

A Reassessment of *Monopyle* (Gloxinieae:Gesneriaceae)

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This dissertation titled
A Reassessment of *Monopyle* (Gloxinieae: Gesneriaceae)

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ABSTRACT

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A Reassessment of *Monopyle* (Gloxinieae: Gesneriaceae)

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Monopyle Moritz ex Benth. is a genus of herbs or suffrutescent herbs distributed from Guatemala southward into northern South America. This assemblage of plants is characterized by the presence of anisophyllous leaves, uncinata trichomes, and campanulate flowers. The genus was last revised in 1945 by Conrad Morton. Since that time, few additional taxa have been recognized. It was comprised of 22 described species in 2011, with two infraspecific taxa. Also, there has been limited sampling of this genus for phylogenetic studies to assess the evolution of the genus. There were two primary foci of this research, a morphological characterization of the species within *Monopyle* and molecular analyses of the species within *Monopyle* and other closely related genera.

A detailed morphological analysis was performed to determine the morphological differentiation between taxa. This analysis also confirmed which diagnostic characters identified in previous studies were valid and useful. This analysis was accomplished by comparing traits of over 3,000 herbarium specimens. This analysis revealed that *Monopyle* is the most taxon rich genus in Gloxinieae, with nearly 100 species and a single infraspecific taxon.

To ascertain the evolutionary relatedness of species within the genus and to other closely related genera, phylogenetic analyses of two genetic markers was utilized. The nuclear marker (*GFLO*) and a chloroplast marker (*trnT-trnL*) were used in the study to assess potential hybridization and polyploidy events. The phylogenetic analysis showed

that *Monopyle* is a monophyletic lineage and that it likely hybridized in the past with a *Diastema*-like lineage and an ancestor of *Phinaea*. These analyses indicate the need to recognize four new genera in Gloxinieae. The nuclear phylogeny also suggested that multiple polyploidy or duplication events have occurred recently in the Gloxinieae. Further study in the tribe and genus should focus on ascertaining the number of duplication events and the amount of hybridization to provide a more clear picture of the evolution of these taxa.

DEDICATION

You knew I would not fail.

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plan my trip to Europe, write keys to the taxa, and for editing some of my original work. She was relentless in helping me move forward at the end of my degree, and I could not have accomplished everything I did without her help. I thank Connie Pollard for always being there, whether I just needed a little advice or help setting up reservations for a major trip. I thank Ohio University, the Graduate Student Senate at Ohio University, and the Gesneriad Society for providing funds for this research. I would especially like to recognize The Gesneriad Society for providing most of the funding for my project and travel. Several members of the society were very helpful to my research. Jeanne Katzenstein provided me with information from Hans Wiehler's collection to help solve several problems with specimens that I had obtained. I thank Nancy and Jerry Kast for providing me with lodging while I visited the Tampa Bay Gesneriad Society, and a substantial amount of live material from several genera in Gesneriaceae. Finally, I thank all of the undergraduates, Donnie Day, Meng Li, and Michael Terbush, who worked on many different research projects with me.

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CHAPTER 1: INTRODUCTION

The family Gesneriaceae belongs to the euasterid I clade and is a basal lineage of the order Lamiales, with an origin around 65 million years ago (MYA) (Bremer et al., 2004). The family comprises approximately 3,500 species in 150 genera, with a significant proportion of epiphytes (Heywood, 2006). It is closely allied to Scrophulariaceae, Plantaginaceae, and Tetrachondraceae. Gesneriaceae can be distinguished from these families by a suite of characters including pair-flowered cymes, five-lobed corollas, parietal placentation, and presence of endosperm in most species. Some of these traits are variable within the family and are found in closely related families (Smith, 1996; Weber, 2004). Recent molecular phylogenetic studies show that even with the lack of consistent morphological synapomorphies, Gesneriaceae are well defined (Albach et al., 2001; Bremer et al., 2002).

Gesneriaceae are divided into three subfamilies, Coronantheroideae, Gesnerioideae, and Cyrtandroideae, based on Wiehler's (1983) classification system. Biogeography and morphological characters can be used in combination to circumscribe the subfamilies. Cyrtandroideae are most commonly separated from the other two subfamilies by their superior ovaries and anisocotylous seedlings. The key character separating the Coronantheroideae from the Gesnerioideae is the adnation of the nectary to the ovary. Gesnerioideae are the predominant subfamily in the Neotropics, with approximately 50 genera and 1,500 species. Gesnerioideae are further divided into seven tribes, including Beslerieae, Gesnerieae, Sinningieae, Gloxinieae, Napeantheae, Episcieae, and Sphaerorrhizeae, based on the most current circumscription of the subfamily (Roalson et al., 2005a)

Gloxinieae are characterized by having “scaly” rhizomes, a feature absent in the other tribes in the subfamily. These “scaly” rhizomes are modified underground stems that have reduced leaves allowing the plants to survive periods of drought (Kvist & Skog, 1992). The tribe has also been characterized by chromosome number ($n=13$), although several differences ($n=11$, $n=12$) have been reported within Gloxinieae (Kvist & Skog, 1996; Zimmer et al., 2002). The tribe has been relatively well studied in terms of generic relationships (Roalson et al., 2005b; Roalson et al., 2008; Zimmer et al., 2002). However, the low resolution of the molecular phylogenies and the use of limited morphological characters have made the delimitations of higher groups questionable. The most current phylogeny (Figure 1) is closer to a more comprehensive and definitive delineation of the tribe, but many more taxa need to be included before relationships are well understood.

Diastema Benth. and *Monopyle* Benth. are two closely related genera within Gloxinieae. They are both terrestrial understory herbs distributed from Mexico southward through northern South America. The two genera combined were believed to include approximately 40 species (Weber, 2004). Several species of each genus are only known from type collections or privately cultivated specimens. While these genera are of horticultural value, their habitat, biogeography, and speciation have not been studied. *Monopyle*, as circumscribed by previous authors, included other taxa that were not recognized, while *Diastema* is still undergoing active alpha-taxonomic investigation at the species level. This genus may represent an ancient hybrid lineage between the *Monopyle* clade and the *Kohleria/Pearcea* clade (Roalson et al., 2005a), given its apparent phylogenetic position between these genera. A study of these genera was

undertaken in part to aid in the determination of the circumscription of the rest of Gloxinieae.

Systematics of *Diastema* and *Monopyle*

Diastema was originally described by Bentham (1844) from material brought back on the HMS Sulphur from the Neotropics. The complex morphologies of *Diastema* have confounded most botanists, with species being moved among ten or more genera. *Diastema vexans* H.E. Moore had three illegitimate names before it was finally validly published by Moore (1954). The International Plant Names Index (IPNI) shows a total of forty-six names published in *Diastema* since 1844. The genus has never been properly revised, and the only available keys to species are from local floras. *Monopyle* Benth. has suffered some of the same taxonomic problems as *Diastema* – the genus has very complex morphologies and has been difficult to circumscribe. Twenty-four species of *Monopyle* have been described since 1876, with most of these taxa known only from type collections. Morton (1945) revised the genus for South America, but he examined a limited number of specimens and questioned some of his own determinations. Roalson et al. (2005a) included species that did not necessarily belong to *Monopyle*, but were included for lack of a better generic assignment. Thus, *Monopyle* served as a taxonomic “dumping ground” and desperately required reexamination and perhaps recircumscription as well. My preliminary investigations suggested that it was closely related morphologically to *Diastema*, *Phinaea*, *Nomopyle*, *Gloxinella*, and *Gloxiniopsis*.

Recent molecular phylogenies (Roalson et al., 2005b; Roalson et al., 2008) placed *Monopyle* and *Diastema* as sister to other genera (*Phinaea*, *Gloxiniopsis*, *Nomopyle*, and *Gloxinella*). These studies may not have been accurate because they focused on tribal

level relationships and included relatively few species per genus. The most notable problem within the phylogenies was *Diastema*. *Diastema vexans* H.E. Moore grouped with the *Kohleria/Pearcea* clade, instead of the clade comprising the rest of the species in the genus. *Diastema vexans* may represent a recent hybridization between the *Diastema* and *Kohleria/Pearcea* clade. Hybridization has been shown to occur both interspecifically and intraspecifically, and it has also been proposed to occur intergenerically within Gloxinieae (Kvist & Skog, 1992, 1996). Intergeneric hybrids have been shown to exist in natural populations within Gesnerieae, the most closely related tribe to Gloxinieae (Skog, 1976). Kvist and Skog (1992) speculated in a revision of *Kohleria* that *Diastema* might be a satellite genus derived from *Kohleria*. The ancient or recent hybridizations between genera may explain the overall morphological similarity among genera in the tribe and the lack of resolution in phylogenies.

Biogeography

The biogeographic origins of *Diastema* and *Monopyle* have not been directly studied. However, two competing hypotheses of origin (Central or South America) have been examined at the tribal level (Roalson et al., 2008), but have not been resolved. The rapid radiation events that occurred during the formation of the Caribbean Islands and the complex connection of Central America to South America (Raven & Axelrod, 1974), likely confound phylogenetic analysis. This area experienced a catastrophic event around 65 MYA when an extraterrestrial bolide impacted the Earth in the Yucatan region, causing widespread extinctions (Iturralde-Vinent, 2006). The formation of the Greater Antilles/Aves Ridge, around 35-33 MYA, allowed for dispersal of terrestrial organisms again between North and South America (Roalson et al., 2008). Gesneriads presumably

dispersed from South America to the Caribbean Islands and parts of Mexico. It was not until approximately 9 MYA that the Panamanian isthmus started to form, providing a more permanent dispersal corridor between South and North America (Iturralde-Vinent, 2006). This corridor formed around the time that members of *Diastema* and *Monopyle* would have diverged from their closest ancestor, ~ 7 MYA (Roalson et al., 2008). *Diastema* and *Monopyle* disperse their seeds from splash cups. The seeds may be carried by small animals or birds, so dispersal to Central America would have taken a long time with no direct connection between the continents (Skog, 1976).

Objectives

1. Morphological study to assess the boundaries between *Monopyle* and other taxa within Gloxinieae.
2. Molecular study of the *Monopyle* clade.
3. Taxonomic synopsis of *Monopyle*.

Morphological study

Morphological studies were used to test the previous circumscription of species. These studies were conducted on nearly 3,000 specimens from herbaria worldwide including: Field Museum (F), Geneva (G), Kew (K), Leiden (L), Missouri Botanic Garden (MO), New York Botanic Garden (NY), Marie Selby Botanic Gardens (SEL), National Museum of Natural History (US), University of California (UC). Several herbaria were visited in the United States (MO, SEL, and US) and Europe (K and P) as well to ascertain diversity in Gloxinieae. *Monopyle* has been distinguished by its uncinat trichomes, campanulate flowers, and anisophyllous leaves (Roalson et al., 2005a; Skog, 1979). *Monopyle* was compared to *Diastema* as well as the other members

of Gloxinieae to identify additional characters to distinguish each genus. Careful morphological study, along with molecular phylogenies, identified possible hybridization events and allowed species and generic circumscriptions of material with intermediate characters. Characters examined for the morphological analysis including leaf shape, leaf arrangement, leaf margins, leaf size, calyx structure, flower number, androecium, gynoecium, and pubescence. Pubescence was examined for stems, leaves, inflorescence bracts, style, ovary, limb, tube, and stamens. Other data, including chromosome counts, were used to evaluate hypotheses of relationships among the material available. Mapping fruit characters onto the phylogenetic trees did not provide definite patterns of fruit development in Gloxinieae. Clark et al. (2012) noted the need for a detailed examination to select characters that were homologous, as morphological convergences within Gesneriaceae are common. This was especially true within *Monopyle*, which has very little variation in floral color (corolla white and lobes purple) and shape (campanulate). Detailed analyses of the characters listed above yielded insights into other floral variation, including size and subtle shape differences in corolla gibbosity.

Molecular studies of *Monopyle*

Previous analyses of Gloxinieae showed that the chloroplast *trn L-F* intergenic spacer and the nuclear internal transcribed spacer (*ITS*) provided poorly resolved phylogenies (Roalson et al., 2005b; Zimmer et al., 2002). Other studies that included *Diastema*, a closely related genus, showed that cloning was necessary for *ITS* sequences (Smith et al., 2004). The low resolution and the prospect of cloning prompted me to select other markers that were of greater phylogenetic utility. These markers included the *trnT(UGU)-trnL(UAA)* intergenic spacer to delimit the genera, and the low copy nuclear

marker *LEAFY/FLORICAULA* for species level comparisons. The *LEAFY* region had been used in Gesneriaceae to test the altered expression of Gesneriaceae *FLORICAULA* (*GFLO*) in *Titanotrichum oldhamii* (Hemsl.) Soler. (Wang et al., 2004). Wang et al. (2004) also stated that the sequences were easy to align at the genus level and might provide a potential region easier to amplify for phylogenetic studies. The primer combinations and protocols from Wang et al. (2004) were used as a model for my own experiments. Further adjustments were needed to generate sequences, including the development of an extraction protocol for herbarium material and fresh tissue. The *GFLO* nuclear marker was used in conjunction with the chloroplast marker to assess possible hybridization events between taxa. Multiple representatives of each species were sequenced to check for polyploidy or hybridization events. Both molecular and morphological characters were assessed for intermediate taxa to identify possible hybrids in the samples. Many additional sequences and more variable genetic markers will be needed to reconstruct a relative complete phylogeny of *Monopyle*.

Dissemination

Project details and objectives were presented at the World Gesneriad Research Conference in October 2010. Preliminary results were presented at the Botanical Society of America meetings in St Louis, MO (2011), Columbus, OH (2012), and New Orleans, LA (2013). Preliminary results were also presented in several invited talks to The Gesneriad Society. The molecular phylogenies will be submitted to *Systematic Botany* or another appropriate journal. All DNA sequences will be submitted to GenBank before the final manuscript is submitted. New species descriptions will be submitted to either *Taxon* or *Systematic Botany*. The monograph of *Monopyle* will be submitted to

Systematic Botany Monographs after the species descriptions are completed.

Molecular protocols, including the new extraction method, will be submitted to

Applications in Plant Sciences as a protocol note.

