TYPE: Peru. San Martîn: Mariscal Caceres, trail between La Playa Camp and Papayas camp, Río Abiseo National Park, 25 July 1987, *Young & León 4977* (holotype U; isotype HUT).

53. ***M. jactans*** J.R. Grant, Harvard Pap. Bot. 9(1): 2004. **INED**. TYPE: Ecuador. Napo: P.N. Napo-Galeras, Cordillera de Galeras, sendera hacia el Río Pucuno, 20 March 1997, *Alvarez et al. 1726* (holotype QCNE; isotype MO).

54. ***M. luna-gentiana*** J.R. Grant & Struwe, Harvard Pap. Bot. 8(1): 72. 2003. TYPE: Ecuador. Loja: Km 21 on road from Yangana to Cerro Toledo, 14 February 2001, *Grant & Struwe 01-4028* (Holotype: US; isotypes: LOJA, NEU, NY, QCA, QCNE).

55. ***M. maguirei*** Weaver & J.R. Grant Harvard Pap. Bot. 8(1): 95. 2003. TYPE: Peru. Cuzco: Paucartambo, in valley of Paucartambo along road between Cuzco and

Pilcopata, 27 September 1968, *Maguire* & *Maguire 61569* (Holotype: NY [3 sheets]; isotype GH).

56. ***M. normae*** J.R. Grant, Harvard Pap. Bot. 8(2): 2003. **INED**. TYPE: Peru. Cuzco: Convención, Choquellohuanca-Lucumaya, 28 April 1944, *Vargas 4196* (Holotype: CUZ; isotypes: MO, NY)

57. ***M. obnubilata*** J.R. Grant, Harvard Pap. Bot. 8(2): 2003. **INED**. TYPE: Peru. Huánuco: Prov. Huánuco, Trocha entre Carpish y Pati, 15 January 1987, *Díaz & Baldéon 2256* (holotype U; isotypes HAM, NEU).

58. ***M. ostentans*** J.R. Grant, Harvard Pap. Bot. 8(2): 2003. **INED**. TYPE: Peru. Pachitea, region of Pucallpa, western part of the "Sira Mountains" and adjacent lowland, c. 24-26 km SE to c. 26 km ESE of Puerto Inca, 9 June 1988, *Wallnöfer 129688* (holotype U; isotype WU).

59. ***M. pachystyla*** Gilg, Bot. Jahrb. Syst. 22: 336. 1896. TYPE: Peru. Chicoplaya, *Tafalla s.n*. (type B? [destroyed]; Lectotype: MA-Ruiz & Pavon [2 sheets]; isolectotypes: G), selected by Grant (2002).

= *Macrocarpaea corymbosa* (Ruiz & Pav.) Ewan, Contr. U. S. Natl. Herb. 29: 242. 1948. Based on: *Lisianthus corymbosus* Ruiz & Pav., Fl. Peruv. Chil. 2: 14. 1799, *nom illeg.* TYPE: Peru. Huánuco: *Ruiz* & *Pavon s.n.* (Lectotype: MA-Ruiz & Pavon [2 sheets]; isolectotypes: BM [5 sheets], F [2 sheets], G [2 sheets]), selected by Grant (2002).

60. ***M. revoluta*** (Ruiz & Pav.), Gilg in Engl. & Prantl, Nat. Pflanzenfam. 4(2): 94. 1895. Based on: *Lisianthus revolutus* Ruiz & Pav., Fl. Peruv. Chil. 2: 14. 1799. *Helia revoluta* (Ruiz & Pav.) Kuntze, Rev. Gen. 428. 1891. TYPE: Peru. Huánuco: *Ruiz* & *Pavon s.n.* (Lectotype: MA-Ruiz & Pavon; isolectotypes: BM [2 sheets], MA-Ruiz & Pavon [3 sheets], F, G [3 sheets]), selected by Grant (2002).

61. ***M. tahuantinsuyuana*** J.R. Grant, Harvard Pap. Bot. 8(2): 2003. **INED**. TYPE: Peru. Pasco: 2-4 km E of Oxapampa, 11 March 1984, *Smith, D.N. et al. 6282* (NEU, NY, U, USM).

62. ***M. viscosa*** (Ruiz & Pav.) Gilg, Bot. Jahrb. Syst. 22: 337. 1896. Based on: *Lisianthus viscosus* Ruiz & Pav., Fl. Peruv. Chil. 2: 14. 1799. *Helia viscosa* (Ruiz & Pav.) Kuntze, Rev. Gen. 428. 1891. TYPE: Peru. Huánuco: *Ruiz* & *Pavon s.n.* (Lectotype: MA-Ruiz & Pavon; isolectotype: MA-Ruiz & Pavon, selected by Grant (2002).

63. ***M. weigendiorum*** J.R. Grant, Harvard Pap. Bot. 8(2): 2003. **INED**. TYPE: Peru. Ucayali: Prov. Aguaytia, road from Aguaytia to Tingo Maria, km 33, Abra Divisoria, 26 March 2001, *Weigend* et al. *5363* (Holotype: BSB; isotypes: F, GH, HUT [2 sheets], NY [2 sheets], U, US).

64. ***M. zophoflora*** Weaver & J.R. Grant, Harvard Pap. Bot. 8(1): 100. 2003. TYPE: Peru. Amazonas: Chachapoyas, south side of Molinopampa-Diosan pass, 8 August 1962, *J.J. Wurdack 1618* (Holotype: US [2 sheets]; isotypes: F, GH, K [2 sheets], NY [2 sheets], P, S, UC, USM).

Fig. 66. Representatives of *Macrocarpaea* sect. *Magnolifoliae*. A–B *Macrocarpaea canoëifolia*. A, habit of flowering stem; B, flower. C–F *M. tahuantinsuyuana*. C, habit of flowering stem; D, flower; E, immature fruit; F, mature fruits. G–H *M. obnubilata*. G, habit of flowering stem; H, bud. I–J *M. viscosa*. I, leaf and habit of flowering stem; J, calyx. A drawn from *Woytkowski 35417* (UC); B drawn from *Gentry et al. 40187* (HAM); C–E drawn from van der Werff 8657 (USM); F drawn from *Woytkowski 6672A* (MO); G–H drawn from *Díaz & Baldéon* 2256 (MO); I–J drawn from *Foster et al. 10511* (USM).

MACROCARPAEA SECT. CHORIOPHYLLA

5. 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* is comprised mostly of 34 taxa largely of the Central Andes, especially around of the Huancabamba region of Ecuador and Peru, but also extending to north to Colombia and south to Bolivia. Species 65–98.

65. ***M. angelliae*** J.R. Grant & Struwe, Harvard Pap. Bot. 5(2): 490. 2001. TYPE: Ecuador. Zamora-Chinchipe: *Romoleroux 804* (Holotype: NY, isotypes: AAU, QCA).

66. ***M. angustifolia*** J.S. Pringle, Novon 12(1): 80. 2002. TYPE: Peru. Pasco: *Foster 7747* (Holotype: MO; isotype: USM).

67. ***M. apparata*** J.R. Grant & Struwe, Harvard Pap. Bot. 8(1): 63. 2003. TYPE: Ecuador. Loja: 28.8 km S of Yangana, 11 February 2001, *Grant & Struwe 01-4002* (Holotype: US; isotypes: G, LOJA, NEU, NY, MO, QCA, QCNE, S).

68. ***M. bangiana*** Gilg, Bot. Jahrb. Syst. 22: 335. 1896. TYPE: Bolivia. LA PAZ: *Bang 520* (type B? [destroyed]; Lectotype: NY [2 sheets]; isolectotypes: BM, E, G [3 sheets], GH [2 sheets], K, M, MANCH, MICH, MO, US [2 sheets], W, selected by Grant [Mac V 2003]).

69. ***M. bubops*** J.R. Grant & Struwe, Harvard Pap. Bot. 8(1): 66. 2003. TYPE: Ecuador. Zamora-Chinchipe: Along new road Loja-Zamora, 25 April 1987, *van der Werff & Palacios 8986* (Holotype: NY; isotypes: AAU, G, GB).

70. ***M. dillonii*** J.R. Grant, Harvard Pap. Bot. 8(2): 2003. **INED**. TYPE: Peru. Amazonas: Prov. Amazonas, Dist. Vista Alegre, Puente sobre el Río Salas, 30 June 1998, *Sánchez Vega, Dillon & Zapata 9572* (CPUN, F, HAO, NEU, U).

71. ***M. elix*** J.R. Grant, Harvard Pap. Bot. 8(2): 2003. **INED**. TYPE: Ecuador. Azuay: highway Cuenca-Cola de San Pablo, km 88, secondary forest, 14 February 1977, *Boeke* & *Loyola 988* (Holotype: NY; isotypes: AAU, QCA).

72. ***M. ericii*** J.R. Grant, Harvard Pap. Bot. 8(2): 2003. **INED**. TYPE: Peru. Cajamarca: San Ignacio, Huarango, Localidad Romerillo, Cordillera entre Romerillo y Nuevo Mundo, 27 July 1997, *Campos*, *Rodríguez*, & *Nuñez 4296* (Holotype MO).

73. ***M. gracilis*** Weaver & J.R. Grant, Harvard Pap. Bot. 8(1): 95. 2003. TYPE: Peru. Locality unknown (probably Cajamarca, see below), 1909-1914, *Weberbauer 6116* (Holotype: F [2 sheets, #627868 flowering, # 627867 fruiting]).

74. ***M. gravabilis*** J.R. Grant, Harvard Pap. Bot. 8(2): 2003. **INED**. TYPE: Colombia. Antioquia: Trail from Encarnacíon to Parque Nacional de los Orchídeas, 27 January 1979, *Gentry* & *Renteria 24569* (Holotype MO; Isotype COL).

75. ***M. harlingii*** J.S. Pringle, Fl. Ecuador 53(159A): 101. 1995. TYPE: Ecuador. Zamora-Chinchipe: *Harling 23531* (Holotype: GB; isotype: QCA).

76. ***M. innarrabilis*** J.R. Grant, Harvard Pap. Bot. 8(2): 2003. **INED**. TYPE: Peru. Amazonas: Rodrigues de Mendoza, July-August 1963, *Woytkowski 8018* (U);

77. ***M. jalca*** J.R. Grant, Harvard Pap. Bot. 8(2): 2003. **INED**. TYPE: Peru. Cajamarca: Prov. Cutervo, 10 km NW of Socota, 10 December 1938, *Stork* & *Horton 10118* (Holotype: US; isotypes: F, K, UC).

78. ***M. jensii*** J.R. Grant & Struwe, Harvard Pap. Bot. 8(1): 68. 2003. TYPE. Ecuador. Zamora-Chinchipe: Parque Nacional Podocarpus (San Francisco entrance), trail leading west from San Francisco, 16 February 2001, *Grant & Struwe 01-4047* (Holotype: US; isotypes: LOJA, QCNE, NEU, NY).

79. ***M. kayakifolia*** J.R. Grant, Harvard Pap. Bot. 8(2): 2003. **INED**. TYPE: Peru. Huánuco: Carpish Hills, trail downslope from San Pedro de Carpish, 3 km E of tunnel, 15 January 1987, *Stein et al. 3864* (Holotype: USM; isotypes: HAM, NEU, U).

80. ***M. kuelap*** J.R. Grant, Harvard Pap. Bot. 8(2): 2003. **INED**. TYPE: Peru. Amazonas: Prov. Bongará, between Río Utcubamba and Pomacocha, km 327 east of Olmos and Rioja road, 31 January 1964, *Hutchinson* & *Wright 3903* (Holotype: US [2 sheets]; isotypes: F, K, MO, NY [2 sheets], UC [2 sheets], USM [2 sheets]).

81. ***M. kuepferiana*** J.R. Grant, Harvard Pap. Bot. 8(2): 2003. **INED**. TYPE: Peru. Puno: Carabaya, San Gabán, Hda. Quillabamba pte. Ario, ladera abierta, 8 February 1967, *Vargas 18928* (CUZ).

82. ***M. lenae*** J.R. Grant, Harvard Pap. Bot. 8(1): 70. 2003. TYPE: Ecuador. Zamora-Chinchipe: 5 km S of Zamora towards P.N. Podocarpus (Bombuscara entrance), 13 February 2001, *Grant & Struwe 01-4013* (Holotype: US; isotypes: LOJA, QCA, QCNE, NEU, NY, MO, S).

83. ***M. loranthoides*** (Griseb.) Maas Cat. Fl. Pl. Gymn. Peru (Mon. Syst. Bot. Missouri Bot. Gard. 45): 1256. 1993. Based on: *Lisianthus loranthoides* Griseb., Gen Sp. Gent. 179. 1839. TYPE: Peru. Amazonas: *Mathews 1315* (Holotype: K; isotypes: E, OXF).

= *Macrocarpaea chlorantha* Gilg, Feddes Repert. Sp. Nov. Regni Veg. 2: 53. 1906. TYPE: Peru. Amazonas: *Weberbauer 4411* (type B? [destroyed]; Lectotype: G, selected by Grant [Mac V 2003]).

84. ***M. luya*** J.R. Grant, Harvard Pap. Bot. 8(2): 2003. **INED**. TYPE: Peru. Amazonas: Prov. Luya, Camporredondo, Tullanga, Cerro Huicsocunga o Condorpuna, September 1989, *Díaz* & *Campos 3786* (Holotype: USM; isotype: MO).

85. ***M. maryae*** J.R. Grant, Harvard Pap. Bot. 8(2): 2003. **INED**. TYPE: Colombia. Chocó: North ridge of Alto de Buey, 8 August 1976, *Gentry* & *Fallen 17369* (Holotype: COL [2 sheets]; isotype: U [2 sheets]).

86. ***M. micrantha*** Gilg, Bot. Jahrb. Syst. 22: 338. 1896. TYPE: Peru. San Martín: *Spruce 4618* (type B? [destroyed]; Lectotype: NY; isolectotypes: BM, BR, C, E, G [3 sheets], GH, GOET, K [2 sheets], LD, OXF [2 sheets], P, W [2 sheets], selected by Grant [Mac V 2003]).

= *Macrocarpaea weberbaueri* Gilg, Feddes Repert. Sp. Nov. Regni Veg. 2: 54. 1906. TYPE: Peru, *Weberbauer 4655* and *Weberbauer 5006* [both destroyed?]. Excluded by Grant (Mac V 2003).

87. ***M. neillii*** J.R. Grant, Harvard Pap. Bot. 9(1): 2004. **INED**. TYPE: Ecuador. Zamora-Chinchipe: Nangaritza, Cordillera de Nanguipa, Cerro Colorado, 8 km SSE of Nambija, 20 km ESE of Zamora, 18 February 2002, Neill et al. 13758 (holotype QCNE; isotype LOJA).

88. ***M. noctiluca*** J.R. Grant & Struwe, Harvard Pap. Bot. 8(1): 76. 2003. TYPE: Ecuador. Loja: Nudo de Sabanilla, 15 km S of Yangana, 10 February 2001, *Grant & Struwe 01-3977* (Holotype: US; isotypes: LOJA, QCA, QCNE, NEU, NY).

89. ***M. pajonalis*** J.R. Grant, Harvard Pap. Bot. 8(2): 2003. **INED**. TYPE: Peru. Pasco: San Gutardo, Oxapampa-Cerro de Pasco road 30-35 km W of Oxapampa, 3 February 1983, *Gentry et al. 39988* (Holotype USM; isotype HAM).

90. ***M. pringleana*** J.R. Grant, Harvard Pap. Bot. 8(2): 2003. **INED**. TYPE: Ecuador. Pastaza: Puyo-Puerto Napo Road, 14-18 km N of Puyo, 25 April 1978, *Luteyn & Lebron-Luteyn 5830* (holotype NY; isotype GH [2 sheets]).

91. ***M. quechua*** J.R. Grant, Harvard Pap. Bot. 9(1): 2004. **INED**. TYPE: Peru. San Martín: San Martín, trail to television antenna, km 17.5 of Tarapoto-Yurimaguas road (2.5 km N of Cataratas de Ahuashiyacu), 7 August 1986, Knapp 7911 (holotype U; isotypes HAM, NEU, USM).

92. ***M. risibilis*** J.R. Grant, Harvard Pap. Bot. 9(1): 2004. **INED**. TYPE: Colombia. Caquetá: Comisaría del Caquetá, 3 April 1940, Cuatrecasas 9034 (holotype COL; isotype US).

93. ***M. sodiroana*** Gilg, Bot. Jahrb. Syst. 25: 724. 1898. TYPE: Ecuador. Pichincha: *Sodiro 101/1* (type B? [destroyed]; Lectotype: QPLS; isolectotypes: QPLS [2 sheets]), selected by Grant (2002).

94. ***M. stenophylla*** Gilg, Bot. Jahrb. Syst. 22: 337. 1896. TYPE: Peru. Amazonas: Stübel 24 (type B? [destroyed]; neotype *Williams 7582* (F)), selected by Grant & Struwe (2000).

95. ***M. subsessilis*** Weaver & J.R. Grant, Harvard Pap. Bot. 8(1): 91. 2003. TYPE: Ecuador. Loja: Between Tambo Cachiyacu, La Entrada, and Nudo de Sabanilla, 7 October 1943, *Steyermark 54436* (Holotype: US; isotypes: F, NY [2 sheets]).

96. ***M. tabula-fluctivagifolia*** J.R. Grant, Harvard Pap. Bot. 8(2): 2003. **INED**. TYPE: Peru. Huánuco: Southwestern slope of the Rio LlullaPichis watershed, on the ascent of Cerros del Sira, at edge of steep embankment near Camp 3 (Laguna), 15 July 1969, *Wolfe 12333* (Holotype: F; isotypes: NA, NY, USM).

97. ***M. wallnoeferi*** J.R. Grant, Harvard Pap. Bot. 8(2): 2003. **INED**. TYPE: Peru. Huánuco: Pachitea, region of Pucallpa, western part of the "Sira Mountains" and adjacent lowland, c. 24-26 km SE to c. 26 km ESE of Puerto Inca, 20 March 1988, *Wallnöfer 18-20388* (Holotype: WU; isotype: U).

98. ***M. xerantifulva*** J.R. Grant, Harvard Pap. Bot. 9(1): 2004. **INED**. TYPE: Peru. Cajamarca: San Ignacio, La Coipa, vista Florida-La Laguna, 11 June 1997, *Campos & García 3960* (holotype MO; isotype U).

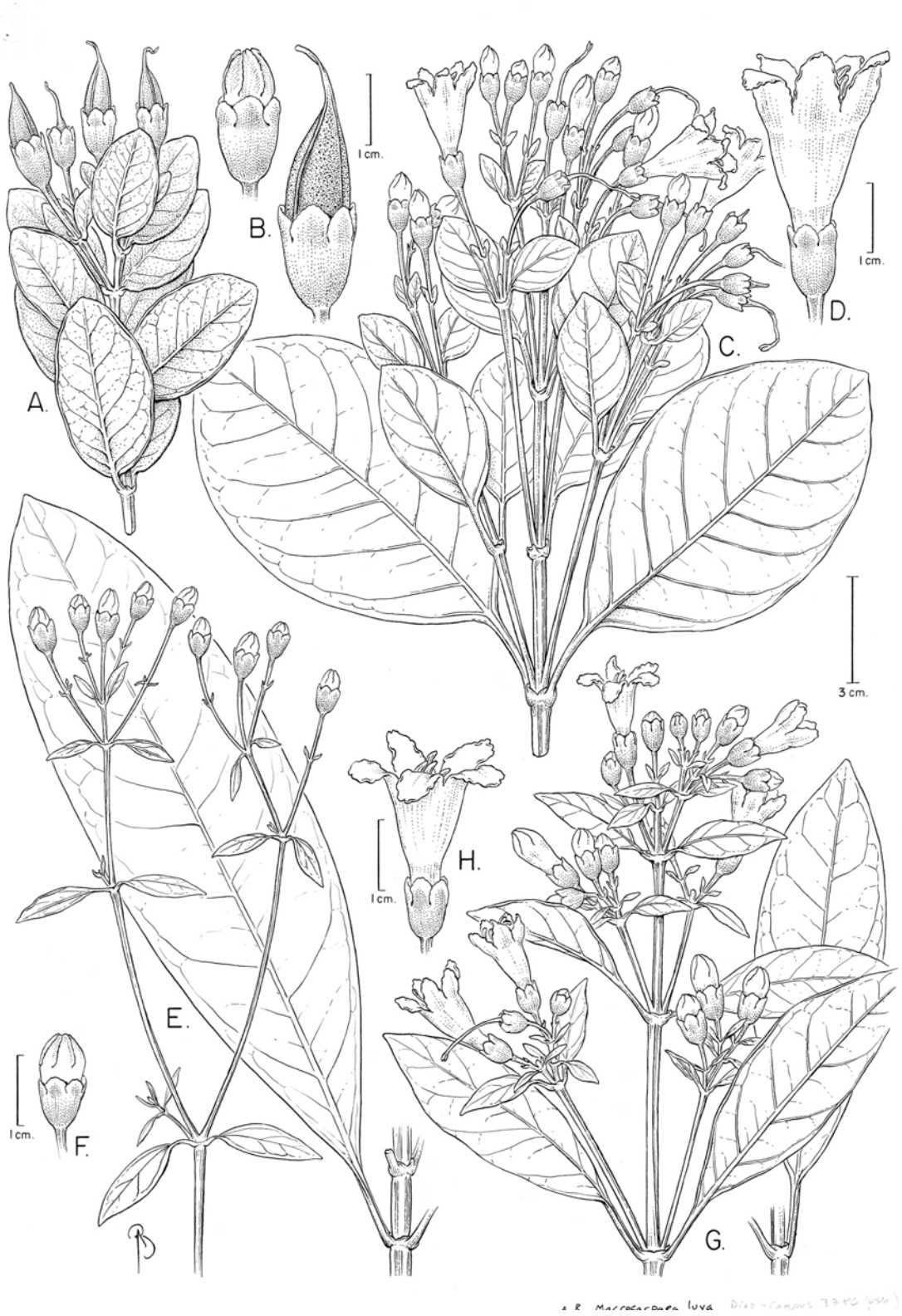


Fig. 67. Representatives of *Macrocarpaea* sect. *Choriophylla*. A–B *Macrocarpaea luya.* A, habit of flowering stem; B, bud and fruit. C–D *M. innarrabilis.* C, habit of flowering stem; D, flower. E–F *M. tabula–fluctivagifolia.* E, habit of flowering stem, leaf and interpetiolar ridge; F, bud. G–H *M. revoluta.* G, habit of flowering stem, leaf and interpetiolar ridge; H, flower. A–B drawn from *Diaz* & *Campos 3786* (USM); C–D drawn from *Matthews 1314* (K); E–F drawn from *Wolfe 12333* (F); G–H drawn from *Smith 2748* (HAM).

DOUBTFUL AND EXCLUDED TAXA

Lisianthus ovalis Ruiz & Pav., Fl. Peruv. Chil. 2: 13. 1799. *Helia ovalis* (Ruiz & Pav.) Kuntze, Rev. Gen. Pl. 428. 1891. *Macrocarpaea ovalis* (Ruiz & Pav.) Ewan, Contr. U. S. Natl. Herb. 29: 234. 1948. Does not have a type, and has therefore been excluded from use (Grant 2003). This name may actually correspond to *M. pajonalis* J.R. Grant (Grant 2003).

Macrocarpaea guttifera Ewan, Contr. U. S. Natl. Herb. 29: 237-238. 1948 = *Ravenia biramosa* Ducke (Rutaceae) (Grant 2001).

Macrocarpaea weberbaueri Gilg, Feddes Repert. Sp. Nov. Regni Veg. 2: 54. 1906. TYPE: Peru, *Weberbauer 4655* and *Weberbauer 5006* [B, both destroyed? In WWII]. Does not have an extant type, and is therefore excluded from use (Grant 2003C). This may be a synonym of *M. micrantha* (Ewan 1948).

Macrocarpaea sp. Based on *Dannouse s.n*. (NY), determined and discussed by Ewan (1950: 164-165) = *Tabernaemontana crassa* (Apocynaceae) (Grant 2003).

NOMINA HERBARIORA

Six nomina herbariora, "nomen herbariorum" (unpublished names written on herbarium sheets), have been discovered in the course of examination of material. They consist of six unpublished species names in *Macrocarpaea*, and a new genus and new species "Axelsonia globiflora". For a complete accounting of all names concerning *Macrocarpaea*, even though never published, these names and synonymy are as follows:

"Axelsonia globiflora Dusén, ined." Written on *Dusén 17288* (S) (Brazil) [= *M. rubra* Malme]

"Macrocarpaea buchtienii Gilg, ined." Written on *Buchtien 1186* (US) and *Buchtien 5639* (NY) (Bolivia) [= *M. cinchoniifolia* (Gilg) Weaver]

"Macrocarpaea ekmanii Ewan, ined." Written on *Ekman 6846* (S); *Ekman 15947* (S); *Wright 1347* (BR) (Cuba) [= *M. pinetorum* Alain]

"Macrocarpaea gilgiana Rusby, ined." Written on *Rusby 1172* (NY) (Bolivia) [= *M. cochabambensis* Gilg-Benedict]

"Macrocarpaea peduncularis Rusby, ined." Written on *Williams 1561* (NY) (Bolivia) [= *M. bangiana* Gilg]

"Macrocarpaea tabacifolia Ewan, ined." Written on *Rusby 1173* (US) (Bolivia) [= *M. cinchoniifolia* (Gilg) Weaver]

Tab. 6. Index of Scientific Names: A synonymized checklist to the species of *Macrocarpaea*

Species	Auth	Synonymy	Section
affinis	Ewan		*Macrocarpaea*
angelliae	J.R. Grant & Struwe		*Choriophylla*
angustifolia	Pringle		*Choriophylla*
apparata	J.R. Grant & Struwe		*Choriophylla*
arborea	(Britton) Ewan	= *Rogersonanthus arboreus* (Britton) Maguire & Boom	–
arborescens	Gilg		*Magnolifoliae*
auriculata	Weaver & J.R. Grant		*Macrocarpaea*
autanae	Weaver		*Macrocarpaea*
ayangannae	J.R. Grant, Struwe & Boggan		*Macrocarpaea*
bangiana	Gilg		*Choriophylla*
biremis	J.R. Grant		*Macrocarpaea*
bogotana	Gilg	= *M. glabra*	*Macrocarpaea*
bracteata	Ewan		*Macrocarpaea*
browallioides	(Ewan) A. Robyns & S. Nilsson		*Macrocarpaea*
bubops	J.R. Grant & Struwe		*Choriophylla*
caatingae	J.R. Grant		*Tabacifoliae*
calophylla	Gilg		*Macrocarpaea*
canoëifolia	J.R. Grant		*Magnolifoliae*
cerronis		= *Rogersonanthus tepuiensis* (Gleason) Maguire & Boom	–
chlorantha	Gilg	= *M. loranthoides*	*Choriophylla*
cinchonifolia	(Gilg) Weaver		*Magnolifoliae*
cochabambensis	Gilg-Benedict		*Magnolifoliae*
corymbosa	(Ruiz & Pav.) Ewan	= *M. pachystyla*	*Magnolifoliae*
densiflora	(Benth.) Ewan		*Macrocarpaea*
dillonii	J.R. Grant		*Choriophylla*
domingensis	Urb. & Ekman		*Caribbigenes*
duquei	Gilg-Benedict		*Macrocarpaea*
elix	J.R. Grant		*Choriophylla*
ericii	J.R. Grant		*Choriophylla*
ewaniana	Weaver & J.R. Grant		*Macrocarpaea*
fortisiana	J.R. Grant		*Magnolifoliae*
fosteri	J.R. Grant		*Magnolifoliae*
gattaca	J.R. Grant		*Macrocarpaea*
gaudialis	J.R. Grant		*Macrocarpaea*
glabra	(L.f.) Gilg		*Macrocarpaea*
glaziovii	Gilg		*Tabacifoliae*
gondoloides	J.R. Grant		*Macrocarpaea*
gracilis	Weaver & J.R. Grant		*Choriophylla*
gran-pajatena	J.R. Grant		*Magnolifoliae*
gravabilis	J.R. Grant		*Choriophylla*
gulosa	J.R. Grant		*Macrocarpaea*
guttifera	Ewan	= *Ravenia biramosa* (Rutaceae)	_
harlingii	Pringle		*Choriophylla*

hartii	Krug & Urban	= *M. thamnoides*	*Caribbigenes*
hilarula	J.R. Grant		*Macrocarpaea*
illecebrosa	J.R. Grant		*Macrocarpaea*
innarrabilis	J.R. Grant		*Choriophylla*
jactans	J.R. Grant		*Magnolifoliae*
jalca	J.R. Grant		*Choriophylla*
jensii	J.R. Grant & Struwe		*Choriophylla*
jocularis	J.R. Grant		*Macrocarpaea*
kayakifolia	J.R. Grant		*Choriophylla*
kuelap	J.R. Grant		*Choriophylla*
kuepferiana	J.R. Grant		*Choriophylla*
lacrossiformis	J.R. Grant		*Macrocarpaea*
laudabilis	J.R. Grant		*Macrocarpaea*
lenae	J.R. Grant		*Choriophylla*
loranthoides	(Griseb.) Maas		*Choriophylla*
luctans	J.R. Grant		*Macrocarpaea*
luna-gentiana	J.R. Grant & Struwe		*Magnolifoliae*
luteynii	J.R. Grant & Struwe		*Macrocarpaea*
luya	J.R. Grant		*Choriophylla*
macrophylla	(Kunth) Gilg		*Macrocarpaea*
maguirei	Weaver & J.R. Grant		*Magnolifoliae*
marahuacae	Struwe & V. Albert		*Macrocarpaea*
maryae	J.R. Grant		*Choriophylla*
micrantha	Gilg		*Choriophylla*
neblinae	Maguire & Steyerm.		*Macrocarpaea*
neillii	J.R. Grant		*Choriophylla*
nicotianiifolia	Weaver & J.R. Grant		*Macrocarpaea*
noctiluca	J.R. Grant & Struwe		*Choriophylla*
normae	J.R. Grant		*Magnolifoliae*
obnubilata	J.R. Grant		*Magnolifoliae*
obtusifolia	(Griseb.) Gilg		*Tabacifoliae*
obtusifolia var. constricta	Griseb.	= *M. glaziovii*	*Tabacifoliae*
ostentans	J.R. Grant		*Magnolifoliae*
ovalis	(Ruiz & Pav.) Ewan	excluded	_
pachyphylla	Gilg		*Macrocarpaea*
pachystyla	Gilg		*Magnolifoliae*
pajonalis	J.R. Grant		*Choriophylla*
papillosa	Weaver & J.R. Grant		*Macrocarpaea*
pauciflora	Alain	= *M. pinetorum*	*Caribbigenes*
pinetorum	Alain		*Caribbigenes*
piresii	Maguire		*Macrocarpaea*
polyantha	Gilg	= *M. glabra*	*Macrocarpaea*
pringleana	J.R. Grant		*Choriophylla*
quechua	J.R. Grant		*Choriophylla*
quelchii	(N.E. Brown) Ewan	= *Rogersonanthus quelchii* (N.E. Brown) Maguire & Boom	–
revoluta	(Ruiz & Pav.) Gilg		*Magnolifoliae*
risibilis	J.R. Grant		*Choriophylla*

rubra	Malme		*Tabacifoliae*
rugosa	Steyerm.		*Macrocarpaea*
salicifolia		= *Rogersonanthus arboreus* (Britton) Maguire & Boom	–
schultesii	Weaver & J.R. Grant		*Macrocarpaea*
sodiroana	Gilg		*Choriophylla*
stenophylla	Gilg		*Choriophylla*
subcaudata	Ewan		*Macrocarpaea*
subsessilis	Weaver & J.R. Grant		*Choriophylla*
tabula-fluctivagifolia	J.R. Grant		*Choriophylla*
tahuantinsuyuana	J.R. Grant		*Magnolifoliae*
tepuiensis	(Gleason) Steyerm.	= *Rogersonanthus tepuiensis* (Gleason) Maguire & Boom	–
thamnoides	(Griseb.) Gilg		*Caribbigenes*
umerulus	J.R. Grant		*Macrocarpaea*
valerii	Standl.		*Macrocarpaea*
viscosa	(Ruiz & Pav.) Gilg		*Magnolifoliae*
wallnoeferi	J.R. Grant		*Choriophylla*
weaveri	J.R. Grant		*Macrocarpaea*
weberbaueri	Gilg	excluded	_
weigendiorum	J.R. Grant		*Magnolifoliae*
wurdackii	Weaver & J.R. Grant		*Macrocarpaea*
x acuminata	Weaver		*Macrocarpaea*
x mattii	J.R. Grant		*Choriophylla*
xerantifulva	J.R. Grant		*Choriophylla*
ypsilocaule	J.R. Grant		*Macrocarpaea*
zophoflora	Weaver & J.R. Grant		*Magnolifoliae*

ETYMOLOGY AND EPONYMY

It is important that a certain degree of humor should exist in science. Therefore I have challenged myself to form species names that are innovative and amusing. Many of the new names derive from the shape of their leaves. Instead of tiring traditional name such as "lanceolata" or "obovata", names have been formed such as *biremis* (two-oared), *canoëifolia* (canoe-shaped leaves), *gondoloides* (gondola-like), *kayakifolia* (kayak-shaped leaves), *lacrossiformis* (lacrosse-stick shaped), and *tabula-fluctivagifolia* (surfboard-shaped leaves). I often retain the orthography of the word in the language from which it derives, e.g., *gondoloides* [Italian], *lacrossiformis* [French, English], or transliterate the name into Latin such as in *tabula-fluctivagifolia*.

Other names derive from other morphological features on the plant, such as the unique dots at the base of leaves in some species, leading to the name *bubops* (owl-eyed). Others derive from an adjective that may describe the "personality" of a species, *gaudialis* (joyful), *gravabilis* (troublesome), *gulosa* (dainty), *hilarula* (cheerful), *illecebrosa* (alluring), *innarrabilis* (indescribable), *jactans* (showing off), *ostentans* (ostentatious), and *risibilis* (smiling). Other names are derived from events that took place during the discovery or realization that the species was new. *Apparata* derives from the Harry Potter word "apparating" (Rowling 1998), the plants having magically appeared in front of us in the field in Ecuador. *Gattaca* derives from four letters A,C, G, and T that form the DNA that led to the first realization it was a distinct species. *Luctans* derives from my efforts "wrestling" with the taxonomy of that species, and *umerulus* (shoulder-like) derives from the nodding (or shoulder-shaped) position of the flowers, coined when I had a cast on my own shoulder after breaking it in a roller-blading crash in Avenches, Switzerland on September 1, 2001.

One of the greatest things a monographer can do is to honor the collectors of the plant specimens he studies. Therefore I have attributed names to a number of collectors of South American plants who have made important collections of *Macrocarpaea*. These include: Michael Dillon (*M. dillonii*), Eric Rodriquez (*M. ericii*), Robin Foster (*M. fosteri*), Jens Madsen (*M. jensii*), James Luteyn (*M. luteynii*), Mary Endress (*M. maryae*), David Neill (*M. neillii*), Norma Salinas (*M. normae*), Richard Evans Schultes† (*M. schultesii*), Bruno Wallnöfer (*M. wallnoeferi*), Maximilian & Katja Weigend (*M. weigendiorum*), and John J. Wurdack† (*M. wurdackii*). Important researchers of the Gentianaceae also are acknowledged: Joseph Ewan† (*M. ewaniana*), Philippe Küpfer (*M. kuepferiana*), Lena Struwe (*M. lenae*), James Pringle (*M. pringleana*), and Richard E. Weaver, Jr. (*M. weaveri*). Bobbi Angell (*M. angelliae*) is acknowledged for preparing illustrations of over 70 species of *Macrocarpaea*, and Ernest Fortis (*M. fortisiana*) for tirelessly managing all my incoming and outgoing loans of specimens. I have also incorporated words or place-names from the indigenous people of South America such as in *kuelap*, *luya*, *quechua*, and *tahuantinsuyuana*.