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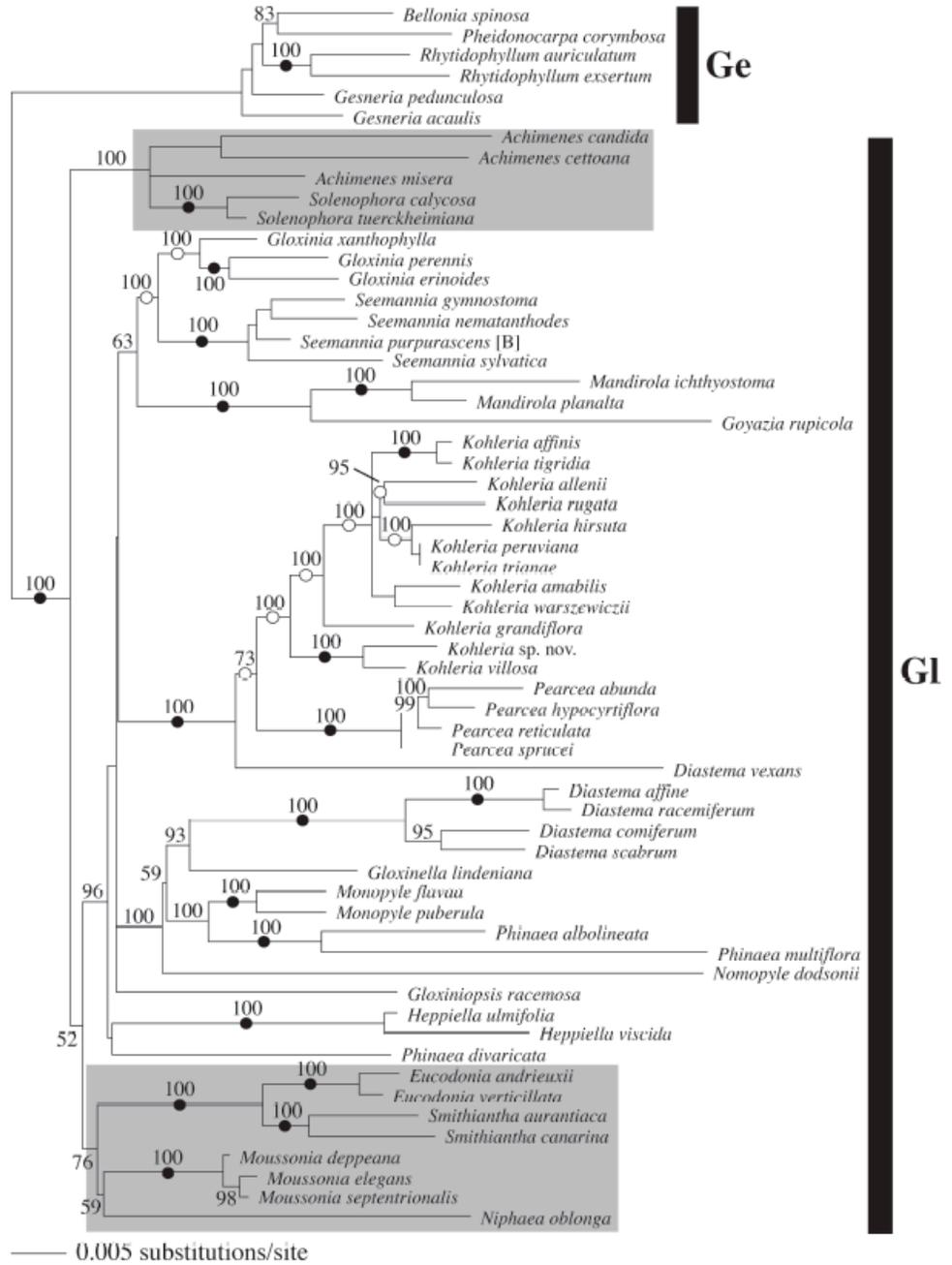


Figure 1. Maximum likelihood phylogeny of Gloxinieae relationships based combined ITS/trnL-F datasets (Roalson et al., 2008).

CHAPTER 2: REXAMINATION OF MORPHOLOGICAL CHARACTERS AND CRITICAL TYPIFICATIONS IN *MONOPYLE*

Introduction

The mostly Neotropical subfamily Gesnerioideae is divided into nine different tribes based on morphological and molecular data (Clark et al., 2006; Roalson et al., 2005a; Roalson et al., 2005b; Smith, 1996, 2000; Smith & Atkinson, 1998; Smith et al., 1997; Smith et al., 2004). The tribe Gloxinieae is sister to Gesnerieae and differs in its “scaly” rhizomes and base chromosome number ($n=11, 12, \text{ or } 13$) (Roalson et al., 2005b; Wiehler, 1983). *Monopyle* Moritz ex Benth. is the largest genus in the tribe, with approximately 100 species. The genus is distributed from Guatemala to northern South America and is found along streams or rock faces in humid forest. Historically, a suite of characters, including anisophyllous leaves, uncinata trichomes, wholly inferior ovary and campanulate flowers, were used to distinguish *Monopyle* from other closely related genera (e.g., *Diastema* Benth.). Hybridizations, both ancient and modern, have shaped the genus and made morphological distinction of some taxa difficult.

In this study, *Monopyle* is distinguished from other genera by its variably thickened internodes (Figure 2), nodal ridge, anisophyllous leaves (Figure 2), and uncinata trichomes (Figure 3), although several species lack the uncinata trichomes (see below). Many other characters including fruit shape, inflorescence structure, and calyx structure, overlap with other genera. The genera most commonly confused with *Monopyle* include: *Gloxinia* L’Hér., *Gloxiniopsis* E.H. Roalson & Boggan, *Gloxinella* (H.E. Moore) E.H. Roalson & Boggan and *Nomopyle* E.H. Roalson & Boggan. They all differ in several key characters including inflorescence structure, presence of a floral

nectary, fruit type, and trichome structure. *Gloxinia* has a terminal bracteolate racemose cyme with one flower per node, an annular or absent nectary disk, a dry capsule, pubescent filaments, and isophyllous leaves. *Gloxiniopsis* differs from *Gloxinia* in its glabrous filaments and many pairs of secondary veins per leaf. *Nomopyle* differs in having strictly axillary inflorescences, pustulate-based trichomes on the corolla, and stomata in indistinct groups. *Gloxinella* is very similar to *Nomopyle* except for its ovoid, rather than cylindrical, fruits and the adaxial leaf color patterning. *Gloxinella* also lacks the pustulate base trichomes on the corolla found in *Nomopyle*. The new genus *Lomocheilus* (see Chapter 3) is quite similar to *Gloxiniopsis* and has been identified as *Gloxiniopsis* in previous work (Roalson et al., 2005b). *Lomocheilus* differs in inflorescence structure, with only axillary inflorescences, lacks a nectary, and has dense glandular trichomes on the margins of the corolla.

A morphological study of characters within *Monopyle* was undertaken to determine which characters were informative for delineating species and supporting recognition of the genus as distinct from related genera in the tribe. These characters are defined below and were used to confirm material for lectotypification of the genus *Monopyle* and several species.

Materials and Methods

Specimens of *Monopyle*, along with several other genera, were requested from F, G, K, L, MO, P, SEL, US, and UC (acronyms follow Index Herbariorum). Additional specimens, photographs, and scans were provided by other researchers and herbaria from around the world. All of these sources provided the material used to confirm morphology and color information and identify previously unknown structures. Flowers were

rehydrated overnight in a mixture of water, soap, and glycerin. The glycerin made the flowers more pliable and easier to flatten on herbarium paper (Christian Feuillet, pers. comm.). Flower dissections of all species were performed multiple times, if material was available, to confirm floral characters. Leaves from several *Monopyle* specimens and closely related genera were cleared with a 10% sodium hypochlorite solution. The cleared leaves were then stained with Safranin-O or Cotton Blue. The stained leaves were mounted on microscope slides and examined under polarized light to visualize crystal patterns. The leaves were also examined under white light to visualize stomatal and venation patterns.

Results

Rhizome. The Gloxinieae are distinguished from other tribes by the presence of “scaly” rhizomes. These highly reduced stems and leaves provide a way for the plants to survive adverse environmental conditions and may also help with dispersal. Other genera (i.e., *Kohleria*, *Achimenes*) scarcely have an internode between the scaly leaves, and the rhizomes that form are compact. *Monopyle* has very loose rhizomes with long internodes and larger fleshy leaves. They appear to form during times of stress and are not always present on the plants, as they are in many other genera in the tribe. The rhizomes in *Monopyle* appear to be mostly dark red to maroon with few trichomes, which is not the case in other genera. *Kohleria*, for example, tends to have green to red rhizomes with many trichomes.

Stem. The stem does not vary much within the tribe or *Monopyle*. The stems in *Monopyle* are fleshy and variable in width, with the largest stems less than one centimeter in diameter. Many of the stems are dorsi-ventral (Figure 2), meaning that all of the

leaves are in a single plane, similar to *Columnea* L.. The genus also tends to have variably swollen internodes (Figure 2). They can be swollen distally, medially, or proximally. There is also a structure at each node that appears stipule-like, but it should be considered a nodal ridge. This ridge can have trichomes and appears as a darkened line across the stem of pressed specimens.

Leaf Symmetry. The leaves are anisophyllous (Figure 2) in all the species of *Monopyle*. This can vary from nearly isophyllous (i.e., *Monopyle isophylla* (Benth.) Keene) to strongly anisophyllous (i.e., *Monopyle subsessilis* Benth.) with scarcely an opposing leaf. The amount of anisophylly is diagnostic and makes the identification of some species quite straightforward. Few other taxa in the Gloxinieae tribe have this feature, but it is present in *Kohleria* Regel, *Pearcea* Regel, and *Regeliantha* ined.

Leaf Lamina. The leaves have three different types of surfaces: smooth, mammillate or bullate. The mammillate leaves vary from a few scattered nipple-like projections to dense projections over the entire surface of the leaf. This character can be quite variable in a species and may be under some type of environmental control. Bullate to rugose leaves are common in the genus with nearly all the other taxa being somewhat rugose. There are few species with flat adaxial surfaces of the leaves, but they might actually have impressed veins before being pressed. Fresh material would be required to confirm whether any species truly have flat leaves. Most of the species have bicolorous leaves and it is possible to find two different leaf color forms in a species. There are some species in which this is far more apparent (i.e., *Monopyle axillaris* Keene) and useful. The lamina is almost always asymmetrical. This asymmetry makes many leaves appear falcate. The lamina base is also variably oblique and the degree or amount of obliqueness

can be used to distinguish species. The apex of the leaf is almost always attenuate to acuminate and is of little taxonomic importance.

Indument. The indument varies greatly and is very useful in the circumscription of species. The indument can be pilose, villous, strigose, or puberulent (see Table 1 and Figures 3 and 4). I have used the following definitions (adapted from Beentje, 2010) to separate the different types of indument. Puberulent is pubescent with minute soft trichomes. Pilose is pubescent with straight soft trichomes. Villous is pubescent with long, soft, weak trichomes that are not matted together on the surface. Strigose is straight, appressed trichomes (i.e., *Monopyle panamensis* C.V. Morton). These indument types tend to be different on several surfaces (i.e., adaxial or abaxial leaf surface). The trichomes can be minute, intermediate, or long (see Table 1 and Figures 3 and 4). They can also be septate, uncinata, glandular, or eglandular. These different types are typically mixed across different surfaces of the plants. The septate trichomes tend to be very long and give the surfaces a very shiny appearance (i.e., *Monopyle nitida*). Uncinate trichomes (fish-hook shaped) (Figures 3 and 4) are a synapomorphy for the genus and can be found on every species, except for *Monopyle panamensis* and *Monopyle longicarpa* J.L. Clark & Keene. These species are both from Panama and are closely related. Glandular trichomes are present in some species, but are difficult to find on many specimens, because the glandular tips are sheared off during the collection process. Trichome density varies greatly, from glabrous to densely pubescent, depending on the species. The trichomes can also vary in color from brown to golden or dark red (i.e., *Monopyle erythrochaete* Keene). Finally, in a few different species there are minute, glandular trichomes on the margins of the corolla lobes.

Inflorescence. The inflorescences within *Monopyle* differ significantly, from axillary to highly branched paniculate cymes (Figure 2). The inflorescence position of most species is terminal, with few species having mixed terminal/axillary or strictly axillary inflorescences. Axillary inflorescences have evolved several times within *Monopyle* and do not represent a single lineage (see Chapter 3). Most of the intermediates (with both terminal and axillary inflorescences) are found in Colombia; these taxa are very difficult to identify because some sheets will have only one inflorescence type or the other. Many specimens of each species need to be examined to determine which inflorescence types are present. The inflorescences can also be erect or lax, although erect is more common. The degree or orders of branching appears to be fixed within each species. Inflorescences that branch once or twice have a racemose or fasciculate appearance. The fasciculate inflorescences have very short secondary or tertiary peduncles, so the inflorescences look constricted. The racemose inflorescences have slightly long secondary peduncles and the cymules are held in a more open arrangement. The paniculate inflorescences have long peduncles and branch five times or more, forming large, open inflorescences (i.e., *Monopyle paniculata* Benth.). Peduncle length is useful in many species. Species with very long peduncles (as above) have more open inflorescences. The axillary inflorescences may only have a highly reduced peduncle, with nearly sessile flowers. The number of nodes per rachis and cymules per node appear to have some taxonomic significance, but a full evaluation of these characters requires many specimens in good condition. The bracts at each node are typically ovate or lanceolate and not very large. A few species have large leaf-like bracts, making them relatively easy to identify (i.e., *Monopyle archidonaensis* Keene).

There are also three species that have bracts with serrate to fimbriate margins (i.e., *Monopyle connata* Keene).

Calyx. Calyx lobes are fused at the base from approximately half to three quarters of the length of the lobes. The fused calyx base can vary from smooth to deeply ridged or verrucose. The base is also occasionally bright red. The calyx may be radially symmetrical, or it may be zygomorphic, with three dorsal lobes and two ventral lobes. The lobes can be appressed or reflexed at the base. They can also be reflexed at just apex. The shape and length of the lobes also greatly varies from nearly orbicular to linear. *Monopyle maxonii* C.V. Morton, for example, has short, orbicular calyx lobes that are reflexed at the apex. The lobes also vary greatly in color from a light green to nearly maroon. *Monopyle campanulata* Keene has lobes that are fused, forming a campanulate calyx.

Corolla. The corollas of *Monopyle* range from pure white to yellow, purple, or pink. Most species have a white corolla tube with pink, purple, or yellow markings on the lobes and/or in the throat. The markings may take the form of discrete spots (maculae), or the entire lobe might be suffused with color. The interior base of the corolla tube in many species is bright yellow, highlighting the osmophore. There are reports of flowers having a scent to attract pollinators, and the scent may be produced by the osmophore. The base of the throat can also have small purple markings or large purple blotches. Color is often imbued by trichomes on the outside of the corolla. The position of the corolla relative to the calyx, is either in a straight line with the calyx lobes, or deflexed at an angle to the calyx lobes. The flowers can also bend at the pedicel and nod towards the ground, though most species have lateral flowers. The stigma is stomatomorphic (mouth-

shaped) and slightly lobed when receptive. It is held directly below glandular trichomes on the dorsal surface of the interior corolla tube, along with the anthers. The anthers are held on filaments that retract before the stigma is receptive, providing a spatial barrier to self-fertilization. The nectary tissue in *Monopyle* is greatly reduced compared to other closely related genera. It is usually present in a rudimentary ring between the base of the corolla and the apex of the ovary. The shape of the corolla varies from infundibuliform to nearly ventricose. The ventral portion of the corolla is almost always gibbous. The gibbosity makes the corollas of a few species seem almost ventricose. *Monopyle grandiflora* Wiehler has a sigmoid corolla that is abruptly deflexed at the base before bending at a 90° angle halfway down the tube.

Fruit. The fruit in *Monopyle* vary from small globose to long cylindrical fleshy capsules (Figure 2). They dehisce along a single suture on the dorsal surface and the suture begins to split medially. The fruits can vary from a few millimeters (i.e., *Monopyle leucantha* Moritz ex Benth.) to nearly three centimeters long (i.e., *Monopyle longicarpa*). There are few reports of fruit color, but pictures of mature fruits from Panama show a variation from light green to orange to a deep red. This character may be of great significance once more data can be collected. The calyx is often accrescent in fruit and care has to be taken to get accurate measurements.

Discussion

Past treatments of *Monopyle* have characterized the genus based on the degree of anisophylly, the presence of uncinata trichomes, inferior ovaries and campanulate flowers (Roalson et al., 2005b; Wiehler, 1983). Detailed morphological analyses show that these characters, aside from ovary position, are quite useful in the delimitation of the genus

Monopyle. The genus tends to have subinferior ovaries (half to three-quarters inferior).

Monopyle reflexa (Rusby) E.H. Roalson & Boggan has been a problematic species because it lacks anisophyllous leaves. This species, however, appears to match the new genus *Lomocheilus* ined. in both morphology and *GFLO* copy number (see Chapter 3). The exclusion of this species from the genus makes *Monopyle* a coherent group of species, with the above-mentioned characters.

Flower color reports vary dramatically between specimen sheets. This variation appears to be due to the presence of colored trichomes on the corolla. These trichomes, typically red, give the corolla exterior a pink appearance. Most flowers that are reportedly pink are probably white with red trichomes. Pink petals are present in the genus, but are not as prevalent as the specimen labels might indicate. Photographs of fresh flowers are a much more reliable source of flower coloration than specimen label data.

Species Diversity

Diversity in *Monopyle* has been grossly underestimated, with nearly seventy-five percent of the species previously unrecognized. Almost all specimens obtained from herbaria had been determined as belonging to one of four different species. *Monopyle macrocarpa* Benth. is the most common determination on specimens from both Central and South America. This species, however, is endemic to Peru and is distinguished by long cylindrical fruits, a lax inflorescence, and the presence of dense uncinata trichomes on the abaxial leaf surface. This confusion is due to the improper synonymization of *M. macrophylla* Benth. and *M. pilosula* C.V. Morton with *M. macrocarpa* in Skog (1979). Two varieties of *M. macrocarpa* have also been described. One of these, *M. macrocarpa*

var. *costaricana* Hemsl., represents the same species as *M. puberula*, and the other, *M. macrocarpa* var. *isophylla* Benth., represents a separate species. *Monopyle isophylla* (Benth.) Keene can be distinguished from *M. macrocarpa* by the position of the inflorescence, fruit size, and nearly isophyllous leaves. Many specimens from Central America have been identified as *M. maxonii* or *M. puberula*. It appears that most of these determinations are based on flower color and calyx structure. *Monopyle maxonii* is distinguished by the presence of long, septate trichomes on the adaxial surface of long petioles; and ovate calyx lobes that reflex at the apex. *Monopyle puberula* has lanceolate to slightly deltoid calyx lobes not reflexed at the apex; and glabrescent, sessile petioles. These species are widely distributed and hybridize with other species where their ranges overlap. Species recognition in Central America, with a few easily distinguishable species, is not as problematic as in South America.

The South American species *M. sodiroana* Fritsch was particularly difficult to resolve. Described by Fritsch in 1914 as having terminal inflorescences, it was illustrated by Hans Wiehler (1977) as having axillary inflorescences with colored corollas. This illustration, in combination with his ID book (Wiehler, 2002), was widely used by botanists to identify specimens of *Monopyle* from South America, resulting in many erroneous determinations. All *Monopyle* specimens from South America with axillary inflorescences were determined as *M. sodiroana*. This species, however, has terminal inflorescences that revert to vegetative growth at the apex, making the inflorescence appear axillary. The flowers were described as white in the protologue, but the type material shows flowers that are spotted on the ventral lobe, in contrast to the colored (presumably light purple) corollas in Wiehler's book. Almost all species of *Monopyle*

with axillary inflorescences have flowers that are heavily spotted purple to maroon on all five corolla lobes. Material with axillary inflorescences represents eleven species, distributed from Colombia through Peru.

Nomenclature and Typification

The nomenclatural history of *Monopyle* is relatively uncomplicated because species diversity in the genus has been severely underestimated by previous authors. Bentham published *Monopyle* as a genus in *Genera Plantarum* in 1876, without naming any species, and then published six species of *Monopyle* in Hooker's *Icones Plantarum* in the same year. Morton (1972) stated that the species were published in April while the genus was published in May, which would constitute invalid publication of the species according to Art. 38.11 of the ICN (McNeill et al., 2012). However, Stafleau and Cowan (1976-1988) lists both publications as May 1876, so they can be considered simultaneous publications and the species are therefore valid. In 1945, Morton selected one of Bentham's original species, *M. leucantha*, as the type of *Monopyle* and treated *M. leucantha* as a synonym of *M. subdimidiata* (Klotzsch & Hanst.) Mansf. However, type material of *M. leucantha* does not represent the same species as material of *M. subdimidiata*. Bentham's protologue listed five specimens, among them *Moritz 868*, which Morton and Denham (1972) designated as the lectotype of *M. leucantha*. The basionym of *M. subdimidiata* is *Koellikeria subdimidiata* Klotzsch & Hanst., and although no specimen numbers were cited at the time of publication, the authors referred to a Moritz collection from Valencia, Venezuela. The description also mentioned features (small flowers, glandular nectary ring) that are not present in *Monopyle*. Mansfield (1935) examined material of *Koellikeria subdimidiata* at Berlin and noted that

another specimen *Moritz 241* from Caracas represented the same material as the “type” of *K. subdimidiata* and had been so identified by Klotzsch. Although the Valencia specimen at Berlin was destroyed, duplicates of *Moritz 241* in the Hamburg herbarium have “*Treverania subdimidata* Kl.” written on the labels in Klotzsch’s handwriting. These specimens are *Gloxinia erinoides* (DC.) E.H. Roalson & Boggan and do not represent material of *Monopyle*. Mansfield’s note on the identification of the *Moritz 241* specimens, combined with Klotzsch & Hanstein’s original description, demonstrate that *M. subdimidiata* should be excluded as a species of *Monopyle* and synonym of *M. leucantha*. *Moritz 241* at HBG will be designated as the lectotype of *K. subdimidiata*, and *Moritz 868* at BM will be designated as the lectotype of *M. leucantha*, which is the type of *Monopyle*.

Monopyle sodiroana Fritsch was described in 1913, from material collected by Sodiro, but no specimen was designated as the type. Sodiro’s collection (*119/1*) was noted in Fritsch’s original description of the species. There are duplicates of this collection at Biblioteca Ecuatoriana Aurelio Espinosa Pólit (QPLS) and Muséum National d’Histoire Naturelle (P). The duplicate at P will be designated as the lectotype for this species because it shows the inflorescence change to vegetative growth and will be more accessible to future researchers.

Scoliotheca triana Baill. is a synonym of *Monopyle macrophylla*, as noted previously by Skog (1979). There are at least two sheets of *Triana 2540* at P. One sheet (P00603486) will be designated as the lectotype of *Scoliotheca triana*.

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Table 1.

The different types of trichomes and how they are recognized in *Monopyle*. See text for specific definitions of trichomes types.

Indument	Trichome size	Trichome Length	Other features
Puberulent	minute	Minute hairs up to 0.5 mm Up to 2 septa	glandular, pustular bases, uncinata, septate
Pilose, villous, strigose	intermediate	0.5–1.0 mm usually 2–5 septa	
	long	1.0 mm and greater 5 or more septa	



Figure 2. *Monopyle ecuadorensis* A. Habit showing anisophyllous leaves and paniculate cyme. *Monopyle iserniana* B. Habit showing strong anisophylly, terminal reduced cymose inflorescence, and variably thickened internodes. *Monopyle uniflora* C. Habit showing strong anisophylly and reduced axillary inflorescence.

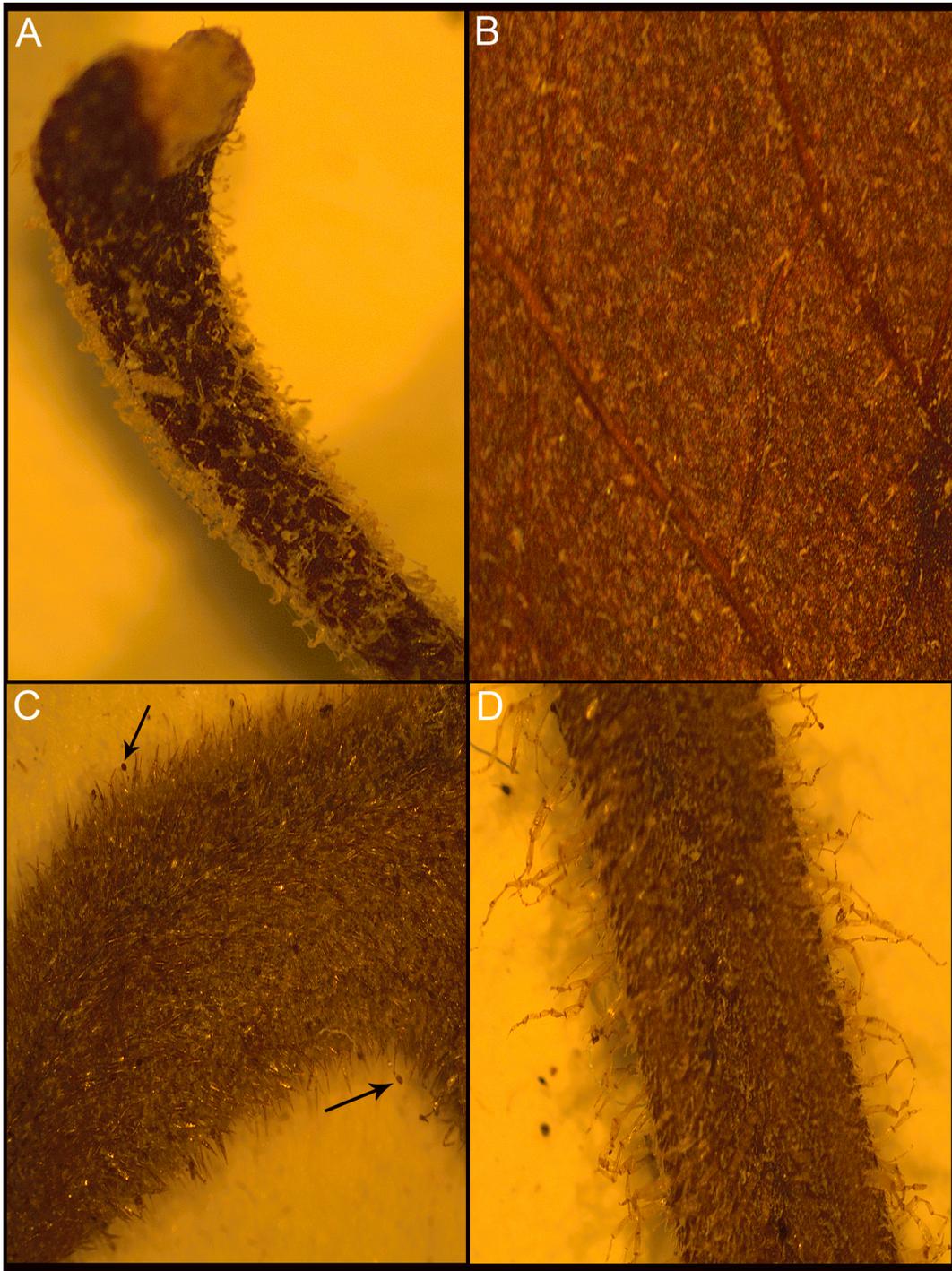


Figure 3. *Monopyle ecuadorensis* A. style puberulent with uncinata trichomes. *Monopyle puberula* B. Leaf abaxial surface puberulent with uncinata trichomes. *Monopyle panamensis* C. Calyx base showing intermixed strigose and glandular trichomes (arrows). *Monopyle multiflora* D. Stem showing intermixed villous septate and minute uncinata trichomes.

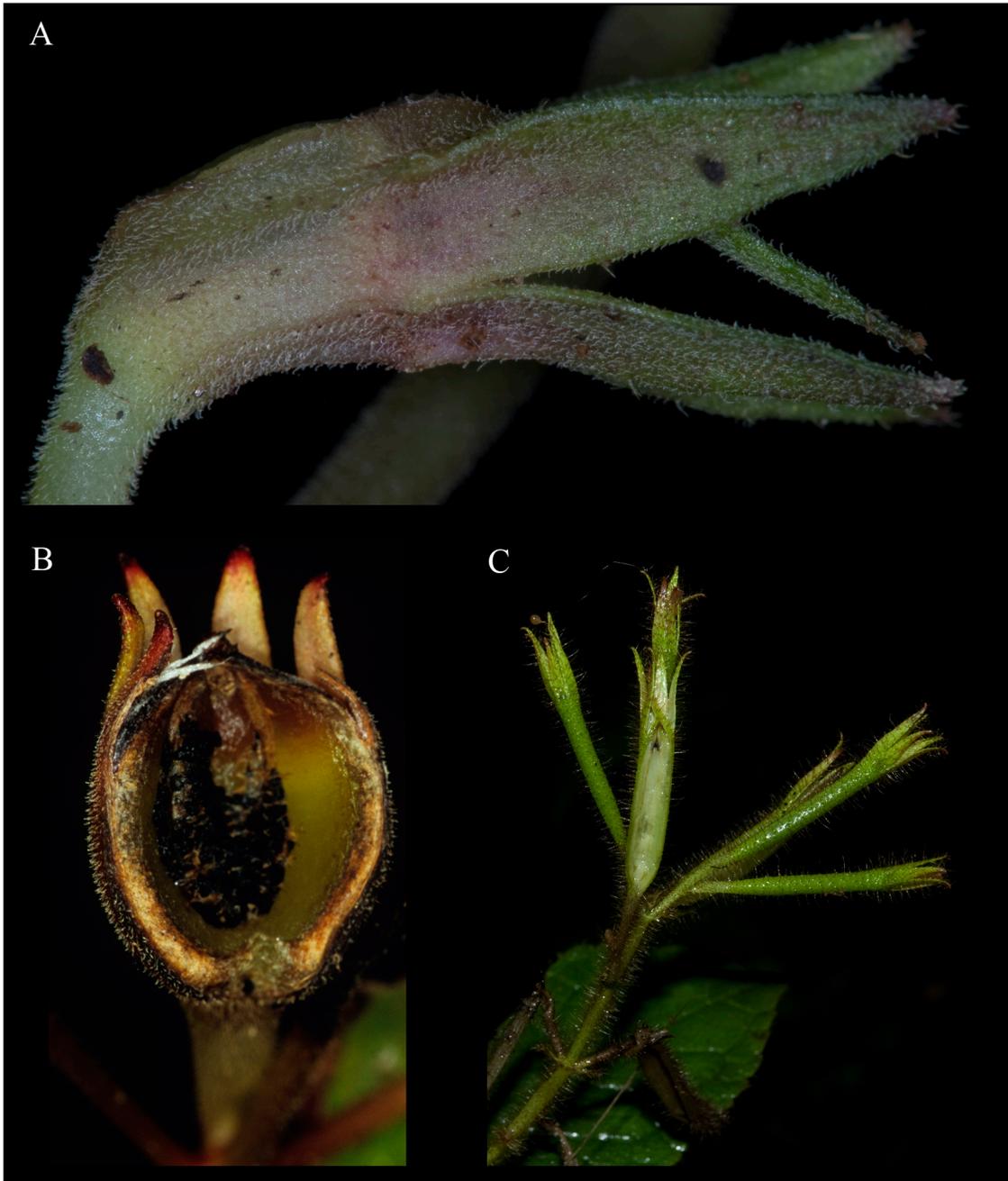


Figure 4. *Monopyle subsessilis* A. Fruit with puberulent uncinata trichomes. *Monopyle paniculata* B. Fruit showing inferior ovary and ovoid fruit shape. *Monopyle longicarpa* C. inferior ovary and cylindrical fruit shape.