HYBRIDS

Hybridization between species has been reported in several groups of Gentianaceae, particularly *Gentiana* of tribe Gentianeae and *Centaurium* of the Chironieae. Numerous hybrids between species of *Gentiana* can be found in the Alps in Europe, e.g., (*G. lutea* × *G. purpurea* = *G.* ×*hybrida*) (Anchisi et al. 1989), and in the American Midwest (e.g., *G. andrewsii* × *G. puberula* = *G.* ×*billingtonii*) (Pringle 1965). *Centaurium* ×*bianoris* of Majorca, Spain, recently has been shown to be a local allotetraploid resulting from the hybrid of *C. maritimum* with *C. tenuiflorum* (Guggisberg & Mansion unpubl.). Likewise, ancient hybridization events appear to have led rise to complex species and generic assemblages within the *Swertia* alliance (Chassot, pers. comm.)

Previous to my studies, no natural or man-made hybrids had been reported between any species in the gentian tribe Helieae. However, I have found what appear to be two natural hybrids, *Macrocarpaea* ×*acuminata* (*M. subcaudata* × *M. valerii*), and *M.* ×*mattii* (*M. noctiluca* × *M. subsessilis*). Both appear to be hybrid individuals only known from single collections. The scarcity of hybrids in the Helieae indicates that gene exchange between species is a rare. Considering that many species of *Macrocarpaea* share the same pollinator species of bats, hummingbirds, moths, and insects, the lack of hybrids is surprising. Unknown barriers to hybridization that are rarely breached are probable. Even though both hybrids are only known from single collections, I feel that naming them is important, giving recognition to their unique taxonomic status, and level of importance which might otherwise be left unacknowledged.

Macrocarpaea ×*acuminata* Weaver (Fig. 70) originally was described as a new species from material from the Tapantí area in Cartago, Costa Rica by Weaver (1972). Since then, no other specimens have ever been identified as identical to that material. From that type locality are many herbarium collections of two other well-known taxa, *M. subcaudata* (Fig. 67), and *M. valerii* (Fig. 69). Based on its intermediate morphological characters, *M.* ×*acuminata* appears to be a single hybrid individual between these two species. On the label of the specimen that later was described as *M. acuminata*, the collector Jiménez remarked "Casi igual al No. 2022, pero la planta más alta y las hojas más pequeñas. Pueder ser una planta más vieja" [Somewhat equal to No. 2022, but the plant taller and the leaves smaller. Might be an older plant]. His number 2022 is a classic herbarium example of *M. valerii*.

Macrocarpaea ×*mattii* J.R. Grant (Fig. 73) is an undescribed natural hybrid (Grant unpubl.), and clearly intermediate between its parents *M. noctiluca* (Fig. 72) and *M. subsessilis* (Fig. 71). I have traveled to Cerro Toledo twice, yet have unfortunately not been able to find any individuals of *M.* ×*mattii*. Its parents are both common species in the area, *M. noctiluca* at generally lower elevations, and *M. subsessilis* at generally higher elevations. An overlap in distribution occurs on the road that climbs from Yangana to Cerro Toledo, where the chance hybridization event occurred. The notable intermediate characters are in the calyx and bracteoles. *Macrocarpaea subsessilis* has a large calyx and two prominent spatulate bracteoles; *M. noctiluca* has a small calyx, and extremely reduced bracteoles; and *M.* ×*mattii* is intermediate in calyx size, yet has the spatulate bracteoles of *M. subsessilis*. Even further up the same road in elevation, *M. luna-gentiana* occurs, but no hybrids are known with this species.

Fig. 68. *M. subcaudata* Ewan, from Tapantí, Costa Rica. *Herrera 5421* (MO).

Fig. 69. *M. valerii* Standley, from Tapantí, Costa Rica. *Jiménez 2022* (GH).

Fig. 70. The hybrid *M.* ×*acuminata* Weaver, from Tapantí, Costa Rica. *Jiménez 2023* (GH).

Fig. 68-70 show the parent species *M. subcaudata* (Fig. 68) and *M. valerii* (Fig. 69), and their hybrid *M.* ×*acuminata* (Fig. 70).from Costa Rica.

Macrocarpaea ×*acuminata* shows intermediate morphological features in terms of leaf shape and calyx size. The leaves of *M. subcaudata* are narrowly lanceolate, whereas those of *M. valerii* are broadly obovate to ovate. In *M.* ×*acuminata* the leaves are generally elliptic, being intermediate in size and shape between *M. subcaudata* and *M. valerii*.

Fig. 71. *M. subsessilis* Weaver & J.R. Grant, from Cerro Toledo, Loja, Ecuador. *Matt12* (ER).

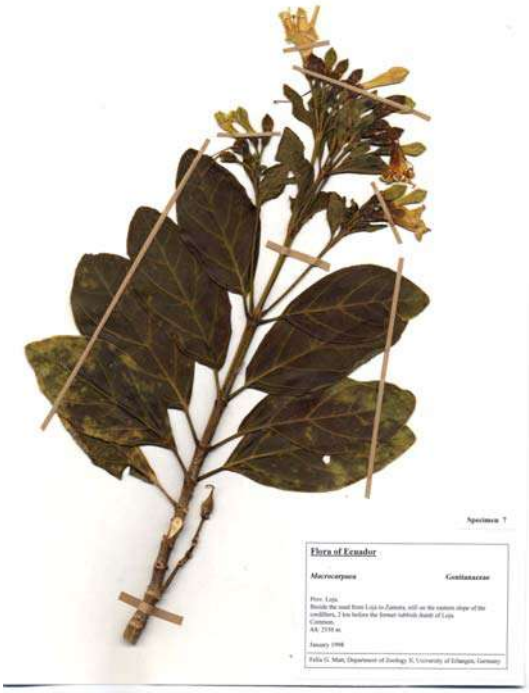


Fig. 72. *M. noctiluca* J.R. Grant & Struwe, from Cerro Toledo, Loja, Ecuador. *Matt 7* (ER).

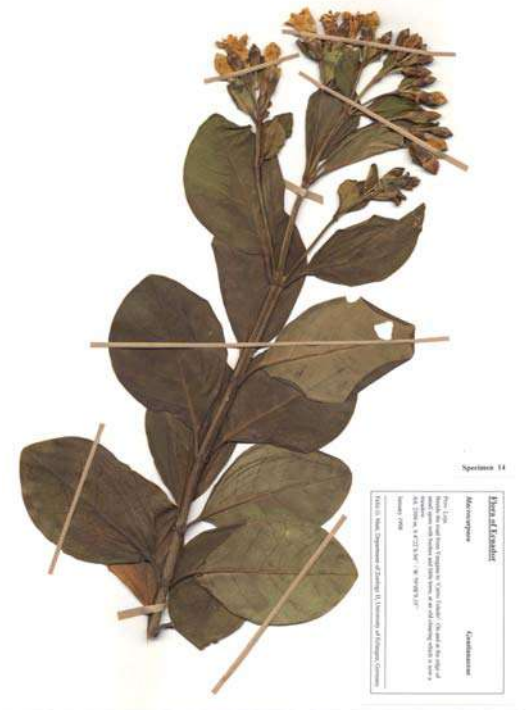


Fig. 73. The hybrid *M.* ×*mattii* J.R. Grant, from Cerro Toledo, Loja, Ecuador. *Matt 14* (ER).

Fig. 71–73 show the parent species *M. subsessilis* (Fig. 71) and *M. noctiluca* (Fig. 72), and their hybrid *M.* ×*mattii* (Fig. 73) from Ecuador.

Macrocarpaea ×*mattii* shows intermediate morphological features in terms of leaf shape, inflorescence architecture, and calyx size. The leaves of *M. subsessilis* are short-petiolate coriaceous and generally obovate, whereas those of *M. noctiluca* are generally long-petiolate elliptic to ovate and thin-textured. In *M.* ×*mattii* the leaves are broadly elliptic, with petioles intermediate in length between *M. subsessilis* and *M. noctiluca*.

5. BIOGEOGRAPHY AND DISTRIBUTION

Macrocarpaea has a relatively broad distribution in mountainous regions of the Neotropics. The Neotropics comprise the tropical parts of the New World: North America, Mesoamerica, and South America. The gentian tribe Helieae, to which *Macrocarpaea* belongs is restricted to the Neotropics (Struwe et al. 2002).

Map 8. Distribution of *Macrocarpaea* as viewed on a map of Earth.

Four different types of distributions are discussed and mapped. 1)All species of *Macrocarpaea* are divided among five taxonomic sections, 2) identified to occur in a discrete geographic area, and 3)noted as to which ecological zone they belong. First, the distribution of the genus is mapped on a map of the Neotropics, and the five sections of *Macrocarpaea* are delineated (Map 1). Secondly, the distributions of the related genera *Chorisepalum* and *Tachia* are mapped against that of *Macrocarpaea* (Map 2). Then above is a map of the distribution of *Macrocarpaea* on a map of the world (Map 3). Fourthly is the delineation of discrete geographic areas in which species of *Macrocarpaea* occur (Map 4).

General Distribution Patterns

The overall distribution pattern of *Macrocarpaea* is typical of many Neotropical taxa. The genus is basically found in five major geographic regions (Tab. 7; Map 9): Southeastern Brazil (4 species), the Greater Antilles of the Caribbean (3 species), the Pantepui of the Guayana Shield (6 species), Southern Mesoamerica (Costa Rica and Panama) (4 species), and the Andes (81 species). Southeastern Brazil is divided into the Atlantic Forest (2 species), and Espinhaço Range (2 species). The Andes are divided into three major sections, Northern, Central, and Southern. *Macrocarpaea* is absent from the Southern Andes (the mountains from Bolivia to Chile). Here, the Northern and Central Andes are further divided into 8 regions: Northern Andes: Sierra Nevada de Santa Marta, Colombia (1 species); Northern Andes: Cordillera de Mérida, Venezuela (3 species); Northern Andes: Cordillera Oriental, Colombia (11 species); Northern Andes: Cordillera Central, Colombia (8 species); Northern Andes: Cordillera Occidental, Colombia and Ecuador (8 species); Central Andes: Huancabamba region of Ecuador and Peru (29 species) [further divided into Huancabamba of Ecuador (8 species); Huancabamba of the Cordillera de Condor, Ecuador and Peru (7 species); and Huancabamba of Peru (14

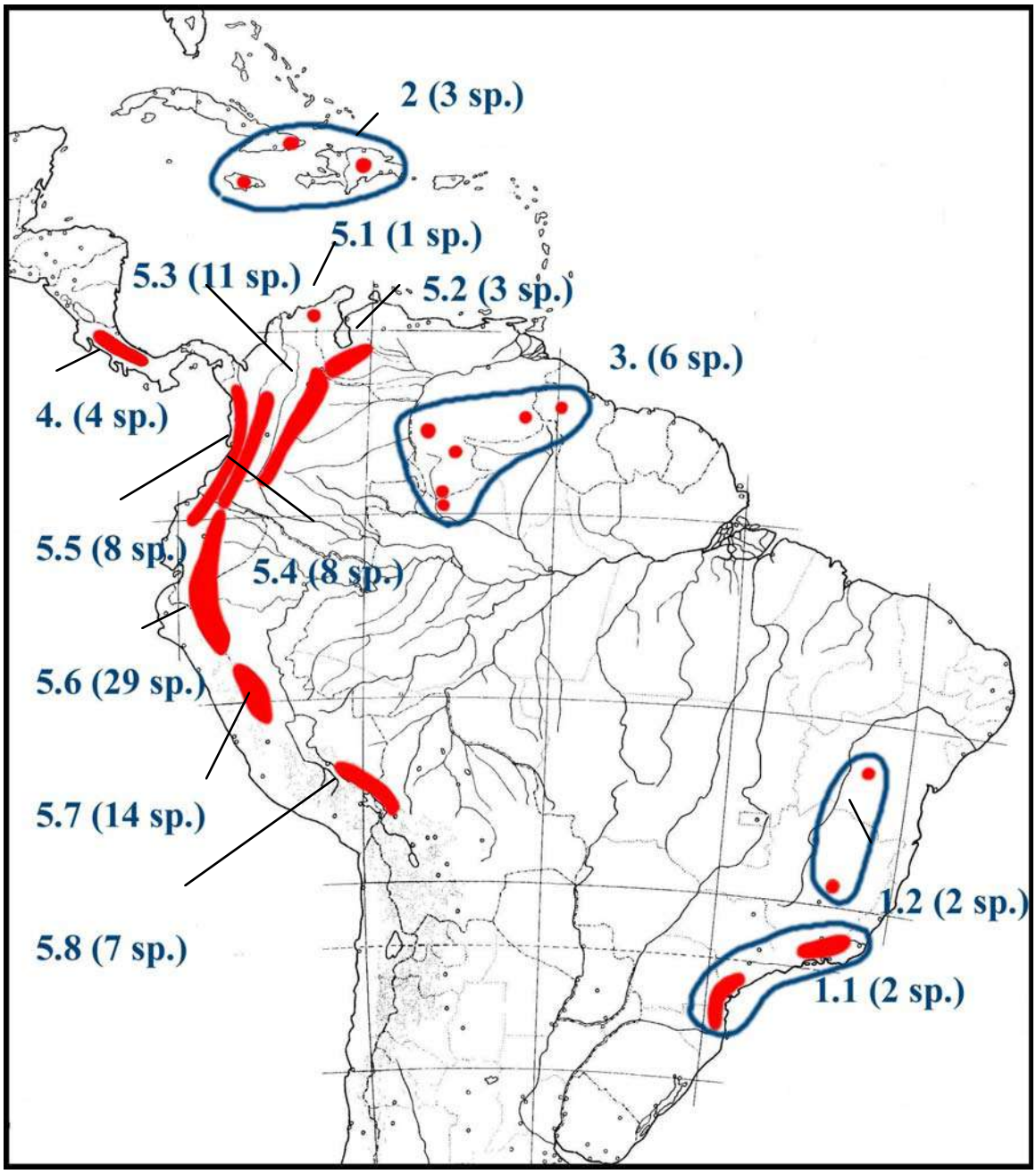
species)]; Central Andes: Cordillera Central, Peru (14 species); and Central Andes: Cordillera Oriental, Peru and Bolivia (7 species).

The center of species diversity of the genus appears to be in the Andes of Colombia, Ecuador, and Peru, where the largest number of species and nearly all the undescribed species are found. Please note that the species numbers in all charts reflect the number of **endemic** species to each region. Only a few cases have been found in which species occur in more than one region (e.g., *M. macrophylla* of the Cordillera Central occurs in the Cordillera Occidental in Colombia as well as in Southern Mesoamerica in Panama).

A total of 98 species are recognized in *Macrocarpaea*, 63 of which were identified during the preparation of this thesis. Previously, 35 species were recognized, for a 64% increase in species number. Of the five major regions, the Andes show by far the largest increase in species numbers. Previously only 21 species were recognized in the Andes, whereas 81 are recognized at present, an increase of 74%.

Reg.	Biogeographical Area	a) # sp	b) # sp prior	c) # new sp	d) % inc in sp #
1	Southeastern Brazil	[4]	[3]	[1]	25
1.1	Southeastern Brazil: Atlantic Forest	2	2	0	0
1.2	Southeastern Brazil: Espinhaço Range	2	1	1	50
2	Greater Antilles of the Caribbean	3	3	0	0
3	Pantepui of the Guayana Shield	6	5	1	17
4	Southern Mesoamerica (Costa Rica and Panama)	4	3	1	0
5	Andes	[81]	[21]	[60]	[74]
5.1	Northern Andes: Sierra Nevada de Santa Marta, Colombia	1	1	0	0
5.2	Northern Andes: Cordillera de Mérida, Venezuela	3	1	2	66
5.3	Northern Andes: Cordillera Oriental, Colombia	11	2	9	82
5.4	Northern Andes: Cordillera Central, Colombia	8	4	4	50
5.5	Northern Andes: Cordillera Occidental, Colombia and Ecuador	8	1	7	88
5.6	Central Andes: Huancabamba region, Ecuador and Peru	[29]	[5]	[24]	[83]
5.6.1	Huancabamba of Ecuador	8	1	7	88
5.6.2	Huancabamba of the Cordillera de Condor, Ecuador/Peru	7	2	5	71
5.6.3	Huancabamba of Peru	14	2	12	86
5.7	Central Andes: Cordillera Central, Peru	14	4	10	71
5.8	Central Andes: Cordillera Oriental, Peru and Bolivia	7	3	4	57
		98	35	63	64

Tab. 7. This figure illustrates the **biogeographical areas** where *Macrocarpaea* species occur, and the number of **endemic** species in each region. For each biogeographical area, statistics on the number of species that occur there are enumerated: a) the number of species **currently** recognized, b) the number of species **previously** recognized, c) the number of **new** species identified in this thesis, and c) the **percentage increase** in species numbers.



Map 9. **Biogeographical regions of *Macrocarpaea* in the Neotropics**.

1.1 Atlantic Forest (2 sp.).
1.2 Espinhaço Range (2 sp.).
2. Greater Antilles of the Caribbean (3 sp.).
3. Pantepui of the Guayana Shield (6 sp.).
4. Southern Mesoamerica (Costa Rica and Panama) (4 sp.).
5.1 Sierra Nevada de Santa Marta, Colombia (1 sp.).
5.2 Cordillera de Mérida, Venezuela (1 sp.).
5.3 Cordillera Oriental, Colombia (11 sp.).
5.4 Cordillera Central, Colombia (8 sp.).
5.5 Cordillera Occidental, Colombia and Ecuador (8 sp.).
5.6 Huancabamba region of Ecuador and Peru (29 sp).
5.7 Cordillera Central, Peru (14 sp.).
5.8 Cordillera Oriental, Peru and Bolivia (7 sp).

Map 10. Distribution of the eleven **centers of diversity** of *Puya* (Bromeliaceae): I. Sierra Nevada de Santa Marta, II. Eastern Cordillera of Colombia and Mérida Andes, III. Cundinamarca, IV. southwestern Colombia and northern Ecuador, V. south-central Ecuador, VI. northern Peru, VII. central Peru, VIII. Titicaca, IX. southern Bolivia, X. northwestern Argentina, and XI. Chile. The genus also ranges to Mesoamerica and the Guayana Shield.

Many of the regions delimited here for *Macrocarpaea* are mirrored in other groups. Varadarajan (1990) described the patterns of geographic distribution in the genus *Puya* (Bromeliaceae). Eleven centers of diversity of *Puya* were found (Map 10): Sierra Nevada de Santa Marta, Eastern Cordillera of Colombia and Mérida Andes, Cundinamarca, southwestern Colombia and northern Ecuador, south-central Ecuador, northern Peru, central Peru, Titicaca, southern Bolivia, northwestern Argentina, and Chile. Please note that these are centers of diversity, and not overall distributions of the genus, compared to my analysis of genus-wide distribution of *Macrocarpaea*. *Puya* does in fact have representatives in Southern Mesoamerica (Costa Rica and Panama), and on the Guayana Shield, though absent from the Greater Antilles and Southeastern Brazil. *Macrocarpaea* is absent from southern Bolivia, northwestern Argentina, and Chile. Nevertheless, *Macrocarpaea* and *Puya* generally have a similar pattern of species distribution, especially in regard to major centers of species diversity.

1. Southeastern Brazil

Macrocarpaea occur in two distinct biogeographic areas in southeastern Brazil, Mata Atlântica (*M. glaziovii* and *M. rubra*), and Espinhaço Range (*M. caatingae* and *M. obtusifolia*). *Macrocarpaea rubra* is the southernmost species of the genus, ranging from São Paulo, Paraná, and Santa Catarina, and unlike its name suggests, the flowers are actually yellow, not red. It is also unique within the genus being a perennial herb (all remaining species are shrubs to small trees), with an urceolate corolla (all remaining have campanulate corollas). According to molecular data, these species form a monophyletic basal lineage recognized here as sect. *Tabacifoliae* (Fig. 63).

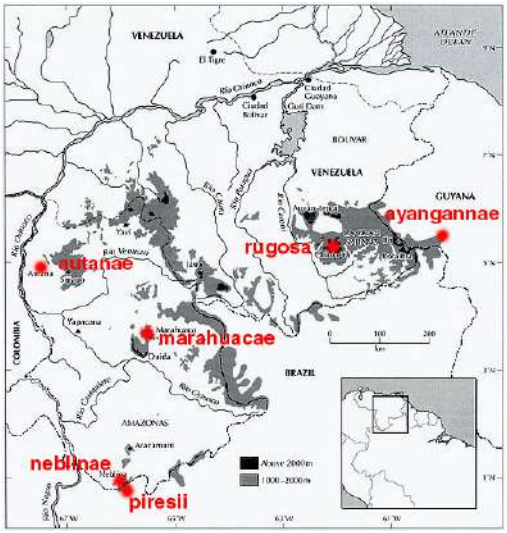
2. Greater Antilles of the Caribbean

Three species occur on islands in the Greater Antilles in the Caribbean (Map 11). *Macrocarpaea domingensis* is endemic to Hispaniola, *M. pinetorum* to eastern Cuba (Thiv & Grant 2002), and *M. thamnoides* to Jamaica. According to molecular data, these species form a monophyletic sub-basal lineage here recognized as sect. *Caribbigenes* (Fig. 64).

Map. 11. Distribution of Macrocarpaea on the Greater Antilles.

3. Pantepui of the Guayana Shield

Pantepui refers to the entirety of the tepui complex that sits on the Guayana Shield, a two-billion-year-old Pre-Cambrian geologic formation. Six widely disjunct species occur on different mountain peaks (Map 12): *Macrocarpaea autanae* (Cerro Autana, Venezuela), *M. ayangannae* (Mt. Ayanganna, Guyana), *M. marahuacae* (Cerro Marahuaca, Venezuela), *M. neblinae* (Cerro de la Neblina, Venezuela), *M. piresii* (Serra da Neblina, Brazil), and *M. rugosa* (Macizo del Chimantá, Venezuela). Unlike the species of the Mata Atlântica or Greater Antilles, these species do not form a monophyletic group. Rather, they appear to originate from separate long-range dispersals from the Andes.



Map 12. Distribution of the six disjunct species of *Macrocarpaea* on Pantepui of the Guayana Shield..

The Guayana Shield may have had at least two dispersals. The eastern species *M. ayangannae*, *M. marahuacae*, and *M. rugosa* are morphologically different (notably being hairy to spiculate) from the glabrous western species *M. autanae*, *M. neblinae*, and *M. piresii*. Though the latter three have characters generally consistent with sect. *Choriophylla*, all six species are here provisionally recognized in sect. *Macrocarpaea* until molecular data can determine differently.

Several notable gaps appear in the distribution of *Macrocarpaea* on the Guayana Shield, especially from species-rich areas as Auyan-tepui, Cerro Jaua, Serra Parima, and Roraima. Additional species of *Macrocarpaea* probably will be found on the Guayana Shield, possibly from these areas.

4. Southern Mesoamerica (Costa Rica and Panama)

Five species (4 endemic) occur in Costa Rica and Panama: *M. auriculata* (Costa Rica), *M. browallioides* (Costa Rica, Panama), *M. macrophylla* (Colombia, Panama), *M. subcaudata* (Costa Rica, Panama), and *M. valerii* (Costa Rica). Additionally, the taxon previously recognized as the species *M. acuminata* is recognized here as a the hybrid *M.* × *acuminata* [*M. subcaudata* × *M. valerii*] (Costa Rica). Although the Costa Rica-Panama region is distinct geographically from the Andes, the species do not form a monophyletic group that might suggest a single radiation. Rather, several different species radiations from Colombia have spread to Panama and Costa Rica, indicating that the genus is expanding northwards.

5. The Andes

The distribution of *Macrocarpaea* in the Andes covers eight distinct regions: 5.1 Sierra Nevada de Santa Marta, Colombia. 5.2 Cordillera de Mérida, Venezuela. 5.3 Cordillera Oriental, Colombia. 5.4 Cordillera Central, Colombia. 5.5 Cordillera Occidental, Colombia and Ecuador. 5.6 Huancabamba region of Ecuador and Peru. 5.7 Cordillera Central, Peru. 5.8 Cordillera Oriental, Peru and Bolivia.

5.1. Northern Andes: Sierra Nevada de Santa Marta, Colombia
The Sierra Nevada de Santa Marta is an isolated group of mountains in northern Colombia, an extension from the Cordillera Oriental. A single species has been collected here, Macrocarpaea calophylla, only known from two collections: the type found in 1843, and a more "recent" collection from 1948. Since there are no modern collections, this species may be extinct.

5.2. Northern Andes: Cordillera de Mérida, Venezuela
Three species occur on the Cordillera de Mérida in Venezuela: *Macrocarpaea bracteata*, *M. ewaniana*, and *M. papillosa*. *Macrocarpaea weaveri* occurs along both sides of the Colombia/Venezuela border, but falls within the geographical region of the Cordillera Oriental of Colombia.

5.3. Northern Andes: Cordillera Oriental, Colombia
The eastern Cordillera of the Andes in Colombia has eleven species including *M. affinis*, *M. glabra*, *M. gulosa*, *M. hilarula*, *M. jocularis*, *M. lacrossiformis*, *M. nicotianifolia*, *M. risibilis*, *M. schultesii*, *M. umerulus*, and *M. weaveri*. *Macrocarpaea glabra* is one of the most commonly represented species in herbaria, likely due to its close proximity to Bogotá.

5.4. Northern Andes: Cordillera Central, Colombia
The central Cordillera of Colombia and N Ecuador has eight species including *M. densiflora*, *M. duquei*, *M. gaudialis*, *M. illecebrosa*, *M. laudabilis*, *M. macrophylla*, *M. pachyphylla*, and *M. ypsilocaule*. *Macrocarpaea macrophylla* is one of the more widespread species in the genus, ranging from (Colombia: Antioquia, Caldas, Cauca, Chocó, Nariño, Risaralda, Valle; Panama: Darien). *Macrocarpaea gaudialis*, *M. illecebrosa*, *M. pachyphylla*, and *M. ypsilocaule* occur in the southern part of this zone just south of where the Andes begins to divide into the western, central, and eastern cordilleras. *Macrocarpaea densiflora* and *M. ypsilocaule* range into N Ecuador from their primarily Colombian distributions.

5.5. Northern Andes: Cordillera Occidental, Colombia and Ecuador
The Chocó flora extends along lowlands and western slopes of the Cordillera Occidental from the Colombian departments of Chocó, Valle, Cauca, Nariño, and to the Ecuadorian provinces of Carchi, Esmeraldas and Pichincha. Inclusion of the Ecuadorian provinces in the Chocó region was suggested by Webster & Rhode (2001). The Chocó has eight species, including *Macrocarpaea biremis*, *M. gattaca*, *M. gondoloides*, *M. gravabilis*, *M. luctans*, *M. luteynii*, *M. maryae*, and *M. sodiroana*. What really sets this region apart is that all its members occur on the western side of the Andes. No other species of *Macrocarpaea* occurs on western slopes any further south, i.e., all other species of *Macrocarpaea* occur on east-facing slopes of the Andes. Likewise, the Chocó is where *Macrocarpaea* species reach some of the lowest elevations. Two species have relatively broad distributions for species of *Macrocarpaea*: *M. gondoloides* (Colombia: Chocó, Nariño; Ecuador: Carchi); and *M. sodiroana* (Colombia: Cauca, Nariño, Putumayo, Valle; Panama: Carchi, Pichincha).

5.6. Central Andes: Huancabamba region of Ecuador and Peru
The Huancabamba region of Ecuador and Peru represents an area of extreme species diversity among many plant groups (Weigend 2002). *Macrocarpaea* becomes most speciose within this area with 29 species. For mere convenience, three loosely

defined and overlapping geographical sub-regions may be identified: Huancabamba of Ecuador (8 sp.), Huancabamba of the Cordillera de Condor (7 sp.), and Huancabamba of Peru (14 sp.). The following 29 species occur in the Huancabamba region: *M. angelliae*, *M. apparata*, *M. arborescens*, *M. bubops*, *M. dillonii*, *M. elix, M. ericii*, *M. gracilis*, *M. gran-pajatena*, *M. innarrabilis*, *M. jalca*, *M. jensii*, *M. harlingii*, *M. jactans*, *M. kuelap*, *M. lenae*, *M. loranthoides*, *M. luna-gentiana*, *M. luya, M. micrantha*, *M. neillii*, *M. noctiluca*, *M. pringleana, M. quechua*, *M. stenophylla*, *M. subsessilis*, *M. wurdackii*, *M. xerantifulva*, and *M. zophoflora*. Additionally, the hybrid *M.* × *mattii* (*noctiluca* × *subsessilis*) occurs here.

5.6.1. Huancabamba of Ecuador

Southern Ecuador is one of the richest areas in *Macrocarpaea* species diversity. Eight species are endemic here including *M. angelliae*, *M. apparata*, *M. arborescens*, *M. elix, M. jensii*, *M. lenae*, *M. luna-gentiana*, and *M. subsessilis*, as well as the hybrid *M.* × *mattii* (*noctiluca* × *subsessilis*). In one locality, the San Francisco site of Parque Nacional Podocarpus, four species are sympatric, *M. bubops*, *M. jensii*, *M. harlingii*, and *M. noctiluca*.

5.6.2. Huancabamba of the Cordillera de Condor, Ecuador and Peru

The Cordillera del Condor is divided along its north-south backbone by the international borders of Ecuador and Peru. Seven species of *Macrocarpaea* occur in here including *M. bubops*, *M. harlingii*, *M. jactans*, *M. micrantha*, *M. neillii*, *M. noctiluca*, and *M. pringleana*.

5.6.3. Huancabamba of Peru

Northern Peru is a hotspot of species diversity with 14 species including *M. dillonii*, *M. ericii*, *M. gracilis*, *M. gran-pajatena*, *M. innarrabilis*, *M. jalca*, *M. kuelap*, *M. loranthoides*, *M. luya, M. quechua*, *M. stenophylla*, *M. wurdackii*, *M. xerantifulva*, and *M. zophoflora*.

5.7. Central Andes: Cordillera Central, Peru

Central Peru has 14 diverse species including *M. angustifolia*, *M. canoëifolia*, *M. fosteri*, *M. kayakifolia*, *M. obnubilata*, *M. ostentans*, *M. pachystyla*, *M. pajonalis*, *M. revoluta*, *M. tabula-fluctivagifolia*, *M. tahuantinsuyuana*, *M. viscosa*, *M. wallnoeferi*, and *M. weigendiorum*. The zone is particularly rich in species of section *Magnolifoliae*, where the center of species diversity of the section exists.

5.8. Central Andes: Cordillera Oriental, Peru and Bolivia

Seven species occur on the Cordillera Oriental of Peru and Bolivia, representing the gradual tapering off of species numbers of *Macrocarpaea* in the Andes. These species are *Macrocarpaea bangiana*, *M. cinchonifolia*, and *M. cochabambensis*, *M. fortisiana*, *M. kuepferiana*, *M. maguirei*, and *M. normae.*

6. NATURAL HISTORY

The natural history of a plant involves *where* is lives (geographical area, elevation, and vegetation type), and *how* it reproduces (pollination biology and dispersal). *Macrocarpaea* occurs in eighteen biogeographical areas of the Neotropics as identified and discussed above (Tab. 7; Map 9). A generally montane genus, species are found from [30–]1000–3600 m in elevation in four vegetations types: dry caatinga, lower montane rain forest, upper montane rain forest, and subpáramo. *Macrocarpaea* is visited or pollinated by bats, moths, hummingbirds, and insects, and its seeds are dispersed by wind or rain.

Elevation

The elevation at which at which an individual plant of *Macrocarpaea* occurs is an important criterion in determining its identification. Most species are restricted to narrow elevation zones within their geographical area that also correspond to *vegetation type*. For example, at one site in Ecuador, three species and one hybrid occur in overlapping distributions on the mountainside of Cerro Toledo, Loja. In the 'Upper montane rain forest' where *M. noctiluca* (1900–3220 m) and *M. subsessilis* (2450–2700 m) overlap, a hybrid has formed, *M.* ×*mattii* (2500 m) (Fig. 71–76). *Macrocarpaea luna-gentiana* occurs at higher elevations (3100–3450 m) in subpáramo vegetation, and is not involved in any hybridization.

Habitats

Following a reliable and consistent taxonomy of ecological zones in *Macrocarpaea* is difficult since several varying classifications exist (e.g., Harling 1979; Holdridge 1967). Some have few ranks and broad definitions, while others are multi-layered with narrow definitions; some appear to conflict with another. The categories used here follow Webster (1995) who provided an overview of the classification of neotropical cloud forests where most species of *Macrocarpaea* occur. The páramo region follows Luteyn (1999). A map of the broad categories of vegetations types in the Neotropics is illustrated where the distribution of *Macrocarpaea* largely corresponds to "Montane forests" (Map 13).

Species of *Macrocarpaea* are distributed in both dry and humid, broadleaf forests. Two species occur in dry forests (caatinga), while the majority (96 species) occur in humid (i.e., wet and rainy) forests, further divided into Lower montane rain forest, Upper montane rain forest, and Subpáramo:

1. Dry Tropical Broadleaf Forest
- 1.1 Caatinga [2 sp.]

2. Humid Tropical Broadleaf Forest
- 2.1 Lower montane rain forest ([400–]1000–2500 m) [50 sp.]
- 2.2 Upper montane rain forest (cloud forest) (2500–3500 m) [28 sp.]
- 2.3 Subpáramo ([2800–]3000–3500 m) [18 sp.]

Dry Tropical Broadleaf Forest

1.1 Caatinga
Two species occur in this extreme habitat on the Espinhaço Ridge in Brazil: *M. caatingae* (Chapada do Diamatina), and *M. obtusifolia* (Serra do Cipó).

Humid Tropical Broadleaf Forest

2.1 Lower montane rain forest ([400–]1000–2500 m) (Fig. 75-77)
50 species including: *M. affinis*, *M. angustifolia*, *M. auriculata*, *M. autanae*, *M. ayangannae*, *M. browallioides*, *M. canoëifolia*, *M. dillonii*, *M. domingensis*, *M. ericii*, *M. fortisiana*, *M. fosteri*, *M. glaziovii*, *M. gondoloides*, *M. gravabilis*, *M. harlingii*, *M. hilarula*, *M. innarrabilis*, *M. jactans*, *M. jensii*, *M. kuepferiana*, *M. lenae*, *M. luctans*, *M. luteynii*, *M. maryae*, *M. micrantha*, *M. neblinae*, *M. normae*, *M. obnubilata*, *M. ostentans*, *M. pachystyla*, *M. pinetorum*, *M. piresii*, *M. pringleana*, *M. quechua*, *M. revoluta*, *M. risibilis*, *M. rubra*, *M. rugosa*, *M. sodiroana*, *M. subcaudata*, *M. tabula-fluctivagifolia*, *M. tahuantinsuyuana*, *M. thamnoides*, *M. umerulus*, *M. valerii*, *M. wallnoeferi*, *M. weigendiorum*, *M. wurdackii*, and *M. xerantifulva*.

2.2 Upper montane rain forest (Cloud forest) (2500–3500 m) (Fig. 74).
28 species including: *M. apparata*, *M. bangiana*, *M. biremis*, *M. bubops*, *M. cinchonifolia*, *M. cochabambensis*, *M. elix*, *M. gattaca*, *M. gaudialis*, *M. gracilis*, *M. gran-pajatena*, *M. gulosa*, *M. kayakifolia*, *M. kuelap*, *M. lacrossiformis*, *M. laudabilis*, *M. loranthoides*, *M. macrophylla*, *M. maguirei*, *M. marahuacae*, *M. neillii*, *M. nicotianifolia*, *M. noctiluca*, *M. pajonalis*, *M. papillosa*, *M. schultesii*, *M. viscosa*, and *M. zophoflora*.