CHAPTER 3: MOLECULAR STUDY

Introduction

Gesneriaceae are a moderately sized family comprising approximately 3,500 known species (Weber, 2004). The family is divided into two distinct subfamilies based on the development of the cotyledons. Cyrtandroideae are anisocotylous and for the most part are restricted to the Paleotropics, whereas Gesnerioideae are isocotylous and found only in the New World, except for the Coronanthereae (Burtt, 1963). In the Gesnerioideae, there are many instances of convergent evolution of floral morphology. For example, the hypocyrtoid corolla is present in species of three different tribes (Wiehler, 1983). The high degree of convergence in morphology has led to many inaccurate taxonomic hypotheses over time. However, with the advent of molecular systematics a taxonomy based on phylogenetic relatedness can be generated regardless of convergence in various morphological characters.

Within Gesnerioideae, the tribe Gloxinieae is unique in having “scaly” rhizomes. This tribe has been recircumscribed several times based on various vegetative and floral characters, and most recently based on phylogenies that combined morphological and molecular data (Roalson et al, 2005a; Roalson et al., 2005b). Of the genera within the Gloxinieae, *Monopyle* Moritz ex Benth. is the most diverse with 22 species having been described. However, it has been inadequately sampled in molecular studies, with only *M. flava* L.E. Skog, *M. macrocarpa* Benth., *M. maxonii* C.V. Morton, and *M. puberula* C.V. Morton included (Roalson et al., 2005b; Smith et al., 2004; Zimmer et al., 2002). Aside from *M. flava*, the above names have been applied almost haphazardly to a diverse assortment of specimens for the last 60 years or more. The majority of these specimens

have been determined as *M. macrocarpa*, which upon further examination appears to be an endemic species from Northern Peru. Convergent characters (e.g. white corolla with purple lobes and uncinata trichomes) have misled many taxonomists into merging this well-defined species into a large and heterogeneous species complex, with many other divergent taxa. Species with broader geographic ranges may also hybridize with narrow endemics in areas where species co-occur. Such hybridization, whether ancient or more recent, may also have greatly increased the confusion of interpreting taxa within the genus.

Hybridization occurs frequently in plants and is an important process in the evolution of many angiosperm groups (Soltis & Soltis, 2009). Hybridization can occur between species or even between genera, if reproductive barriers are not substantial. Although hybrids may be sterile, plants have the ability to overcome this obstacle through polyploidization (Kim et al., 2008). These processes pose problems to phylogenetic tree construction because the gene trees of the chloroplast and nuclear markers are often discordant (Pillon et al., 2013). Recent studies (de Villiers et al., 2013; Kim et al., 2008) showed that this discordance is useful because the evolutionary patterns between the maternally inherited chloroplast markers and the biparentally inherited nuclear markers can be compared. This comparison provides a method to identify potential hybridization events by examining the discordant placement of taxa between the gene trees. Additionally, more than one copy of a putatively single copy nuclear marker may indicate potential polyploidization.

Therefore, the purpose of this study is two fold. First, to more accurately delimit *Monopyle* and related genera in the Gloxinieae using molecular data and discrete

morphological characters. Second, the evolutionary relationships among species and possible hybridization, recombination, or gene duplication events will be investigated using a putative single copy nuclear gene as well as a chloroplast gene.

Methods

Taxon Sampling. Twenty-seven specimens representing twenty-two species of *Monopyle* were selected. Additional genera closely related to *Monopyle* were sampled to elucidate generic relationships in the Gloxinieae tribe. The ingroup consisted of sixty-five accessions, with twenty-two species of *Monopyle* and thirty-three species representing *Achimenes* Pers., *Amalophyllon* Brandegee, *Chautemsia* A.O. Araujo & V.C. Souza, *Diastema* Benth., *Eucodonia* Hanst., *Gloxinia* L'Hér, *Gloxiniopsis* E.H. Roalson & Boggan, *Gloxinella* (H.E. Moore) E.H. Roalson & Boggan, *Kohleria* Regel, *Moussonia* Regel, *Niphaea* Lindl., *Nomopyle* E.H. Roalson & Boggan, *Pearcea* Regel, *Phinaea* Benth., *Seemannia* Regel, and *Smithiantha* Kuntze. *Gesneria acaulis* L. and *Gesneria rupicola* Urb. were chosen as outgroup taxa based on previous subfamily and tribal level phylogenetic analyses (Roalson, et al., 2005b; Zimmer et al., 2002). Specimens of the generic type species were preferentially selected for the ingroup genera. Multiple specimens of several fairly morphologically ambiguous species within *Monopyle* were analyzed to confirm their identification. These species appeared to be hybridizing with other taxa along their geographic ranges. Complete names of taxa and voucher information are provided in Appendix 1.

DNA extraction, Amplification, and Sequencing. Genomic DNA was extracted from approximately 30 mg of herbarium tissue or 100 mg of fresh tissue using the Nucleospin Plant II Mini kit (Macherey-Nagel, Düren, Germany). The lysis step was

modified from the manufacturer's protocol by the addition of 95 μ l 5M NaCl, 120 μ l 5% sodium N-lauroyl sarcosine, and 60 μ l 10 % polyvinylpyrrolidone (PVP), after the method used by Fleischmann and Heubl (2009). The incubation step was also lengthened to one-and-a-half hours for herbarium material. The *trnT*(UGU)-*trnL*(UAA) intergenic spacer was amplified using primer pairs (a and b) from Taberlet et al. (1991). The Gesneriaceae *FLORICAULA/LEAFY* homologue (*GFLO*) nuclear region was also amplified for comparison with the chloroplast region. Primers for a portion of the first intron region of *GFLO* were designed using Geneious 6.1 (Biomatters, Auckland, New Zealand), based on previously published sequences (Wang, Möller, & Cronk, 2004b). The forward primer was anchored in exon 1 and amplified multiple paralogues of varying length, with two distinct bands of 300 and 600 bp. These paralogues were designated *GFLOA* and *GFLOB*, and additional paralogues were amplified in some samples. The additional paralogues were not sequenced successfully. All gene regions were amplified using the KAPA3G Plant PCR Kit (Kapa Biosystems, Woburn, Massachusetts), following the protocol of Schori et al. (2013). The reaction volume was reduced to 25 μ l and the $MgCl_2$ concentration was increased from 2 mM to 3 mM for samples as needed. The reactions contained the following: KAPA3G Plant Buffer, $MgCl_2$ (2 mM), 20 mM of each primer, 0.5 U of KAPA3G enzyme, 1 μ l DNA and PCR-grade water to volume for fresh or silica-dried tissue. Recalcitrant herbarium tissue required additional $MgCl_2$ (3mM) for consistent amplification. The thermal cycling program had an initial denaturation (95°C, 10 min) followed by 40 cycles of denaturation (95°C, 45 sec), annealing (52–56°C, 1 min), and extension (72°C, 1 min), with a final extension (72°C, 3 min). PCR products were visualized by running on a 1% agarose gel and staining with

ethidium bromide. PCR products were cleaned using the Promega Wizard® SV Gel and PCR Clean-Up System (Promega Corp., Madison, Wisconsin, USA). Cycle-sequencing reactions were performed at the Ohio University Genomics Facility using an ABI 3130xl Genetic Analyzer (Applied Biosystems, Carlsbad, California, USA). Each reaction contained 2 µl 5× buffer (Applied Biosystems), 0.5 µl dimethyl sulfoxide (DMSO; Sigma, St. Louis, Missouri, USA), 0.5 µl Big Dye (Applied Biosystems), 0.1 µl ThermoFidelase (Fidelity System, Gaithersburg, Maryland, USA), a 30 second denaturation step is done prior to adding the enzyme, 10–40 ng template DNA, and PCR water for a final volume of 8 µl. Prior to adding the enzyme to the reactions a 30–60 second denaturation step was performed to increase the efficiency of the sequencing reactions. Sequencing products were cleaned with the BigDye X Terminator Purification Kit (Applied Biosystems, Foster City, California).

Phylogenetic Analysis. Sequences were aligned using MAFFT v. 7 (Katoh & Standley, 2013) and corrected manually within Geneious 6.1.6. The MAFFT alignments used default parameters with the scoring matrix set to 1PAM / $\kappa=2$. The scoring matrix was adjusted to account for the close relationships among all analyzed taxa. The nuclear (*GFLOA*) and chloroplast datasets were not combined because species sequenced for the two markers did not fully overlap. The two tree topologies were quite different and combining datasets could have altered the signal in the final analysis. Maximum parsimony (MP) analyses were performed on each dataset in PAUP* v4.0b10 (Swofford, 2003). The heuristic search was set to stepwise with TBR (tree-bisection-reconnection) branch swapping, 1,000 random replicates, Multiple Trees on, with no topological constraints. Branch support for each MP analysis was obtained from a stepwise heuristic

search with TBR branch swapping and sequences added at random for 1,000 bootstrap replicates. Each alignment was analyzed in jModeltest 2.1.2 (Darriba, Taboada, Doallo, & Posada, 2012) to select the best substitution model based on the Akaike Information Criterion (AIC) for use in Bayesian inference (BI) and maximum likelihood (ML) analyses. The general time reversal model with gamma distributed rate variation among sites (GTR + G) was selected for both the nuclear and chloroplast datasets. Maximum likelihood analyses were completed on each dataset in RAxML 7.2.8 (Stamatakis, 2006) with the GTR + G model, 1,000 bootstrap replicates, and all other settings on default. Bayesian analyses were completed using MrBayes 3.2.1 (Ronquist et al., 2012). The analyses were set to run for ten million generations with the GTR + G model. The high number of generations was needed to overcome the number of replicates that were discarded due to burn-in. The burn-in for each dataset was calculated using Tracer 1.5 (Rambaut & Drummond, 2007) and discarded for each. Final trees were edited and images were added in Dendroscope 3.2.8 (Huson & Scornavacca, 2012).

Results

The final *trnT*(UGU)-*trnL*(UAA) alignment included a total of 651 characters, of which 498 characters were invariant, 85 variable characters were not parsimony informative, and 68 characters were parsimony informative. This dataset produced 221 most parsimonious trees with a length of 195 steps, which had a consistency index (CI) of 0.85 and a retention index (RI) of 0.87. The ML analysis based on the GTR + G model generated a tree with a ln likelihood score of -1958.8898. The *GFLOA* alignment included a total of 505 characters, of which 269 characters were invariant, 152 variable characters were not parsimony informative, and 84 characters were parsimony

informative. *Monopyle* had two distinct deletions (10 and 84 bp each) in the *GFLOA* that allowed for easy identification of the sequences in the alignment. This dataset produced 413 most parsimonious trees with a length of 398 steps, which had a CI of 0.81 and a RI of 0.75. The ML analysis based on the GTR + G model generated a tree with a ln likelihood score of -2358.0560. The same tree topology was retained in all three analyses. Support values are reported below in the following format: ML bootstrap/MP bootstrap/BI posterior probabilities. There was strong incongruence between the chloroplast and nuclear trees (Fig. 4). Relationships among species of *Monopyle* appeared to correlate with geography in the chloroplast tree (Fig. 4), but this was unsupported in the nuclear tree (Fig. 4). Although *GFLO* was assumed to be single-copy in Gesneriaceae (Wang et al., 2004), multiple copies were present in *Monopyle* and other genera (Table 1). The number of *GFLO* copies appears to have evolved among lineages, as shown in Figure 4. *Monopyle* was recovered as a monophyletic lineage (50/90/65) with the generic type nested within the clade in the nuclear tree. The hypothesis of relationships among species of *Monopyle* was incongruent between the chloroplast tree and the nuclear tree. *Nomopyle dodsonii*, *Phinaea albolineata*, and a new red flowered *Diastema*-like species were placed within the *Monopyle* clade in the chloroplast tree. The nuclear tree indicated that *Nomopyle* belonged to a separate lineage from *Monopyle*, but *Nomopyle* was only represented by a single, potentially new, species. *Phinaea albolineata* was supported as sister to *Monopyle* in the nuclear tree.

The *Diastema*-like species was not sequenced for *GFLO* due to multiple copies, so its relationship to *Monopyle* cannot be ascertained. One problematic species, *Monopyle reflexa* (Rusby) Roalson & Boggan, was not successfully sequenced for either

gene region. An undescribed species of *Nomopyle* was nested within a clade containing *Gloxiniopsis racemosa* in the nuclear phylogeny, though the generic type was not sequenced successfully for *GFLOA*. *Phinaea* was not maintained as a monophyletic lineage in either tree, with *Phinaea pulchella* sister to a clade containing *Gloxiniopsis racemosa*. *Diastema* was not shown to be monophyletic in either tree. *Amalophyllon* was supported as a separate genus from *Diastema* in the chloroplast tree, but was more closely related to core *Diastema* in the nuclear tree. The other genera sampled were in similar placements to previous phylogenies.

Discussion

Relationships within Monopyle. *Monopyle* as a genus is highly diverse morphologically and from a taxonomic perspective is woefully underdescribed; no studies to date have adequately sampled the diversity. Previous studies (Zimmer et al., 2002; Smith et al., 2004; Roalson et al., 2005b) also have not included the generic type to confirm the assumption of monophyly for *Monopyle*. The genus *Monopyle* in the current investigation was recovered as monophyletic, although hybridization is apparent, both between species and potentially with other genera, from the strong incongruence between the gene phylogenies and observations of morphological intermediacy. Several taxa that have been treated as species of *Monopyle* by some authors were not in the *Monopyle* sensu stricto clade, and their morphology supports segregation into other genera. *Monopyle reflexa*, which was not included in previous phylogenetic studies (Roalson et al., 2005b; Zimmer et al., 2002) of tribal level relationships, was originally described as a *Gloxinia* species. It was later transferred to *Monopyle*, due to the lack of morphological similarity to the circumscription of the genus *Gloxinia* (Roalson et al., 2005a). This

species, along with a few other undescribed species, will be later segregated into a new genus *Lomacheilus* ined. *Lomacheilus* is characterized by fimbriate corollas with prominent glandular trichomes on the fringed lobes, long cylindrical fruits, and three copies of *GFLO* in the species sampled. There is evidence of a strong phylogeographic signal in the chloroplast tree for *Monopyle*, suggesting that ancestors of those species have been differentiating allopatrically for a long time in those regions. However, different relationships portrayed by the nuclear DNA variation suggests that hybridization has occurred at some point in the more recent past to obscure the phylogeographic split. Many of the narrowly circumscribed species are endemic to particular watersheds and may be pollinator limited, as are island endemics (Bernardello et al., 2001), requiring them to compensate through other reproductive means. Several of these species are autogamous or apomictic (Keene, unpublished data) and putatively produce viable seeds without cross-pollination. Pollination studies involving emasculation would be needed to confirm the production of seeds without fertilization. Apomixis has been hypothesized in other genera in the family (Roelofs, 1979; Martén-Rodríguez & Fenster, 2008; Chen et al., 2009) and is likely the source of the divergence in lineages after recombination events.

Other Taxa and Tribal Relationships. Although Roalson et al. (2005b) recircumscribed many generic boundaries in the tribe, their sampling was incomplete and some of the genera are likely to be polyphyletic. Molecular data from the chloroplast indicated that at least four different genera have hybridized with members of *Monopyle* in the past. *Gloxinella*, *Nomopyle*, *Phinaea*, and a red flowered *Diastema*-like species were all included in a clade with *Monopyle* in the chloroplast tree, indicating potential

chloroplast capture, gene duplication, horizontal transfer or some combination of these processes. *Gloxinella* and *Nomopyle* are both relatively similar to *Monopyle*, but have several key morphological features (e.g., inflorescence architecture and fruit dehiscence) that separate them. These genera probably arose from ancient hybridization events with species of *Monopyle*. In the nuclear tree, these genera were excluded from the *Monopyle* sensu stricto clade. *Nomopyle* was nested within *Gloxiniopsis* in the nuclear tree, which is likely due to limited taxon sampling. The two genera are morphologically distinct and the placement of *Nomopyle* within *Gloxiniopsis* does not seem to be problematic. These genera are small, with only three to four species each (Keene, unpublished data). The genera both contain three or more copies of *GFLO*, which appears to be a recent event (see Table 2). This similarity in *GFLO* copy number is the most reasonable explanation for the genera being nested in the phylogeny. *Diastema* was shown to be polyphyletic in both the nuclear and chloroplast trees. *Diastema racemiferum*, the type of the genus, formed a clade with *D. luteolum* in the chloroplast tree. In the nuclear tree, *Diastema luteolum* was sister to another morphologically similar species. Other species appeared elsewhere in both trees with relatively high levels of support, warranting the recognition of three additional generic segregates from *Diastema*: *Regeliantha* ined., *Crataegophyllus* ined., and *Pseudodiastema* ined. These genera each were supported in both trees and the consensus tree (Figure 6). The genera are also distinguished by unique or unusual morphological traits (e.g., fruit shape, dehiscence, and inflorescence architecture). Previous studies (Roalson et al., 2005b; Clark et al., 2011) have suggested that *Diastema* was polyphyletic and placed a taxon formally subsumed under *Diastema* (now *Regeliantha*) near *Phinaea pulchella*, but the authors concentrated on flower

similarity and ignored other potentially informative morphological traits. They did not segregate the genera, hypothesizing that they could be hybrids or were being influenced by some other evolutionary process (Roalson et al., 2005a; Roalson et al., 2005b). The chloroplast and nuclear phylogenies suggest that *Amalophyllon* could be sister to the core *Diastema* clade, as opposed to a separate lineage. Additional sampling and detailed morphological analyses are required to establish the boundaries of *Amalophyllon*. The odd red-flowered *Diastema*-like species probably represents another undescribed genus, but additional sampling and further morphological study will be required to confirm the placement and distinctiveness of this taxon. Finally, additional data will be required to delimit *Phinaea pulchella*. This species is only known from the Caribbean and may represent a separate lineage that has evolved in isolation from the rest of *Phinaea*. *Phinaea albolineata* is sister to *Monopyle* and the ancestors to these genera came into contact with each other in the past. The only other species in the genus, *Phinaea multiflora*, was not sequenced due to a lack of available material. This species has a similar fruit shape and dehiscence features to *P. albolineata*. Further examination of *Amalophyllon* and *Phinaea* will be required to determine the evolutionary history and affinities of these genera.

Evolutionary implications. The phylogenetic analyses demonstrated that the complex evolutionary history of *Monopyle* and the entire Gloxinieae tribe is still not very well understood. The presence and mechanisms of hybridization have been largely overlooked, with a few exceptions in morphological studies (Kvist, 1990; Kvist & Skog, 1992, 1996). It appears that hybridization, perhaps coupled with increased ploidy, have played important roles in speciation within Gloxinieae. These two processes, combined

with autogamy and apomixis, would explain why support values tended to be low in phylogenetic reconstructions for the tribe. Increased sampling to obtain a conclusive copy numbers for *GFLO* in different lineages may overcome this limitation, and would also help to determine when the duplication event(s) occurred in the tribe. The *GFLO* exon may also yield phylogenetically informative sequence data because it seemed to be variable in the taxa examined.

Future Research. Elucidating relationships within Gloxinieae will involve a significant effort in both the field and laboratory to start teasing apart the processes that have shaped their evolutionary history. Future studies should focus on chromosome counts to establish ploidy levels, chromosomes mapping to examine the positions of *GFLO* copies establishing whether they are suitable for tracing inheritance patterns, and the identification of nuclear regions that are more informative than *trnT*(UGU)-*trnL*(UAA) and *GFLO*.

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Table 2.

Number of GFLO copies identified for each taxon.

Taxon	Number of individuals	Number of <i>GFLO</i> copies
<i>Achimenes misera</i>	1	2 or more
<i>Amalophyllon aff. divaricatum</i>	1	2
<i>Diastema racemiferum</i>	1	2
<i>Chautemsia calicola</i>	1	2
<i>Crataegophyllus glabratus</i>	1	2
<i>Gloxinella lindeniana</i>	2	2
<i>Gloxiniopsis racemosa</i>	2	3 or more
<i>Lomacheilus velutinus</i>	2	3 or more
<i>Monopyle ambigua</i>	1	2
<i>Monopyle dichotoma</i>	2	2
<i>Monopyle mammillata</i>	8	2
<i>Monopyle maxonii</i>	2	2
<i>Monopyle puberula</i>	2	2
<i>Monopyle reflexa</i>	1	3 or more
<i>Nomopyle dodsonii</i>	2	2 or more
<i>Pearcea schimpfii</i>	1	2
<i>Pearcea hypocrytiflora</i>	1	2
<i>Phinaea albolineata</i>	2	2
<i>Phinaea pulchella</i>	1	3 or more

Table 2. cont.

Number of GFLO copies identified for each taxon.

Taxon	Number of individuals	Number of <i>GFLO</i> copies
<i>Pseudodiastema pilosa</i>	1	2
<i>Regeliantha vexans</i>	2	2
<i>Gesneria acaulis</i>	1	3 or more
<i>Gesneria rupicola</i>	1	3 or more

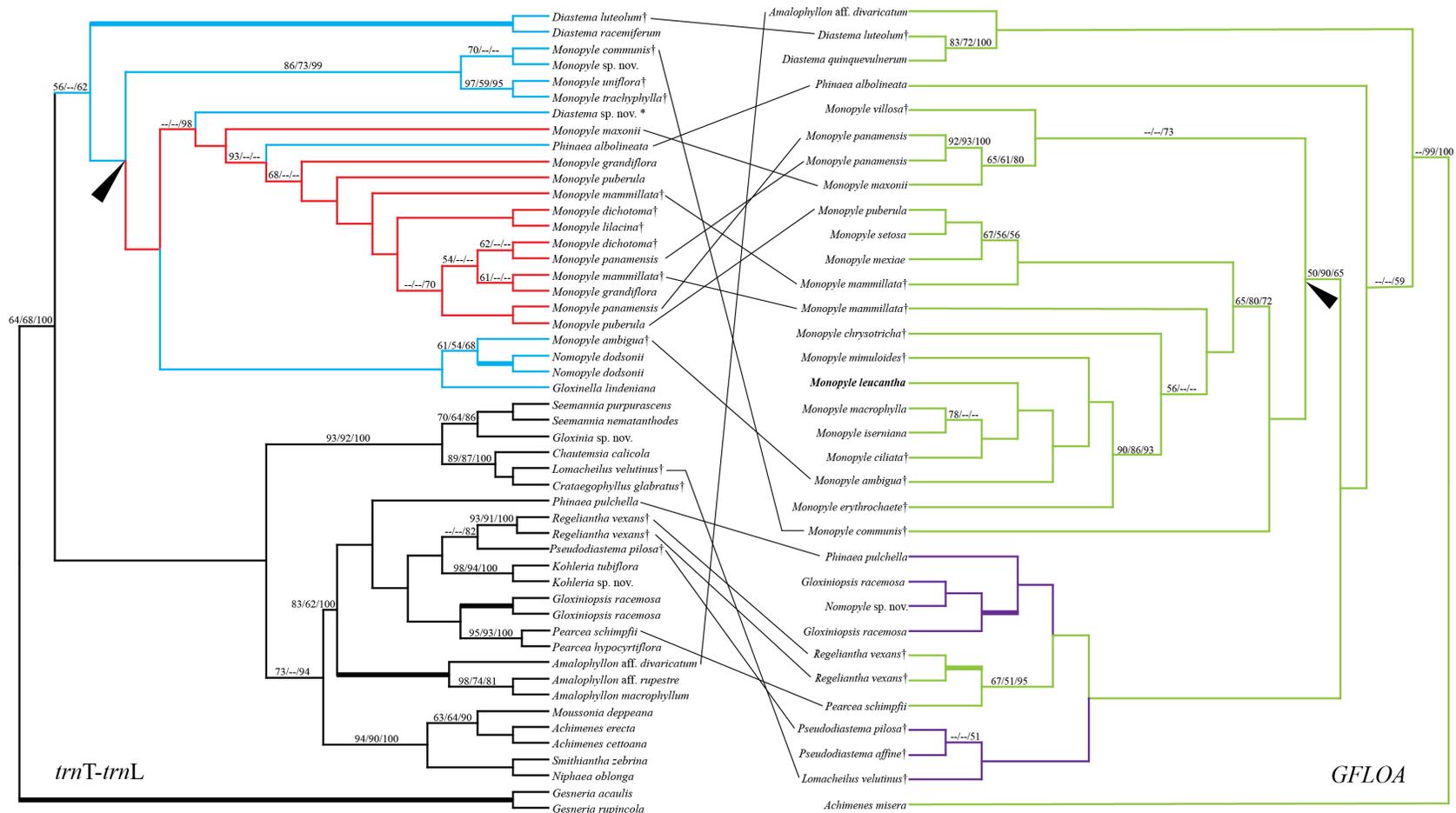


Figure 5. Maximum likelihood phylogenies of *Monopyle* and related genera in Gloxinieae based on *trnT-trnL* and *GFLOA*. Support values at the nodes are indicated as ML bootstrap/MP bootstrap/BI posterior probabilities. Nodes with support above 0.95 for all three are shown as thickened lines. Arrows indicate the clades containing *Monopyle*. Lines between phylogenies indicate taxa in different placements in each tree. Color in the *trnT-trnL* phylogeny indicate geographic distribution, South America (cyan) and Central America (red). Color in the *GFLOA* phylogeny indicates copy number, two copies (light green) and three or more copies (purple). The generic type of *Monopyle* is indicated with bold type in the *GFLOA* phylogeny. † indicates undescribed taxa and * indicates another possible *Diastema*-like lineage.

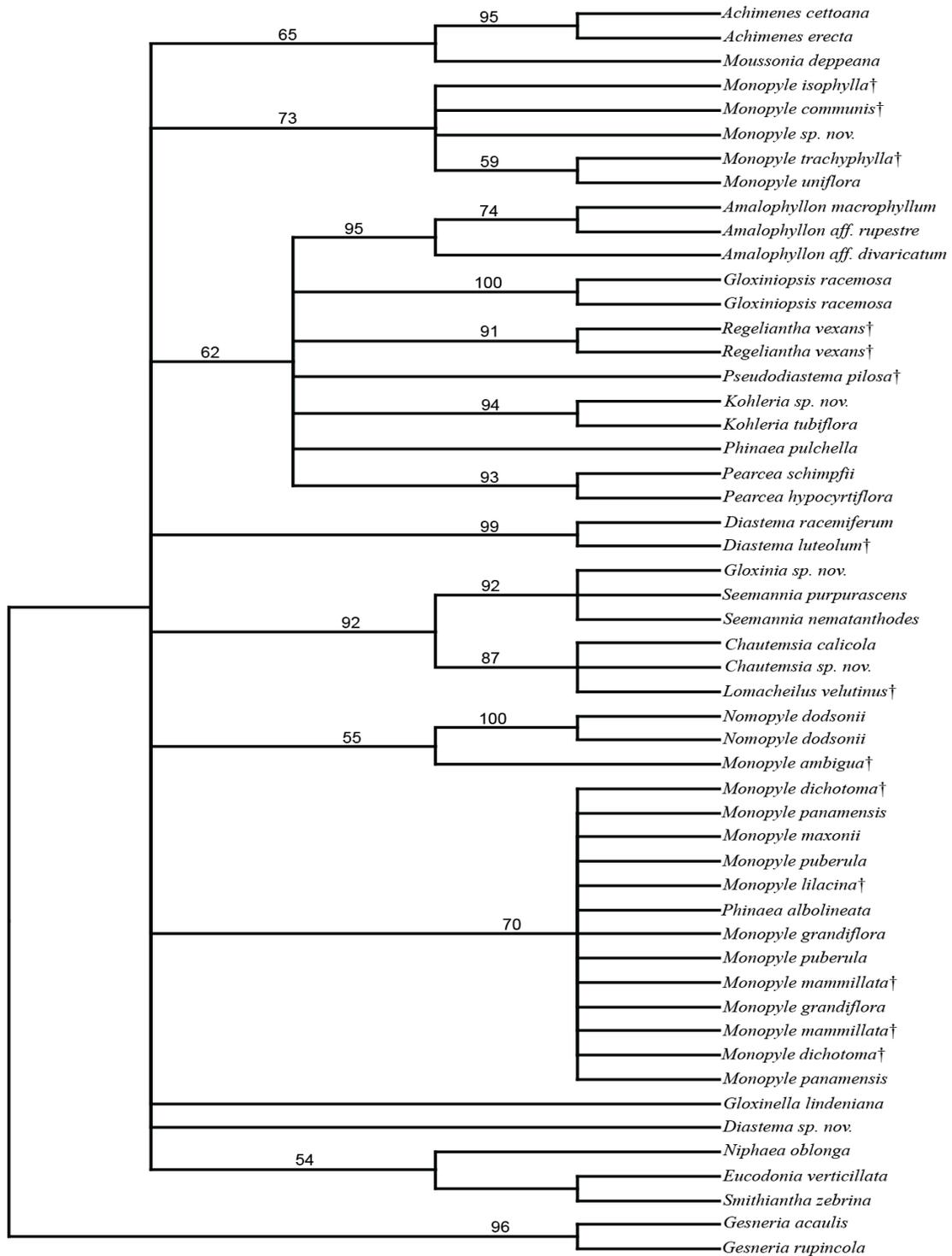


Figure 6. Majority rule consensus tree of *Monopyle* and related genera in Gloxinieae based on *trnT-trnL*. Support values at the nodes are MP bootstraps. † indicates undescribed taxa.

Appendix

This appendix is a list of all of the taxa that were sampled for the molecular study in Chapter 3. All samples were taken from herbarium specimens on loan from Missouri Botanic Gardens (MO) and are noted by Collector and Collector #. Collections noted as “live collection” are from live research collections and vouchers have been processed.