Five species may be referable to *jalca* vegetation, which occurs in the higher elevation areas of the Huancabamba region in Peru: *M. kuelap*, *M. luya*, *M. stenophylla*, *M. viscosa* and *M. zophoflora*. Three species of Bolivia and southern Peru may be are referable to *puno* or *yungas* vegetation, including *M. cinchonifolia*, *M. cochabambensis*, and *M. maguirei*.

2.3 Subpáramo ([2800–]3000–3500 m) (Fig. 78).
18 species including: M. *angelliae*, *M. arborescens*, *M. bracteata*, *M. calophylla*, *M. densiflora*, *M. duquei*, *M. ewaniana*, *M. glabra*, *M. illecebrosa*, *M. jalca*, *M. jocularis*, *M. luna-gentiana*, *M. luya*, *M. pachyphylla*, *M. stenophylla*, *M. subsessilis*, *M. weaveri*, and *M. ypsilocaule*. Eighteen species range to or generally are restricted to zones above 3000 m. The highest ranging species in the genus is M. glabra in Colombia, recorded from 3400–3600 m. Eleven of 18 species recorded from subpáramo vegetation are from sect. *Macrocarpaea*, occurring mostly in Colombia.

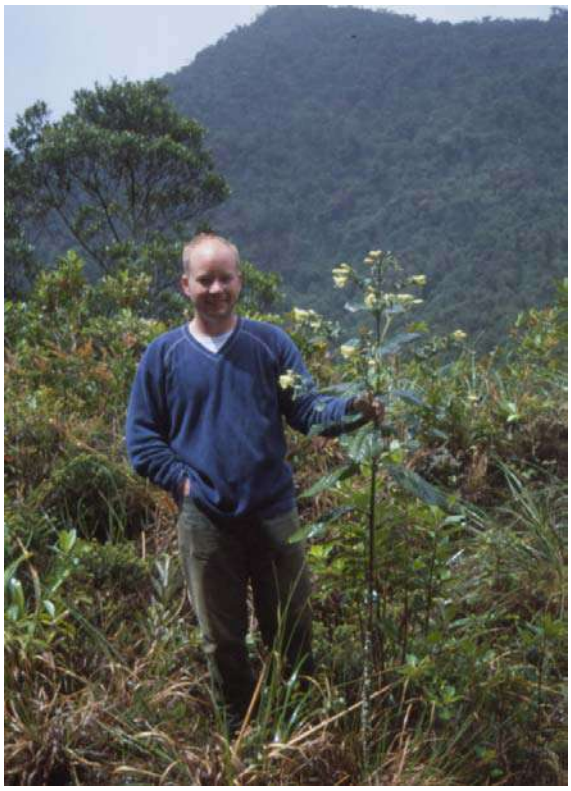


Fig. 74. **Upper montane rain forest**. JRG with *M. noctiluca*, Ecuador. Photo by L. Struwe.

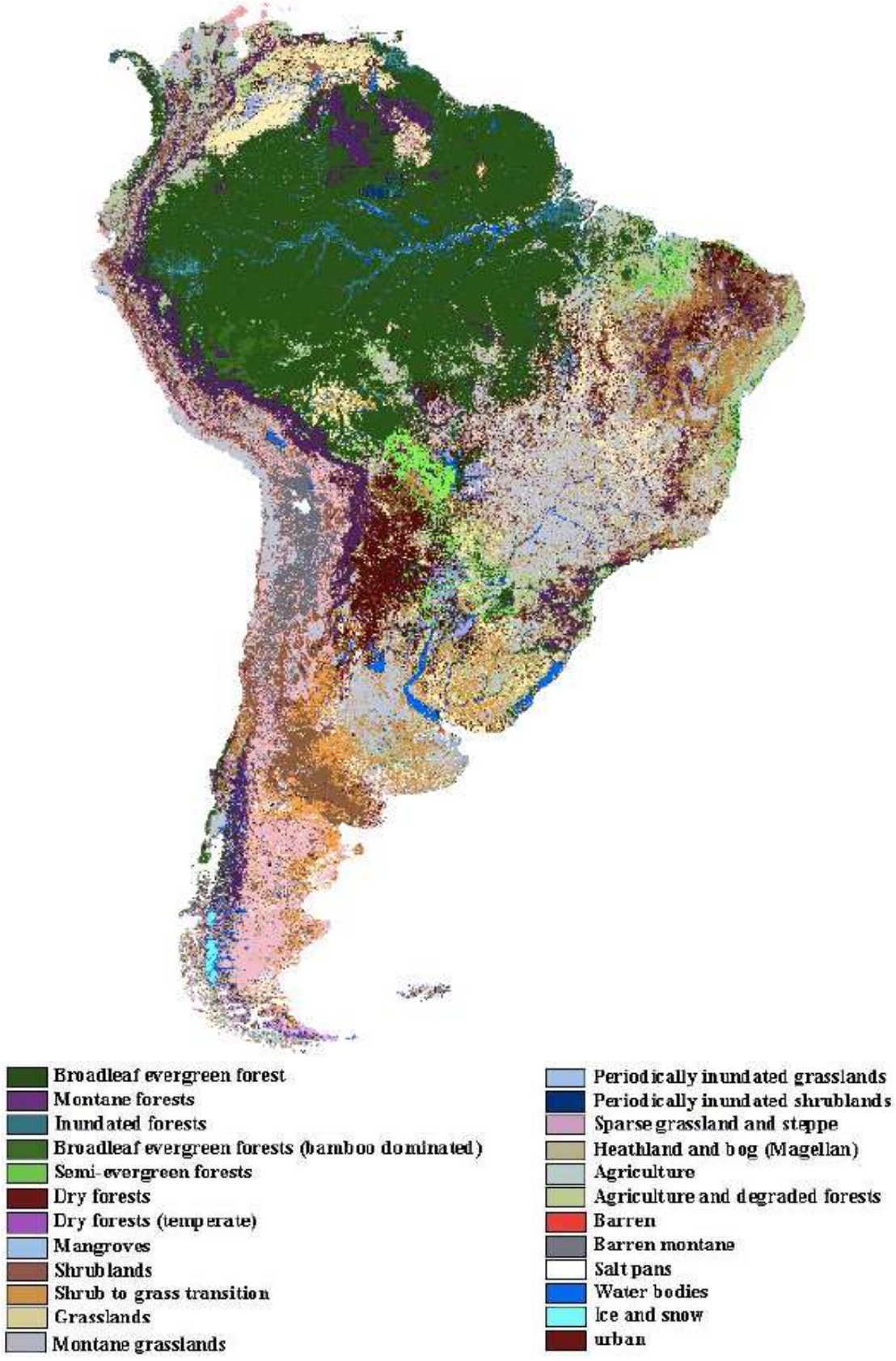
Fig. 75. **Lower montane rain forest**. Maquipucuna, Ecuador. Photo by J. Torres**.**

Fig. 76. **Lower montane rain forest**. Maquipucuna, Ecuador. Photo by J. Torres**.**

Fig. 74-78 Habitats of *Macrocarpaea*.

Fig. 77. **Lower montane rain forest** Maquipucuna, Ecuador. Photo by J. Torres**.**

Fig. 78. **Subpáramo**. JRG with *M. luna-gentiana*, Ecuador. Photo by L. Struwe.



Map 13. "A vegetation map of South America", Eva et al. (2002). The distribution of *Macrocarpaea* largely corresponds to "Montane forests", identified in purple.

POLLINATION BIOLOGY AND DISPERSAL

The flowers of *Macrocarpaea* are a typical example of night blooming and nocturnal pollination. They are generally large (2.0–7.5 cm long), wide-mouthed, funnelform, rubbery-firm, white, yellow, to light green in color, with fragrances most pronounced at nighttime, produce large quantities of nectar and pollen, and a have remote position on large open thyrses to facilitate visitors in the dark (e.g., bats due to sonar system limitations). Since the genus is specialized for nocturnal pollination, the diurnal (typically morning) visitors may be generalists simply be attracted to lingering fragrances and any remaining nectar.

Macrocarpaea is pollinated nocturnally by bats and moths, and diurnally by hummingbirds and insects. Matt (2001) has shown that the level of nectar production across five species is at the highest just after the flower opens, and steadily decreases throughout the night till the early morning. The nocturnal visits by bats and moths reap the greatest rewards in terms of nectar and pollen, while significantly less remains by morning for the diurnal visits of hummingbirds and insects (ants, beetles, bees). Studies on the pollination biology of *Macrocarpaea* are only now beginning. It should prove to be a fascinating model since there are so many different types of visitors to the flowers.

Once pollinated, fruits develop into dry dehiscent capsules with hundreds of miniscule seeds. Wind and the rain-wash or rain-splash effect are the probable modes of dispersal. It seems unlikely that animals would be attracted to the seeds as they are miniscule and offer no reward (like a fleshy pericarp).

VECTORS OF POLLINATION

BATS

Most species of bats are insectivorous (insect eating). Nectarivorous (nectar and pollen eating) species are less common, and have likely derived as a specialization from frugivorous (fruit eating) species (Gibson 2001). Bat pollination by nectarivorous species occurs nearly exclusively in tropical regions where the bats search out large flowers with large amounts of sugary nectar rewards (such plants are largely absent in non-tropical regions). Nectarivorous bats have a well-developed sense of smell, and are attracted to flowers with strong fruity or musky odors. The flowers are located by scent and sonar echolocation, and secondarily in short range by sight and sense on their whiskers when inserting the nose into the flower. The nectarivorous bats are attracted to the large reward of sucrose-rich nectar and pollen. Pollination occurs when large amounts of pollen are deposited on the head of the bat while it is feeding on nectar. The anthers and stigma are located in the same place in all *Macrocarpaea* flowers, so when the bat visits the next flower, pollen may be released from the bat on to the new flower, effectuating pollination. Since bats are known to forage long-distances from their day-time roots, effective cross-pollination across wide areas may occur (Gibson 2001).

Pollination by bats in *Macrocarpaea* has been anecdotally noted in various texts, yet without confirmation of the species of *Macrocarpaea* nor the species of bat. The first report of possible chiropterophily (bat-pollination) in *Macrocarpaea* was by Vogel

(1969) who compared the gentian genera *Chelonanthus*, *Macrocarpaea*, and *Symbolanthus*. However, specific examples were not cited as his comments were predictive (Vogel 1969; and pers. comm.). Félix Matt (Universität Erlangen, Germany) has extensively studied pollination in five species of *Macrocarpaea* at the Parque Nacional Podocarpus (Loja and Zamora-Chinchipe) Ecuador. Matt (2001) has observed two species of bats, *Anoura caudifera* (Tailed tailless bat) and *A. geoffroyi* (Hairy-legged Long-tongued Bat), visiting five species of *Macrocarpaea* (Tab. 8). The bat genus *Anoura* belongs to the Order Chiroptera, Family Phyllostomidae, Subfamily Glossophaginae: the Leaf-nosed Bats, which are obligate nectarivores. An additional report also indicates *Anoura geoffreyi* as the pollinator of *Macrocarpaea neblinae* on the tepui Cerro Neblina on the Guayana Shield (Renner 1989).

Latin Name Pollinator	**Common Name**	***arb***	***har***	***len***	***lun***	***neb***	***noc***
Anoura caudifera	Tailed Tailless Bat		**x**	**x**			**x**
Anoura geoffroyi	Hairy-legged Long-tongued Bat	**x**	**x**		**x**	**x**	**x**

Tab. 8. The two bat pollinators, and the six species of *Macrocarpaea* visited in S Ecuador (arb = *M. arborescens*), (harl = *M. harlingii*), (len = *M. lenae*), (lun = *M. luna-gentiana*), and (noc = *M. noctiluca*), and Venezuela (neb = *M. neblinae*).

Fig. 79. *Anoura caudifera*, the Tailed Tailless Bat, in flight pollinating the passionflower *Passiflora ovalis*. Photo by Ivan & Marlies Sazima, downloaded from http://www.aultimaarcadenoe.com/morcegofoto1.htm

Fig. 80. *Anoura caudifera*, the Tailed Tailless Bat, pollinating the passionflower *Passiflora ovalis* (Passifloraceae). Photo downloaded from http://www.aultimaarcadenoe.com/morcegofoto1.h

Fig. 81. *Anoura geoffroyi*, the Hairy-legged Long-Tongued Bat, in flight pollinating the passionflower *Passiflora ovalis*. Photo by Ivan & Marlies Sazima, downloaded from http://www.aultimaarcadenoe.com/morcegofoto1.htm

Fig. 82. *Anoura geoffroyi*, the Hairy-legged Long-Tongued Bat. Photo downloaded from http://www.aultimaarcadenoe.com/morcegofoto1.htm

MOTHS

Studies on pollination in *Macrocarpaea* recently have begun at the Reserva Maquipucuna, Pichincha, Ecuador, by Joseph Torres, a diploma student at the Université de Neuchâtel. A single species occurs at this reserve, *M. sodiroana*. Torres has photo-documented and sampled at least 11 species of moths: *Antiblemma* sp., *Coronidia* sp., *Desmia* sp., *Elmiotis* sp., *Erinnyis ello*, *Geometridae* sp., *Hemiceras* sp., *Notodontidae* sp., *Nystalea* sp., *Opharus* sp., and *Uraniinae* sp. Photos of these pollinators are illustrated as Fig. 83–91, and have also been placed on the following web site: http://www.ekuador.ch/macrocarpaea/. By placing the photos on the internet, new identifications by specialists in different moth groups have been made possible. Although reports of these visitors are made, their actual pollination results remain unknown, and will be also addressed in the studies of Torres. Various experiments using *Macrocarpaea sodiroana* as a model species are the first pollination studies in the genus. For example, is *Macrocarpaea* selfing or self-incompatible? Which visitors effectuate pollination, and which are robbers?

Additionally, specimen vouchers of moths have been prepared (e.g., Fig. 84–85), and compared by Torres to specimens of known identifications at the Instituto Nacional de Biodiversidad, Costa Rica. This institution (InBio) contains the largest and best curated collection of insects in the Neotropics.

Fig. 83. Living *Erinnyis ello*.visiting *M. sodiroana*.

Fig. 84. *Coronidia* sp. preserved as a specimen (see also Fig. 89–90).

Fig. 85. Dead *Erinnys ello* preserved as a specimen. Identification by Torres was based on photographs, comparison of specimens to a voucher collection at InBio, Costa Rica, and the help of Isidro Chacon and Dan Janzen.

Fig. 86. *Opharus* sp.

Fig. 87. *Nystalea* sp.

Fig. 88. *Antiblemma* sp.

Fig. 89. *Coronidia* sp.

Fig. 90. *Coronidia* sp.

Fig. 91. *Antiblemma* sp.

Fig. 86–91. Moths visiting *M. sodiroana*, Maquipucuna, Ecuador. Photos by J Torres

HUMMINGBIRDS

Pollination by hummingbirds has been observed on a number of species in *Macrocarpaea* (Tab. 9). Although more species certainly visit, eleven species have been recorded to date: *Acestrura* sp., *Aglaeactis cupripennis*, *Campylopterus duidae*, *Chalcostigma herrani*, *Coeligena iris*, *Coeligena lutetiae*, *Coeligena torquata*, *Eriocnemis vestitus*, *Heliangelus amethysticollis*, *Pterophanes cyanopteris*, and *Urosticte benjamini* (Fig. 92-96).

Stein & Todzia on their herbarium label of *Stein & Todzia 2322* (year 1985) recorded the visits of *Heliangelus amethysticollis* to *Macrocarpaea pajonalis* in central Peru. Renner (1989) reported *Campylopterus duidae* as a common visitor of *M. neblinae* on Cerro Neblina on the Guayana Shield of Venezuela. Felix Matt (2001) observed eight species of hummingbirds visiting five nearly sympatric species of *Macrocarpaea* at Parque Nacional Podocarpus (Loja and Zamora-Chinchipe) Ecuador. The species recorded include *Acestrura* sp., *Aglaeactis cupripennis*, *Chalcostigma herrani*, *Coeligena iris*, *Coeligena lutetiae*, *Coeligena torquata*, *Eriocnemis vestitus*, and *Pterophanes cyanopteris* visiting *M. arborescens*, *M. harlingii*, *M. lenae*, *M. luna-gentiana*, and *M. noctiluca* (Tab. 8). Joseph Torres (unpubl.) has recorded visits to *M. sodiroana* by *Urosticte benjamini* (Fig. 92-93).

Hummingbirds may be generalist flower visitors, simply testing all flowers that are available. *Macrocarpaea* has a classical nocturnal floral syndrome and is best adapted to nocturnal visitors. However, visits by hummingbirds have been reported, e.g., in *M. sodiroana* in the morning by *Urosticte benjamini* when floral fragrances that are most pronounced at night may be lingering and still attractive (Torres unpubl.).

Pollinator	**Common Name**	***arb***	***har***	***len***	***lun***	***neb***	***noc***	***paj***	***sod***
Acestrura sp.	Woodstar			**x**					
Aglaeactis cupripennis	Shining Sunbeam						**x**		
Campylopterus duidae	Buff-breasted Sabrewing					**x**			
Chalcostigma herrani	Rainbow-bearded Thornbill				**x**				
Coeligena iris	Rainbow Starfrontlet	**x**							
Coeligena lutetiae	Buff-winged Starfrontlet				**x**				
Coeligena torquata	Collared Inca	**x**	**x**						
Eriocnemis vestitus	Glowing Puffleg	**x**					**x**		
Heliangelus amethysticollis	Amethyst-throated Sunangel							**x**	
Pterophanes cyanopteris	Great Sapphirewing				**x**				
Urosticte benjamini	Purple-bibbed Whitetip								**x**

Tab. 9. Hummingbird visitors to species of *Macrocarpaea* (arb = *M. arborescens*; har = *M. harlingii*; len = *M. lenae*; lun = *M. luna-gentiana*; neb = *M. neblinae*; and noc = *M. noctiluca*; paj = *M. pajonalis*; and sod = M. *sodiroana*).

Fig. 92. *Urosticte benjamini* visiting *M. sodiroana* in Ecuador. Photo by J. Torres.

Fig. 93. *Urosticte benjamini* visiting *M. sodiroana* in Ecuador. Photo by J. Torres.

Fig. 94. *Coeligena torquata*, Collared Inca.

Fig. 95. *Coeligena iris*, Rainbow Starfrontlet.

Fig. 96 *Pterophanes cyanopteris*, Great Sapphirewing.

Fig 92-96, hummingbird pollinators of *Macrocarpaea*.
http://www.focusonnature.com/FONT's%20Hummer%20Gallery.htm#Humming-bird%20Photos
http://www.nationalgeographic.com/wildworld/profiles/photos/nt/nt0174aS.htm

INSECTS

Beetles and ants are common visitors to *Macrocarpaea* flowers, attracted by the copious amounts pollen and nectar produced (Fig. 97-99). Spiders (Fig. 99) have been observed crouching on the flowers, possibly waiting to catch a pollinator of the flower. To date there are no studies on the visits of insects to *Macrocarpaea*.

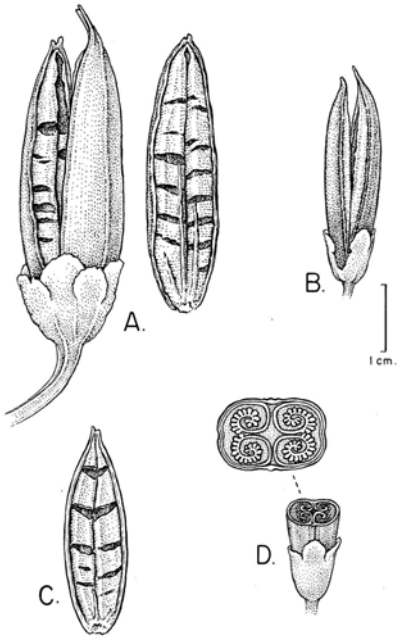
Fig. 97. Beetles and ants visiting *M. subsessilis* in Ecuador. Photo by J.R. Grant.

Fig. 99. Spider waiting on flower of *M. sodiroana* in Ecuador, perhaps for a lunchtime meal of an insect pollinator or visitor to the flower. Photo by J. Torres

Fig. 98. Insects visiting *M. gattaca* in Ecuador. Photo by J. Torres.

DISPERSAL

The fruit of *Macrocarpaea* is a dry, woody, 2–carpelled, bilocular and dehiscent capsule (Fig. 100-101). Seeds are flattened, polygonal, rimmed, winged or winged perimetrically, miniscule, ca. 0.2–1.6 x 0.2–0.6 mm (Fig. 42). In some species the seeds are fairly substantial in size, such as in *M. obtusifolia* (Fig. 42C) (the largest found so far), which are chunky enough to make distinct pattering noises when 50 or so are bounced upon a piece of paper. At the other extreme, the seeds of *M. micrantha* are so light and dust-like, that they momentarily lift into the air before silently floating down to the paper (Fig. 42Q). Each capsule may have 200+ seeds. The seeds fall out through salt-shaker-like holes (fenestrations) on the locules of the dehisced capsule (Fig. 100A,C). They may be blown out by the wind, or knocked out in the rain-wash or rain-splash effect where water droplets jolt a capsule in turn knocking out a few seeds at a time. Since neither the capsule nor seeds offer any enticing reward (such as a fleshy pericarp), dispersal by animals seems unlikely. The seeds are miniscule and may only be of interest to small insects, if anything.



Above. Fig. 100. Dehisced capsules of *M. noctiluca*. Photo by J.R. Grant

Left Fig. 101. Capsules of *Macrocarpaea*. A, *M. jactans*. B. *M. pringleana*. C. *M. maguirei*. D. *M. nicotianifolia*

Chance dispersal is the likely scenario for the genus migrating between southeast Brazil and the Caribbean, and then from the Caribbean to northwest South America. It seems unlikely (though possible) that vicariance could explain the extant distribution of the genus unless several large-scale extinction events of ancestral *Macrocarpaea* species or extinctions over large areas of Amazonia are taken into consideration.

Winged seeds have arisen several times in the genus. In sect. *Macrocarpaea*, the four known epiphytic species have developed extended rims to wings (from an otherwise polygonal group) that may facilitate distribution in epiphytic habitats. True winged seeds occur in sects. *Magnolifoliae* and *Choriophylla*. The rapid and diverse speciation in these groups may be due to the winged seeds that could disseminate the genus further than taxa with polygonal seeds and no wings.

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FUTURE WORK

1. Finish preparation of the *Flora Neotropica* monograph. This work involves describing the remainder of new species in several articles, then assembling all descriptions into *Flora Neotropica* format.

2. Continue floral biology studies of *Macrocarpaea* in Ecuador with Joseph Torres, a diploma student at the Université de Neuchâtel.

3. Travel to Colombia to visit herbaria, e.g., COAH, COL, CUVC, HUA, JAUM, MEDEL TULV, UDBC, and VALLE.

4. Begin a detailed morphological study of the seeds of *Macrocarpaea* by using Scanning Electron Microscopy (SEM).

5. Prepare website of *Macrocarpaea* images, keys, descriptions, etc.

6. Begin anatomical studies on alcohol-preserved flowers of *Macrocarpaea*.

7. Study the relationship of *Macrocarpaea* to the monotypic Cuban endemic genus *Zonanthus*. *Macrocarpaea* appears to be related to this enigmatic genus that has only been collected a few times since its discovery over 100 years ago. Fieldwork in Cuba would also address the Cuban endemic *Macrocarpaea pinetorum*.

APPENDIX A

Grant, J. R. and L. Struwe. 2000.

Morphological evolution and neotropical biogeography in *Macrocarpaea* (Gentianaceae: Helieae).
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APPENDIX B

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(2): 489-498

APPENDIX C

Thiv, M. and J.R. Grant. 2002.

Macrocarpaea (Gentianaceae) in Flora de la República de Cuba Fasc. 6(1): 23-26

APPENDIX D

Grant, J.R. 2003.

De Macrocarpaeae Grisebach (ex Gentianaceis) speciebus novis II:
Typification of the Ruiz & Pavon Names.
Harvard Pap. Bot 7(2): 423-436

APPENDIX E

Grant, J. R. and L. Struwe. 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(1): 61-81

APPENDIX F

Grant, J. R. and R.E. Weaver. 2003.

De Macrocarpaeae Grisebach (ex Gentianaceis) speciebus novis IV:
Eleven new species of *Macrocarpaea* (Gentianaceae: Helieae) from Central and South America, and the first report of the presence of stipules in the family.
Harvard Pap. Bot. 8(1): 83-109

APPENDIX G

Grant, J.R.

Macrocarpaea (Gentianaceae) in Catálogo de las Plantas Vasculares de Bolivia.
Submitted April 2003

APPENDIX H

Grant, J.R.

De Macrocarpaeae Grisebach (ex Gentianaceis) speciebus novis V:
Thirty-four new species of *Macrocarpaea* (Gentianaceae: Helieae) from Colombia, Ecuador, and Peru, and typification of all species in the genus.
Harvard Pap. Bot. To submit September 2003

APPENDIX I

Pollen morphological data and vouchers for Gentianaceae taxa with monads (adapted from Nilsson 2002)

APPENDIX J

Catalogue of Herbarium specimens cited by Ewan in the only monograph of *Macrocarpaea* (Ewan 1948)

APPENDIX K

List of Exsiccatae:
A Catalogue of Herbarium Specimens of *Macrocarpaea* (Gentianaceae)

Coprophilous species exhibit a series of "adaptations" to their unique habitat: they produce chemicals that attract insects that look for dung to lay their eggs; the sterile tissue below the sporangium is expanded allowing for insects to land on the sporophyte; they produce small sticky spores; their capsule wall contracts upon drying and the spores are continupously pushed up to the mouth of the sporangium by a psuedocolumellea subtending the spore mass. Entomochorous taxa (i.e., those that use insects to disperse their spores) have traditionally been considered derived within the family, with *Splachnum* representing the ultimate product of this evolutionary trend. Here we present phylogenetic analyses of sequences of two chloroplast loci (trnL-trnF and rps4) for about 100 accessions, including exemplars of all genera considered closely related to the Splachnaceae. Maximum parsimony and likelihood analyses yield topologies wherein *Splachnum* is resolved sister to a clade comprising all remaining taxa. Within the latter, *Tetraplodon* whose species are all thought to be entomophilous too, is sister to the Taylorioideae. *Brachymitrion*, the sole genus lacking any feature associated with entomophily, and occurring primarily in epiphytic habitst, composes the most derived lineage. Most noticeable is the recurrent association of anemophilous (using wind for spore dispersal) and entomophilous species. Based on these results it is hypothesized that entomophily was acquired early in the evolutionary history of the Splachnaceae and subsequently lost multiple times. This scenario would suggest that although highly specialized taxa may be evolutionary dead ends, that they offer a source for subsequent evolution of less specialized taxa, and thus may play in a significant part in the diversification of these lineages.

385 GRAHAM, SEAN W*, HARDEEP RAI, PATRICK REEVES, HEATH O'BRIEN, AND RICHARD OLMSTEAD. Dept. of Biological Sciences, University of Alberta, Edmonton AB, Canada T6G 2E9; Dept. of Botany, University of Washington, Seattle WA 98195—*Inference of seed plant phylogeny from multiple chloroplast genes.*

The reconstruction of seed plant relationships is recognized as one of the most difficult problems in plant systematics. A range of studies using various lines of evidence from morphology and molecules have given different and often strongly conflicting results. It is not clear, for example, whether the Gnetales represent the extant sister group of the flowering plants (the "anthophyte hypothesis"). Recent molecular studies suggest that they are instead closely related to (or even nested within) the conifers. The root of the seed plants, and the issue of gymnosperm monophyly, are likewise unclear. Long-branch attraction appears to be a major problem in seed plant phylogenetic inference, and may be partly responsible for the strongly discordant results from different studies. We have sampled large amounts of DNA sequence data from a variety of slowly evolving chloroplast genes, across taxa that span the major lineages of the seed plants, in order to try to explore these issues. The impact of long-branch attraction and of different levels of gene and taxon sampling on seed plant phylogenetic inference will be addressed.

386 GRANT1, JASON R.* AND LENA STRUWE2. 1 Laboratoire de phanérogamie, Institut de botanique, Université de Neuchâtel, ch. de Chantemerle 18, 2007 Neuchâtel, Switzerland, 2 The Lewis B. & Dorothy Cullman Program for Molecular Systematics Studies, The New York Botanical Garden, Bronx, NY 10458 USA—*Morphological evolution and neotropical biogeograpy in* Macrocarpaea *(Gentianaceae: Helieae).*

The genus *Macrocarpaea* consists of 50-60 species of herbs, shrubs (some epiphytic), and small trees restricted to the neotropics. The majority of its species are distributed in mid- to upper-elevation rain or cloud forests in the Andes. Additional species occur in the mountains of southeastern Brazil, the Guayana Highlands, Central America, and the Greater Antilles. A monographic treatment of the genus based on over 1500 herbarium specimens on loan from over 40 different herbaria has been initiated. Nomenclature problems will be resolved, dozens of new species will be described, and dubious taxa will be confirmed. *Macrocarpaea* is one of only a few genera among that gentians that have hairy leaves in some species. Scanning electron microscopy studies of indumentum anatomy will be evaluated and presented. Large micromorphological variation can also be found in seed and pollen anatomy, as well as in macromorphological characters. Species level cladistic analyses based on ribosomal 5s-NTS and nuclear ITS (internal transcribed spacer) sequences are presented and will eventually be combined with morphological data. Preliminary molecular data suggests that within the distribution area of the genus, the most ancestral lineages are present in the peripheral regions (i.e. Brazil and the Caribbean), with the Andean species representing more recent and more species-rich radiations.

DE MACROCARPAEAE GRISEBACH (EX GENTIANACEIS) SPECIEBUS NOVIS I: AN INTRODUCTION TO THE GENUS *MACROCARPAEA* AND THREE NEW SPECIES FROM COLOMBIA, ECUADOR, AND GUYANA

JASON R. GRANT[1] AND LENA STRUWE[2]

Abstract. A monographic revision of the neotropical genus *Macrocarpaea* (Gentianaceae: Helieae) has been initiated. The taxonomic and nomenclatural background is provided as an introduction in this first of several papers. These gentians are typically montane shrubs with large, funnelform, night-blooming, bat-pollinated flowers and have a high rate of species endemicity. It is also an excellent group from which to study neotropical montane biogeography, since they occur in all major neotropical montane habitats. Three new species are described and illustrated: *Macrocarpaea angelliae* (Ecuador) in discussion with *M. stenophylla* where a neotype is selected, *M. ayangannae* (Guyana), and *M. luteynii* (Colombia). New synonymy is reported for one published species [*Macrocarpaea guttifera* = *Ravenia biramosa* (Rutaceae)] and six "nomen herbariorum": "Axelsonia globiflora Dusén, ined." = *M. rubra*, "M. buchtienii Gilg, ined." = *M. cinchoniifolia*, "M. ekmanii Ewan, ined." = *M. pinetorum*, "M. gilgiana Rusby, ined." = *M. cochabambensis*, "M. peduncularis Rusby, ined." = *M. bangiana*, and "M. tabacifolia Ewan, ined." = *M. cinchoniifolia*.

Keywords: Gentianaceae, Helieae, *Macrocarpaea*, morphology, Neotropics.

Macrocarpaea is a genus of herbs, shrubs, and small trees that occur primarily in montane regions of the Neotropics. The flowers are generally large (2.0–7.5 cm long), funnelform, night-blooming, and bat-pollinated. With some 65+ species, it is the largest genus in the tribe Helieae, has a high rate of species endemicity, and exhibits a wide range of morphological variation. Important and taxonomically consistent morphological characters at the species rank that are readily visible on herbarium material include the architecture of the inflorescence (a thyrse, where the primary branching is racemose, and the secondary is cymose); position of the flowers before and after anthesis (erect, spreading, horizontal, nodding); calyx size, shape (lobes acute, acuminate, cuspidate, obtuse, rounded), vestiture (glabrous, scabrous, hairy); and leaf size and shape (linear, lanceolate, ovate, elliptical, obovate).

Macrocarpaea is positioned in the tribe Helieae of the Gentianaceae (Clade C in Thiv et al., 1999) and is itself monophyletic (Grant and Struwe, 2000; Grant and Struwe, unpubl.). The genus has a geographic distribution pattern typical of many groups in the Neotropics. Within the primary range (Costa Rica and Panama, and the Andes of Venezuela through Colombia, Ecuador, and Peru to Bolivia), there are around 52 species of narrow endemics and relatively few wide-ranging species (e.g., *Macrocarpaea sodiroana* and *M. revoluta*). Outside this primary and generally contiguous range, there are four species endemic to the Greater Antilles

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(Cuba, Dominican Republic, and Jamaica), six species endemic to the Guayana Highlands (Brazil, Guyana, and Venezuela), and three species endemic to southeastern Brazil. The center of diversity of the genus appears to be in the Andes of Colombia, Ecuador, and Peru, where the largest number of species and nearly all the undescribed species are found.

Grisebach (1839) described *Lisyanthus* sect. *Macrocarpaea*, which was elevated to the genus rank by Gilg (1895). In the latter work, Gilg also described the monotypic genus *Rusbyanthus* based on a species with warty pollen [*R. cinchoniifolius* Gilg] that Weaver (1974) reduced to synonymy under *Macrocarpaea*. The only revision ever made of *Macrocarpaea* was published by Ewan (1948), who recognized 31 species based on 95 herbarium collections. Since then, the five species that have pollen in tetrads [*M. arborea* (Britton) Ewan, *M. quelchii* (N. E. Brown) Ewan, *M. cerronis* Ewan, *M. salicifolia* Ewan, and *M. tepuiensis* (Gleason) Steyerm., the latter three being placed in synonymy under *Rogersonanthus arboreus* (Maguire and Boom, 1989; Struwe et al., 1999) were segregated by Maguire and Boom (1989) as the new genus *Rogersonanthus*. This resulted in the genus *Macrocarpaea* being specifically defined as having pollen only in monads (Nilsson 1968, 1970). Additionally, since Ewan (1948) to the present time, 13 species have either been transferred to *Macrocarpaea* or described as new (Ewan, 1950, 1951; Alain, 1955; Steyermark, 1963; Robyns and Nilsson, 1970; Weaver, 1972, 1974; Maguire, 1981; Maas, 1993; Pringle, 1995; Struwe and Albert, 1998). Several works have addressed *Macrocarpaea* taxonomy in specific regional areas (Costa Rica—Weaver, 1972; Panama—Sytsma, 1987; Ecuador—Pringle, 1995; and the Venezuelan Guayana—Struwe et al., 1999); however, no modern comprehensive treatment exists for the genus. This paper is part of an in-progress revision of the entire genus, based on the examination of over 1700 herbarium specimens on loan from over 50 herbaria throughout the world. Several species recognized by Ewan will be synonymized, and at least 65 species will be accepted, a third of which are so far undescribed. Three of these new species are described here in this first of a series of papers on *Macrocarpaea* systematics.

Macrocarpaea stenophylla Gilg, Bot. Jahrb. Syst. 22: 337. 1896. NEOTYPE: PERU. Amazonas: Central Cordillera of the Andes, Chachapoyas to Moyabamba, small shrub, La Jalca, 2700–3300 m, 20 January 1930, *Williams 7582* (Neotype: F, here designated).

Gilg (1896) based *Macrocarpaea stenophylla* on a single specimen, *Stübel 24* (B). Since this material cannot be currently located, it was presumably destroyed when the Berlin-Dahlem herbarium was partially destroyed during the Second World War. No isotypes have been found, so our identification of the species is based entirely on the original description and locality information. Ewan (1948) cited *Stübel 24* (B) and *Williams 7582* (F) as the two specimens he knew of *M. stenophylla*. Because the Stübel collection is missing, and since the Williams material does in fact match the protologue, the latter is here selected as the neotype for *M. stenophylla*.