Genus	Species	Collector	Collector #
Achimenes	cettoana	Live Collection	
Achimenes	erecta	Live Collection	
Achimenes	misera	Live Collection-Kew	39538
Amalophyllon	aff. divaricatum	van der Werff	15590
Amalophyllon	aff. rupestre	Live Collection	RM-2006
Amalophyllon	macrophyllum	J. L. Clark	12904
Chautemsia	calicola	Live Collection	
Crataegophyllum	glabratus	Núñez & Ortiz	12739
Diastema	aff. racemiferum	Live Collection	
Diastema	luteolum	Live Collection	
Diastema	quinquevulnerum	Croat & Gaskin	80394
Diastema	sp. nov.	Live Collection	GRF 9754
Eucodonia	verticillata	Live Collection	
Gesneria	acaulis	Live Collection	
Gesneria	rupicola	Live Collection	
Gloxinella	lindeniana	Live Collection	
Gloxinia	sp. nov.	Gesneriad Research Foundation	9669
Gloxiniopsis	racemosa	Live Collection	
Gloxiniopsis	racemosa	J. L. Clark	8838
Kohleria	tubiflora	Live Collection	
Lomacheilus	velutinus	Vargas	12272
Monopyle	ambigua	Londono & Kvist	156
Monopyle	bilsaensis	J. L. Clark	12131
Monopyle	chrysotricha	J. L. Clark	7190
Monopyle	ciliata	Sytsma et al.	4243
Monopyle	dichotoma	J. L. Clark	8621
Monopyle	dichotoma	Luteyn	14892
Monopyle	erythrochaete	Beltran & Foster	1113
Monopyle	grandiflora	Herrera et al.	861
Monopyle	grandiflora	D'Arcy & McPherson	16196
Monopyle	iserniana	Cumacas	107
Monopyle	isophylla	Leeuwenberg	2024
Monopyle	lilacina	Salazar et al.	673
Monopyle	mammillata	Croat & Zhu	76570
Monopyle	mammillata	Nevers & Gonzalez	3652
Monopyle	maxonii	J. L. Clark	8603
Monopyle	mexiae	Berlin	1805
Monopyle	mimuloides	Amaya & Smith	608
Monopyle	panamensis	J. L. Clark	8756
Monopyle	panamensis	Churchill & Nevers	4951
Monopyle	pilosula	Neill et al.	12465
Monopyle	puberula	Moran & Amasifuen	7978
Monopyle	puberula	Boyle et al.	6317
Monopyle	setosa	Jaramillo et al.	1076
Monopyle	sp. nov.	Live Collection	

			61
Monopyle	subdimidiata	Wingfield	8104
Monopyle	trachyphylla	van der Werff et al.	12373A
Monopyle	uniflora	J. L. Clark	11162
Monopyle	villosa	Rodriguez et al.	1141
Moussonia	deppeana	Live Collection	
Niphaea	oblonga	Live Collection	
Nomopyle	dodsonii	J. L. Clark	8784
Nomopyle	sp. nov.	Ancuash	190
Pearcea	hypocyrtiflora	Live Collection	
Pearcea	schimpfii	Live Collection	
Pearcea	sp. nov.	Live Collection	
Phinaea	albolineata	Live Collection	
Phinaea	pulchella	J. L. Clark	
Pseudodiastema	affine	J. L. Clark	7534
Pseudodiastema	pilosa	Monteagudo et al.	4981
Regeliantha	vexans	Croat & Gaskin	79729
Regeliantha	vexans	Live Collection	
Seemannia	nematanthodes	Live Collection	
Seemannia	purpurascens	Live Collection	
Smithiantha	zebrina	Live Collection	

CHAPTER 4: TWO NEW SPECIES OF *MONOPYLE* (GESNERIACEAE) FROM
NORTHERN ECUADOR

This manuscript was published in the Journal of the Botanical Research Institute of Texas in 2011. It describes two new species collected by my collaborator Dr. John L. Clark.

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Abstract

Two new species of *Monopyle* Benth. are described from the pluvial lowland forests of northwestern Ecuador in the province of Esmeraldas. They are both locally endemic and are of conservation concern. The two species are segregated from other *Monopyle* species by axillary inflorescences and indument type. *Monopyle uniflora* J.L. Clark & Keene is distinguished by having basally appressed inflorescence bracts, glandular trichomes on the calyx, and a singular axillary flower. The densely villous indument and inflorescence of multiple flowers differentiate *Monopyle multiflora* Keene & J.L. Clark from *Monopyle uniflora*.

Resumen

Dos especies de *Monopyle* son descritas de los bosques de lluvias en las tierras bajas del noroeste de Ecuador en la provincia de Esmeraldas. Estas especies son tanto endémicas localmente así como de interés para su conservación. Las dos especies son segregadas de otras especies de *Monopyle* debido a sus inflorescencias axilares y tipo de indumento. *Monopyle uniflora* J. L. Clark & J. Keene se distingue por tener brácteas adpresadas basalmente en las inflorescencias, tricomas glandulares en el cáliz, y una única flor axilar. El indumento vellosa denso y las inflorescencias de flores múltiples se la distinguen *Monopyle multiflora* J. Keene & J. L. Clark de *Monopyle uniflora*.

Key Words: *Monopyle*, Gesneriaceae, Systematics, Ecuador

Introduction

The family Gesneriaceae is a basal lineage in the order Lamiales, with a hypothesized origin of ~ 65 million years ago (Bremer et al. 2004). The family comprises approximately 3,500 species in 150 genera, with a significant proportion being epiphytes (Weber 2004). The Gesneriaceae can be distinguished from other families in the Lamiales by a suite of characters including reduced pair-flowered cymes, five-lobed corollas, parietal placentation, and presence of endosperm. Some of these traits, however, are variable within the family and found in the other closely related families (Heywood, 2006; Weber, 2004).

The Gesnerioideae is the largest subfamily of Gesneriaceae in the Neotropics with approximately 50 genera and 1,500 species (Weber, 2004). The subfamily is Neotropical in distribution and recognized by having isocotylous seedlings (Burt & Wiehler 1995). The most current circumscription of the tribes (Roalson et al. 2005) further divides the

Gesnerioideae into seven tribes, including Beslerieae, Gesnerieae, Sinningieae, Gloxinieae, Napeantheae, Episcieae and Sphaerorrhizeae. The Gloxinieae is characterized by having “scaly” rhizomes, a feature separating it from other tribes in the subfamily. These “scaly” rhizomes are modified underground stems with reduced succulent leaves that allow the plants to survive through periods of drought (Kvist and Skog 1992).

Monopyle Benth. (Gloxinieae: Gesneriaceae) is a genus of Neotropical terrestrial understory herbs, comprising over 20 species (Weber, 2004). These plants are distributed from Guatemala southward through northern South America. The genus was revised for South America by Morton (1945), but limited material was examined and he doubted some of his own determinations. The genus is characterized morphologically by anisophyllous opposite leaves, campanulate flowers, and the presence of uncinat trichomes (Roalson et al., 2005; Weber, 2004). Preliminary investigations by the first author of *Monopyle* for a revisionary work show that these characters along with indument type, density, and inflorescence architecture are diagnostic for the genus. We focus here on the description of two new species with axillary inflorescences that are closely related morphologically to *Monopyle sodiroana* (Keene, Unpublished Data). These taxa have been misplaced within *Monopyle sodiroana* and are here segregated from that species. A distribution map (Fig. 5), a table of characters (Table 3), figures of live collections and a dichotomous key are provided to distinguish the newly described taxa.

Monopyle multiflora Keene & J.L. Clark, sp. nov.

TYPE: ECUADOR. Esmeraldas: Cantón San Lorenzo, Parroquia Santa Rita, Tundaloma Lodge, km 17 Hwy San Lorenzo–Ibarra, Sector Calderón, 01°10'59"N,

78°45'3"W, 31 m, 29 May 2008, J.L. Clark, B. Bisvicutth, S. Ginzburg, & J. Melton 10407 (Holotype: US; Isotypes: K, MO, NY, QCNE, SEL). (Table 3 & Figs. 7 & 8)

Species Diagnosis. *Species nova Monopyles a speciebus aliis axillaribus multifloris inflorescentiis, villosis trichomatibus in abaxialibus foliorum lateribus, et absentia glandulosorum trichomatum in inflorescentiis differt.*

Terrestrial or epiphytic herb, roots fibrous, shoots dorsiventral, ca., 60 cm tall, densely villous with long straight trichomes intermixed with minute uncinata trichomes throughout; lateral shoots absent in the axils of leaves. Leaves opposite, strongly anisophyllous; larger leaf with petioles 8–12(–18) mm long (length decreasing towards stem apex), pubescence same as above; lamina asymmetrical elliptic to ovate, base oblique, apex acuminate, (8.7–)10.5–15.9 × 3.3–7.8 cm, base entire becoming shallowly serrate to deeply serrate towards apex; adaxially dark green to maroon, sparsely villous with long straight trichomes, abaxially maroon, dense puberulent uncinata trichomes intermixed with long straight trichomes (mostly on the veins); smaller leaf with petioles 4(–9) mm long, some appearing sessile, densely villous with long straight trichomes intermixed with minute uncinata trichomes; lamina orbicular to ovate, base subequilateral to oblique, apex acuminate to cuspidate, 1.0–3.4(–5) × (0.70–)1.1–2.7(–3.4) cm, entire to serrate; adaxially densely puberulent with minute uncinata trichomes intermixed with long straight trichomes; abaxially same as large leaf. Inflorescence axillary with two or more flowers per axil; peduncles 1–2 mm long, densely villous with long straight trichomes intermixed with minute uncinata trichomes, floral bracts, 1.6 × 0.8 mm not basally appressed on the peduncle, persistent, opposite, adaxially densely villous, abaxially sparsely villous; pedicel to 2.8 mm long, villous with long straight trichomes

intermixed with uncinata trichomes. Calyx green to maroon, lobes five, 6.0–10(–13) × 0.7–2(–4) mm, connate 2–3(–6) mm from base, apex acuminate, abaxially villous with long straight trichomes intermixed with minute uncinata trichomes, adaxially few long straight trichomes. Corolla white with varying amounts of violet spots in and also yellow blotch at the base of the throat, 18.3 × 9.6 mm, villous with long straight trichomes intermixed with uncinata trichomes on the outer surface, short gland-tipped papillae on the inner surface of the tube confined to the yellow blotch at the base of the throat (osmophore?); limb glabrous, upper lobes 6.1 × 5.3 mm, lower lobe to 11 mm wide and always significantly wider than upper lobes. Androecium four stamens, didynamous, anthers connivent for 1.4 mm. Nectary usually absent, some flowers with small amounts of raised tissue dorsally at the base of the ovary. Gynoecium ovary half-inferior, to 2 mm wide, sparsely pubescent with minute uncinata trichomes, style to 4 mm long, sparsely pubescent with minute uncinata trichomes, stigma stomatomorphic. Fruits 7–10 × 3–5 mm, accrescent, dehiscent along dorsal surface, calyx persistent in fruit; seeds numerous, oblong, with tubular and bell-shaped protuberances, 0.6 × 0.4 mm, dark brown to black.

Phenology. Collected in flower and fruit in May and September.

Distribution and Ecology. *Monopyle multiflora* has been collected from areas noted on herbarium labels as tropical humid forest and transitional montane/premontane to lowland wet forest. It is also noted to be growing in the understory of the following canopy trees: *Carapa guianensis* Aubl. (Meliaceae), *Humiriastrum procerum* (Little) Cuatrec. (Humariaceae), *Jacaranda copaia* (Aubl.) D. Don (Bignoniaceae), and *Jessenia bataua* (Mart.) Burret. This species is known from the Esmeraldas province in Ecuador. It

is likely that additional populations will be discovered near the type locality in pluvial forests in adjacent Colombia where limited fieldwork has been conducted.

Conservation and IUCN Red List category. *Monopyle multiflora* is known from two populations in the Esmeraldas province along the foothills of the eastern Andean slopes of northern Ecuador (Fig. 9). The type collection was made in Tundaloma Lodge, a small private reserve located 17 km east of the town San Lorenzo (sector Calderón) in northern Ecuador. The Tundaloma Lodge is owned and managed by Andres Chiriboga and it is a destination for bird watchers. Most of the forest along the San Lorenzo-Ibarra highway has been converted to African Palm plantations as a result of the recent completion of the highway. Some patches of isolated forest exist in the hilly areas along the highway, but the habitat that is most threatened is the lowland flat areas near San Lorenzo where *Monopyle multiflora* is located. It is not found in any formally protected area in Ecuador and additional fieldwork in adjacent forests in Colombia may result in the documentation of additional populations. According to the IUCN Red List criteria (IUCN 2001) for limited geographic range (B2a, less than 10 km² and known to exist at only a single location) and considering the uncertain future of habitat conservation along the San Lorenzo-Ibarra highway, *Monopyle multiflora* should be listed in the category CR (Critically Endangered).

Etymology. The specific epithet, *multiflora*, reflects the species typically having many flowers per axillary inflorescence.

Paratypes: ECUADOR. Esmeraldas: Entre el Estero Molina–Hcda. Montero Riera [between the Molina stream and the Montero Riera Farm], San Marco, 140 m, 7 Sep 1991, *J. Jaramillo, E. Grijalva & M. Grijalva 13811* (NY).

Monopyle uniflora J.L. Clark & Keene, *sp. nov.*

TYPE: ECUADOR. Esmeraldas: Cantón San Lorenzo, flat forest near highway Ibarra–San Lorenzo, near Rio Durango, Centro de Manejo Lote #1 (Fundacion Sirua), Sendero Hola, 1°5'5"N, 78°41'12"W, 87 m, 4 Jun 2009, *J.L. Clark & Gesneriad Research Expedition Participants 11162* (Holotype: US; Isotypes: K, MO, QCNE, SEL) (Table 3 & Figs. 8 & 10).

Species Diagnosis. *Species nova Monopyles a speciebus aliis axillaribus inflorescentiis singulari flore cum amplectenti bractea, et praesentia uncinatorum et glandulosorum trichomatum in inflorescentiis differt.*

Terrestrial herb, roots fibrous, stems dorsiventral to erect, 40–80 cm tall, puberulent with loosely appressed uncinata trichomes throughout, green with some red coloration. Leaves opposite, strongly anisophyllous; larger leaf with petioles 5.1–15.9 mm (length decreasing towards apex), densely puberulent with short uncinata trichomes intermixed with scattered long straight trichomes; lamina elliptic to falcate, base oblique, apex falcate-acuminate, 5.6–8.5(–14.2) × (2.5–)3.4–6.7 cm, shallowly serrate to deeply serrate towards apex; adaxially dark green, sparsely puberulent with minute uncinata trichomes intermixed with scattered long straight trichomes, abaxially light green, minute uncinata trichomes (mainly on the veins); small leaf with petioles 1.6–4.6 mm, dense puberulent uncinata intermixed with long straight trichomes; lamina orbicular to ovate, base subequilateral to oblique, apex cuspidate, (1.0)1.9–2.8(–5.5) × 3.3–4.9 cm, serrulate to serrate; adaxially bullate, evenly spaced minute uncinata trichomes intermixed with sparse long straight trichomes; abaxially sparse to somewhat dense puberulent uncinata trichomes. Inflorescence axillary, a reduced pair-flowered cyme with one to two flowers;

peduncles 0.9–2.1 mm, puberulent with uncinata trichomes, bracts 1.1–1.3 mm × 0.4 mm appressed basally on the peduncle, persistent, opposite, sparsely to densely villous; pedicel 2.2–4.5 mm, puberulent with uncinata trichomes intermixed with long glandular trichomes. Calyx light green, lobes five, equal, 5.1–6.3 × 0.9–1.7 mm, connate 1.8–2.4 mm from base, apex acuminate, puberulent with uncinata trichomes intermixed with long straight glandular and non-glandular trichomes, adaxial surface with few long straight trichomes. Corolla white to light lavender with broad yellow blotch in the base of the throat, 14.8–17.3 × 7.2–10 mm, sparsely pubescent with short sharply pointed trichomes on the outer surface, short gland-tipped papillae confined to the yellow blotch on the inner surface of the tube (osmophore?); limb glabrous, upper lobes 5–7 × 7–9 mm, lower lobe to 13 mm long, always significantly wider than upper lobes. Androecium with two pairs of stamens, anthers connivent for 1.1 mm. Nectary usually absent, some flowers with small amounts of raised tissue at base of ovary. Gynoecium ovary half-inferior, to 1.6 mm wide, puberulent with uncinata trichomes, style to 4 mm long, sparsely pubescent with uncinata trichomes, stigma stomatomorphic. Fruits 6–9 × 2–4 mm, accrescent, dehiscent on dorsal side only, calyx persistent in fruit; seeds numerous, oblong, with tubular and bell-shaped protuberances, 0.4 × 0.2 mm, cream to light tan.

Phenology. Collected with flowers and fruits in June and October.

Distribution and Ecology. *Monopyle uniflora* has been collected from areas noted as flat forest and humid tropical primary forest on herbarium labels. It is likely that additional populations will be discovered near the type locality in pluvial forests in adjacent Colombia where limited fieldwork has been conducted.

Conservation and IUCN Red List category. *Monopyle uniflora* is known from two collections in the Esmeraldas province along the foothills of the eastern Andean slopes of northern Ecuador (Fig. 9). The type collection is from a remnant patch of lowland flat forest that is managed by Fundacion Sirua, a foundation dedicated to the conservation of biodiversity along the Ibarra–San Lorenzo highway. According to the IUCN Red List criteria (IUCN, 2001) for limited geographic range (B2a, less than 10 km²) and considering the uncertain future of habitat conservation along the San Lorenzo–Ibarra highway, *Monopyle uniflora* should be listed in the category CR (Critically Endangered).

Etymology. The specific epithet, *uniflora*, comes from the species typically producing a single flower per axillary inflorescence.

Paratypes: ECUADOR. Esmeraldas: San Lorenzo Cantón, Reserva Etnica Awá, Centro Ricaurte, 01°10'N, 78°32'W, 300 m, 27 Oct 1992, G. Tipaz, C. Aulestia, & M. Pascal 2218 (MO, QCNE, US).

Key To Differentiate New Species From *Monopyle sodiroana*

1. Inflorescences terminal.

Monopyle sodiroana

1. Inflorescences axillary.

2. Calyx with glandular trichomes and bracts basally appressed.

Monopyle uniflora

2. Calyx lacking glandular trichomes and bracts not basally appressed.

Monopyle multiflora

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Table 3.

Main diagnostic features between Monopyle multiflora, M. uniflora and M. sodiroana.

Diagnostic character	<i>Monopyle multiflora</i>	<i>Monopyle uniflora</i>	<i>Monopyle sodiroana</i>
Glandular trichomes on the calyx	Absent	Present	Absent
Stem indument	Villous	Puberulent	Puberulent
Inflorescence	Axillary	Axillary	Terminal
Inflorescence bract base	Spreading	Appressed	Spreading

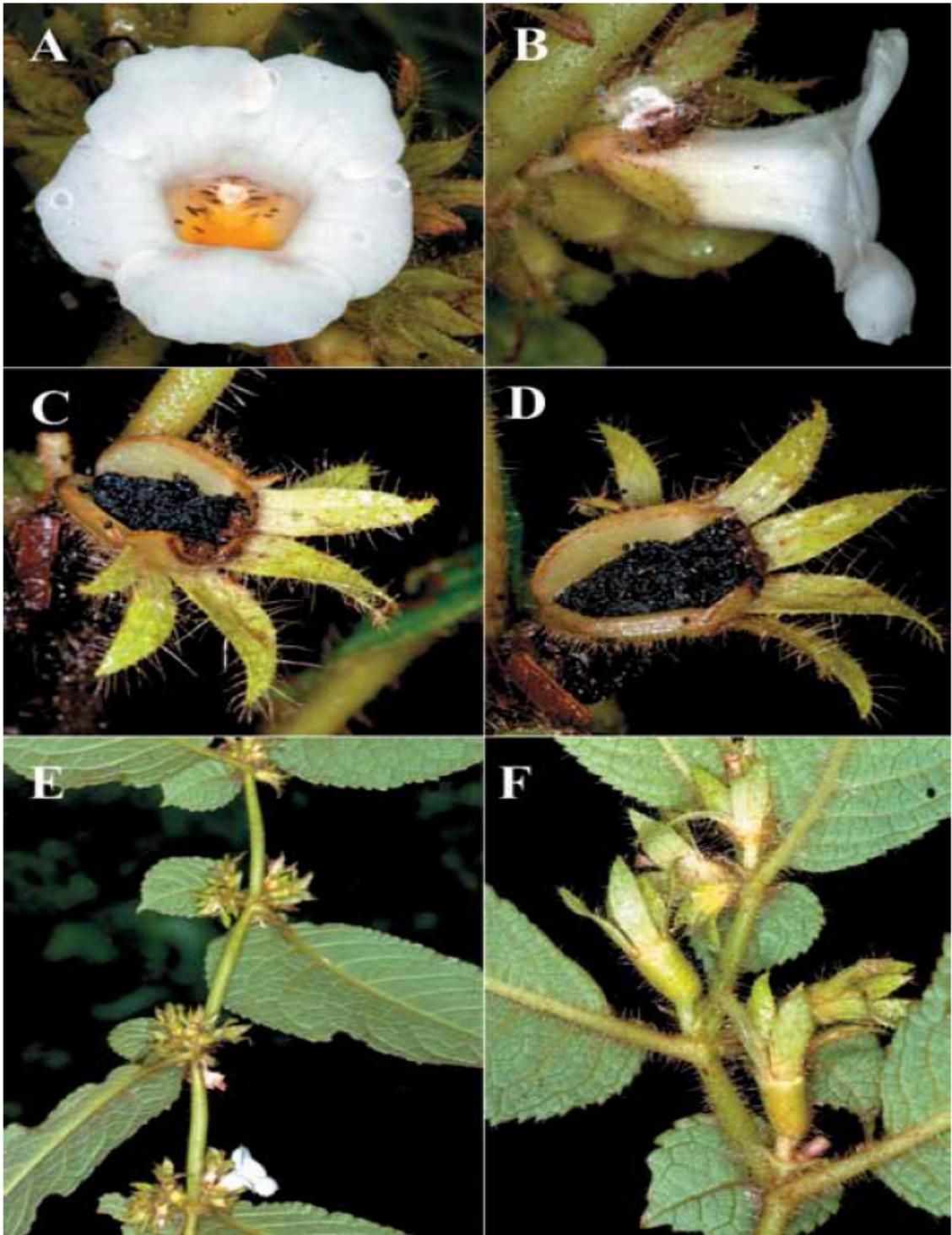


Figure 7. Monopyle multiflora. A. Face view of flower (Yellow blotch – osmophore?). B. Lateral view of flower. C & D. Mature fruit. E. Habit showing strongly anisophyllous leaves. F. Immature Fruits (Photos by J.L. Clark; voucher from the holotype, J.L. Clark, B. Bisvicuth, S. Ginzburg & T. Melton 10407 at US).

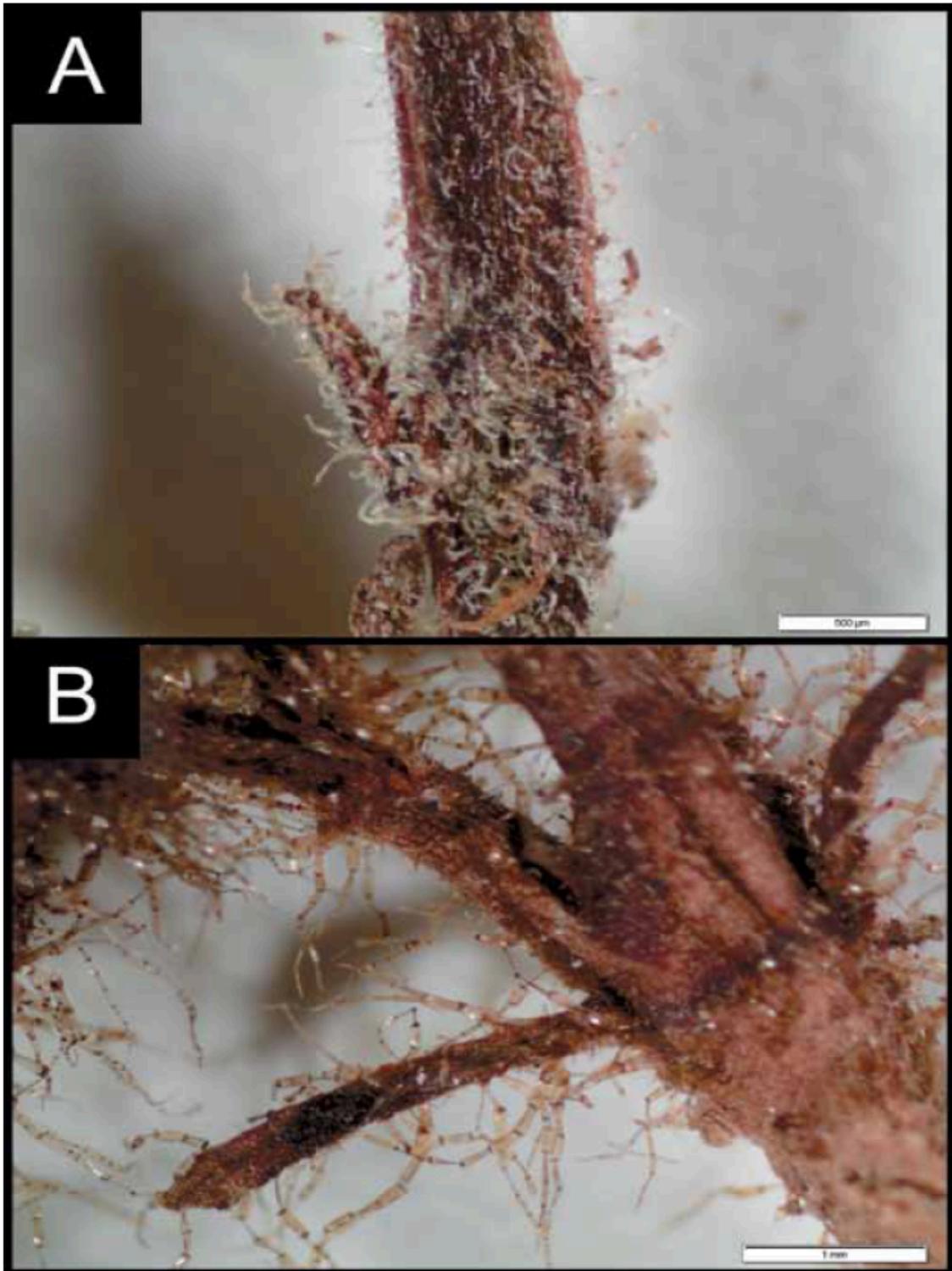


Figure 8. A. *Monopyle uniflora* showing peduncle with basally appressed bracts. B. *Monopyle multiflora* showing peduncle with the bracts not basally appressed. (Photos by Jeremy Keene; voucher from the holotype: J.L. Clark & Gesneriad Research Expedition Participants 11162 at US).

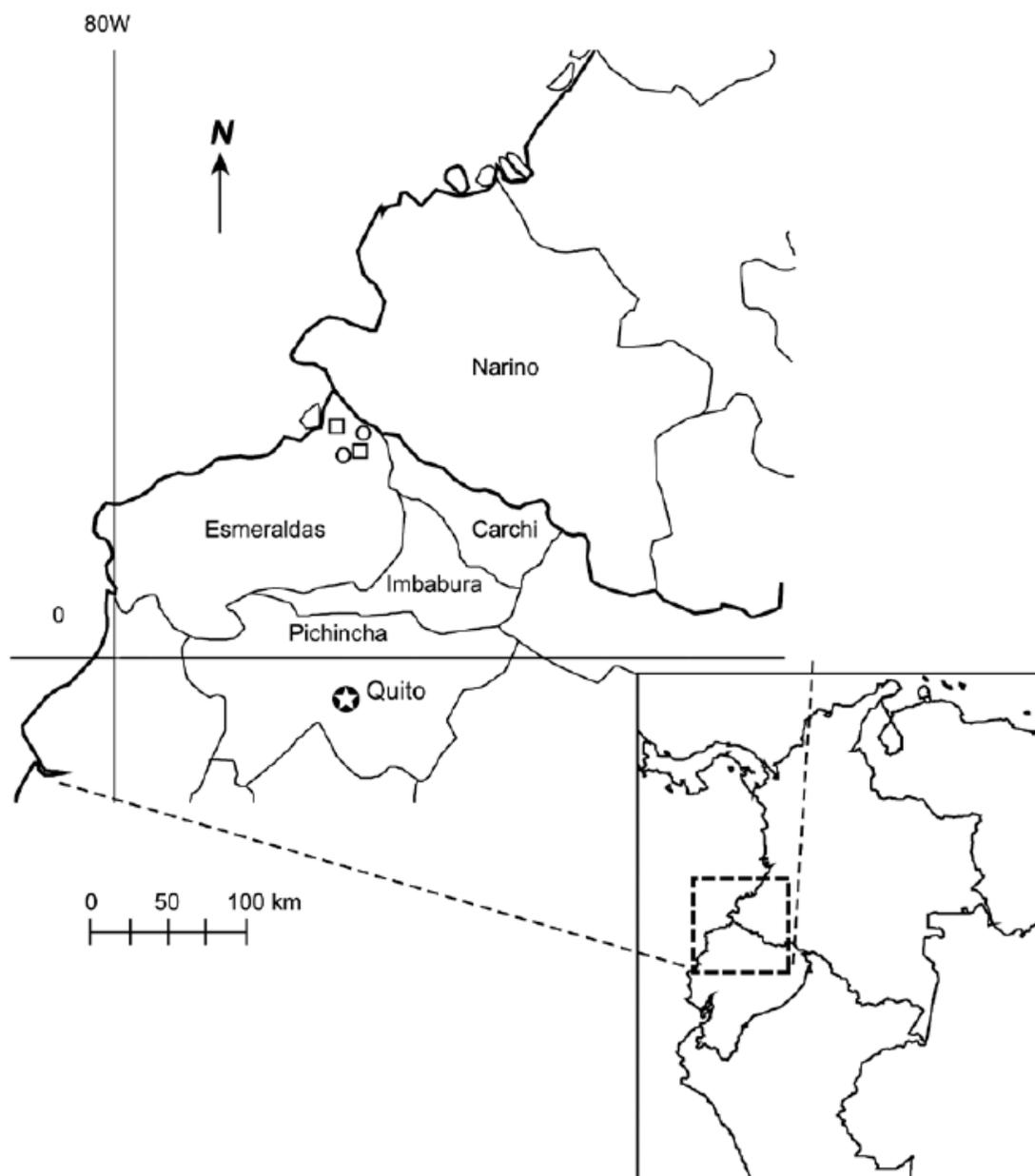


Figure 9. Distribution map of *Monopyle uniflora* (open circle) and *Monopyle multiflora* (open square).