During the research on these specimens of *Macrocarpaea stenophylla*, as well as the material cited by Pringle (1995: 97–98) in *Flora of Ecuador*, a problem emerged. The Ecuadorian material cited by Pringle clearly represented a taxon quite different from the Peruvian. Therefore, the three Peruvian specimens alone are here identified as *M. stenophylla*, while the Ecuadorian material represents a new species that is described below as *M. angelliae*.

Additional material examined: PERU. Amazonas: Cerro de Fraijaco (Huaui-Huni), NE of Tambo de Ventilla, 3200-3400 m, shrub, corolla pale yellow (baryta y.), dry sandy soil, 7 July 1948, *Pennell 15861* (PH). Cajamarca: Prov. San Ignacio: San José de Lourdes, Llanos, forest remnants, peat bog and open jalca area over sandstone, 1900–2100 m, shrub in dryish areas in grassland, leaves strongly coriaceous, dark green, flowers strongly zygomorphic, pale greenish-yellow, 10 June 1998, *Weigend et al. 98/500* (M).

Macrocarpaea angelliae J. R. Grant & Struwe, *sp. nov.* TYPE: ECUADOR. Zamora-Chinchipe: Carretera Loja-Zamora, cerca al Paso, 2800–2900 m, sufrutex de 1.0–1.5 m, brácteas verdes, sépalos amarillo-verdosos, vegetación representiva de *Clusia*, *Simplocos*, *Psychotria*, 15 March 1989, *Romoleroux 804* (Holotype: NY; Isotype: AAU). Fig. 1.

= *Macrocarpaea stenophylla* in part *sensu* Pringle, *Flora of Ecuador* 53: 97–98. 1995.

A Macrocarpaea stenophylla Gilg cui affinis, sed foliis ovatis, ellipticis, lanceolatis, apicibus

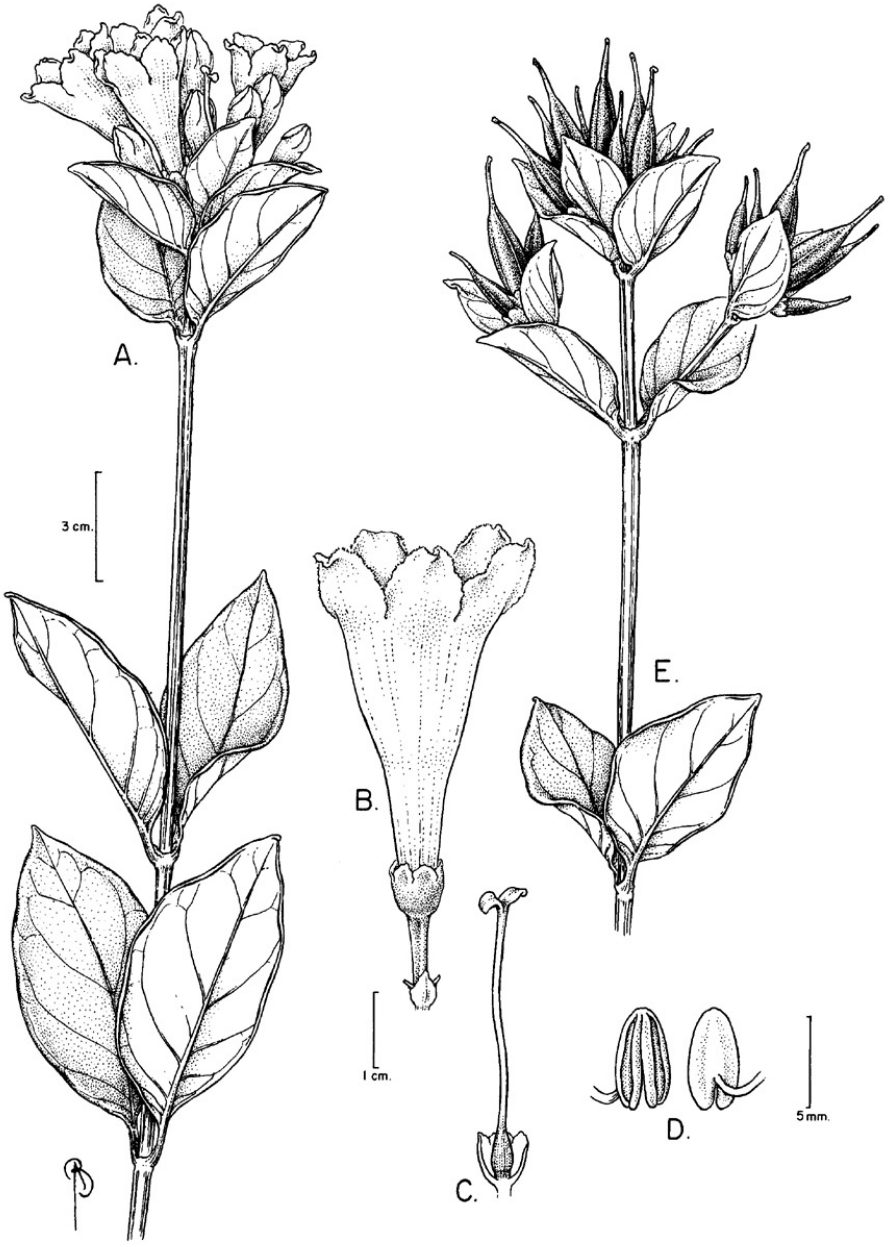

FIGURE 1. *Macrocarpaea angelliae*. A, habit of flowering stem; B, flower; C, gynoecium; D, anthers; E, fruiting stem. From *Øllgaard 91065* (AAU).

acutis vel acuminatis, et bracteis longioribus foliiformibus differt.

Shrubs 1.0–1.5 m tall; stems terete, solid or hollow, up to 8 mm in diameter, glabrous throughout except lower leaf surfaces. Leaves short-petiolate, ovate, elliptical to lanceolate, 5.5–13 × 2.5–6.0 cm, glabrous, edges strongly revolute (at least when dried), the base rounded to slightly attenuate, the apex acute to acuminate, leathery-coriaceous, the upper side dark green with slightly impressed veins, the lower contrasting light green with raised veins and short brown sessile stellate hairs; interpetiolar ridge 4–6 mm high; petioles 3–11 mm long. Inflorescence 4-11 cm long, 6- to 20-flowered; bracts large, leaf-like, ovate, apex obtuse, 2.5–6.6 × 1..9–3.1 cm, clasping each cyme. Flowers pedicellate, erect, not spreading; pedicels 8–11 mm. Bracteoles inconspicuous, scabrous, ovate 2–5 × 2.0-4.5 mm, sessile to the receptacle. Calyx campanulate, 6–8 mm long, yellowish-green, the lobes rounded, 1–3 mm, with hyaline margins, remaining erect in fruit. Corolla yellowish-green, 3.5–5.1 cm long, funnelform, the lobes ovate to elliptical, 8–13 × 8–12 mm, lobe apex obtuse. Stamens reaching the base of the corolla lobes; filaments of unequal length, filiform, straight; anthers linear, 4.5–5.0 mm long, sagittate, versatile. Gynoecium 3 cm long, ovary 5–6 × 3–4 mm, style 24–25 x 1.0 mm, stigma 2-lobed, each lobe circular, 2–3 × 2 mm. Capsules erect to slightly spreading from another, slightly woody, 2.5–3.0 cm (excluding the style base), rugose, shiny, with a persistent, elongate style base to 15 mm long. Seeds unknown.

Macrocarpaea angelliae differs from *M. stenophylla* in its generally more robust appearance, ovate, elliptical to lanceolate leaves with acute to typically acuminate apices (vs. ovate, elliptical to obovate leaves with acute apices), and larger, more leaf-like bracts. In *M. stenophylla*, the two bracts (or bracteoles) that immediately subtend each flower are distinctly spatulate to obovate, 9–15 × 5–6 mm at broadest, contrasting to the bracts that subtend the inflorescence that are 2.1–5.2 × 1.4–2.9 cm. In *M. angelliae*, the bracteoles that subtend each flower are minute, scabrous, ovate 2–5 × 2.0-4.5 mm, while the bracts that subtend each inflorescence are 2.5–6.6 × 1..9–3.1 cm. *Macrocarpaea stenophylla* grows in dry sandy soils in "la jalca" vegetation, and has a pale yellow to pale-greenish-yellow corolla, while *M. angelliae* occurs in wet montane forests and ridges, and has a yellowish-green corolla.

This species ranges between Loja and Zamora-Chinchipe provinces in southern Ecuador (Fig. 2). At least nine species occur in this area, making it one of the most species-rich regions for *Macrocarpaea*. In particular, to date, Parque Nacional Podocarpus is known to

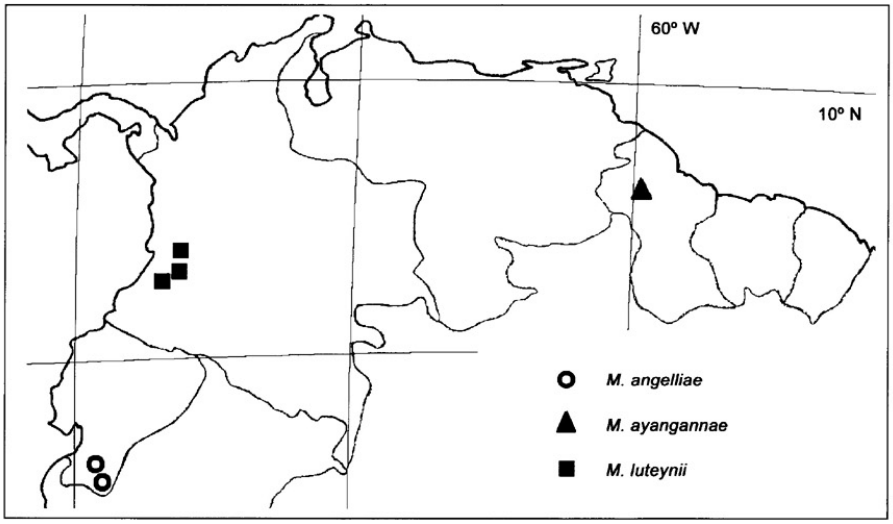

FIGURE 2. Distribution of *Macrocarpaea angelliae* (Ecuador), *M. ayangannae* (Guyana), and *M. luteynii* (Colombia) in northern South America.

be the single richest area in diversity, containing *M. angelliae* J.R. Grant & Struwe, *M. harlingii* J.M. Pringle, *M. micrantha* Gilg, *M. ovalis* (Ruiz & Pav.) Ewan, *M. pachyphylla* Gilg, *M. revoluta* (Ruiz & Pav.) Gilg, and *M.* cf. *sodiroana* Gilg.

Etymology: this species is named in honor of Bobbi Angell (1955–), Marlboro, Vermont, who has so skillfully prepared not only the illustrations of each of the three new species in this article but many others that will appear in forthcoming installments of this series.

Paratypes: ECUADOR. Loja: Yangana-Valladolid Rd., 2500–3000 m, 10 December 1989, *Madsen 86683* (AAU); Parque Nacional Podocarpus, ca. 1 km along trail towards Numbala at pass on the Yangana-Valladolid road, on ridge with low shrub vegetation, 4° 28' S, 79° 10' W, 3000 m, shrub to 1.5 m high, flowers yellow-green, 16 January, 1990, *Knudsen 8* (S). Zamora-Chinchipe: Parque Nacional Podocarpus, road Yangana-Valladolid, just S and E of the pass (Nudo de Sabanilla), mule-track from pass toward Quebrada Honda, wet montane forest and low exposed ridgetop vegetation, 4° 27' S, 78° 08' W, 2750–2950 m, 1.5 m tall shrub on open ridge, 18 February 1989, *Øllgaard 90630* (AAU); Parque Nacional Podocarpus, road Yangana-Valladolid, just S and E of the pass (Nudo de Sabanilla), mule-track from pass toward Quebrada Honda, wet montane forest and low exposed ridgetop vegetation, 4° 27' S, 78° 08' W, 2750–2950 m, 2750–2950 m, 1 m tall, unbranched, woody, flowers greenish yellow, 14 March 1989, *Øllgaard 91065* (AAU).

Macrocarpaea ayangannae J. R. Grant, Struwe, & J. K. Boggan, *sp. nov.* TYPE: GUYANA. Region Cuyoni-Mazaruni: Mt. Ayanganna, easternmost peak, summit and steep slopes, 05° 25' N, 59° 57' W, 1350–1380 m, elfin forest dominated by *Bonnetia roraimae*, *Clusia* spp., and various Myrtaceae, tree 3.5m x 4 cm, calyx and leaves dark green, corolla yellowish-green, 11 March 1987, *Pipoly et al. 11103* (Holotype: US [2 sheets, # 3378137 and # 3378517]. Five duplicates of this specimen apparently exist but could not be located during this study). Fig. 3–4.

A Macrocarpaeae rugosae Steyermark cui affinis, sed petiolos longioribus, foliis ovatis, apicibus acutis, basibus rotundatis, inflorescencia paucifloribus, et calyces brevioribus differt.

Trees 3.5 m tall; stems terete, hollow, up to 4 cm in diameter, brownish puberulent with short simple hairs on stems, petioles, leaves, inflorescences, calyces, and corolla lobes. Leaves long petiolate, broadly ovate to elliptic, 7.5–22.0 × 5.5–11.0 cm, slightly rugose, dark green, the base rounded, the apex bluntly acute, margin entire, not revolute, with slightly impressed veins above and slightly raised veins below, all veins brownish puberulent; interpetiolar ridge 1–2 mm high; petiole 1–5 cm long, terete. Inflorescences 7–26 cm long, 9- to 12-flowered; bracts leaf-like, broadly ovate-elliptic with bluntly acute apices, 1.0–6.0 × 0.5–4.0 cm. Flowers pedicellate, erect to horizontal; pedicels 0.9–2.1 cm. Calyx campanulate, 7–10 mm long, thin-coriaceous, dark green, the lobes elliptic, 3–5 × 4–5 mm, with slightly hyaline margins. Corolla yellowish-green, 3.2–3.8 cm long, funnelform, the tube narrowed in the lower third, the lobes ovate to elliptic, 6–8 mm long, lobe apex rounded. Stamens reaching the base of the corolla lobes; filaments of unequal length, filiform, straight; anthers linear, 5–6 mm long, sagittate, versatile. Gynoecium 4 cm long, ovary 8–9 × 3–4 mm, style 31–32 × 1 mm, stigma 2-lobed, each lobe obovate, 4.0–4.5 × 1.0–2.0 mm. Capsules unknown.

This species occurs on Mt. Ayanganna in the Pakaraima Mountains, on the easternmost edge of the Guayana Shield (Fig. 2). It is most similar to *Macrocarpaea rugosa* Steyerm. (the geographically closest species, from the Macizo del Chimantá, Bolívar, Venezuela) and *M. marahuacae* Struwe & V.A. Albert (from Cerro Marahuaca, Amazonas, Venezuela). It differs from *M. rugosa* by its ovate (vs. elliptical) leaf shape, acute leaf apices (vs. broadly rounded), rounded leaf bases (vs. cordate), fewer-flowered inflorescences, and shorter calyces. From *M. marahuacae* it is immediately distinguished by the much finer degree of leaf venation, and ovate (vs. elliptical to obovate) leaf shape.

This is the sixth species found on the tepuis of the Guayana Shield of northern South America, the others being *Macrocarpaea autanae* Weaver, *M. marahuacae* Struwe & V. A. Albert, *M. neblinae* Maguire & Steyerm., *M. piresii* Maguire, and *M. rugosa* Steyerm. (Struwe et al., 1999). This group forms a geographically coherent unit, yet some species may be more closer related to Andean species groups than to each other. A preliminary molecular analysis of *Macrocarpaea* based on 5S-NTS sequences including two species from this group shows support for two separate origins

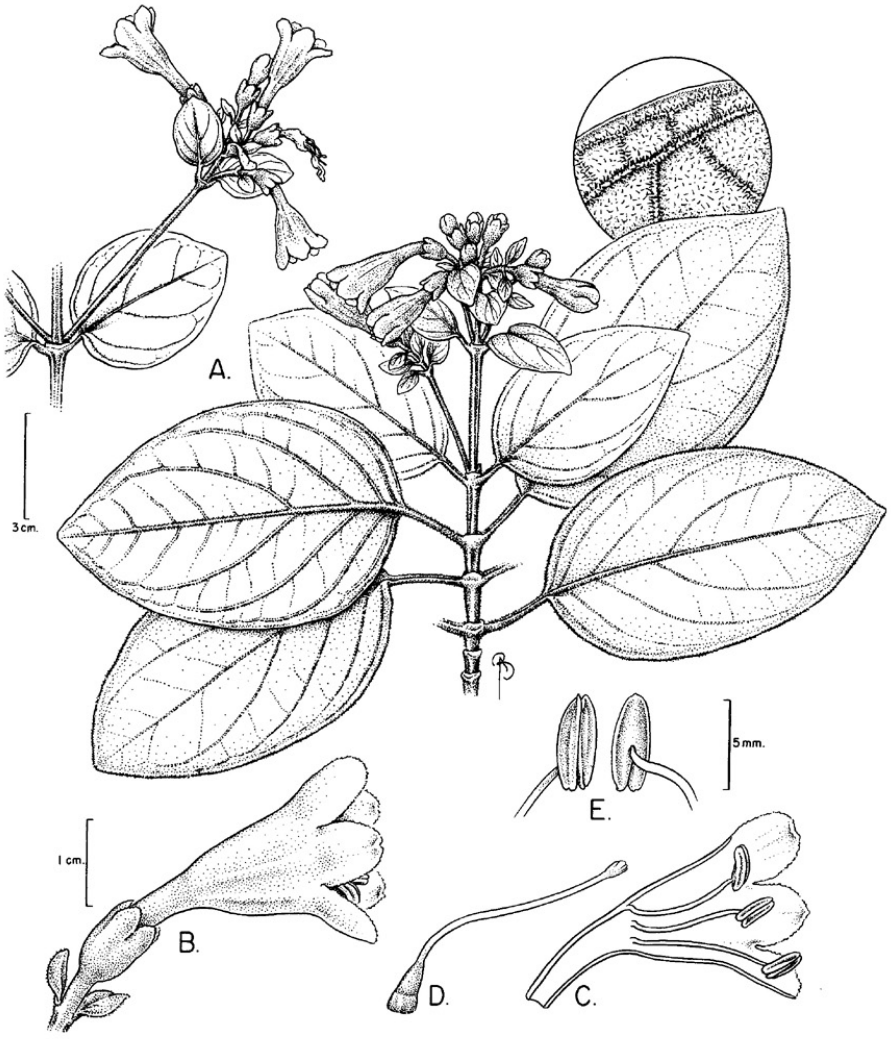

FIGURE 3. *Macrocarpaea ayangannae*. A, habit of flowering stems, with magnified upper leaf surface showing papillate hairs; B, flower; C, internal cross-section of corolla showing; D, gynoecium; E, anthers. From *Pipoly 11103* (US).

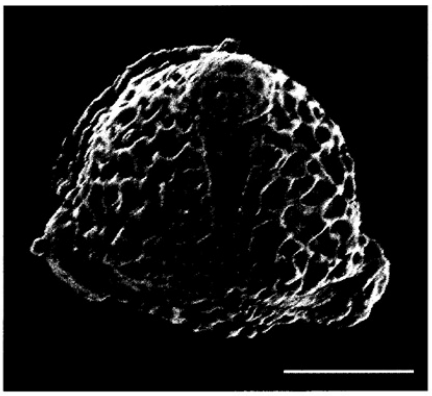

FIGURE 4. *Macrocarpaea ayangannae*, pollen grain. From *Pipoly et al. 1103* (US). Bar equals 10 μm.

from the Andes (Grant and Struwe, 2000; Grant and Struwe unpubl.). This is the first report known to us showing species that occur on the Guayana Shield having an origin in the Andes. A synopsis of the Guayana Shield species of *Macrocarpaea* with a discussion of their biogeography and molecular systematics will be presented in a separate paper.

Etymology: this species is named for the mountain on which it was collected, Mt. Ayanganna in western Guyana.

Macrocarpaea luteynii J. R. Grant & Struwe, *sp. nov.* TYPE: COLOMBIA. Cauca: Parque Nacional Munchique, km 50–55 along road above Uribe, cloud forest, 1875–2256 m, shrub 1.5 m tall, fruits green, 25 April 1979, *Luteyn et al. 7466* (Holotype: NY; Isotypes: COL, F, HAM, MO, U, US). Fig. 5–6.

A Macrocarpaea browallioides (Ewan) A. Robyns & S. Nilsson cui affinis, sed inflorescencia multifloribus, calyces campanulatis, foliis lanceolatis, ovatis, ellipticis, a M. subcaudata Ewan foliis brevioribus differt.

Shrubs to 1.5–3.0 m that are erect, leaning, climbing or epiphytic, glabrous to puberulent with short simple hairs on stems, petioles, leaves, inflorescences, calyces, and corolla lobes; stems terete, solid to hollow, up to 8 mm in diameter. Leaves petiolate, linear-lanceolate, lanceolate, elliptical to ovate, 6–11(–14) × 1.3–4.0(–5.3) cm, generally glabrous above and puberulent below, the base attenuate and decurrent into the petiole, margin slightly revolute; venation with impressed veins above and raised veins below, the apex acute to acuminate; interpetiolar ridge 1–2 mm high; petiole 5–23 mm long, slightly winged. Inflorescences 11–18 cm long, 9- to 35-flowered; bracts leaflike, ovate to lanceolate, 2.5–6.0 × 1.5–2.5 cm, apex acute. Flowers pedicellate, erect to horizontal; pedicels 7–31 mm. Calyx campanulate, 5–7 mm long, the lobes elliptic, 2–3 mm long, with hyaline margins, spreading or recurving in fruit. Corolla pale yellow to yellow-green, 1.8–2.4 cm long, funnelform, the lobes ovate to elliptic, 4–5 × 4–5 mm, lobe apex acute. Stamens reaching the corolla lobes; filaments of unequal length, filiform, straight; anthers linear, 2.5–3.5 mm long, sagittate, versatile. Gynoecium 1.9–2.1 cm long, ovary 5–6 × 2 mm, style 13.0–16.0 × 0.5–1.0 mm, stigma 2-lobed, the stigmatic area hardly any wider than the width of the style, with each lobe less than 0.5 mm long. Capsules conspicuously nodding, shiny, rugose, 9–15 mm long (excluding the style base), yellow-green immature, with a persistent, elongate style base to 8–10 mm. Seeds flattened, conspicuously winged, 0.3–1.0 mm.

This species differs from the Central American species *Macrocarpaea browallioides* in its many-flowered inflorescence, campanulate calyx, and generally lanceolate (vs. ovate to elliptical) leaves. The flaring calyx of *M. browallioides* is the most distinct in the genus with its ovate-triangular cuspidate lobes, whereas most species have obtuse to elliptical to rounded lobes. *Macrocarpaea luteynii* differs from *M. subcaudata* in its typically lanceolate (vs. the linear-long), shorter and broader leaves, measuring 60–110(–140) × 13–40(–53) mm (vs. 80–210 × 18–38 mm).

Along with *Macrocarpaea browallioides* (Ewan) A. Robyns & S. Nilsson and *M. subcaudata* Ewan, both of Panama and Costa Rica, this new species is the third in the genus known to be facultatively epiphytic. *Macrocarpaea luteynii* has been found as an erect, leaning, climbing or epiphytic shrub. *Cabrera & van der Werff 15768* and *15772* were collected on the same day and at the same locality. Collection *15772* is typical of *M. luteynii*, consisting of an upright, epiphytic, or terrestrial shrub. However, collection *15769* stands apart from the remaining collections of *M. luteynii* in having a shorter, compact inflorescence and leaves that are generally smaller, ovate, and uniform in size throughout the stem, as opposed to the typical progression of larger to smaller leaves toward

FIGURE 5. *Macrocarpaea luteynii*. A, habit of fruiting stem; B, interpetiolar ridge between opposite leaves, typical of *Macrocarpaea*; C, fruit; D, flower; E, internal cross-section of corolla; F, gynoecium. A-C from *Luteyn 7466* (NY); D-F from *Ruíz et al. 196* (MA).

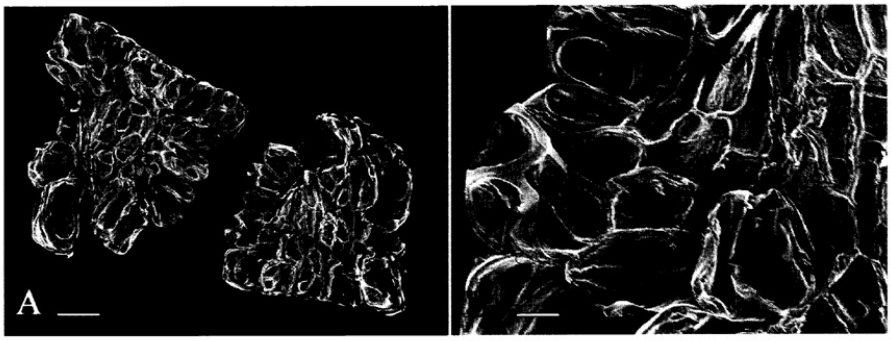

FIGURE 6. *Macrocarpaea luteynii*. A, seeds; B, edge of seed. From *Luteyn 7466* (NY). Bars equal 100 μm.

the inflorescence in other collections. Despite these differences, the inflorescence, flowers, and fruits are identical, making it unlikely that it represents a different species.

This species ranges between Cauca and Valle Provinces in southwestern Colombia (Fig. 2). This area, where at least eleven species of *Macrocarpaea* occur, represents another of several important hot spots of diversification in the genus.

Etymology: this species is named in honor of James Leonard Luteyn (1948–) of the New York Botanical Garden, specialist of the páramo and Ericaceae of South America, who has collected many *Macrocarpaea* including the type of this species.

Paratypes: COLOMBIA. Cauca: "La Gallera," Micay Valley, 1900–2000 m, herb, corolla yellow-green, 1 July 1922, *Killip 7940* (GH, US); Parque Nacional Munchique, El Sopadero, 1950 m, arbusto, 28 March 1979, *Lobo 45* (COL); Parque Nacional Munchique, El Tambo, vereda La Romelia, La Gallera, 1950 m, hierba trepadora de 2 m, corola verde-amarillento, 25 July 1993, *González et al. 2832* (COL, MA); Parque Nacional Munchique, El Tambo, camino de la carretera a Nueva Granada, 2280 m, hierba erecta de 1.5 m, flores verde claro, 28 August 1993, *Ruíz, N. et al. 196* (COL, MA). Valle: San Antonio (Cerro La Horqueta), Cordillera Occidental, vertiente oriental, cerca a km 17 de carretera Cali-Buenaventura, bosque nublado, 2060–2100 m, arbusto inclinado, hojas coriáceas, cáliz verde, corola en yema amarillo pálido, ápice pentagonal, estilo blanco-amarillento, estigma verde, fruto jóven verde, 20 January 1986, *Silverstone-Sopkin et al. 2119* (CUVC, U [2 sheets]); km 18 y km 20 de la carretera de Cali a Buenaventura entrando por la finca Zingara, cumbre de la Cordillera Occidental, precipitación pluvial por año, relictus de la selva nublada y bastante intervenida antropogénicamente, 1500–2000 m, epífita leñosa, tallos y hojas quebradizas, botones verdes y flores verde-amarillentas, frutos en cápsulas secas y coriáceas, 28 February 1988, *Cabrera & van der Werff 15769* (COL, U); km 18–20 carr. Cali-Buenaventura, 1500–2000 m, epífita arbustiva, en la selva clímax nublada y muy húmeda, tallos y hojas quebradizos, botones verdes, flores amarillo-verdosas, cáliz verde oscuro, anteras amarillas, 28 February 1988, *Cabrera & van der Werff 15772* (COL).

NEW SYNONYMY

Macrocarpaea guttifera Ewan, Contr. U. S. Natl. Herb. 29: 237–238. 1948.

Macrocarpaea guttifera has always been an anomalous species. Ewan himself stated, "The systematic position of *Macrocarpaea guttifera* cannot be suggested from the several unusual characters that it displays, which, indeed, may be subject to reinterpretation when additional material is available." Richard E. Weaver alerted us to the notion that this species was not a gentian. When we received the type on loan, we concurred but could not place it in a family. Consequently we e-mailed a scan of the specimen to numerous specialists. Barry Hammel (MO/INB) suggested Rutaceae, so we sent it to Rutaceae specialist Jackie Kallunki (NY), who identified the specimen as *Ravenia biramosa* Ducke (Rutaceae). Therefore, *Macrocarpaea*

guttifera is excluded from *Macrocarpaea* and indeed the Gentianaceae and is reduced to synonymy under *Ravenia biramosa* Ducke (1935).

Six "nomen herbariorum" (unpublished names written on herbarium sheets) have been discovered in the course of examination of material. They consist of six unpublished species names in *Macrocarpaea*, and a new genus and new species "Axelsonia globiflora". For a complete accounting of all names concerning *Macrocarpaea*, even though never published, these names and their new synonymy is as follows:

"Axelsonia globiflora Dusén, ined." Based on *Dusén 17288* (S) (Brazil) [= *M. rubra* Malme]

"Macrocarpaea buchtienii Gilg, ined." Based on *Buchtien 1186* (US) and *Buchtien 5639* (NY) (Bolivia) [= *M. cinchoniifolia* (Gilg) Weaver]

"Macrocarpaea ekmanii Ewan, ined." Based on *Ekman 6846* (S); *Ekman 15947* (S); *Wright 1347* (BR) (Cuba) [= *M. pinetorum* Alain]

"Macrocarpaea gilgiana Rusby, ined." Based on *Rusby 1172* (NY) (Bolivia) [= *M. cochabambensis* Gilg-Benedict]

"Macrocarpaea peduncularis Rusby, ined." Based on *Williams 1561* (NY) (Bolivia) [= *M. bangiana* Gilg]

"Macrocarpaea tabacifolia Ewan, ined." Based on *Rusby 1173* (US) (Bolivia) [= *M. cinchoniifolia* (Gilg) Weaver]

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U s o s : Tiene las mismas propiedades como el *Eustoma exaltatum* (Roig 1874: 450-452).

N o m b r e s c o m u n e s : Centaurilla de las Guyanas (Grosourdy 1864: 106), acelga cimarrona, tabaco de flor rosada, tabaco de sabana (Roig 1963: 53, 885).

Mapa 9. *Schultesia guianensis* (Aubl.) Malme

6. Macrocarpaea (Griseb.) Gilg in Engler & Prantl, Nat. Pflanzenfam. 4(2): 94. 1895 ≡ *Lisianthius* sect. *Macrocarpaea* Griseb., Gen. Sp. Gent.: 173. 1838[1].
Tipo (Ewan 1948: 210, 215): *Lisianthius glaber* L. f. (*Macrocarpaea glabra* (L. f.) Gilg).

Arbustos, arbolitos o raramente hierbas perennes sufruticosas. Ramas cuadrangulares a teretes, ramosas. Hojas pecioladas o raramente sésiles; lámina de forma variable, mayormente oval, ovada u obovada, a menudo coriácea, aguda a obtusa; base cordiforme a atenuada. Inflorescencias terminales, en dicasio laxo, multifloro. Flores 5-meras, pediceladas, con pequeñas bractéolas lineares. Cáliz campanulado, con tubo más corto o más largo que los lóbulos; coléteres presentes. Corola verde, amarilla o blanca, infundibuliforme o raramente tubular, con tubo mucho más largo que los lóbulos. Estambres insertados en el medio del tubo de la corola, a veces no todos al mismo nivel en androceo ligeramente zigomorfo; filamentos ± filiformes; anteras sagitales, recurvadas después de la antesis; polen en granos sueltos. Disco presente en la base del ovario. Ovario ovoide a elipsoideo, bilocular en su base; estilo filiforme, persistente;

[1] Con la colaboración de J. Grant, Laboratorio de Botánica Evolutiva, Instituto de Botánica, Facultad de Ciencias, Universidad de Neuchâtel, rue Émile-Argand 11, CH-2007 Neuchâtel, Suiza.

lobos estigmáticos orbiculares. Fruto una cápsula septicida. Semillas numerosas, poliédricas, a veces aplanadas.

D i s t r i b u c i ó n : Abarca 104 especies mayormente de bosques húmedos de montaña en Suramérica tropical, Centroamérica y las Antillas Mayores. Está pendiente una revisión, por J. Grant para "Flora Neotropica", de la última monografía del género (Ewan 1948). Una sola especie crece en Cuba.

C i t o l o g í a : Se conoce el número cromosómico de *Macrocarpaea thamnoides* (Griseb.) Gilg, $2n = 42$ (Weaver 1969).

6.1. Macrocarpaea pinetorum Alain in Mem. Soc. Cub. Hist. Nat. "Felipe Poey" 22: 114. 1955. Holótipo: [espécimen] Cuba, Prov. Holguín, "Oriente, La Breña, Moa", 27-VI-1945, *Clemente 4401* (HAC [n.v.], isótipos GH!, US!).

= *Macrocarpaea pauciflora* Alain in Mem. Soc. Cub. Hist. Nat. "Felipe Poey" 22: 115. 1955. Holótipo: [espécimen] Cuba, Prov. Guantánamo, "Oriente, Laguna del Galano, Sierra del Frijol", 2-I-1954, *Alain 3855* (HAC [n.v.]; isótipo: NY!).

– *"Lisyanthus thamnoides"* sensu Grisebach, Cat. Pl. Cub.: 180. 1866 [non *Lisianthius thamnoides* Griseb., Fl. Brit. W.I.: 424. 1862].

– *"Irlbachia thamnoides"* sensu M. Gómez in Revista Fac. Letras Ci. Univ. Habana 7: 247. 1908 [non *Irlbachia thamnoides* (Griseb.) M. Gómez, l.c.]. – Fig. 6.

Arbusto o arbolito de hasta 4 m de alto. Hojas con pecíolo de 19-55 mm de largo; lámina oval a obovada, de 12,5-24,5 × 3,8-8,8 cm, acuminada o mucronada a cuspidada; base atenuada a cuneiforme. Inflorescencias 15-30-floras; brácteas ovadas a estrechamente ovales, de 9-75 × 3-32 mm, agudas; base atenuada. Pedicelos de 0,7-1,8 cm de largo. Cáliz con costillas no carinadas; tubo de 3,4-4,9 mm de largo; lóbulos anchamente ovales a espatulados, de 3-4,3 × 2,4-3,7 mm, obtusos a mucronados. Corola amarilla, infundibuliforme; tubo de 12-20 mm de largo; lóbulos anchamente ovales, de 5-6,3 × 4,1-5,7 mm, obtusos. Estambres con filamentos de 9,7-16 mm de largo, ensanchados hacia la base; anteras de 3-4 × 1,2-1,5 mm. Ovario ovoide, de 6,3-8 × 1,7-2,6 mm, atenuado en el estilo; estilo de 10-19 mm de largo; lobos estigmáticos de 0,7-0,9 × 0,7-0,8 mm. Fruto fusiforme a ovoide, de 14-20 × 4-7 mm. Semillas de 0,6-0,8 mm de diámetro. – Fl.: VIII-V; Fr.: IX-VI.

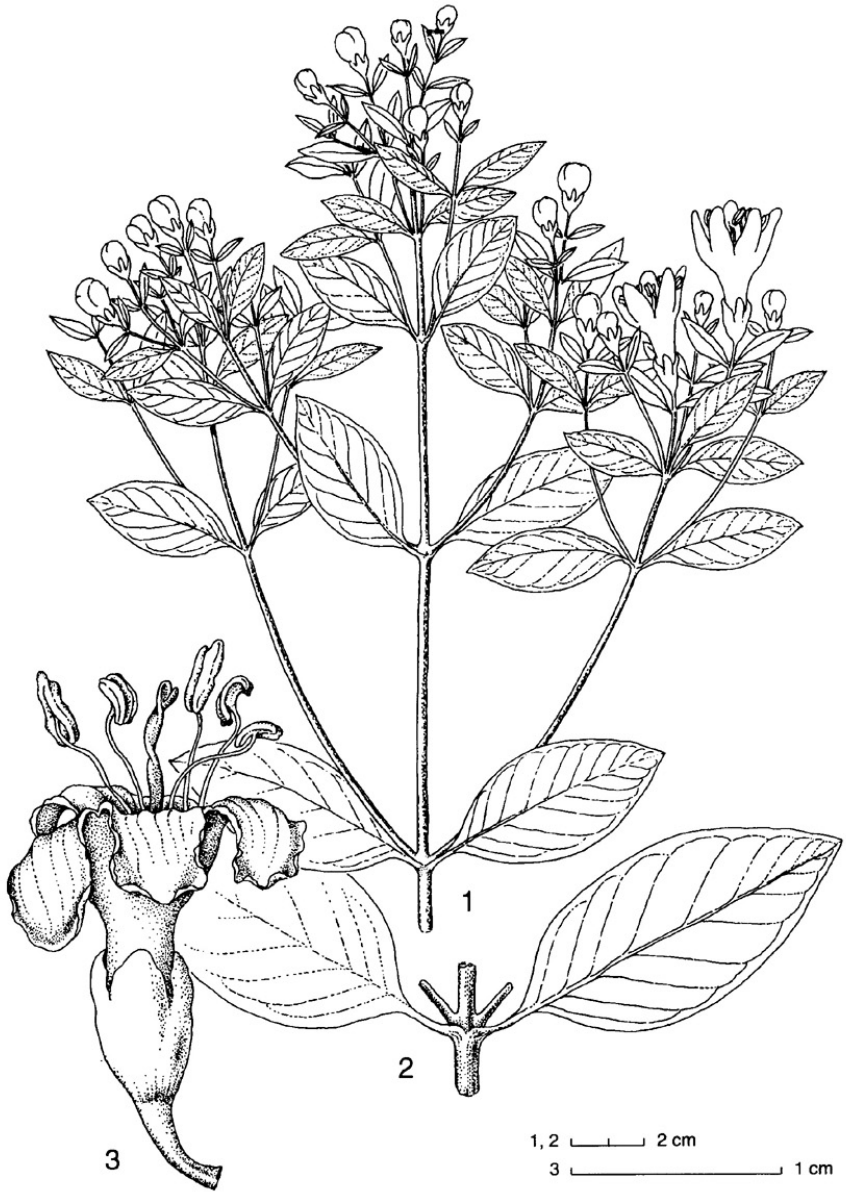

Figura 6. *Macrocarpaea pinetorum* Alain (1-2: espécimen *PFC 53383,* JE; 3: espécimen *PFC 52172,* B; dibujos de Michael Rodewald).
1. Rama con flores; 2. Nudo en la parte estéril, con hojas; 3. Flor.

Distribución: Endémica en Cuba oriental: Ho, SC (Mayarí Arriba: Sierra del Cristal), Gu. En bosques húmedos de montaña. – Mapa 10.

Mapa 10. *Macrocarpaea pinetorum* Alain

7. Zonanthus Griseb. in J. Linn. Soc., Bot. 6: 145. 1862.
Tipo: *Zonanthus cubensis* Griseb.

Arbustos o arbolitos. Ramas teretes, ramosas. Hojas caulinares pecioladas, con una pequeña ócrea caediza; lámina oval, coriácea, obtusa a mucronada; base atenuada. Inflorescencias axilares unifloras. Flores 5-meras, pediceladas, involucradas por la base concrescente y ciatiforme de dos bractéolas foliáceas, anchamente espatuladas, coriáceas. Cáliz tubular, coriáceo, con tubo más corto que los lóbulos; coléteres presentes. Corola verdusca, ciatiforme, con tubo mucho más largo que los lóbulos. Estambres insertados en la parte superior del tubo de la corola, no todos al mismo nivel en androceo ligeramente zigomorfo; filamentos filiformes, curvados en la antesis; anteras sagitales, torcidas después de la dehiscencia; polen en granos sueltos. Ovario cónico u ovoide a oblongo, estrechado en el estilo, unilocular pero 4-locular en su base; estilo filiforme; lobos estigmáticos suborbiculares. Fruto una cápsula septicida cónica a oblongo-ovoide. Semillas numerosas, poliédricas, oblongas a globosas.

Distribución: Género uniespecífico, endémico en bosques de montaña de Cuba oriental.

7.1. Zonanthus cubensis Griseb. in J. Linn. Soc., Bot. 6: 145. 1862. Lectótipo (designado aquí): [espécimen] Cuba, prov. Guantánamo, "prope villam Monte Verde dictam", I a VII-1859, *Wright 1346* (GOET!; isótipos?: BM!, BR!, G!, GH!, K!, P!, PH!, MO!). – Fig. 7.

DE MACROCARPAEAE GRISEBACH (EX GENTIANACEIS) SPECIEBUS NOVIS II: TYPIFICATION OF THE RUIZ AND PAVON NAMES

JASON R. GRANT[1]

Abstract. Ruiz and Pavon described four species of *Lisianthus* (Gentianaceae) that are now recognized in the genus *Macrocarpaea*: *Lisianthus corymbosus*, *L. ovalis*, *L. revolutus*, and *L. viscosus*. These species were described from specimens collected in the province of Huánuco, Peru, and are here identified as relatively narrow endemics largely of that province. Their complicated taxonomic or nomenclatural history has required a careful review that revealed interesting details relevant to their circumscriptions. Lectotypes are selected for *Lisianthus corymbosus*, *L. revolutus*, *L. viscosus*, *Macrocarpaea arborescens*, *M. pachystyla*, and *M. sodiroana*. *Lisianthus corymbosus* is recognized as an illegitimate name, and is therefore reduced to synonymy under the next validly published name, *Macrocarpaea pachystyla*. *Lisianthus ovalis* does not have a type, and is therefore excluded from use. *Macrocarpaea arborescens* is identified here as a species of southern Ecuador, previously recognized as *M. ovalis*. The name "Macrocarpaea magnifica Ewan, ined" is a *nomen herbariorum*, here recognized as *M. arborescens*. The previously broadly circumscribed *Macrocarpaea sodiroana* is here recognized as restricted to the province of Pichincha, Ecuador. A new identification is reported where the anomalous specimen *Dannouse s.n.* (NY) previously identified as "*Macrocarpaea* sp." by Ewan (1948) is identified as *Tabernaemontana crassa* (Apocynaceae).

Keywords: Gentianaceae, *Macrocarpaea*, Neotropics, nomenclature, Pavon, Ruiz, Sodiro, Tafalla, typification.

Four species of *Macrocarpaea* were described from collections brought back from Ruiz and Pavon's *Expedición Botánica al Virreinato de Perú y Chile (1777–1788)*: *Lisianthus corymbosus*, *L. ovalis*, *L. revolutus*, and *L. viscosus* (Ruiz and Pavon, 1799). This is an account of the collection and description of these species and subsequent typification herein.

On 8 April 1777, Hipólito Ruiz Lopez (1754–1815) was given orders from King Carlos III of Spain to travel to his dominions in America to study their botanical natural history (Ruiz, 1940: 9; 1998). José Antonio Pavon y Jiménez (1754–1844) was appointed as second botanist, and José Burnette and Isidro Gálvez as draftsmen. French naturalist Joseph Dombey (1742–1794) also accompanied the travels. The expedition left Madrid on 19 September 1777 and Cádiz on 19 October, arriving at the port of Callao (Lima) nearly six months later on 8 April 1778. On 14 November 1784, Juan José Tafalla (1755–1811) and Francisco Pulgar also joined the expedition in Peru (Ruiz, 1998: 29). Ruiz and Pavon remained in Peru and Chile for nearly eleven years, departing on 1 April 1778, returning some seven months later in Cádiz on 12 October 1778, and in Madrid on 16 December 1778. Dombey had left previously, arriving in Cádiz on 22 February 1785 (Steele, 1964), while Tafalla remained in Peru and Ecuador continuing to send back specimens to Madrid until his death in Lima.

In Ruiz and Pavon's major scientific works, *Prodromus* (Ruiz and Pavon, 1794), *Flora Peruviana et Chilensis* (Ruiz and Pavon, 1798–1802), and *Systema* (Ruiz and Pavon,

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1798), some 1900 new taxa were described from notes and illustrations made in the field, and herbarium specimens brought back to Madrid. Four of these species are of interest here, *Lisianthus corymbosus*, *L. ovalis*, *L. revolutus*, and *L. viscosus* (Ruiz and Pavon, 1799: 13–15). The two other species described in *Lisianthus* are *L. calygonus* Ruiz & Pav. [= *Symbolanthus calygonus* (Ruiz & Pav.) Griseb.], and *L. acutangulus* Ruiz & Pav. [=*Chelonanthus alatus* (Aubl.) Pulle].

In these Ruiz and Pavon's texts, there is little information on when or where the specimens were collected. Ruiz had planned to publish such information in a manuscript entitled *Viaje* that disappeared soon after his death in 1815. A version of this manuscript later surfaced and was published as *Relación del Viaje Hecho a los Reynos del Perú y Chile por los Botánicos y Dibuxantes Enviados para aquella Expedición, Extractado de los Diarios por el orden que Llevó en ellos su Autor Don Hipólito Ruiz* (Ruiz, 1931). It was translated into English by Bror Eric Dahlgren, and published as *Travels of Ruiz, Pavon, and Dombey in Peru and Chile (1777–1788)* (Ruiz, 1940). Jaime Jaramillo-Arango located another manuscript at the British Museum, and combined the manuscript versions into a single text that included a reordering of chapters in chronological order entitled *Relación Histórica del Viaje que Hizo a los Reynos del Perú y Chile el Botánico D. Hipólito Ruiz en el Año de 1777 hasta el de 1778, en cuya Epoca Regresó a Madrid* (Ruiz, 1952). The English translation of Jaramillo's work prepared largely by Richard Evans Schultes has been recently published as *The journals of Hipólito Ruiz, Spanish botanist in Peru and Chile 1777–1788* (Ruiz, 1998). When these four texts are considered in concert with Ruiz and Pavon's protologues, the herbarium material can be studied in a proper timeframe.

Between 1 August–1 September 1780, the expedition worked near the cities of Huánuco and Chinchao where they collected *Lisianthus corymbosus* and *L. ovalis* (Ruiz, 1940: 81). However, several unfortunate incidents befell these collections. In April 1784, they sent back to Spain via the *San Pedro de Alcántara* 53 cases containing all the pressed plants and illustrations made to that date. By July 1786 Ruiz had learned that the ship had first encountered a storm off the coast of Chile and all the living plants were swept overboard, then on approaching the coast of Portugal, hit rocks and sank on 2 February 1786 with all the dried plant specimens (Steele, 1964). Dombey had sent his collections (perhaps of similar material collected by Ruiz and Pavon) back to France on the *El Peruano*. Relevant material to *Lisianthus* and *Macrocarpaea* may be among the Dombey collections at Paris (P), but has not been searched for by this author. Earlier on 6 August 1785 a fire in Macora destroyed all of Ruiz' manuscripts of plant descriptions. Therefore, within a relatively short period of time, they had lost all of their herbarium specimens, drawings and manuscripts made from 1778–1785, including presumably all material of *L. corymbosus* and *L. ovalis*. Though this was a tremendous setback, Ruiz soon began rewriting the descriptions with plant specimens and illustrations newly collected at Macora and elsewhere. *Lisianthus ovalis* was soon recollected near Puzuzo (Ruiz, 1940: 204), and was redescribed. From 15 August–24 September 1786, they botanized in the region of Muña, collecting *Lisianthus revolutus* and *L. viscosus*. Herbarium specimens of *L. corymbosus*, *L. revolutus*, and *L. viscosus* are extant at Madrid, though there are none of *L. ovalis*. The original elements of *L. corymbosus*, *L. revolutus*, and *L. viscosus* include their protologue, published illustrations, and herbarium specimens. Typification of each of these names is discussed in detail below.

1. *Macrocarpaea pachystyla* Gilg, Bot. Jahrb. Syst. 22: 336. 1896. TYPE: PERU. Chicoplaya, *Tafalla s.n.* (Type: B? [destroyed]; Lectotype: MA-Ruiz & Pavon [2 sheets], selected here; Isolectotypes: G [G-BOISS, G sheet number 8647/14]). Figs. 1–2.

Synonym : *Lisianthus corymbosus* Ruiz & Pav., Fl. Peruv. Chil. 2: 14. 1799, *nom illeg., syn. nov. Macrocarpaea corymbosa* (Ruiz & Pav.) Ewan, Contr. U. S. Natl. Herb. 29: 242. 1948. TYPE: PERU. Huánuco: Habitat in Peruviae nemoribus inter Acomayo et Chinchao ad Pati praedium, *Ruiz & Pavon s.n.* (Lectotype: MA-Ruiz & Pavon [2 sheets], selected here; Isolectotypes: BM [5 sheets, BM sheet numbers 583101, 583102, 583107, 583108, 583109], F [2 sheets, F sheet numbers 842844, 843438], G [2 sheets, G sheet numbers 8647/9, 867/13 (G-BOISS)]. Figs. 3–4.

FIGURES 1–4. 1, *Macrocarpaea pachystyla*, lectotype *Tafalla s.n.* (MA-Ruiz & Pavon). Photo Jason R. Grant; 2, *Macrocarpaea pachystyla*, label of lectotype *Tafalla s.n.* (MA-Ruiz & Pavon). Photo Jason R. Grant; 3, *Macrocarpaea corymbosa* original illustration in Ruiz & Pav., Fl. Peruv. Chil. 2: 14. 1799, fig. CXXIV; 4, *Macrocarpaea corymbosa*, lectotype *Ruiz & Pavon s.n.* (MA-Ruiz & Pavon). Photo Jason R. Grant.

Additional material examined: PERU. Without province or locality, 1835, *Matthews 2065* (BM, E, K, OXF, P, W); *Stockholm Herbarium s.n.* (S). Huánuco: Peruvia subandina, Cuchero, 1 February 1930, *Poeppig 1666* (W); Rondos, 24 April 1962, *Schunke-Vigo 5880* (F, US); Huamilies, Monzón, Paujil, 22 March 1972, *Schunke-Vigo 5298* (F, G, GH, MO, NY, US). San Martín: Mariscal Caceres, Tocache Nuevo, 4 May 1971, *Schunke-Vigo 4848* (COL).

The type of *Macrocarpaea corymbosa* (described as *Lisianthus corymbosus*) was collected between 1 August–1 September 1780, near Huánuco and Chinchao (Ruiz, 1940: 81). The type material consists of ten sheets in four different herbaria (BM, F, G, and MA). The most complete sheet at Madrid is selected as the lectotype. Four other sheets here identified as the type material of *M. pachystyla* have been previously thought to partially represent original material of *M. corymbosa*. While the original material is thought to have been lost when *San Pedro de Alcántara* sank, there are in fact Ruiz and Pavon collections at Madrid that must represent collections made as replacements after the original set was lost.

When Ruiz and Pavon described *Lisianthus corymbosus*, they cited *Lisianthus glaber* L.f. [Suppl. Pl. 134. 1781] as a synonym. Therefore, *Lisianthus corymbosus* is a superfluous renaming of *Lisianthus glaber*. This opinion is shared by Kunth (1818: 185), Grisebach (1839: 173–174), and Gilg (1896: 337). However, in the only monograph of *Macrocarpaea*, Ewan (1948: 242–243) disagreed, providing a lengthy discussion on the problems surrounding *Lisianthus corymbosus* and *L. glaber*, but missing the key point that Ruiz and Pavon cited *L. glaber* in synonymy. Ewan transferred *L. corymbosus* to *Macrocarpaea* as *M. corymbosa* (Ruiz & Pav.) Ewan. While Ruiz and Pavon effectively described and illustrated *Lisianthus corymbosus*, their synonymy of *L. glaber* can not be overlooked and the name must be considered superfluous. *Lisianthus glaber*, now recognized as *Macrocarpaea glabra*, is a distinct species from the Bogotá region of Colombia.

To explain the matter in further detail, the following chronology may be presented. Linnaeus filius (1781) described *Lisianthus glaber* based on a Colombian Mutis icon. J. E. Smith (1789) expanded on Linnaeus filius's description, and provided an illustration of the plant that we now refer to as *Macrocarpaea glabra* from Bogotá. Ruiz and Pavon (1799) described and illustrated *Lisianthus corymbosus* from Peru; however, they simultaneously cited *Lisianthus glaber* in synonymy. Kunth (1818), Grisebach (1839), and Gilg (1896: 337) recognized *Lisianthus glaber* L.f. They regarded *L. corymbosus* as a synonym of *L. glaber*, recognizing that Ruiz and Pavon's publication of *L. corymbosus* was illegitimate. However, Gilg (1896: 337) seems to consider *L. glaber* as a Peruvian plant when he recognized *L. corymbosus* as a synonym. And therefore, since the Colombian species needed a new name, Gilg (1896: 337) described *Macrocarpaea bogotana* as "*L. glaber* Kunth, not L.f'. Gilg based *M. bogotana* on a Colombian specimen that is identical to that of *Lisianthus glaber* L.f. Gilg (1896: 336), then described *Macrocarpaea pachystyla* based on similar Peruvian Ruiz and Pavon [Tafalla!] herbarium specimens that Ruiz and Pavon had described *L. corymbosus*. Could Gilg's *Macrocarpaea bogotana* and *M. pachystyla* be "new names" for *L. glaber* Kunth not *L. glaber* L.f., and *L. corymbosus nom. illeg.*, respectively? Though seemingly logical, there is nothing to suggest this as fact in the text, so all hypotheses must be left to supposition. Ewan (1948: 226, 242–243) recognized *Macrocarpaea bogotana* as a synonym of *M. glabra*, and *Macrocarpaea corymbosa* and *M. pachystyla* as two separate species, but knew that each was based on Ruiz and Pavon collections from Peru.

Gilg (1896) described *Macrocarpaea pachystyla* from material thought to have been collected by Ruiz and Pavon. However, the handwriting and style of the labels are consistent with those of Juan Tafalla, as is discussed further in a similar situation with *M. ovalis* below. Also, the herbarium specimens have a slightly different appearance than the known Ruiz and Pavon collections of *M. corymbosa*. Since *M. pachystyla* appears to be conspecific with *M. corymbosa*, *M. pachystyla* is therefore recognized as the next validly published name for this taxon.

While studying the Ruiz and Pavon collections at Madrid, I was puzzled by the annotation labels of Ernst Gilg. I had first thought that they had been transcribed by someone else making herbarium revisions after the publication of his articles. However, with comparison of verified handwriting samples and annotation labels from Berlin, I was able to determine that the annotations are in fact in his hand. Part of the Ruiz and Pavon collections in Madrid had

been sent to Berlin for study.[2] We may presume that these specimens of *Macrocarpaea* were part of the loan from Madrid to Berlin, were annotated by Gilg, and were returned prior to the partial destruction of the Berlin herbarium in 1945 when all *Macrocarpaea* collections including most Gilg types were lost.

2. *Macrocarpaea ovalis* (Ruiz & Pav.) Ewan, Contr. U. S. Natl. Herb. 29: 234. 1948.

Basionym: *Lisianthus ovalis* Ruiz & Pav., Fl. Peruv. Chil. 2: 13. 1799. TYPE: PERU. Huánuco: Habitat in Peruviae nemoribus per Chinchao runcationes, *Ruiz & Pavon s.n.*; original material no longer extant.

Synonym: *Helia ovalis* (Ruiz & Pav.) Kuntze, Rev. Gen. Pl. 428. 1891.

The type of *Lisianthus ovalis* was collected between 1 August–1 September 1780, near Huánuco and Chinchao (Ruiz, 1940: 81). However, all specimens were presumably lost when the *San Pedro de Alcántara* sank. It was soon recollected near Puzuzo and apparently dried and redescribed (Ruiz, 1940: 204). Nevertheless, no definitively authentic material of *L. ovalis* is extant, nor was an illustration published that could be used as a lectotype. Therefore this name is excluded from use.

While I state here that no authentic material of *Lisianthus ovalis* is currently extant, that assessment comes only after much research that has revealed an example of Ruiz and Pavon's replacement in their herbarium of their own specimens lost in the fires and shipwreck with material later collected by Juan Tafalla. There *are* herbarium specimens labeled as *Macrocarpaea ovalis* in the Ruiz and Pavon herbarium at Madrid, as well as duplicates at BM, F, and G that date to the time period of Ruiz and Pavon. This material has always been considered to be type material of *M. ovalis*, e.g. by Ewan (1948). However, the first clue that these specimens could not be the type material of *M. ovalis* was when I identified the mounted specimens as a locally common species of Loja, Ecuador (*M. arborescens*). The problem is that Ruiz and Pavon described *M. ovalis* from Huánuco, Peru, and while it is not impossible in principle for this species to occur in both countries, no species of *Macrocarpaea* has such a wide disjunction. The hunt was then on to determine whether Ruiz and Pavon could have named *M. ovalis* based on specimens from Ecuador rather than Peru. While I knew that the specimens represented an Ecuadorian species, I needed proof to show that they could not be *M. ovalis*. While I had the duplicates on loan from BM, F, and G, I needed to verify the primary set. Therefore, I examined the original set of Ruiz and Pavon collections in Madrid. Regarding these other sets, the British Museum (BM) material came from the auction after the death of Aylmer Bourke Lambert, who had purchased the specimens directly from Pavon (Ruiz, 1952: XXVI; 1998: 27). The Geneva (G) material had been sent to de Candolle directly from Pavon. The Field Museum (F) material was distributed directly by Madrid likely during Joseph MacBride's *Flora of Peru* project based at the Field Museum during the mid-20th century. Additional material may also be in the Webb herbarium at Florence (FI), but has not been searched for by this author.

When I first examined the "Ruiz and Pavon" collections of *Macrocarpaea ovalis* at Madrid I was disappointed since I quickly recognized that they represented the Ecuadorian species, not the Peruvian species as I had hoped. However, the missing puzzle piece soon came into place when I compared verified handwriting samples of botanists who collected during the time period of Ruiz and Pavon in the New World, e.g. Dombey, Mutis, Nee, Pavon, Ruiz, Tafalla. The handwriting on the labels of the specimens of *M. ovalis* at Madrid was different than that of Ruiz or Pavon, but easily matched that of Tafalla! Juan Tafalla collected with Ruiz and Pavon in Peru, and remained in Peru and

[2] "Die Direktion des Botanischen Museums in Madrid hat in sehr anerkennenswerter Weise das dort aufbewahrte Herbar von Ruiz und Pavon zur Bearbeitung zur Verfügung gestellt; einzelne Teile des Herbars werden leihweise übersandt und nach Durchsicht und Revision des Materials zurückgeschickt; die Originale zu den Beschreibungen und Abbildungen in der Flora Peruviana, dem für die Flora von Peru sowie Teilen von Chile grundlegenden Werk, können somit mit neueren Material verglichen werden, soweit sie nicht schon in früher verteilten Dubletten in Berliner Herbar vorhanden waren." Anonymous, Notizbl. Bot. Gard. Berlin-Dahlem 103: 161. 1931.

[The directors of the Botanical Museum in Madrid have made the commendable decision to make the herbarium of Ruiz and Pavon housed at their institution available for examination. Individual parts of the herbarium will be loaned out for examination and review. Materials will then be returned to the Museum. Under this arrangement, the originals used as a basis for the descriptions and illustrations in *Flora Peruviana*, the seminal work for the flora of Peru and portions of Chile, can be compared with more recent materials. This is particularly important for specimens that were not previously available in the Berlin herbaria.]

later Ecuador after Ruiz and Pavon returned to Spain. Tafalla continued to send specimens from his travels for Ruiz and Pavon to describe, or "replace" in their collections the missing specimens lost during Ruiz and Pavon's travels (Ruiz, 1940: 257).

The Tafalla labels on the "*M. ovalis*" specimens have cryptic abbreviations. Yet, this seemingly coded information saw new light once Tafalla was identified as the collector. There are three sheets, two of which have full label data that read "Pentand. Monog., Lisianthus, F.H.D. N. 540., Ex Hualaseo, A° 805" [the second sheet is a duplicate of #540], and "Pentand. Monog., Lisianthus, N. 572 S.L., Ex Loxa, A° 805" (also Tafalla, 1989: 26). After the handwriting samples identified the collector as Tafalla, and by comparing it to known Tafalla labels, it now makes sense. The "F.H." of Tafalla labels refers to his *Flora Huayaquilensis*, which has only been recently published (Tafalla, 1989). This is a flora of the Guayaquil area of Ecuador that also covers species collected on his expedition to Loja in search of *Cinchona* (Rubiaceae), from which quinine was extracted to treat malaria. The locality Hualaseo is in the province of Cuenca (Tafalla, 1989: LXXVII), and "Loxa" is Loja, both in Ecuador. The "A° 805" can be identified as "Año 1805" [year 1805], the year Tafalla is known to have collected in Loja, Ecuador (Tafalla, 1989). The text of *Flora Huayaquilensis* also confirms the identity of specimen numbers 540 and 572 of Tafalla as originating in Loja (Tafalla, 1989: 26; Cevallos, 1991).

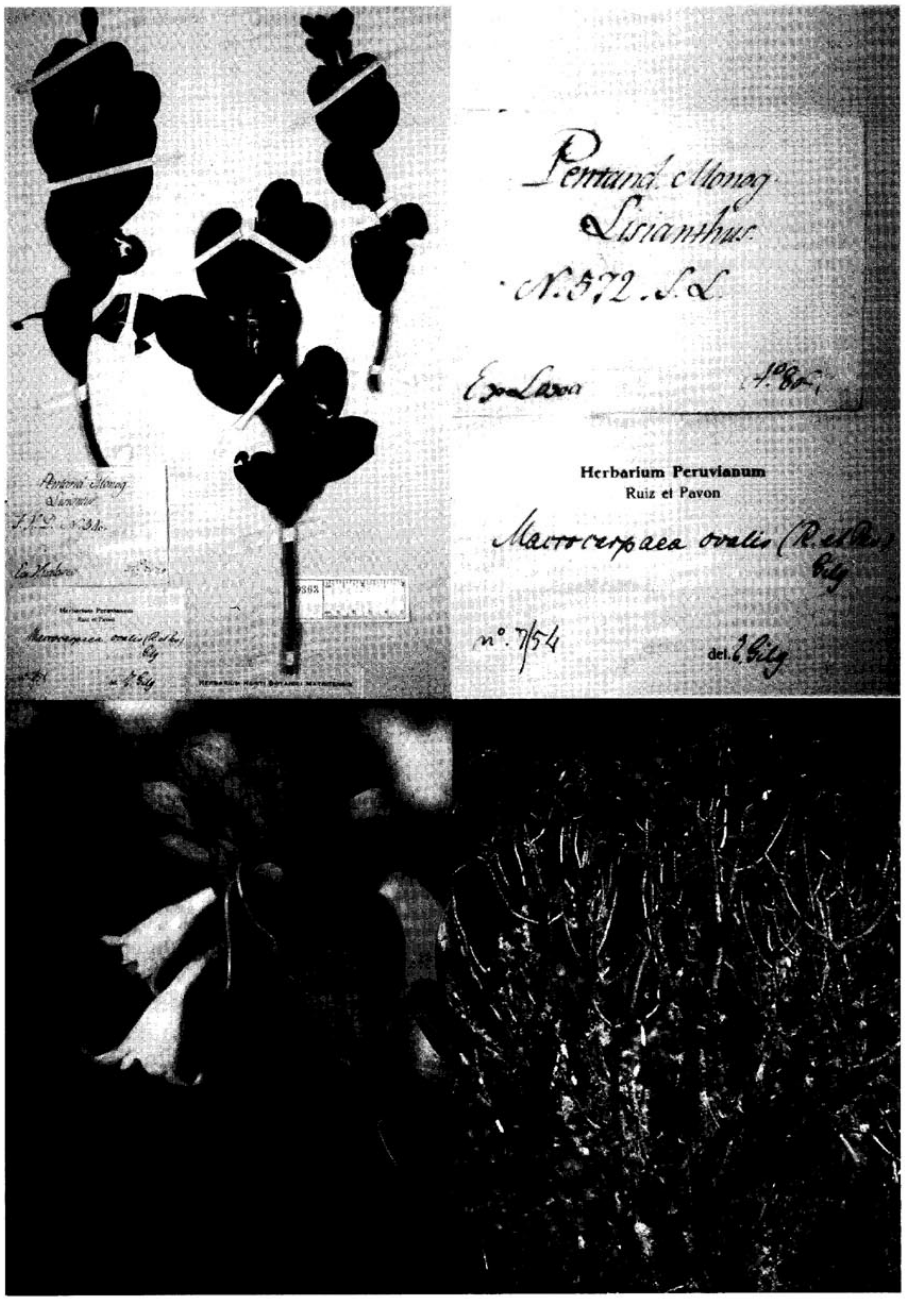
Therefore, the specimens long regarded as the type material of *Macrocarpaea ovalis* were in fact collected by Tafalla in 1805 in Loja, Ecuador. They can't possibly be type material of *Lisianthus ovalis* since the name was published earlier, in 1799. Since no type material of *L. ovalis* is known to exist, nor was there an illustration published as was the case for *L. corymbosus*, *L. revolutus*, and *L. viscosus*, the name must be excluded.

Since *Macrocarpaea ovalis* has been shown to be restricted to central Peru, it left the Ecuadorian taxon that has traditionally held the name *M. ovalis* momentarily nameless. However, the name *Macrocarpaea arborescens* is available, yet with a full set of problems of its own (see below).

3. *Macrocarpaea arborescens* Gilg, Bot. Jahrb. Syst. Beibl. 111: 50. 1913. TYPE: COLOMBIA. Cauca: W Andes of Popayán, 1800-2500 m, *Lehmann 5450* (Type: B? [destroyed]; Lectotype: GH, selected here; Isolectotypes: F, K, US). Figs. 5–8.

Synonym: "Macrocarpaea magnifica" Ewan, nomen herbariorum 1983, *ined.* Based on: ECUADOR. Azuay: Páramo de Castillo, 2745–3355 m, 18 August 1945, *Camp 4795* (NO).

Additional material examined: ECUADOR. Azuay: Páramo de Castillo, 18 August 1945, *Camp 4795* (NO, NY, S); Sevilla de Oro, 29 August 1996, *Garmendia & Cisneros 1113* (QCNE); Sevilla de Oro, 31 August 1996, *Garmendia & Cisneros 1171* (QCNE); Sigsig-Gualaquiza, Molón, 11 December 1968, *Harling et al. 8236* (GB, QCA); Pica Sevilla de Oro-Méndez, 7 August 1983, *Jaramillo 5588* (QCA); Carr. Zigzig-Molón-Gualaquiza, 6 August 1986, *Jaramillo et al. 8856* (AAU, NY, QCA); Km 74 de Cuenca, Carr. Zigzig-Molón-Gualaquiza, 6 August 1986, *Jaramillo et al. 8866A* (QCA). Cañar: Pindilig-Rivera, 9 March 1985, *Harling & Andersson 22989* (GB, QCA). Loja: Loja, 1 December 1896, *André 4549* (F, GH, NY); Loma de Oro, 10 km S of Saraguro, 2 January 1981, *Balslev 1385* (AAU, NY); Road Loja-Saraguro, 15 February 1987, *Bohlin et al. 1357* (GB, QCA); Nudo de Cajanuma, 2 July 2000, *Chassot 00-15* (NEU); 5 km S of Saraguro, 7 October 1988, *Ellemann 66594* (AAU, LOJA, QCA); Hac. Horta-Naque 7 November 1946, *Espinosa, R. 897* (K); Cajanuma Field Station, and trail to Mirador, 17 February 2001, *Grant & Struwe 01-4066* (LOJA, NEU, NY, QCA, QCNE, US); From Loja-Saraguro road, then 2.2 km on road towards Fierro Urco, 18 February 2001, *Grant & Struwe 01-4075* (LOJA, NEU, NY, QCA, QCNE, US); From Loja-Saraguro road, then 3 km on road towards Fierro Urco, 18 February 2001, *Grant & Struwe 01-4084* (LOJA, NEU, NY, QCNE, US); Loma de Loro, 11 February 1985, *Harling & Andersson 21918* (GB); Laraguro and San Lucas, 8 September 1865, *Jameson 67* (K); Loma del Oro, 4 August 1986, *Jaramillo et al. 8816* (QCA); Saraguro-Loja, km 12.4, turnoff towards Fierro Urco, 7 December 1994, *Jørgensen et al. 1314* (HAM, LOJA, MO, NY, QCA); P.N. Podocarpus, Cajanuma, 29 October 1977, *Lewis 3674* (AAU); Páramos de Saraguro, 2 January 1979, *Luteyn et al. 6669* (NY, QCA); P.N. Podocarpus, Nudo de Cajanuma, 6 September 1988, *Madsen & Elleman 75280* (AAU, LOJA, QCA); P.N. Podocarpus, Cajanuma 'Mirador', November 1997, *Matt 2* (ER); P.N.



FIGURES 5–8. 5, *Macrocarpaea arborescens,* (though previously thought type of *Lisianthus ovalis*) *Tafalla 540* (MA-Ruiz & Pavon). Photo Jason R. Grant; 6, *Macrocarpaea arborescens*, label of *Tafalla 572* (MA-Ruiz & Pavon), illustrating the handwriting of Juan Tafalla. Photo Jason R. Grant; 7, *Macrocarpaea arborescens*, inflorescence, *Grant & Struwe 01-4084*. Photo Jason R. Grant; 8, *Macrocarpaea arborescens*, habit as a well-branched tree, *Grant & Struwe 01-4066*. Photo Jason R. Grant.

Podocarpus, Cajanuma 'Mirador', November 1997, *Matt 3* (ER); P.N. Podocarpus, S of Loja, 22 February 1985, *Øllgaard et al. 57953* (AAU, LOJA, QCA); P.N. Podocarpus, S of Loja, 22 February 1985, *Øllgaard et al. 57983* (AAU, LOJA, QCA); Ca. km 5 rd Fierro Urco from Pichig, 12 February 1989, *Øllgaard & Madsen 90494* (AAU, LOJA, QCA); Páramo de Saraguro, 17 March 1983, *Pipoly 6393* (GB, NY); Hualaseo, 1805, *Tafalla 540* (MA-Ruiz & Pavon [2 sheets]); Loja, 1805, *Tafalla 572* (MA-Ruiz & Pavon); Tafalla [likely # *540* or *572*, though unmarked] (BM, F, G). Morona-Santiago: Río Yacuambi, Rumetranca, Cooral-Huica, January 1944, *Goetschel 94945* (VEN); Sigsig-Gualaquiza, 9 April 1968, *Harling et al. 8117* (GB). "Peru" Without province or locality, *Lobb 22* (K). "Peru" Without province or locality, *Lobb s.n.* (F, W).

Gilg described *Macrocarpaea arborescens* from material collected by Lehmann with label information indicating Colombia as the country of provenance. However, the plants on Lehmann's sheets represent a species endemic to southern Ecuador. Lehmann is known to have collected in the Loja area of southern Ecuador, and therefore I suggest that Lehmann's labels may have been confused. It is highly unlikely that *M. arborescens* had a historical contiguous distribution from Colombia to southern Ecuador, especially since this type of disjunction between the two countries as is not presently known in *Macrocarpaea*. While it may be a bold assertion to suggest label errors, there is at least one other case within the Gentianaceae that seems to fit the same pattern. *Gentiana dacrydioides* Gilg was also described from a Lehmann collection allegedly from Cauca (Pringle, 1995: 53). Yet, all the specimens currently referred to the species are from southern Ecuador, none from Colombia (J. Pringle, pers. comm.).

Karl Friedrich Lehmann (1850–1903), who collected the type of *Macrocarpaea arborescens* was the German consul in Popayán, Colombia, and made many plant collections in Colombia, Ecuador, and Guatemala, often with other botanists such as Ellsworth Paine Killip (1890–1968). The genus *Lehmanniella* Gilg (Gentianaceae) was named in his honor (Gilg, 1895: 95). He is not to be confused with the more famous Johann Georg Christian Lehmann (1792–1860), botanist of Hamburg, Germany who largely botanized in Europe.

The annotation of the unpublished name "Macrocarpaea magnifica sp. nov." by Ewan in 1983 occurs on the NO sheet of *Camp 4795*. There is no text with the annotation, so one cannot determine what he was thinking. In any case, this specimen falls well within the circumscription here of *Macrocarpaea. arborescens*.

4. *Macrocarpaea revoluta* (Ruiz & Pav.), Gilg in Engl. & Prantl, Nat. Pflanzenfam. 4(2): 94. 1895.

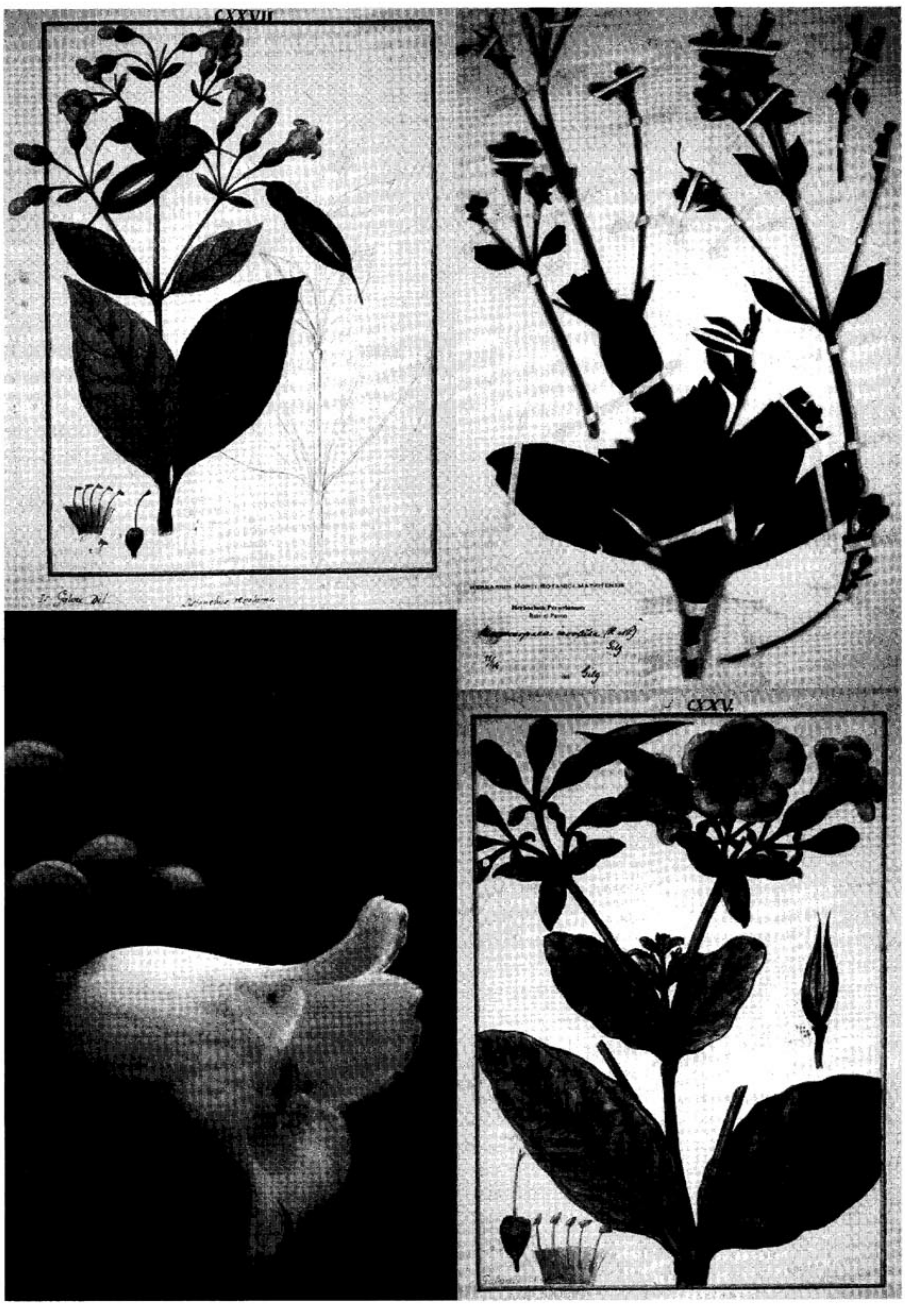
Basionym: *Lisianthus revolutus* Ruiz & Pav., Fl. Peruv. Chil. 2: 14. 1799. TYPE: PERU. Huánuco: Habitat in montibus altis frigidis Muña ad Saria tractum, 15 August–24 September 1796, *Ruiz & Pavon s.n.* (Lectotype: MA-Ruiz & Pavon, selected here; Isolectotypes: BM [2 sheets, BM numbers 582105, 583106], MA-Ruiz & Pavon [3 sheets], F [F sheet 842851], G [3 sheets, G (8647/40), G-BOIS (8647/42), G-DEL (8647/41)]. Figs. 9–11.

Synonym: *Helia revoluta* (Ruiz & Pav.) Kuntze, Rev. Gen. 428. 1891.

Additional material examined: PERU. Huánuco: Carpish, 9 November 1938, *Stork & Horton 9913* (GH, K, UC); Leoncio Prado, road from Huánuco to Tingo Maria, Abra Carpish, just north of tunnel, 22 March 2001, *Weigend et al. 5288* (HUT). Junín: La Merced, 10 August 1923, *MacBride 5224* (F, GH, US).

The type of *Macrocarpaea revoluta* (described as *Lisianthus revolutus*) was collected between August–September 1786, between Huánuco and Muña (Ruiz, 1940: 208–211). The exact locality identified by Ruiz and Pavon (1799: 14) is "*Habitat in montibus altis frigidis Muña ad Saria tractum*". The type material consists of four sheets in the Ruiz and Pavon herbarium at Madrid, and a single sheet at the Field Museum in Chicago (a photo of which appears as plate 4 in Ewan, 1948: between pages 222–223). The most complete sheet at Madrid is selected as the lectotype.

The circumscription here of *Macrocarpaea revoluta* is essentially identical to that of Ewan (1948: 230) except for the exclusion of the specimen *Williams 7596*. Most researchers since Ewan (1948) have used this name to identify to a different, relatively common species from the Chachapoyas area of Amazonas, Peru, where the Williams collection is from. That is a yet-to-be-described new species that will appear in a forthcoming installment of this series to be named after the pre-Columbian Chachapoya fortress Kuelap.



FIGURES 9–12. 9, *Macrocarpaea revoluta* original illustration in Ruiz & Pav., Fl. Peruv. Chil. 2: 14. 1799, fig. CXXVII; 10, *Macrocarpaea revoluta*, lectotype *Ruiz & Pavon s.n.* (MA-Ruiz & Pavon). Photo Jason R. Grant; 11, *Macrocarpaea revoluta*, inflorescence, *Weigend et al. 5288*. Photo Maximilian Weigend; 12, *Macrocarpaea viscosa* original illustration in Ruiz & Pav., Fl. Peruv. Chil. 2: 14. 1799, fig. CXXV.

5. *Macrocarpaea viscosa* (Ruiz & Pav.) Gilg, Bot. Jahrb. Syst. 22: 337. 1896.

Basionym: *Lisianthus viscosus* Ruiz & Pav., Fl. Peruv. Chil. 2: 14. 1799. TYPE: PERU. Huánuco: Habitat in altis locis Muña ad Tambo nuevo tractus, 15 August–24 September 1786, *Ruiz & Pavon s.n.* (Lectotype: MA-Ruiz & Pavon, selected here; Isolectotype: MA-Ruiz & Pavon). Figs. 12–15.

Synonym: *Helia viscosa* (Ruiz & Pav.) Kuntze, Rev. Gen. 428. 1891.

Additional material examined: PERU. Huánuco: 10 km N of Acomayo, bosque Unchog, 10 October 1982, *Graham s.n.* [= *M. Ramírez R. No. 32*] (F); Pachitea, Panao, road from Chaglla to Rumichaca (Tambo de Vaca), 31 March 2001, *Weigend et al. 5429* (BSB, NY).

The type of *Macrocarpaea viscosa* (described as *Lisianthus viscosus*) was collected between 15 August–24 September 1786, between Huánuco and Muña (Ruiz, 1940: 208–211). The exact locality identified by Ruiz and Pavon (1799: 14) is "in altis locis *Muña* ad *Tambo nuevo* tractus". Ruiz (1940: 211) makes the following observations: "The calyces of this small shrub as well as the flower stalks are covered with a white, crystalline gum that dissolves completely in water and crackles in the fire like gum arabic." In dried material this is a common trait and found in many gentians, for example on seeds, leaves and calyces in *Lisianthius*, Chironieae, Helieae, and Potalieae (Struwe, Weaver, pers. comm.) The type material of *Lisianthus viscosus* consists of two herbarium sheets in the Ruiz and Pavon herbarium at Madrid. No duplicates have been found in other herbaria. The sheet with a leaf and an inflorescence is selected as the lectotype, and the sheet with inflorescence only is selected as the isolectotype.

Macrocarpaea viscosa is a distinctive species, yet has been misunderstood by most students of the genus. Notably, when Ewan (1948: 246) had only seen a photograph of the type at Madrid, he attributed three specimens to *M. viscosa* that in fact represent three different species (none of which is *M. viscosa*!). In all actuality, there was a lapse of nearly 200 years from the time Ruiz and Pavon collected *M. viscosa* in 1786 to when it was recollected by Graham in 1982. The more important collections are those of by Weigend in 2000 near Ruiz and Pavon's original locality. Weigend's herbarium material, flowers preserved in alcohol, and color photographs provide the most significant data in our understanding of this rare species.

6. *Macrocarpaea sodiroana* Gilg, Bot. Jahrb. Syst. 25: 724. 1898. TYPE: ECUADOR. Pichincha: In regione temperata secus fluv. Pilatón, 800–1600 m, August flor., *Sodiro 101/1* (Type: B? [destroyed]; Lectotype: QPLS, selected here; Isolectotypes: QPLS [2 sheets]). Figs. 16–17.

Additional material examined: ECUADOR. Pichincha: Collections made along the old road from Quito to Santo Domingo via Chiriboga: 21 March 1980, *Dodson & Gentry 9725* (MO, SEL); 7 April 1984, *Dodson & Thurston 14162* (HAM, MO [2 sheets]); *Fagerlind & Wibom 1925a* (S); *Fagerlind & Wibom 1925b* (S); 26 February 2002, *Grant & Torres 02–4210* (NEU, NY, US); 8 May 1968, *Harling et al. 9221* (GB); 2 February 1982, *Luteyn et al. 8733* (QCA); February 1975, *Ortiz 20* (MO); 4 February 1944, *Scolnik 1616* (PH); 13 December 1987, *Zak & Jaramillo 3169* (HAM, MO); 15 April 1988, *Zak & Jaramillo 3458* (GB, K, NY, US). Collections made at Parroquia Nanegal, Bosque Protectora Maquipucuna: 24 January 1974, *Harling & Andersson 11575* (GB); 20 May 1991, *Tipaz & Quelal 154* (MO); 18 September 1989, *Webster et al. 27733* (DAV); 7 July 1992, *Webster et al. 29065* (DAV); 15 January 1995, *Webster et al. 31346* (DAV); 17 June 1996, *Webster et al. 31550* (DAV); Carretera Calacalí, Los Bancos, en Mindo, 17 May 1997, *Carrera 23* (QCA); Quito Canton, trek from Lloa to Mindo, 8 February 1998, *J.L. Clark 4521* (QCNE); Quito, Parr. Mindo, Bosque Protector Mindo, 15 July 1992, *Delprete et al. 6100* (TEX); Ridge between Río Mindo and Río Bagasal, 14 July 1992, *Webster et al. 29399* (DAV).

Macrocarpaea sodiroana Gilg was described from a specimen collected by Sodiro and likely deposited at Berlin (Gilg, 1898). However, all material of *Macrocarpaea* at B was destroyed during the Second World War. Luckily, most of Gilg and Gilg-Benedict's new species have isotypic material in other herbaria (e.g. BM, BR, C, E, G, GH, GOET, K, LD, M, MANCH, MICH, MO, NY, OXF, P, PH, QPLS, US, and W). Lectotypes will be selected from this material for *M. arborescens* Gilg, *M. bangiana* Gilg, *M. bogotana* Gilg, *M. calophylla* Gilg, *M. chlorantha* Gilg, *M. cinchoniifolia* (Gilg) Weaver, *M. cochabambensis* Gilg-Benedict, *M. duquei* Gilg-Benedict, *M. glaziovii* Gilg, *M. micrantha* Gilg, *M. pachyphylla* Gilg, *M. pachystyla* Gilg,

FIGURES 13–16. 13, *Macrocarpaea viscosa*, lectotype *Ruiz & Pavon s.n.* (MA-Ruiz & Pavon). Photo Jason R. Grant; 14, *Macrocarpaea viscosa*, inflorescence, showing corolla throat from front, *Weigend et al. 5429*. Photo Maximilian Weigend; 15, *Macrocarpaea viscosa* , inflorescence, showing corolla from the side, *Weigend et al. 5429*. Photo Maximilian Weigend; 16, *Macrocarpaea sodiroana*, lectotype *Sodiro 101/1* (QPLS). Photo Jason R. Grant.

FIGURE 17. *Macrocarpaea sodiroana*, inflorescence, *Grant & Torres 02-4210*. Photo Jason R. Grant.

M. polyantha Gilg, *M. sodiroana* Gilg, and *M. weberbaueri* Gilg). The exception is *M. stenophylla* where a neotype was required and recently selected by Grant & Struwe (2001). The first set of Sodiro's specimens is at QPLS, located in the Bibliotheca Ecuatoriana Aurelio Espinosa Polit, Quito Ecuador. Original material of *Macrocarpaea sodiroana* was recently identified, and is here selected as lectotype.

Gilg (1898) cites the type of *Macrocarpaea sodiroana* as *Sodiro n. 101/1*. However, this number does not actually correspond to a Sodiro collection number, rather to an order and family. Sodiro gave numbers to each species he collected, not different collections (Jørgensen and Léon-Yánez, 1999: 34). On the QPLS sheets, there is the following information: "Num. 109/1. Ord. 109. Trib. II. Gen. 35." Gilg possibly misread the handwriting of 109/1 as 101/1, and then referred to it as the collection number of the type specimen of *M. sodiroana*. Here, I recognize the lectotype and isolectotypes of *M. sodiroana* as *Sodiro s.n.* (QPLS).

Macrocarpaea sodiroana is a distinct species endemic to Pichincha, Ecuador, and its broad species circumscription by Pringle (1995) is rejected.

A Sodiro collection at Paris (P) incorrectly annotated as type material of *Macrocarpaea sodiroana* by Alicia Lourteig is here identified as *Chelonanthus alatus* (Aubl.) Pulle [syn. *Irlbachia alata* (Aubl.) Maas]. The specimen citation is as follows: Ecuador. Pichincha: In reg. subtrop. secus, fl. Pilatón, I/1889, *Sodiro s.n.* (P). Numerous Sodiro specimens of *Chelonanthus alatus* with similar data were also seen at QPLS.

NEW IDENTIFICATION

1. *Macrocarpaea* sp. Based on *Dannouse s.n.* (NY), determined and discussed by Ewan (1950:164–165).

The specimen collected by Dannouse in Trinidad, and annotated as the genus *Macrocarpaea* by both Nicholas Edward Brown (1920) and Joseph Ewan (1946), and discussed by Ewan (1950: 164) as a species of *Macrocarpaea*, is not a gentian.

It is unclear why Brown thought this was a member of the Gentianaceae. In penciled handwriting on the herbarium sheet itself, Brown simply writes "Seems to be allied to *Macrocarpaea Hartii* Krug & Urb. Not matched at Kew. Sept 1920. N. E. Brown." Ewan writes on his annotation label "Unique in *Macrocarpaea*, not placed, J. Ewan, 1946." Ewan appears to have had some doubts about the provenance of the specimen. Two additional

annotation labels by Ewan have additional information that was discussed in Ewan (1950): ["Dannouse, paid collector hired by Broadway (?); a number of his collections have not been repeated before or since." John Beard, in lett. to J. Ewan 1 V 1946"]. From the specimen itself, Ewan (1950) notes differences from typical *Macrocarpaea* in the leaves and corolla, but maintains it as a gentian although he does not describe it as a new species or assign it to any previously described species.

Both Brown and Ewan were possibly confused by the specimen because it did not match any other neotropical plant they knew. The problem is that while the plant is said to have been collected in Trinidad, the herbarium specimen must have been made from a cultivated tree. My initial determination of the specimen as Apocynaceae was confirmed by Apocynaceae experts Mary Endress, Barry Hammel, and J. Francisco Morales, yet none could immediately place it in any neotropical group. The specimen is clearly a member of the Apocynaceae as can be seen most noticeably in the twisted corolla, the form of the anthers (revealed in the boiled dissection of a flower), and the structure of the inflorescence. Also, no gentian has an inflorescence without bracts subtending the nodes or flowers, as in this specimen.

Endress and this author then ignoring the locality data, identified the plant to genus and species based on morphology and comparison to herbarium material at Zürich (Z). Relatively easy identification to *Tabernaemontana crassa*, a species native to Africa was confirmed by unique characters in the calyx, inflorescence structure, leaf venation and drying patterns. Additionally, Leeuwenberg (1991) mentions that the tree is cultivated in the New World, notably at the Belém Botanical Garden (Brazil). Although it is native to tropical Africa, it has not been reported to escape from cultivation in the Neotropics.

Ewan's description of *Macrocarpaea guttifera*, that turns out to be a member of the Rutaceae (*Ravenia biramosa*) (Grant & Struwe, 2001), and the identification of the Dannouse collection as a *Macrocarpaea*, that turns out to be a member of the Apocynaceae (*Tabernaemontana crassa*), draws further attention to Ewan's rather problematic treatment of the genus (Ewan, 1948, 1950, 1951).

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DE MACROCARPAEAE GRISEBACH (EX GENTIANACEIS) SPECIEBUS NOVIS III: SIX NEW SPECIES OF MOON-GENTIANS (*MACROCARPAEA*, GENTIANACEAE: HELIEAE) FROM PARQUE NACIONAL PODOCARPUS, ECUADOR

JASON R. GRANT[1] AND LENA STRUWE[2]

Abstract. In preparation for the *Flora Neotropica* monograph of *Macrocarpaea* (Gentianaceae: Helieae) and recent fieldwork in Ecuador, six new species have been identified and are here described from Parque Nacional Podocarpus and its surrounding areas in Loja and Zamora-Chinchipe provinces. These are *Macrocarpaea apparata*, *M. bubops*, *M. jensii*, *M. lenae*, *M. luna-gentiana*, and *M. noctiluca*. For each new species, descriptions, illustrations, and ecological information are provided. The neotropical montane genus *Macrocarpaea* has among the highest biodiversity in Ecuador with over 30 species present. The name "moon-gentian" or "genciana de luna" is coined as the common name for the genus *Macrocarpaea*.

Keywords: Ecuador, Gentianaceae, Helieae, *Macrocarpaea*, morphology, Neotropics.

The treatment of *Macrocarpaea* in the *Flora of Ecuador* (Pringle 1995) is exceedingly conservative at the species rank, likely due to the limited number of herbarium specimens observed. Where Pringle only recognized 8 species, over 30 species for Ecuador will be recognized in the *Flora Neotropica* monograph of *Macrocarpaea* (Grant, in prep.) The genus has a high and previously unexpected amount of species endemism in Colombia, Ecuador and Peru, notably on eastern Andean slopes between 1000–3500 m. *Macrocarpaea* itself belongs to the '*Macrocarpaea* clade' of the tribe Helieae, comprising at least *Chorisepalum*, *Macrocarpaea*, and *Tachia*, and possibly *Zonanthus* (Struwe et al. 2002). This paper results from plant collections made during a collecting expedition to southern Ecuador in February 2001. We collected and made observations on numerous species in the field. Examination of these living plants as well as herbarium specimens has led us to identify six new species. These are *Macrocarpaea apparata*, *M. bubops*, *M. jensii*, *M. lenae*, *M. luna-gentiana*, and *M. noctiluca*.

Southern Ecuador and notably the provinces of Loja and Zamora-Chinchipe with the large and species-rich Parque Nacional Podocarpus represents one of the areas of highest species diversity in *Macrocarpaea*. Some 16 species occur in the region, an increase of seven species from the nine recorded to occur in the region by Grant & Struwe (2001). Many are common throughout the area (e.g., *M. arborescens* Gilg and *M. noctiluca*), while others are only known from basically a single locality (e.g., *M. apparata*), Fig. 1.

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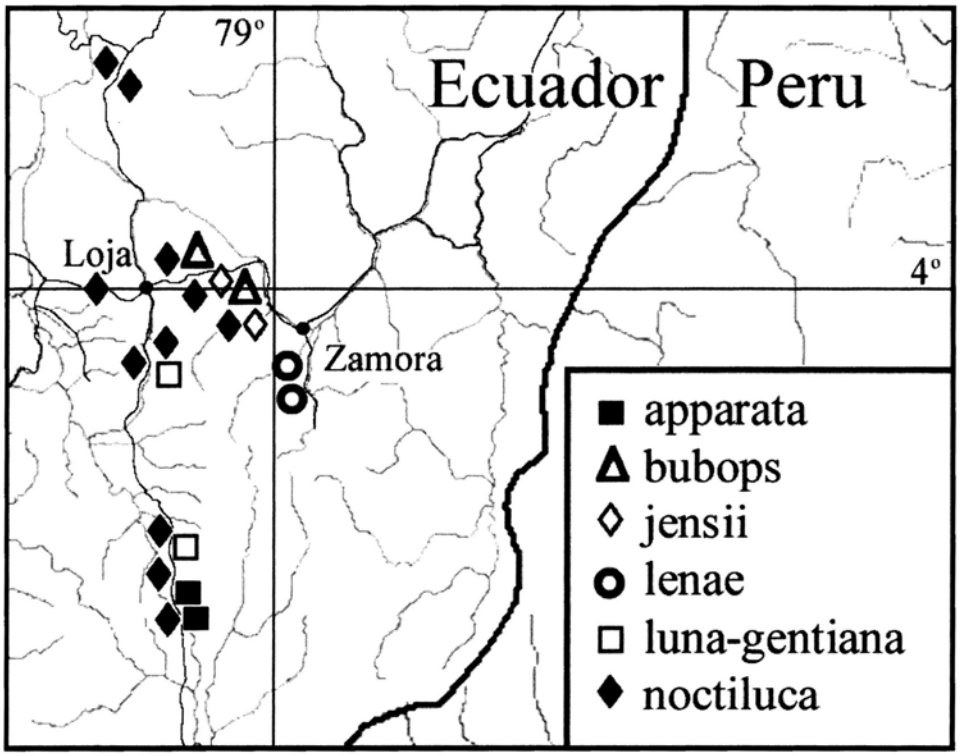

FIGURE 1. Distribution of *Macrocarpaea apparata*, *M. bubops*, *M. jensii*, *M. lenae*, *M. luna-gentiana*, and *M. noctiluca* in Loja and Zamora provinces, southern Ecuador.

The descriptions of the six species below are based on field observations, pickled material from the field, photographs, and herbarium specimens. In order to maintain continuity between written descriptions of other authors (as well as other descriptions of our own made without the benefit of fresh material), all measurements and descriptions here are based on dried pressed specimens since floral material has been known to shrink by up to 50% in drying.

The total length of an inflorescence will generally not be reported since a number of species have large inflorescences that do not fit on a single herbarium sheet (e.g., *M. apparata*). Therefore, measuring and comparing inflorescence fragments on a single herbarium sheet of such a species, to another one where the entire inflorescence will always fit on an entire sheet (e.g., *M. angelliae* J.R. Grant & Struwe), do not lead to parallel descriptions. Therefore, measurements of branch length alone (lateral and terminal branches) will be given for all species, and both such branch length and total inflorescence length for species with comparatively small inflorescences when possible. While the entire inflorescence is a thyrse composed of cymes in a racemose branching pattern, the term "branch" will be used as a general term since any branch may comprise 1–3 or more cymes.

The term "bract" is defined as all leaves in the inflorescence, except the 1–2 "bracteoles" that subtend each flower. The pair of leaves that subtend the entire inflorescence are recognized as true leaves since their size and shape is more consistent with the leaves below than the bracts above. The width of the corolla is measured at the level of the corolla lobe sinuses.

Every plant needs a common name that connects a sense of recognition in a vernacular language. And therefore, after careful consideration, we herald "moon-gentian" or "genciana de luna" for *Macrocarpaea*. The name is fitting since all species known to date are night-blooming, bathed in the glow of the moon, and have pale yellow, light-greenish or

white colored corollas, often with half-moon-shaped corolla lobes. The Latin name *Macrocarpaea* reflects the presence of an unusually large fruit for a gentian. However, this character would not be suitable for translation into a common name in English or Spanish since many other plants have larger capsules within the gentians (e.g., *Fagraea* and *Symbolanthus*).

1. *Macrocarpaea apparata* J.R. Grant & Struwe, *sp. nov.* TYPE: ECUADOR. Loja: 28.8 km S of Yangana, 04° 27'59" S, 079° 08'44" W, 2450 m, roadside secondary vegetation, tree 4–5 m tall, 5 cm in diameter at the base of the trunk, corolla rugose on the outside, calyx medium green, 11 February 2001, *J.R. Grant & Struwe 01-4002* (Holotype: US; isotypes: G [2 sheets], LOJA, NEU [2 sheets], NY, MO, QCA, QCNE, S, SBG). Fig. 2–3A.

A Macrocarpaeae sodiroanae cui affinis, sed arbores excelsis, foliis multo grandibus, et caulibus, petiolis, foliis, inflorescentiis, calycibus et lobis corollae pubescens hyalinis differt.

Dichotomously branched tree, overall branching pattern triangular in outline, 4–5 m tall, hyaline hispid with short simple hairs on stems, petioles, leaves, inflorescences, calyces, and corolla lobes. Trunk to 6.5 cm in diameter, wood hollow (pith 3–19 mm, narrower in trunk, and wider in younger branches), growth rings detectable but not prominent; bark papery thin to scarcely measurable (to 0.05 mm), outer surface smooth to rugose, tan-brown. Stems terete to slightly quadrangular, hollow, 8–16 mm in diameter just below inflorescence. Leaves broadly to narrowly ovate to elliptic, petiolate, 27–60 cm; blades 24–50 × 14–31 cm, base aequilateral to slightly oblique, apex acute, entire, not revolute, papery thin in texture, dark green, with slightly impressed veins above and slightly raised veins below, glabrous above, hyaline to tan pubescent on lower surfaces and especially veins; interpetiolar ridge 3–10 mm high; petioles robust with strong open vagination nearly equaling the length of the petiole, (30–)60–100 mm. Branches of the inflorescence 23–40 cm, 14–30 flowered per branch; bracts ovate to lanceolate to linear, 20–165 × 4–100 mm, base aequilateral to oblique, apex acute to acuminate, petiolate; bract petioles 1–20 mm. Flowers pedicellate, erect to horizontal to oriented in all directions in the inflorescence; pedicels 2–26 mm; bracteoles linear to lanceolate to ovate, 3–25 × 1–8 mm. Calyx narrowly campanulate, 7–10 × 6–8 mm, hyaline puberulent, smooth, medium to dark green, ecarinate, no ridges extend down from calyx lobes; calyx lobes dividing calyx to one third, rounded to obtuse, 2–3 × 3–4 mm. Corolla funnel-shaped, 39–53 mm, 18–22 mm wide at corolla lobe sinuses, whitish-green, rugose to smooth; corolla lobes ovate, apex obtuse to rounded to retuse, 7–14 × 8–12 mm. Stamens 27–33 mm; filaments 20–26 mm, filiform, terete; anthers linear to linear-elliptic, 5.5–7.0 × 2.0–2.5 mm, sagittate, versatile. Pistil 35–39 mm; ovary 7–8 × 3.0–3.5 mm; style 22–26 × 1.0–1.5 mm; stigma 2-lobed, lobes 4–5 × 2.0–2.5 mm, rounded to spathulate. Capsules and seeds unknown.

Macrocarpaea apparata is a large sturdy tree to 4–5 m tall with the largest leaves known to date within the genus (27–60 cm long × 14–31 cm wide). The tobacco-like leaves are broadly ovate to narrowly ovate to elliptic, and sterile plants typically look rather like members of the Rubiaceae or Asteraceae. Even as sterile it is easy to recognize by its winged, vaginated petioles (Fig. 2), a feature that is rare among gentians, and known only in species of *Anthocleista*, *Fagraea*, and *Macrocarpaea*. These winged, vaginated petioles are pronounced in *M. apparata*, *M. bubops*, and several other undescribed species. The wings are essentially elevated ridges along the vagination that extend from the base on either side of the petiole. In smaller leaved species these "wings" between paired opposite leaves may appear as a ring around the stem. However, in larger leaved species as here in *M. apparata*, these wings extend well along the length of the petiole to form this unique morphology.

It is somewhat surprising that this species has never been collected prior to our collections since mature individuals are conspicuous along the roadside. *Macrocarpaea apparata* has affinities to several other undescribed species from southern Ecuador. However, for the purpose of the establishment of the name, comparison to *M. sodiroana* is made even though the two species are not closely related. It differs from *M. sodiroana* in its tall habit, large leaves, and distinct hyaline pubescence of short simple hairs on stems, petioles, leaves, inflorescences, calyces, and corolla lobes.

Etymology. The name *apparata* derives from the English verb "to apparate", made popular in

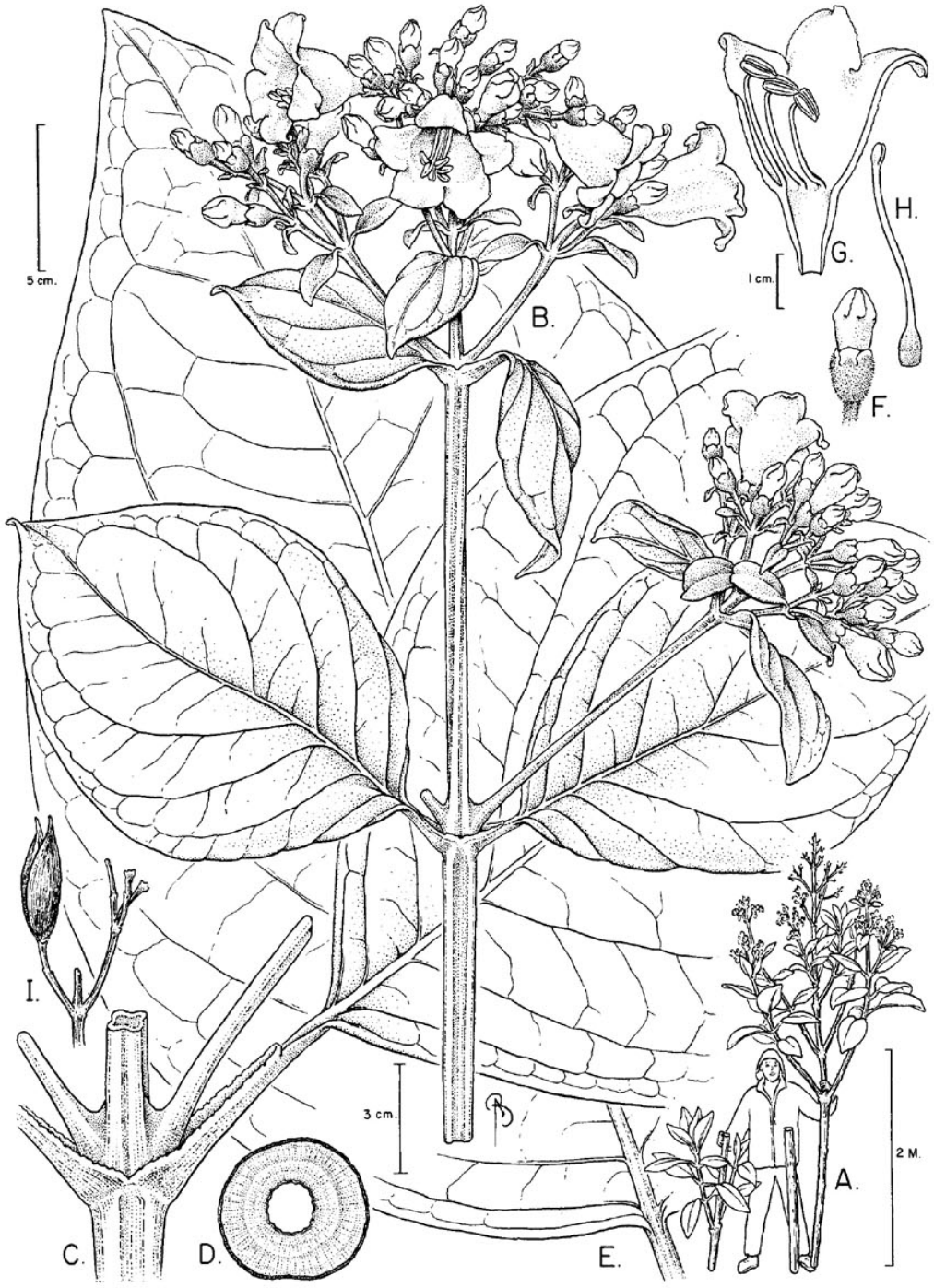

FIGURE 2. *Macrocarpaea apparata*. A, habit of tree in the field, trunk cut into three segments from the base; B, habit of flowering stem; C, interpetiolar ridge; D, wood anatomy of cross-section of main trunk; E, leaf; F, floral bud; G, cross-section of corolla; H, pistil; I, mature dehisced capsule. A, D, F, H from pickles, photos and pressed specimens of *J.R. Grant & Struwe 01-4002*; B, C from *J.R. Grant & Struwe 01-3999* and photos of *J.R. Grant & Struwe 01-4002*; E from *J.R. Grant & Struwe 3998*; I from *J.R. Grant & Struwe 4001*.

FIGURE 3. A–C. *Macrocarpaea* species. A, *Macrocarpaea apparata:* flowering stem with large white campanulate flowers. Photo by Jason R. Grant, 28.8 km S of Yangana, Loja, Ecuador, 11 February 2001, *J.R. Grant & Struwe 01-4002* (type); B, *Macrocarpaea jensii.* Flowering stem with large yellowish-white campanulate flowers. Photo by Jason R. Grant, Parque Nacional Podocarpus (San Francisco entrance), Zamora-Chinchipe, Ecuador, 16 February 2001, *J.R. Grant & Struwe 01-4047* (type); C, *Macrocarpaea lenae.* Lena Struwe holding type material of *M. lenae.* Photo by Jason R. Grant, Parque Nacional Podocarpus (Bombuscaro entrance), Zamora-Chinchipe, Ecuador, 13 February 2001, *J.R. Grant & Struwe 01-4013* (type).

the book 'Harry Potter and the Chamber of Secrets' by J.K. Rowling (1998). The term describes the magical ability to vanish and reappear at your destination (i.e. apparating). When we first found this new species, we could only find sterile individuals. After looking all afternoon, and only just before dusk, we finally found several flowering plants that seem to have 'apparated' in front of us, appearing out of nowhere. Therefore, we present the name the "apparating moon-gentian".

Paratypes: ECUADOR. Loja: Nudo de Sabanilla, ca. 24 km S of Yangana, at border of P.N. Podocarpus, roadside right after stream that crosses the road, roadside secondary vegetation, plant sterile, 2550 m, 11 February 2001, *J.R. Grant & Struwe 01-3995* (LOJA, QCNE, NEU, NY, US [2 sheets]); 29.6 km S of Yangana, 04°27'59"S, 079°08'44"W, 2450 m, roadside secondary vegetation, plant sterile, 11 February 2001, *J.R. Grant & Struwe 01-3998* (LOJA, QCNE, NEU, NY, US [2 sheets]); 29.6 km S of Yangana, 04°27'59"S, 079°08'44"W, 2450 m, roadside secondary vegetation, pickled flowers, stem, petioles, and leaves available, calyx dark green, corolla whitish green, filaments light green, stamens cream-colored, corolla bud rugose on outside, calyx with short, stiff hairs, 11 February 2001, *J.R. Grant & Struwe 01-3999* (LOJA, QCNE, NEU, NY, US [2 sheets]); 30.9 km S of Yangana, 04°27'59"S, 079°08'44"W, 2450 m, roadside secondary vegetation, tree 10 m tall, with flowers and fruits, 11 February 2001, *J.R. Grant & Struwe 01-4001* (LOJA, QCNE, NEU [4 sheets], NY, US [4 sheets]); 30.1 km past Yangana towards Valladolid, 5 November 2002, *J.R. Grant et al 02-4292* (NEU, NY, US).

2. *Macrocarpaea bubops* J.R. Grant & Struwe, *sp. nov.* TYPE: ECUADOR. Zamora-Chinchipe: Along new road Loja-Zamora, moist cloud forest on peaty soil with *Sphagnum* and terrestrial lichens, 2500 m, tree 5 m, flowers greenish yellow, 25 April 1987, *van der Werff & Palacios 8986* (Holotype: NY; isotypes: AAU, G, GB, QCNE). Fig. 4.

A Macrocarpaeae calophylla cui affinis, sed foliis coriaceis, ellipticis vel anguste ovatis (vs. ellipticis), paginae superiore laevibus, inflorescentiis multifloribus, et lobis calycis margine hyalinis differt.

Dichotomously branched tree, much branched from about 2 m above the ground; overall branching pattern conical in outline, 1–10 m tall, glabrous throughout except lower leaf surfaces with short papillae. Trunk to 9.5 cm diameter wood always solid without any hollow cavities, growth rings prominent; bark thick, pithy to 4 mm thick, outer surface rugose, brown. Stems terete, solid, 5–12 mm in diameter just below inflorescence. Leaves narrowly ovate to elliptic, petiolate, 8.5–22.0 cm; blades 7.5–19.5 × 4.0–11.5, cuneate to rounded, margin entire, slightly revolute, base aequilateral to slightly oblique, apex acute, thick, leathery-coriaceous, dark green, with no or few impressed veins above, and slightly raised veins below, glabrous above and typically below, yet often with short tuberculate hairs on lower veins, and on most herbarium specimens (and especially visible on living material) on the underside of most leaves, at the base, on either side of the midrib just above the petiole, there are two orange dots (Fig. 4C); interpetiolar ridge 1–5 mm high; petioles robust with strong open vagination nearly equaling the length of the petiole, 10–35 mm. Branches of the inflorescence 14–36 cm, 5–20 flowered per branch. Bracts narrowly ovate to elliptic to obovate to rounded, 22–60(–170) × 6–32(–80) mm, base aequilateral, apex acute, petiolate; bract petioles 2–14(–30) mm. Flowers pedicellate, erect to horizontal to oriented in all directions in the inflorescence; pedicels 4–20 mm; bracteoles linear to ovate to obovate, 2–20 × 2–9 mm. Calyx narrowly to broadly campanulate, 7–11 × 7–10 mm, glabrous, smooth, green, ecarinate, often with pronounced ridges between calyx lobes extending to the base of the calyx; calyx lobes dividing calyx one third to one half, rounded to obtuse, 3–4 × 3–5 mm, often with a slightly raised orange keel. Corolla funnel-shaped, 32–51 mm, 13–22 mm wide at corolla lobe sinuses, white to greenish yellow, smooth; corolla lobes ovate to elliptic, apex obtuse to rounded to retuse, 5–10 × 7–11 mm. Stamens 17–23 mm; filaments 12–19 mm, filiform, terete; anthers elliptic to oblong, 4–5 × 2.0–2.5 mm, sagittate, versatile. Pistil 22–29 mm; ovary 5–6 × 2.5–4.0 mm; style 14–19 × 0.5–1.0 mm; stigma 2-lobed, lobes 3–4 × 1–2 mm. Capsules and seeds unknown.

Macrocarpaea bubops belongs to a group of species previously circumscribed under a broad interpretation of *M. revoluta* (e.g., Pringle 1995: 95–97). However, *M. bubops* has no morphological affinity to *M. revoluta* and is also

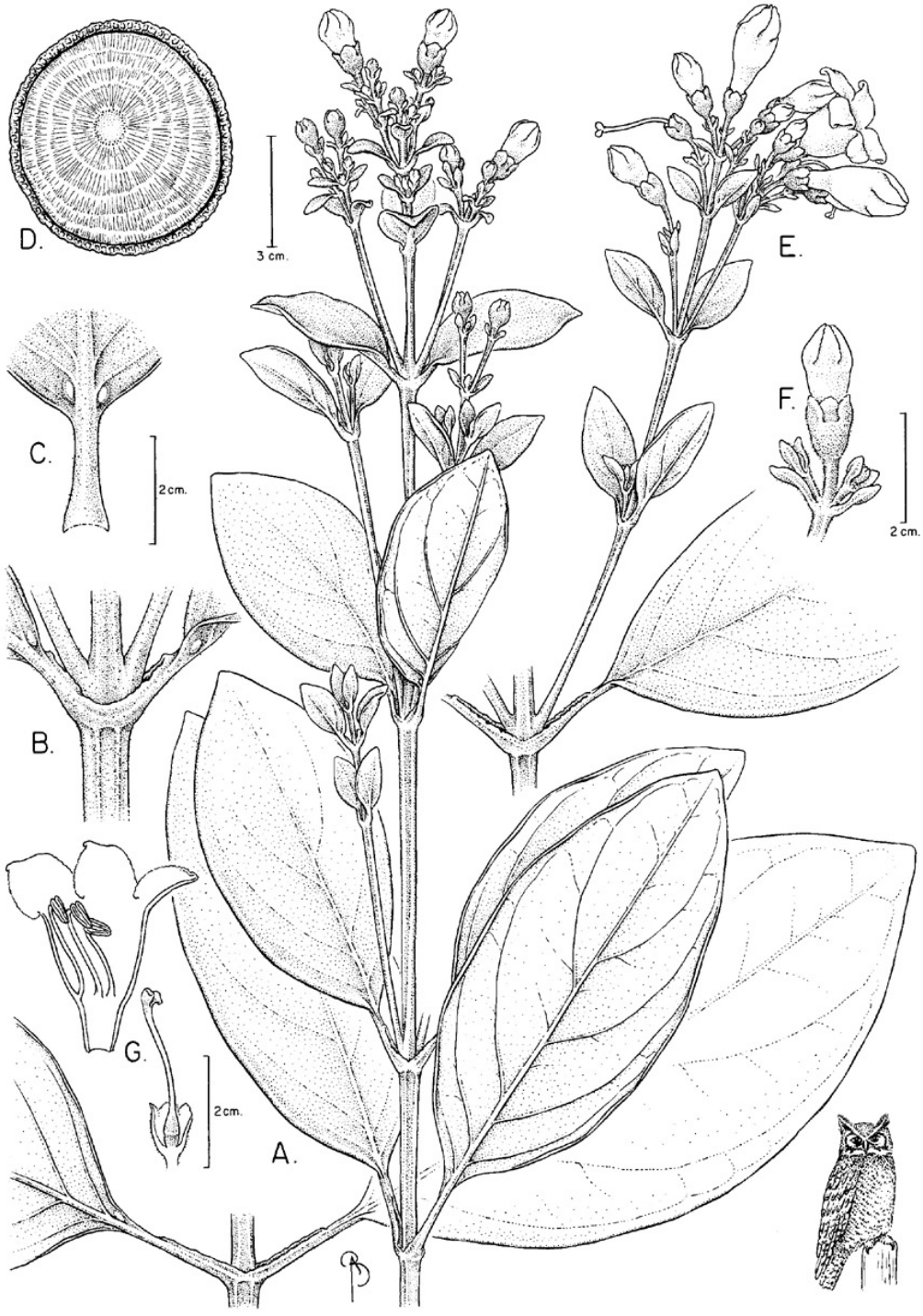

FIGURE 4. *Macrocarpaea bubops*. A, habit of flowering stem and leaves; B, interpetiolar ridge; C, lower surface of leaf showing two orange dots; D, wood anatomy of cross-section of main trunk; E, flowering stem; F, floral bud; G, cross-section of corolla and pistil. A–D, F from pickles, photos and specimens of *J.R. Grant & Struwe 01-4046*; E, G from *Madsen 74050* (AAU).

geographically distinct from its Huánuco and Junín distribution (Grant 2002). *Macrocarpaea bubops* has affinities to *M. calophylla* of Magdalena, Colombia, which may be extinct since it has not been recollected since its original collections made in 1843. These two species are similar in the general shape of the leaves and architecture of the inflorescence. *Macrocarpaea bubops* differs in its thicker, more leathery, elliptic to narrowly ovate (vs. broadly elliptic) leaves with a smooth upper surface, a many-flowered inflorescence, and rounded calyx lobes with a hyaline margin. Interestingly, on the underside of most leaves, at the base, on either side of the midrib just above the petiole, are two, so far as yet unexplained orange dots that become translucent when preserved in alcohol. These dots are part of the plant, and not a fungus, lichen or insect damage. Similar yet yellow-colored dots were also observed on some leaves of *M. noctiluca* in Loja (*J.R. Grant & Struwe 01-4074*).

The Estación Cientifica San Francisco in Parque Nacional Podocarpus is unique in Ecuador in that four species of the genus *Macrocarpaea* occur sympatrically. Individuals of *M. bubops* (*J.R. Grant & Struwe 01-4046*), *M. harlingii* (*J.R. Grant & Struwe 01-4048*; *J.R. Grant & Struwe 01-4049*), and *M. jensii* (*J.R. Grant & Struwe 01-4047*) were collected within 20 m of each other, and *M. noctiluca* (*J.R. Grant & Struwe 01-4062*) within 100 m from them. Each species is a clearly different morphological type, and none appears to be closely related to the other. *Macrocarpaea bubops*, *M. harlingii*, and *M. jensii* are rarely-collected plants that generally occur in primary forest and known best from the San Francisco site, whereas *M. noctiluca* is a commonly collected species that occurs throughout Loja and Zamora-Chinchipe provinces, seen most commonly in disturbed sites along roadsides. *Macrocarpaea bubops* is a tall stately tree to 10 m, perhaps the tallest in the genus. *Macrocarpaea harlingii* is a slender unbranched beanpole-like treelet with its leaves and inflorescence clustered at the apex. *Macrocarpaea jensii* is more slender and stouter than *M. harlingii*, rather shrubby in appearance and 1–5 m tall. *Macrocarpaea noctiluca* is a 1–6 m tree often simply appearing as a large inflorescence. No hybrids were observed.

Etymology. The name *bubops* derives from the Latin "*Bubo*", owl, and the Greek "*ops*", eye. This species is named for the orange dots on the underside of most leaves that are reminiscent of a pair of owl eyes, and hence the name "owl-eyed moon-gentian".

Paratypes: ECUADOR. Loja: En una pista que sale de la carretera de Loja a Zamora, 2600 m, 28 September 1995, *Garmendia & Paredes 311* (QCNE); Loja-Zamora rd, km 11, 79°11'W, 03°59'S, 2630 m, shrub 3 m, floral buds greenish yellow, 23 February 1988, *Jørgensen 65084* (AAU, QCA); Loja-Zamora rd., approx. km 15, disturbed primary and secondary montane forest, 79°08'W, 03°58'S, 2400–2700 m, shrub 1 m, flowers white, 23-24 April 1988, *Madsen 74050* (AAU, LOJA, QCA). Zamora-Chinchipe: Canton Zamora, sector el Tambo, Estación Cientifica "San Francisco", 2170 m, 17 April 2000, *Cerna 109* (QCNE); Carretera Loja-Zamora, Cuenca del rio San Francisco, Fundacion Arco Iris, 2100 m, 03°59'S, 79°05'W, bosque de neblina montano, transectos de 50 × 4 m. × 5 (0.1 Ha.), especies de 2.5 cm. de DAP en adelante (modelo radial), arbol de 7 m × 10 cm. de DAP, flor limon. T. 26, 27 February 2000, *Cerón et al. 40136* (QAP); Parque Nacional Podocarpus (San Francisco entrance), trail leading west from San Francisco, 03°59'24"S, 079°05'48"W, 2100 m, 16 February 2001, *J.R. Grant & Struwe 01-4046* (G [2 sheets], LOJA, MO, NEU [3 sheets], NY, QCA, QCNE, S, SBG, US [3 sheets]).

3. *Macrocarpaea jensii* J.R. Grant & Struwe, *sp. nov.* TYPE. ECUADOR. Zamora-Chinchipe: Parque Nacional Podocarpus (San Francisco entrance), trail leading west from San Francisco, 03°59'24"S, 079°05'48"W, 2100 m, slender tree to 4 m tall, corolla light green, tube yellowish-green, outside of corolla thick and spongy, the corolla lobes warty and uneven, leaves membranaceous, dark green, 16 February 2001, *J.R. Grant & Struwe 01-4047* (Holotype: US [3 sheets]; isotypes: G [2 sheets], LOJA, QCNE, NEU, NY, SBG). Fig. 5, 3B.

A Macrocarpaeae sodiroanae cui affinis, sed foliis longe-petiolatis gracilis, ellipticis-rhombiformibus, et corollae crassis spongiosis differt.

Unbranched tree, overall inflorescence triangular in outline, 1–5 m tall, glabrous throughout; trunk to 1.5 cm diameter wood solid to hollow (pith to 3 mm), growth rings scarcely visible; bark papery thin to scarcely measurable, 0.05 mm thick, outer surface smooth to rugose, tan. Stems terete, solid to hollow, 4–6

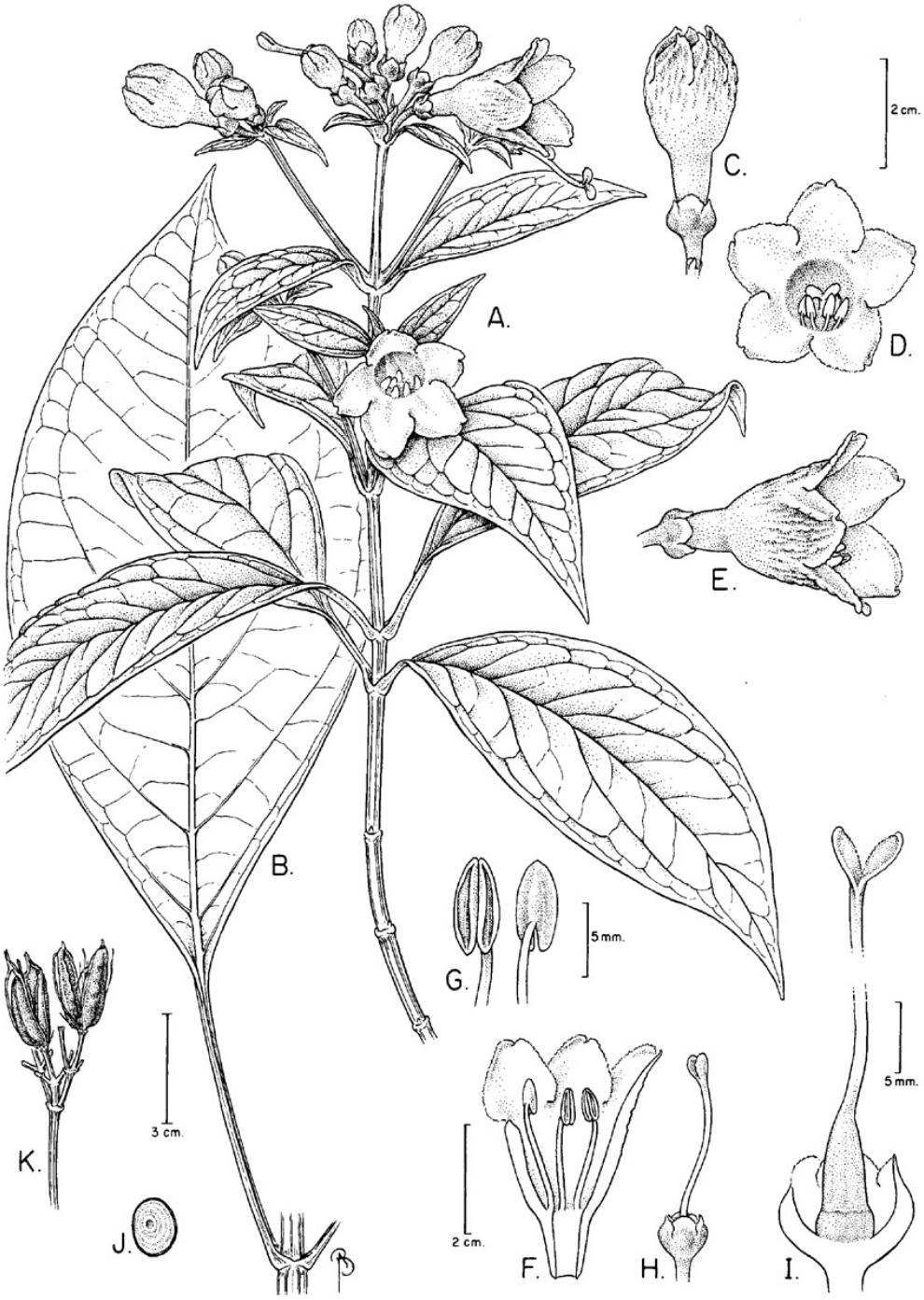

FIGURE 5. *Macrocarpaea jensii*. A, habit of flowering stem; B, leaf; C, floral bud; D, corolla viewed from front; E, side-view of flower at anthesis; F, cross-section of corolla; G, anthers; H, pistil; I pistil with sepals removed to show the ovary; J, wood anatomy of cross-section of main trunk; K, mature dehisced capsules. A-K from pickles, photos and specimens of *J.R. Grant & Struwe 01-4047*.

mm in diameter just below inflorescence. Leaves elliptic-rhomboid to oval, slightly asymmetric, petiolate, 12–32 cm; blades 14–23 × 4.5–11.5 cm, long attenuate and decurrent on the petiole, entire, not revolute, base aequilateral, apex acute to acuminate, membranaceous, thin, flexible, dark green, with slightly impressed veins above, and slightly raised veins below, glabrous above and typically below, yet often with short tuberculate hairs on lower veins; interpetiolar ridge 1–5 mm high; petioles slender with very slight vagination, 30–90 mm. Branches of the inflorescence 6–23 cm, 3–12 flowered per branch. Bracts elliptic-rhomboid to oval, slightly asymmetric, 18–80(–140) × 9–35(–50) mm, base aequilateral to attenuate, apex acute to acuminate, sessile to petiolate; bract petioles 0–10 mm. Flowers pedicellate, erect to horizontal to oriented in all directions in the inflorescence; pedicels 6–17 mm; bracteoles lanceolate to ovate, 1–12 × 1–9 mm, urceolate to campanulate, 7–9 × 7–9 mm, glabrous, smooth, green, ecarinate, no ridges extend down from calyx lobes; calyx lobes dividing calyx one third to one half, apex rounded, obtuse to acute, 2–4 × 3–4 mm. Corolla funnel-shaped, 29–41 mm, 17–25 mm wide at corolla lobe sinuses, yellowish-green, smooth to spongy, fleshy, warty and uneven; corolla lobes ovate, apex obtuse to rounded, 7–14 × 6–13 mm. Stamens 19–21 mm; filaments 16–18 mm, filiform, terete; anthers elliptic to oblong, 3–4 × 2–3 mm, sagittate, versatile. Pistil 26–32 mm; ovary 7–10 × 2.5–3.0 mm; style 17–18 × 0.5–1.0 mm, 2-lobed; stigma 2-lobed, lobes 2–4 × 1–2 mm, spathulate. Capsules dry, bilocular, medially dehiscent, ellipsoidal, 20–26 × 6–11 mm, smooth to very faintly ribbed, faint-orangish tan, erect to slightly nodding, style remnant 2–6 mm. Seeds flattened, angular, roughly triangular in outline, winged, 0.3–1.0 × 0.2–0.5 mm, faint orangish-tan, rugose-reticulate.

Macrocarpaea jensii belongs to a large group of species previously circumscribed under a broad interpretation of *M. sodiroana* (e.g., Pringle 1995: 93–95). However, *M. jensii* is a distinct species with several unique features in the genus. It has the thinnest leaves of any known species (when pressed and dried), contrasting with the thickest and spongiest corolla. It does not appear to have any clear affinities to any other Ecuadorian species, but has been confused with *M. sodiroana*. It is similar to *M. harlingii*, *M. lenae*, and *M. sodiroana* in its habit as a small slender treelet, and to *M. lenae* with its long slender petioles. Its leaves are long-petiolate, elliptic-rhomboid and often slightly asymmetric. It is known best from the 'Estación Cientifica San Francisco' within Parque Nacional Podocarpus.

Etymology. This species is named for Danish botanist Jens Madsen, 1959–, of the University of Aarhus, prolific collector of southern Ecuadorian plants, at whose home in Loja we stayed during our plant-collecting expedition to Parque Nacional Podocarpus. We are grateful for his hospitality, the logistics he provided, and introducing us to the bar "El Viejo Minero" in Loja where they serve the deadly cocktail "El Vikingo", also named for Jens. Therefore, we dedicate this species as "Jens' moon-gentian".

Paratypes: ECUADOR. Zamora-Chinchipe: Loja-Zamora rd., E of the pass, disturbed forest, 2600 m, slender treelet, 4–5 m, corolla yellowish-green, 15 February 1985, *Harling & Andersson 22118* (GB, QCA); At 25 km from Loja (road to Zamora), in the forest of the 'Estación Cientifica San Francisco', south of the river San Francisco, beside the path connecting the hydroelectric station and the entrance of the water channel, 1850 m, January 1998, *Matt 16* (ER); At 25 km from Loja (road to Zamora), in the forest of the 'Estación Cientifica San Francisco', south of the river San Francisco, beside the path connecting the hydroelectric station and the entrance of the water channel, 1850 m, January 1998, *Matt17* (ER); P.N. Podocarpus, La Esmeralda (Cooperativa San Francisco de Numbala Alto), bosque primario alto, 04°22'S, 79°03'W, 2250 m, arbusto de 1 m de altura, cáliz verde oscuro, corolla verde claro, January 1995, *Palacios & Tirado 13033* (MO, U).

4. *Macrocarpaea lenae* J.R. Grant, *sp. nov.* TYPE: ECUADOR. Zamora-Chinchipe: 5 km S of Zamora towards P.N. Podocarpus (Bombuscaro entrance), 04°06'31"S, 078°57'49"W, 1030 m, open area in primary forest, small 4 m tree, sparsely branched, calyx and corolla buds the same glaucous green color, corolla light green, old fruits brown and nodding, 13 February 2001, *J.R. Grant & Struwe 01-4013* (Holotype: US; isotypes: G, LOJA, QCA, QCNE, NEU [2 sheets], NY, MO, S, SBG). Fig. 3C, 6.

A Macrocarpaeae sodiroanae cui affinis, sed calycibus urceolatis glaucis, et foliis longe-

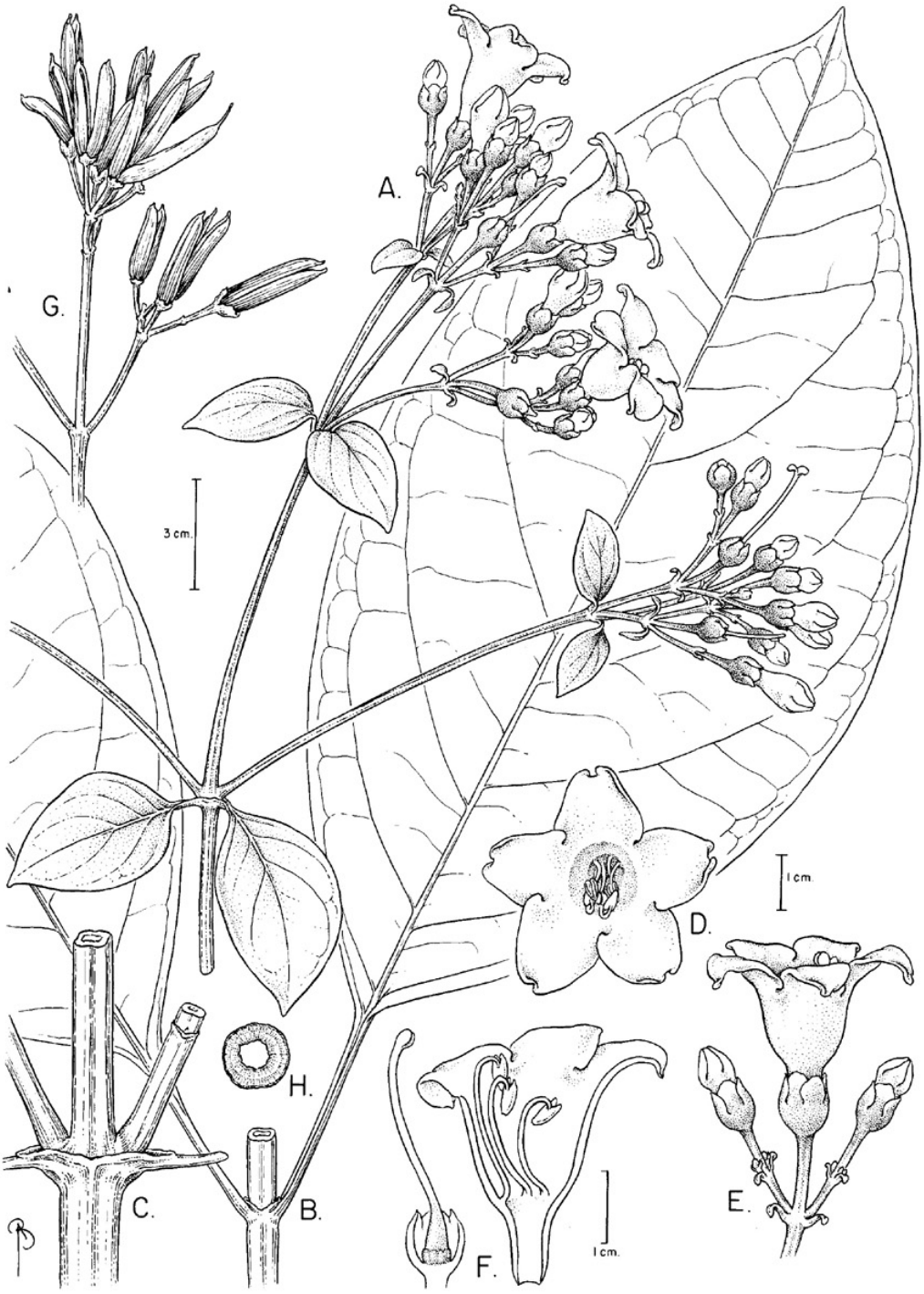

FIGURE 6. *Macrocarpaea lenae*. A, habit of flowering stem; B, leaves; C, interpetiolar ridge; D, corolla viewed from front; E, flower and floral buds; F, cross-section of corolla; G, mature dehisced capsules; H, wood anatomy of cross-section of main trunk. A–H from pickles, photos and specimens of *J.R. Grant & Struwe 01-4013*.

petiolatis differt, et cui petioli tenues homonymiae talis similis.

Unbranched tree, overall inflorescence triangular in outline, 2–3 m tall, glabrous throughout; trunk to 2.7 cm diameter wood always hollow (pith 5–9 mm), growth rings scarcely visible, bark papery thin to scarcely measurable (to 0.05 mm), outer surface smooth to rugose, tan. Stems terete to slightly quadrangular, hollow, 4–6 mm in diameter just below inflorescence. Leaves elliptic, oblong to oval, petiolate, 12–45 cm; blades 10.5–37 × (4.5–) 11.5–19 cm, cuneate to rounded, entire, not revolute, base aequilateral to oblique, apex acute to acuminate, papery thin, dark green, with slightly impressed veins above, and slightly raised veins below, glabrous above and below; interpetiolar ridge 2–8 mm high; petioles slender with very slight vagination, 15–70 mm. Branches of the inflorescence 11–26 cm, 6–20 flowered per branch. Bracts ovate to elliptic, 9–70 × 5–32 mm, base aequilateral, apex acute to acuminate, short-petiolate; bract petioles 1–5 mm. Flowers pedicellate, erect to horizontal to oriented in all directions in the inflorescence; pedicels 7–25 mm; bracteoles linear to ovate, 1–15 × 1–9 mm. Calyx urceolate to campanulate, 8–10 × 6–8 mm, glabrous, smooth, glaucous green, ecarinate; no ridges extend down from calyx lobes; calyx lobes dividing calyx one third to one half, rounded to obtuse, 3–4 × 3.0–4.5 mm. Corolla funnel-shaped, 30–37 mm, 12–21 mm wide at corolla lobe sinuses, light green, smooth; corolla lobes ovate, apex obtuse to retuse, 9–12 × 4–9 mm. Stamens 24–28 mm; filaments 20–24 mm, filiform, terete; anthers elliptic to oblong, 3–4 × 2–3 mm, sagittate, versatile. Pistil 25–31 mm; ovary 5–7 × 2.5–3.5 mm; style 17–20 × 0.5–1.5 mm; stigma 2-lobed, lobes 3–4 × 2.0–2.5 mm, rounded to spathulate. Capsules dry, bilocular, medially dehiscent, ellipsoidal, 24–29 × 8–11 mm, smooth, faint orangish-tan, erect to slightly nodding, style remnant 1–2 mm. Seeds flattened, angular, roughly triangular in outline, winged, 0.3–1.1 × 0.4–0.6, faint orangish-tan, rugose-reticulate.

Macrocarpaea lenae belongs to a large group of species previously circumscribed under a broad interpretation of *M. sodiroana* (e.g., Pringle 1995: 93–95). The two species resemble one another in their open spreading to bending inflorescences, and habit as small lanky 1–3 m tall shrubs to treelets often found in disturbed areas. It differs notably from *M. sodiroana* in its urceolate to campanulate, glaucous calyx, and leaves with long slender petioles (vs. sessile to short-petiolate leaves). As presently known, *Macrocarpaea lenae* is restricted to a small area south of the town of Zamora, Zamora-Chinchipe while *Macrocarpaea sodiroana* is confined to the province of Pichincha in northern Ecuador.

Etymology. This species is named for the co-author of this paper, Swedish botanist Karin Lena Elisabet Struwe, 1967–, of Rutgers University- New Brunswick, NJ. This species is called "Lena's moon-gentian".

Paratypes. ECUADOR. Zamora-Chinchipe: 5 km S of Zamora towards P.N. Podocarpus (Bombuscaro entrance), 04°06'31"S, 078°57'49"W, 1030 m, 1 November 2002, *J.R. Grant et al. 02-4250* (MO, NEU, NY, SEL, US); P.N. Podocarpus, Romerillo, trail at limit of P.N. Podocarpus, mountain rainforest, 78°56'W, 04°13'S, 1650–1700 m, flowers green, 14 February 1990, *Madsen & Knudsen 86854* (AAU, LOJA); hills and pasture and disturbed forest immediately S and SE of Zamora, 78°57'W, 04°04'S, 1000–1250 m, shrub to 3 m, 14 June 1988, *Øllgaard et al. 74846* (AAU, LOJA, QCA); P.N. Podocarpus, Guardería Río Bombuscaro, Sendero al Mirador, bosque primario alto, 1100 m, arbusto de 2 m de altura, flores verdes, January 1995, *Palacios & Tirado 13301* (MO, QCNE, U).

5. *Macrocarpaea luna-gentiana* J.R. Grant & Struwe, *sp. nov*. TYPE: ECUADOR. Loja: Km 21 on road from Yangana to Cerro Toledo, then trail from Cerro Toledo (ca. 300 m below antennas) towards Numbala, (to 1 km down the trail), cool, very rainy, windy páramo, 04°24'01"S, 079°06'42"W, 3350 m, small tree, 6 cm in diameter at the base, leaves coriaceous, glossy green, bullate, revolute edge, corolla buds green, corollas light green, fruits green, 14 February 2001, *J.R. Grant & Struwe 01-4028* (Holotype: US; isotypes: G, LOJA, NEU, NY, QCA, QCNE). Fig. 7, 8.

A Macrocarpaeae pachyphylla cui affinis, sed arbores robustis, inflorescentiis paucifloribus, calycibus longioribus (9–18 vs. 7–12 mm), lobis calycis latis, et floribus magni differt.

Dichotomously branched to unbranched tree, overall branching pattern obtriangular and flat-topped in outline, 2–3 m tall, glabrous to hyaline puberulent with short simple hairs on

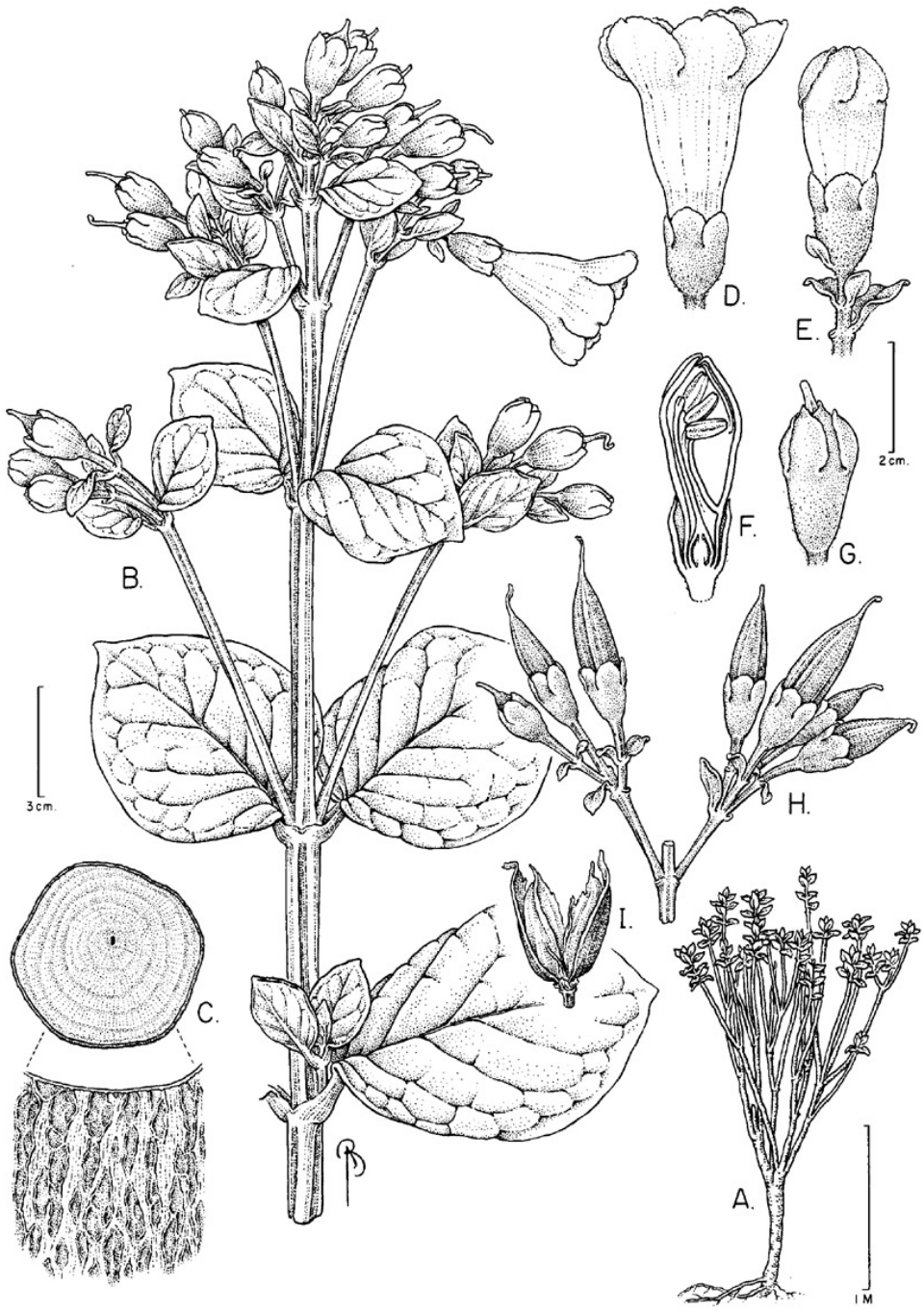

FIGURE 7. *Macrocarpaea luna-gentiana*. A, habit of tree in the field; B, habit of flowering stem; C, wood anatomy of cross-section of main trunk, and bark; D, flower; E, floral bud; F, cross-section of floral bud; G, flower just after anthesis; H, immature capsules; I, mature dehisced capsule. A from a photo of *J.R. Grant & Struwe 01-4027*; B from *Matt 1* (ER); C from *J.R. Grant & Struwe 01-4027*; D–I from *J.R. Grant & Struwe 01-4028*.

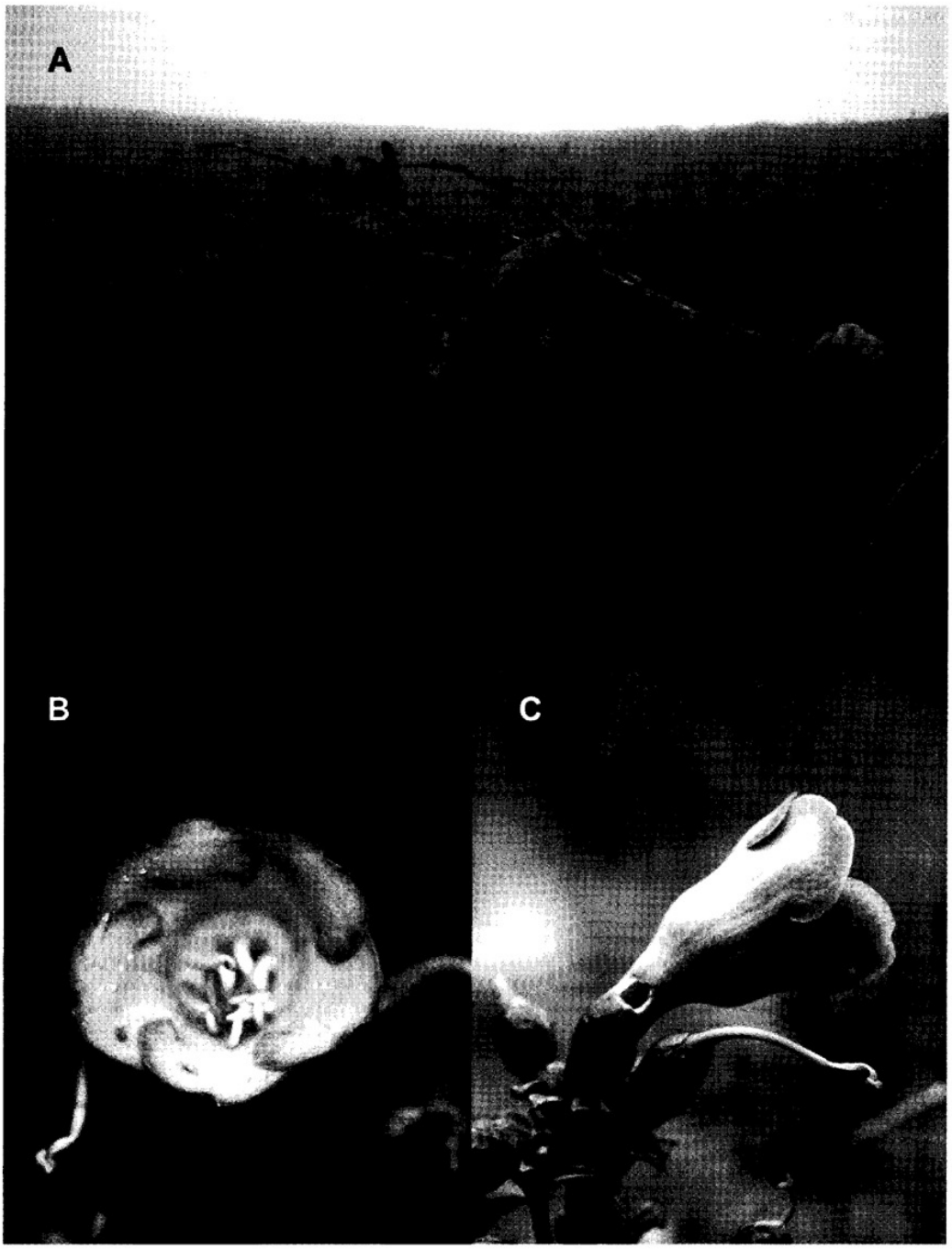

FIGURE 8. A–C. *Macrocarpaea luna-gentiana*. A, Jason R. Grant at type locality carrying a large plant. Photo by Lena Struwe, Cerro Toledo Loja, Ecuador, 14 February 2001, *J.R. Grant & Struwe 01-4028* (type); B, Corolla viewed from front, distinct overlapping corolla lobes. Photo by Jason Grant, Cerro Toledo Loja, Ecuador, 2 November 2002, *J.R. Grant et al. 02-4272*; C, Corolla viewed from side, hole at base of corolla made by nectar robbers. Photo by Jason Grant, Cerro Toledo Loja, Ecuador, 2 November 2002, *J.R. Grant et al. 02-4272*.

stems, petioles, leaves, inflorescences, calyces, and corolla lobes; trunk to 7.7 cm diameter wood solid in trunk, hollow in younger branches (to 0.5), growth rings prominent; bark thin to thick, (to 0.5–4.0 mm), brown background, mottled with distinctive tan rippling and furrowing patterns. Stems terete to slightly quadrangular, solid to hollow, 5–10 mm in diameter just below inflorescence. Leaves broadly ovate, sessile to short-petiolate, 3–12 cm; blades 10–11.5 × 2.5–8.0 cm, entire, slightly revolute, base aequilateral to slightly oblique to cuneate, apex acute, thick, leathery-coriaceous, light to dark glossy green, bullate, with few to strongly impressed veins above, and strongly raised veins below, glabrous above and typically below yet often with long pubescent hairs on the veins of young leaves; interpetiolar ridge 1–5 mm high; petioles flattened to concave, 3–5 mm. Branches of the inflorescence 5–23 cm, 1–10 flowered per branch. Bracts ovate to lanceolate, 33–82 × 10–42 mm, base aequilateral to slightly oblique or rounded, apex acute, sessile to short-petiolate; bract petioles 0–3 mm. Flowers pedicellate, erect to horizontal to oriented in all directions in the inflorescence; pedicels 3–30 mm; bracteoles ovate, 5–18 × 3–7 mm. Calyx broadly campanulate, 9–18 × 13–14 mm, hyaline puberulent to glabrous, rugose, green, ecarinate, no ridges extend down from calyx lobes; calyx lobes dividing calyx one third to one half, rounded, 7–9 × 6–12 mm. Corolla funnel-shaped, 341–62 mm, 15–40 mm wide at corolla lobe sinuses, light green, smooth; corolla lobes half moon-shaped to broadly ovate, apex rounded, 5–21 × 9–24 mm. Stamens 23–35 mm; filaments 18–29 mm, filiform, flattened; anthers elliptic to oblong, 5–6 × 2.5–3.5 mm, sagittate, versatile. Pistil 41–42 mm; ovary 7–8 × 3–4 mm; style 29–30 × 1.0–1.5 mm; stigma 2-lobed, lobes 4–5 × 2.0–2.5 mm, spathulate. Capsules dry, bilocular, medially dehiscent, ellipsoidal to ovoid, 30–49 × 13–19 mm, wrinkled to ribbed, dark brown, erect to slightly nodding; style remnant 4–15 mm. Seeds unknown.

Macrocarpaea luna-gentiana has been previously recognized as *M. pachyphylla* (e.g., Ewan 1948: 232; Pringle 1995: 97). The two species have a similar gestalt especially in the morphology of the leaves, yet the details of the inflorescence are quite different. *Macrocarpaea luna-gentiana* has a generally robust, stout appearance, a few-flowered inflorescence, broad campanulate calyx, rounded calyx lobes, and a broad funnel-shaped corolla with broad rounded to half-moon-shaped corolla lobes. *Macrocarpaea pachyphylla* has a more slender appearance overall, a many-flowered inflorescence, smaller calyx, obtuse to acute to rounded calyx lobes, a narrower corolla, and obtuse to acute corolla lobes.

Macrocarpaea luna-gentiana is a distinct narrow endemic of Loja province, Ecuador, between 2500–3500 m. Its probable sister species *M. pachyphylla* is restricted to Nariño and Putumayo provinces of Colombia at similar elevations of 3000–3400 m. These two species occur in true páramo conditions at some of the highest elevations of any known species in the genus. Other species of the genus occurring at or above 3000 m include *M. arborescens* Gilg, *M. bracteata* Ewan, *M. densiflora* (Benth.) Ewan, *M. duquei* Gilg-Benedict, *M. glabra* (L.f.) Gilg, *M. noctiluca* J.R. Grant & Struwe, and *M. stenophylla* Gilg. It is interesting to note that this species was first collected by Édouard André in 1876, and then not again for more than 100 years until 1985, a similar situation to that of the Peruvian *M. viscosa* (Grant 2002).

Etymology: *Macrocarpaea luna-gentiana* is the seminal name for the common name of the genus, "moon-gentian", derived from the Latin "*luna*", moon, and "*gentiana*", gentian.

Paratypes: ECUADOR. Loja: Loja-Zamora, 3800 m, fleur verte épaisse, arbuste à feuillage jolie, alt 2–3 m., fleur verte épaisse, arbuste à feuillage jolie, alt. 2–3 m, fl. eau de vies, 1 December 1876, *André 4513* (F, K, NY); Loja-Zamora, 3500 m, fleur verte, arbuste alt. de 2–3 m, 1 December 1876, *André 4536* (K, NY); Parque Nacional Podocarpus, Sendero a Cajanuma-Laguna del Compadre-Mirador-Cajanuma, 2750-3200 m, 04°04'S, 79°09'W, Bosque siempreverde montano alto, arbusto de 2 m., botones color verde, fruto capsular color verde, 25 February 2000, *Cerón & Curso de Dendrologia 40077* (QAP); Km 21 on road from Yangana to Cerro Toledo, then trail from Cerro Toledo (ca. 300 m below antennas) towards Numbala, (to 1 km down the trail), cool, very rainy, windy páramo, 04°24'01"S, 079°06'42"W, 3350 m, small tree, 6 cm in diameter at the base, leaves coriaceous, glossy green, bullate, revolute edge, corolla buds green, corollas light green, fruits green, 14 February 2001, *J.R. Grant & Struwe 01-4027* (LOJA, NEU, QCNE, US); Km 21 on road

from Yangana to Cerro Toledo, 2 November 2002, *J.R. Grant et al. 02-4272* (NEU, NY, US); P.N. Podocarpus, Cerro Toledo, montane forest and páramo, 79°07'W, 04°23'W, 2500–3400 m, 30 October 1989, *Madsen 86290* (AAU [2 sheets], LOJA); P.N. Podocarpus, above the refuge of Cajanuma, beside the trail from 'Mirador' on the ridge eastward to the cordillera, 3200 m, November 1997, *Matt 1* (ER); P.N. Podocarpus, S of Loja, above "Centro de información", E of Nudo de Cajanuma, mountain crest with low scrub and páramo, 79°10'W, 04°05'S, 3050–3420 m, 3 m tall shrub, flowers green, 24 February 1985, *Øllgaard et al. 58114* (AAU); P.N. Podocarpus, Yangana-Cerro Toledo, at entrance to crest, subpáramo scrub and bogs in the pass, 70°06'W, 04°23'S, 3100 m, 2 m tall sparsely branched shrub, 26 February 1985, *Øllgaard et al. 58258* (AAU, LOJA, QCA).

6. *Macrocarpaea noctiluca* J.R. Grant & Struwe, *sp. nov.* TYPE: ECUADOR. Loja: Nudo de Sabanilla, 15 km S of Yangana, 04°25'22"S, 079°09'04"W, 2486 m, common, small tree along roadside, flowers yellow, 10 February 2001, *J.R. Grant & Struwe 01-3977* (Holotype: US; isotypes: LOJA, QCA, QCNE, NY). Fig. 9, 10.

A Macrocarpaeae revoluta cui affinis, sed inflorescentiis compactis, foliis late-ovalis oblongis vel ellipticis, costae robustis, apicibus obtusis vel acutis (vs. foliis lanceolatis vel ovatis, costae gracilis, et apicibus acutis) differt.

Dichotomously branched to unbranched tree, overall branching pattern triangular in outline, 1–6 m tall, glabrous throughout; trunk to 4.0 cm diameter wood solid to hollow (pith to 5 mm), growth rings prominent, bark thin 0.005–0.1, outer surface rugose, brown. Stems terete, solid to hollow, 6–12 mm in diameter just below inflorescence. Leaves broadly ovate, oblong to elliptic, sessile to short-petiolate, 8–43 cm; blades 7–35 × 4.5–16.0 cm, entire, slightly revolute, base aequilateral to slightly oblique or rounded, apex acute, papery thin, shiny to opaque, light green to dark green, with slightly impressed veins above, and slightly raised veins below, glabrous above and below; interpetiolar ridge 3–6 mm high; petioles slender with very slight vagination, 10–90 mm. Branches of the inflorescence 17–34 cm, 3–18 flowered per branch. Bracts ovate to lanceolate to oblong to elliptic, 9–135 × 5–75 mm, base aequilateral to attenuate, apex acute to obtuse, sessile to short-petiolate; bract petioles 1–7 mm. Flowers pedicellate, erect to horizontal to oriented in all directions in the inflorescence; pedicels 3–31 mm; bracteoles linear to lanceolate to obovate, 1–13 × 1–8 mm. Calyx narrowly to broadly campanulate, 7–10 × 5–9 mm, glabrous, smooth, green, ecarinate, to sometimes a small keel on the back of calyx lobe, often with pronounced ridges between calyx lobes extending to the base of the calyx; calyx lobes dividing calyx to one third, obtuse, rounded to acute, 2–4 × 2.5–3.0. Corolla funnel-shaped, 30–50 mm, 11–24 mm wide at corolla lobe sinuses, creamy white to yellow to yellowish green, smooth; corolla lobes ovate to elliptic, apex obtuse to rounded, 7–15 × 4–13 mm. Stamens 22–34 mm; filaments 18–28 mm, filiform, terete; anthers linear to linear elliptic, 4–6 × 2.0–2.5 mm, sagittate, versatile. Pistil 25–43 mm; ovary 4–7 × 2.5–3.0 mm; style 18–31 × 1.0–1.5 mm; stigma 2-lobed, lobes 3–5 × 2–3 mm, rounded to spathulate. Capsules dry, bilocular, medially dehiscent, ellipsoidal to ovoid, 29–34 × 10–14 mm, smooth to rugose, dark brown, erect to slightly nodding; style remnant 3–6 mm. Seeds unknown.

Macrocarpaea noctiluca was previously included within a broad interpretation of *M. revoluta* (e.g., Pringle 1995: 95–97) which has since been shown to be restricted to Peru (Grant 2002). It can be distinguished from *M. revoluta* in its more compact inflorescence, and broadly ovate to oblong to elliptic leaves with stout midrib and obtuse to acute apex (vs. lanceolate to ovate leaves with a slender midrib and acute apex).

Macrocarpaea noctiluca is the most common species of the genus in Ecuador, occurring in Azuay, Loja, Morona-Santiago, and Zamora-Chinchipe, and subsequently, the mostly frequently collected. It is mostly commonly observed as a primary colonizer in roadside secondary vegetation. It occurs at different sites with *M. angelliae*, *M. apparata*, *M. arborescens*, *M. bubops*, *M. harlingii*, and *M. jensii*. Often its presence may indicate the occurrence of other more rare species of *Macrocarpaea*.

Vernacular names: zimora del cerro (*Ellemann 66529*), simora del cerro (*Ellemann 75387*), cascarilla (*Ellemann 91665*).

Medicinal uses: medicine for headache: crush the leaves and place or tie it at the forehead

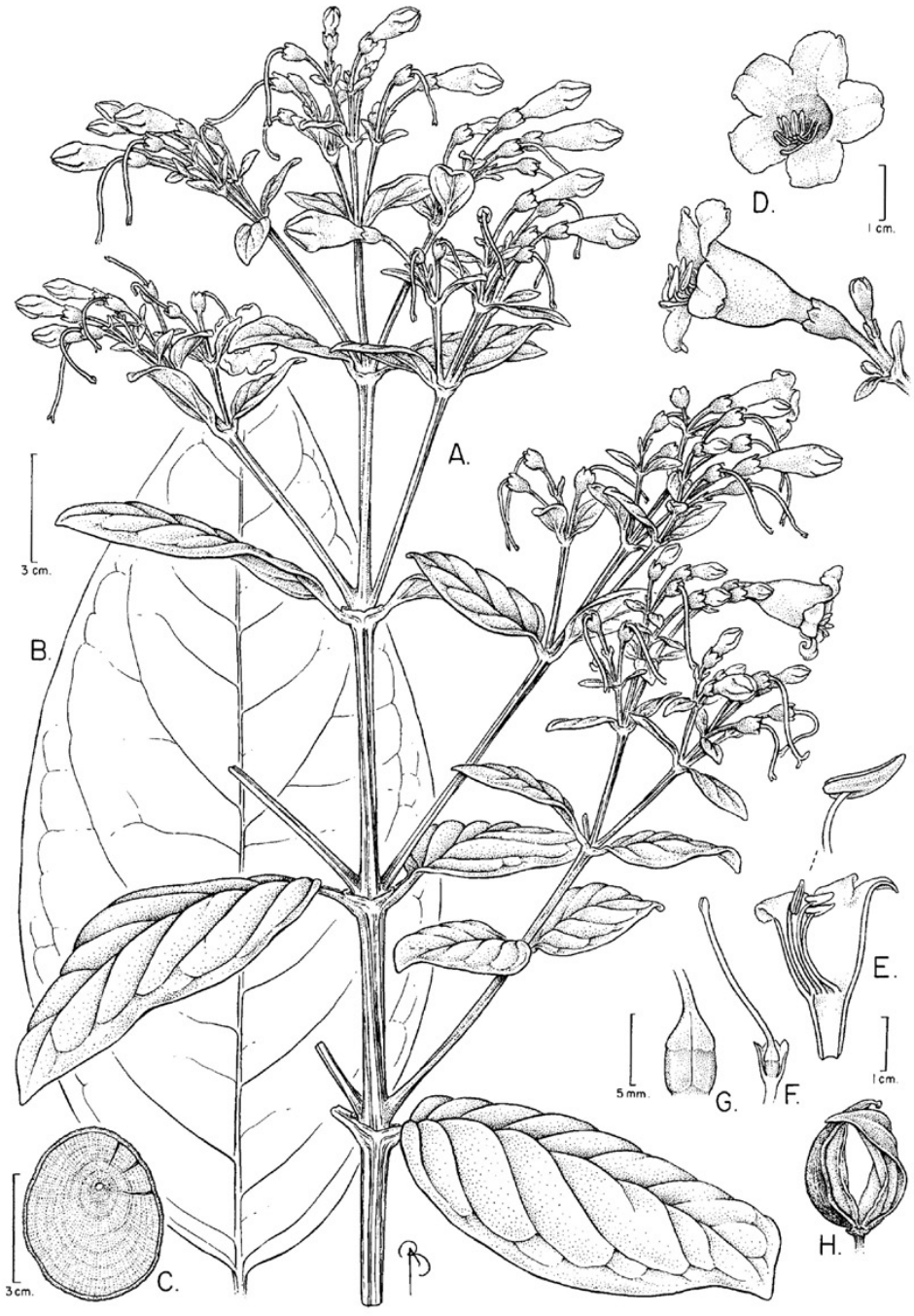

FIGURE 9. *Macrocarpaea noctiluca*. A, habit of flowering stem; B, leaf; C, wood anatomy of cross-section of main trunk; D, corolla viewed from front, and side-view of flower; E, cross-section of corolla, and anther; F, pistil; G, ovary; H, mature dehisced capsule. A from field photo *J.R. Grant & Struwe 01-4021*; B, G from *J.R. Grant & Struwe 01-4074*; C from *J.R. Grant & Struwe 01-3994*; D–F from pickles of *J.R. Grant & Struwe 01-3979*.

FIGURE 10. *Macrocarpaea noctiluca*. Locally common species occurring frequently in roadside secondary vegetation in Loja and Zamora-Chinchipe. Photo by Jason R. Grant, Loja, Ecuador, February 2001.

(*Ellemann 66529*, *Ellemann 75387*; information of vernacular name and use given by Daniel Chalán Cartuche, Saraguro-Indian]); a decoction is used as a medicine for malaria (*Ellemann 91665*; information given by Honorio Gonzales).

Etymology. The name *noctiluca* derives from the Latin "*noctis*", night, and "*lucis*", light, or glowing. The yellowish-white campanulate flowers remind us of small glowing lights. Therefore, we describe the "night-glowing moon-gentian".

Paratypes: ECUADOR. Azuay: Km 74 de Cuenca, carretera Zigzig-Molón-Gualaquiza, 2790 m, 6 August 1986, *Jaramillo et al. 8866* (AAU, GB, QCA); Road Sigsig-Gualaquiza, km 25.6, at the pass on military post road, wet páramo vegetation with large patches of *Neurolepis*, km 3.3 from pass to military post, shrub 3 m, corolla greenish white/cream, stem hollow, 3200-3330 m, 11 January 2000, *Jørgensen et al. 1832* (CHRB, QCNE). Loja: 15 km S of Yangana on the road Loja-Zumba (under construction), slightly disturbed mountain cloud forest, 04°30'S, 79°8'W, 2500 m, shrub 2.5 m, flowers pale yellow, 24 September 1983, *Brandbyge 42299* (AAU, Q); Nudo de Guagrauma, slopes of the Lora de Oro (about 6 km south of Zaraguro), 3000 m, tree 5 m, trunk 6 cm diameter, flowers creamy white, leaves subcoriaceous, dark green and shining above, with dark green veins an shiny below, in the sotobosque, 2 August 1944, *Camp 275* (NY); P.N. Podocarpus, Sendero a Cajanuma, 2550-2700 m, 04°04'S, 79°09'W, bosque de neblina montano, arbusto de 2 m., corola amarillo, fruto capsular color verde 23 February 2000, *Cerón & Curso de Dendrologia 40065* (QAP); Saraguro Canton, along road between Cuenca and Loja, 58.6 km N of Loja (first roundabout after entering the main entrance road), ca. 5 km S of Saraguro), 03°39'S, 79°15'W, 2875 m, 1 m tall, flowers greenish-yellow, 4 March 1992, *Croat 72660* (MO, QCNE); Loja-Zamora, 12 km from Loja, on the finca of Dr. David Espinosa, 03°55'S, 79°09'W, 2600 m, shrub 1 m high, flowers light green, bark light gray, slash green, 1 October 1988, *Ellemann 66529* (AAU, LOJA, QCA); Loja-Zamora, 12 km from Loja, on the finca of Dr. David Espinosa, 03°55'S, 79°09'W, 2400–2600 m, shrub, flowers yellow, 17–18 November 1988, *Ellemann 75387* (AAU, LOJA); 12 km NW of Saraguro on Loma Paredones, 03°36'S, 79°10'W, 2800 m, shrub 2 m high, 9 March 1989, *Ellemann 91665* (AAU, LOJA, QCA); Namandu, S. Loja, 2400–2500 m, flores de color amarillo-verdoso, de bello aspecto, en corimbos terminales y axilares, 18 April 1946, *Espinosa, R. 198* (LOJA, US); Quedrada Honda, en la carretera Yangana-Valladolid, 2470 m, 9 October 1995, *Garmendia & Paredes 639* (QCNE); De la carretera Yangana-Valladolid, antes del refugio de Quebrada Honda, sale un camino de herradura que va a unos potreros, a 10 km de la carretera, cerca del camino, bosque secundario de cresta, arbustivo, 04°28'59"S, 79°9'20"W, 2720 m, 9 October 1995, *Garmendia & Paredes 688* (QCNE); 8 km E of Loja on Loja-Zamora road, 31 October 2002, *J.R. Grant 02-4245* (NEU, NY, US); Nudo de Sabanilla, 20 km S of Yangana, 04°27'12"S, 079°09'11"W, 2485 m, common, small tree along roadside, flowers yellow, 10 February 2001, *J.R. Grant & Struwe 01-3979* (LOJA, QCA, QCNE, NEU, NY, S, US); Nudo de Sabanilla, between 20-28.8 km S of Yangana, 04°27'59"S, 079°08'44"W, 2550 m, roadside secondary vegetation, 1.5 m tall small, single-stemmed tree, calyx dark green, glabrous, 11 February 2001, *J.R. Grant & Struwe 01-3992* (LOJA, QCA, QCNE, NEU, NY, MO, S, US); Nudo de Sabanilla, between 20-28.8 km S of Yangana, 04°27'59"S, 079°08'44"W, 2550 m, roadside secondary vegetation, 1.5 m tall small, single-stemmed tree, calyx dark green, glabrous, 11 February 2001, *J.R. Grant & Struwe 01-3993* (LOJA, NEU, QCNE); Nudo de Sabanilla, between 20-28.8 km S of Yangana, 04°27'59"S, 079°08'44"W, 2550 m, roadside secondary vegetation, 1.5 m tall small, single-stemmed tree, calyx dark green, glabrous, 11 February 2001, *J.R. Grant & Struwe 01-3994* (LOJA, NEU, QCNE, US [2 sheets]); 28.8 km S of Yangana, 04°27'59"S, 079°08'44"W, 2560 m, roadside secondary vegetation, plants 3 m tall, 11 February 2001, *J.R. Grant & Struwe 01-3996* (LOJA, QCNE, US); 28.8 km S of Yangana, 04°27'59"S, 079°08'44"W, 2560 m, roadside secondary vegetation, plants 3 m tall, 11 February 2001, *J.R. Grant & Struwe 01-3997* (LOJA, QCNE, US[2 sheets]); 10 km from Loja on road to Zamora, 03°59'28"S, 079°09'57"W, 2550 m, disturbed forest, flowers the same color as the common local Proteaceae, many seedlings present, 13 February 2001, *J.R. Grant & Struwe 01-4003* (LOJA, NEU, NY, QCA, QCNE); Km 8.9 on road from Yangana to Cerro Toledo, 04°23'08"S, 079°09'03"W, 2450 m, roadside

secondary vegetation, common, single-stemmed, sparsely branched shrub to 3 m, corollas light green, 14 February 2001, *J.R. Grant & Struwe 01-4021* (LOJA, NEU, NY, QCA, QCNE,); From Loja-Saraguro road, then 200 m on road towards Fierro Urco, 03°40'58"S, 079°16'22"W, 2900 m, roadside shrub to 2 m tall with flower buds and old fruits, corollas light greenish-yellow, leaves with two yellow dots at the base of the leaf, growing alongside *Macrocarpaea arborescens* (*Grant & Struwe 01-4075*), 17 February 2001, *J.R. Grant & Struwe 01-4074* (G, LOJA, NEU [3 sheets], NY, QCA, QCNE, US [2 sheets]); Km 8.9 on road from Yangana- Cerro Toledo, 2 November 2002, *J.R. Grant et al. 02-4269* (NEU); Km 10 on road from Yangana- Cerro Toledo, 2 November 2002, *J.R. Grant et al. 02-4275* (MO, NEU, NY, SEL, US); Km 10 on road from Yangana- Cerro Toledo, 2 November 2002, *J.R. Grant et al. 02-4276* (MO, NEU, NY, SEL, US); 30.1 km past Yangana towards Valladolid, 5 November 2002, *J.R. Grant et al. 02-4295* (NEU, NY, US); Road between Loja and Zamora, 2600–2700 m, shrub ca. 2 m high, corolla pale yellow, 20 March 1972, *Harling 11322* (GB); Loma de Loro, 6 km S of Saraguro on road to Loja, 3200 m, treelet 4–5 m tall, corolla greenish-yellow, 11 February 1985, *Harling & Andersson 21910* (GB, QCA); W slope of Nudo de Sabanilla, ca. 10 km above Yangana on road to Valladolid, rainforest with open bog-like areas, 2500 m, shrub 2.0–2.5 m tall, corolla pale greenish-yellow, 3 April 1985, *Harling & Andersson 23594* (GB, QCA); Loja-Zamora rd, 2700–2900 m, shrub 4–5 m, corolla yellow, 8 February 1982, *Harling et al. 20386* (GB); Nudo de Sabanilla, N part, 2400–2600 m, tree ca. 4 m high, corolla pale yellow, 10 February 1982, *Harling et al. 20558* (GB); Carretera Loja-La Palma, bosque húmedo, suelo cascajosa, 2850 m, arbusto de 5 m, cáliz verde, corolla amarilla, 27 December 1988, *Jaramillo 10514* (QCA); Km 10-15 Yangana-Toledo road, subpáramo, 04°24'S, 79°6'W, 3000–3300 m, tree 3 m, fruits green, 1 August 1986 *Jørgensen 61374B* (AAU, QCA, QCNE); Loja-Saraguro, km 58, turnoff towards Fierro Urco, km 1-2, 03°41'49"S, 79°16'22"W, 3000 m, shrub 1.5 m, flowers yellow, fruits brownish-green, 21 April 1994, *Jørgensen et al. 499* (HAM, LOJA, MO, QCA, QCNE); Cerro Uritusinga, Loja-La Palma, km 18-20, montane forest, primary and secondary forest, 04°05'03"S, 79°13'40"W, 2910–3000 m, tree 4 m, calyx green, corolla light yellow, 30 November 1994, *Jørgensen et al. 1050* (HAM, LOJA, MO, QCA, QCNE); Slopes of Cerro Villonaco, ca. 10 km west of Loja, 03°11'80"S, 79°3'10"W, 2850 m, small tree 4 m tall, with yellow flowers, 6 March 1966, *Knight 517* (WIS); 4 km S of Loja, 04°0'40"S, 79°2'15"W, 2600 m, 17 April 1966, *Knight 494* (WIS); Road Loja-Zamora, km 10, vegetación bosque húmedo andino, and secondary roadside scrub mixed with ericaceous scrub forest, 03°58'S, 79°08'W, 2600 m, erect shrub, 2.5 × 5 cm diameter, bark pale brown, leaves dark bottle-green, slightly paler below, calyces dark green, corollas yellowish green, style and stigma green, filaments pale green, anthers creamish white, open areas of bosque margin with crown in open sunlight, 24 October 1996, *Lewis 2709* (LOJA, QCNE); Road Loja-Saraguro, km 26, bosque Cofragia, 03°49'437"S, 79°17'592"W, 2750 m, shrub 3–5 m × 3–6 cm diameter, bark smooth, gray, mottled, stems brittle, wood orange, yellow outer slash, leaves fleshy-rubbery, dark bottle-green above, paler below, calyces green, corollas cream, style pale green, stigma green, filaments creamish green, anthers cream, 17 January 1997, *Lewis et al. 2930* (LOJA, QCNE); Road between Loja and Zamora ca. Km 9, ecotone between cloud forest & páramo, 2500–2750 m, shrub to 3 m tall, calyx green, corolla pale yellowish-green, common, 31 December 1978, *Luteyn et al. 6542* (AAU, CAS, GH, NY, QCA); Cordillera de Sabanilla, ca. 15 km S of Yangana, 2480 m, wet montane forest, sparingly branched shrub 2.2 m tall, calyx green, corolla cream, 30 December 1980, *Madison & Besse 7498* (QCA, SEL); P.N. Podocarpus, about 6.5 km from the park entrance to the refuge Cajanuma, 2500 m, November 1998, *Matt 4* (ER); P.N. Podocarpus, about 6.5 km from the park entrance to the refuge Cajanuma, 2500 m, November 1998, *Matt 5* (ER); P.N. Podocarpus, about 6.5 km from the park entrance to the refuge Cajanuma, 2500 m, November 1998, *Matt 6* (ER); Beside the road from Loja to Zamora, still on the eastern slope of the cordillera, 2 km before the former rubbish dump of Loja, 2550 m, January 1998, *Matt 7* (ER); Beside the road from Loja to Zamora, still on the eastern slope of the cordillera, 2 km before the former rubbish dump of Loja, 2550 m, January 1998, *Matt 8* (ER); Beside the road from Loja to Zamora, still on the eastern slope of the cordillera, 2 km before the former rub-

bish dump of Loja, 2550 m, January 1998, *Matt 9* (ER); Beside the road from Loja to Zamora, still on the eastern slope of the cordillera, 2 km before the former rubbish dump of Loja, 2550 m, January 1998, *Matt 10* (ER); Beside the road from Loja to Zamora, still on the eastern slope of the cordillera, 2 km before the former rubbish dump of Loja, 2550 m, January 1998, *Matt 11* (ER); Amaluza, 5-10 km ENE of the village (Pasaje del Romerillo), montane forest with 4-10 m high trees along river, 2400-2700 m, tree 3 m high, 79°23'W, 04°34'S, 23 September 1976, *Øllgaard & Balslev 9740* (AAU, NY); Carretera Valladolid-Loja, km 4-21, 04°20'S, 79°15'W, 1900–2700 m, arbusto de 2 m, 18 February 1993, *Romoleroux et al. 1536* (QCA, QCNE); western slopes of Cordillera de Condor and northwest slopes of Nudo de Sabanillas, around Tambo Cachiyacu, along Río Cachiyacu, about 2 leagues southeast of Yangana, 2000–3000 m, shrub 1 m tall, corolla creamy-yellow, leaves dull above, paler dull green below, calyx dull green, 19 October 1943, *Steyermark 54812* (F). Morona-Santiago: Path Campamento San Miguel (on road in construction Sigsig-Gualaquiza)- Gualaquiza, shrub ca. 3 m high, corolla yellowish green, 9 April 1968, *Harling et al. 8115* (GB). Zamora-Chinchipe: Quebrada Honda, cuesta carrizal, 2520 m, 26 September 1996, *Garmedia & Igual 1464* (QCNE); Parque Nacional Podocarpus (San Francisco entrance), trail leading west from San Francisco, 03°59'24"S, 079°05'48"W, 2100 m, common shrub in disturbed areas, corolla lemon yellow, 16 February 2001, *J.R. Grant & Struwe 01-4062* (LOJA, QCNE); Above Valladolid on rd to Yangana, montane rain forest, 2700 m, suberect shrub, corolla greenish-white, 2 February 1985, *Harling & Andersson 21462* (GB); Nudo de Sabanilla-Valladolid, horse trail to Caserío Quebrada Honda, montane rainforest, 2400–2600 m, ca. 2.0–2.5 m, corolla sulphur, slightly greenish, 12 February 1993, *Harling & Ståhl 26325* (GB, S); P.N. Podocarpus, road Yangana-Valladolid, km 26, montane forest along ravine, 04°29'S, 79°09'W, 2550 m, shrub 3 m high, flowers cream, 2 December 1988, *Madsen et al. 75753* (AAU, LOJA, QCA, QCNE); P.N. Podocarpus, road Yangana-Valladolid, just S of the pass (Nudo de Sabanilla), quebrada with wet montane forest, and low dense scrub on ridgetop, 04°27'S, 78°08'W, 2640–2770 m, 4 m tall, flowers yellowish green, 16 February 1989, *Øllgaard et al. 90616* (AAU, LOJA, QCA).

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