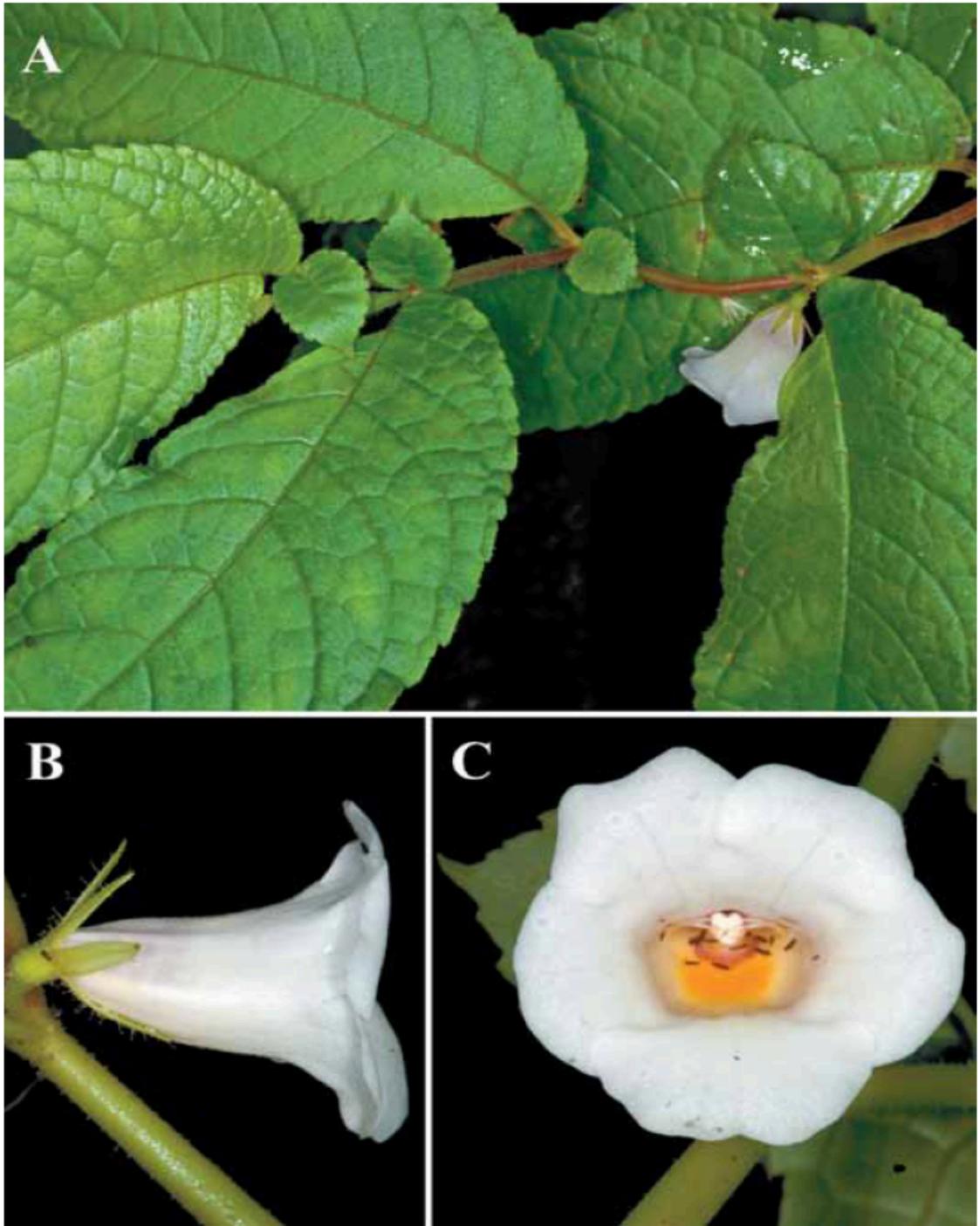


Figure 10. Monopyle uniflora. A. Habit showing strongly anisophyllous leaves and single axillary flower. B. Lateral view of Flower. C. Front view of flower showing yellow blotch (osmophore?) at base of tube (Photos by J.L. Clark; voucher from the holotype: J.L. Clark & Gesneriad Research Expedition Participants 11162 at US.

CHAPTER 5: TWO NEW SPECIES OF *MONOPYLE* (GESNERIACEAE) FROM
PANAMA.

This manuscript was submitted to Novon for review in February 2013. It describes two new species from near a mine site in Panama.

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Abstract

Two new species of *Monopyle* (Gesneriaceae) are described from central Panama near the Caribbean coast in the Panama Copper Concession (Consección Minera Panamá S.A.). The new species are endemic to Panama, are poorly represented in herbaria, and are differentiated from other *Monopyle* by a suite of characters. *Monopyle aurea* Keene & J. L. Clark has yellow flowers with a distinct maroon osmophore and a red fleshy fruit. *Monopyle longicarpa* J. L. Clark & Keene has a villous golden indument and elongate linear fruit. Both species are differentiated from other congeners by the presence of small glandular trichomes along the margin of the corolla lobes.

Resumen

Se describen dos especies nuevas de *Monopyle* (Gesneriaceae) de la Región Central de Panamá, cerca a la costa Caribe, en la Concesión Minera Panamá S.A. Las

especies nuevas son endémica de Panamá, son escasamente representada en colecciones de herbario, y se diferencian de otras especies de *Monopyle* por una serie de características. *Monopyle aurea* Keene & J. L. Clark tiene flores amarillas con un osmóforo marrón distintivo y fruto carnoso rojo. *Monopyle longicarpa* J. L. Clark & Keene tiene indumento viloso dorado y fruto elongado linear. Ambas especies se diferencian de sus congéneres por la presencia de tricomas pequeños glandulares a lo largo de la margen de los lóbulos de la corola.

Key Words: Gesneriaceae, *Monopyle*, Panama, Systematics

Introduction

Monopyle Moritz ex Benth. (Gloxinieae: Gesneriaceae) is a group of terrestrial understory or epiphytic herbs distributed from Guatemala southward through northern South America. The genus currently comprises 22 described species (Weber 2004), but the actual number is much higher because preliminary monographic work suggests that some broadly circumscribed taxa need to be more narrowly defined (Keene, unpublished data). Additionally, recent exploratory expeditions by the second author have resulted in numerous new species not represented in herbaria and collections that have facilitated the recognition of new species poorly represented in herbaria. Here we describe two species that were collected in 2011 during a research expedition facilitated by Minera Panama S.A. (MPSA) in the copper mine concession in the Colón province of central Panama.

Monopyle is morphologically complex and has had little attention since Morton's monographic revision (1945). *Monopyle* is traditionally characterized by strongly anisophyllous opposite leaves, campanulate flowers, and the presence of uncinat trichomes (Roalson et al. 2005; Weber, 2004). An additional diagnostic character that

defines *Monopyle* that was discovered during revisionary work by the first author includes the presence of an osmophore (floral fragrance gland) at the base of the corolla. Many *Monopyle* species are locally endemic and appear to be restricted to a specific watershed. It is likely that narrow distributions are the result of minute seeds limited by a splash-cup dispersal mechanism.

Monopyle aurea Keene & J. L. Clark, sp. nov.

TYPE: PANAMA. Colón: Distrito Donoso, Conseción de Minera Panama S.A. Helipad ZP-P9, 8°51'5"N, 80°40'19"W, 391 m, 20 July 2011, *J. L. Clark & L. Martinez 12564* (holotype: US; isotypes: K, MO, NY, PMA, SEL). Figure 11.

Species Diagnosis. Differs from all other *Monopyle* by the combination of yellow flowers with a dark maroon osmophore, dark red fleshy fruits, and minute glandular trichomes on the margins of the corolla lobes.

Terrestrial suffrutescent herb, roots fibrous, stems erect, red to brown, internodes swollen, 0.5–1.5 m tall, to 5 mm in diameter, pilose to densely pilose with uncinata trichomes intermixed occasionally with longer eglandular trichomes; lateral shoots present in the axils of leaves. Leaves opposite, strongly anisophyllous, interstipular scar present; larger leaf with petioles (1.4–) 2.9–7.9 cm, villous with eglandular trichomes intermixed with uncinata trichomes on the abaxial surface, lamina asymmetrical ovate to elliptic, base oblique, to 8 mm between bases, apex attenuate to acuminate, (10.3–) 13.1–19.9 × (5.6–) 7.1–10.8 cm, serrate with a gland at each point; adaxially green to red, densely villous at leaf base with eglandular trichomes becoming villous and intermixed with uncinata trichomes towards the apex, abaxially red to maroon, sparsely villous along veins with eglandular trichomes; smaller leaf with petioles (0.7–) 1.7–4.5 cm, pubescence

same as large leaf; lamina ovate to elliptic, base oblique (occasionally cuneate), apex acute to attenuate, (2.5–) 5.3–11.2 (–13.9) × (1.9–) 3.2–6.9 (–9.1) cm, serrate; adaxially and abaxially same as large leaf. Inflorescence terminal, erect, compound cyme; peduncle 34–50 mm, densely pilose uncinata trichomes intermixed with longer eglandular trichomes, bracts 6–8 × 0.4–1.1 mm, persistent, opposite, adaxially nearly glabrous, abaxially villous eglandular trichomes; rachis (8.9–) 15.7– 25.3 cm, 2–4 nodes, 6–8 cymules per node; secondary peduncle 15–39 mm, bracteoles 2–4 × 0.5–1 mm; tertiary peduncle 8–13 mm, bracteoles 1–2 × 0.4–0.6 mm; pedicel of terminal flower 2–7 mm, front flower (12–) 22–33 mm. Calyx green to maroon, lobes five, linear to lanceolate, 8–13 × 1–2.5 mm, connate 2–6 mm from base, apex acute, abaxially pilose with uncinata trichomes intermixed with longer eglandular trichomes, adaxially nearly glabrous. Corolla mostly white with yellow throat, 18–24 × 12–15 mm, villous with thin eglandular trichomes, minute gland-tipped trichomes on the inner surface of the tube confined to the dorsal surface above androecium, osmophore at base of corolla dark maroon; limb with minute glandular trichomes along the margin of the corolla lobes, dorsal lobes 6–9 × 4–8 mm, ventral lobe 7–13 × 5–11 mm. Androecium of four stamens, 3–7 mm, didynamous, included, filaments 2–6 mm, adnate to corolla, anthers to 1.0 × 0.6 mm, connivent for up to 0.7 mm. Nectary usually absent, some flowers with small amounts of raised tissue at the base of the ovary. Gynoecium with ovary subinferior, to 1.5 mm wide, densely pilose with uncinata intermixed with eglandular trichomes (mainly at the apex near the base of the style), style to 4.5 mm long, glabrous, stigma stomatomorphic. Fruits 8–12 × 2.5–4 mm, accrescent, dehiscent along dorsal surface, calyx persistent in fruit; seeds numerous,

ovoid to ellipsoid, with many tube-shaped protuberances, $0.3\text{--}0.4 \times 0.2\text{--}0.3$ mm, dark brown to black.

Phenology. Collected in flower and fruit in February, June, July, and November.

Distribution and habitat. *Monopyle aurea* is endemic to Panama and is only known from six collections. The lowland forests (i.e., below 500 m) of the Caribbean slope where *M. aurea* is abundant is classified by Holdridge (1978) as Tropical Wet Forest. All known populations of *M. aurea* are located in the shaded understory of mature forests along streams.

Conservation and IUCN Red List Category. According to the IUCN Red List criteria (IUCN 2001) for limited geographic range (B2a, severely fragmented or known to exist at no more than five locations) and considering the uncertain future of habitat conservation in the area, *Monopyle aurea* should be listed as ER (Endangered).

Etymology. The specific epithet, *aurea*, refers to the yellow coloration of the flowers of this species. Most species of *Monopyle* are blue and the only other known species of *Monopyle* with yellow flowers is *Monopyle flava* L.E. Skog.

Paratypes. PANAMA. Coclé: area between Cano Blanco del Norte, Cano Sucio and Chorro del Río Tife, 3 Feb 1983, *G. Davidse & C. W. Hamilton 23544* (MO); Road from La Pintada to Coclesito, 7 Feb 1983, *C. Hamilton & G. Davidse 2816* (MO); Trail from Rio San Juan to Rio Tife Falls, 10 Jun 1978, *B. Hammel 3378* (MO); Caribbean side of the divide at El Copé, 4 Feb 1983, *C. Hamilton & G. Davidse 2710* (MO, L). Colón: Teck Cominco Petaquilla mining concession, 30 Nov 2007, *G. McPherson 19902* (MO).

Monopyle longicarpa J. L. Clark & Keene, sp. nov.

TYPE: PANAMA. Colón: Distrito Donoso, Conseción de Minera Panama S.A. Helipad ZP-P9, 8°51'5"N, 80°40'19"W, 391 m, 20 July 2011, *J. L. Clark & L. Martinez 12563* (holotype: US; isotype: K, MO, NY, PMA, SEL). Figure 12.

Species Diagnosis. Differs from all other *Monopyle* by the combination of villous golden indument, elongate linear fruit, and minute glandular trichomes on the margins of the corolla lobes.

Terrestrial herb, roots fibrous, shoots dorsiventral, golden to dark red at the base, internodes swollen, 20–40 cm tall, 2.5–5 mm in diameter, villous with multicellular eglandular (occasionally glandular) golden trichomes; lateral shoots absent in the axils of leaves. Leaves opposite, strongly anisophyllous; larger leaf with petioles (4–) 7–17 mm, densely villous, blade asymmetrical ovate to elliptic, base oblique, to 13 mm between bases, apex acuminate, (5.1–) 8.6–23.3 × 3.0–5.8 (–8.1) cm, subentire to serrate; adaxially dark green (occasionally suffused red), villous, abaxially dark green to maroon, villous (more so on veins); smaller leaf with petioles to 5 mm, some appearing sessile, villous; blade ovate to orbicular, base oblique (appearing equilateral), apex acuminate to cuspidate, 0.9–2.4 × 0.5–1.2 cm, entire to serrate towards the apex; adaxially and abaxially same as larger leaf. Inflorescence terminal, erect, compound cyme; peduncle 41.6–50.3 mm, densely villous, bracts 3–5 × 0.5–1.0 mm, persistent, opposite, adaxially nearly glabrous, abaxially villous; rachis 35.4–41.6 cm, 2–3 nodes, 2 cymules per node; secondary peduncle 5–9 mm, bracteoles 1–2 × 0.2–0.4 mm; pedicel 6–9 mm. Calyx green to maroon, lobes five, linear, 11–15 × 1–2 mm, connate 4–8 mm from base, apex acute, reflexing, abaxially villous, adaxially nearly glabrous. Corolla white with varying

amounts of violet, 18–24 × 10–13 mm, pilose with thin eglandular trichomes, minute gland-tipped trichomes on the inner dorsal surface of the tube (above androecium), osmophore present; corolla lobes with minute glandular trichomes along margin of the lobes, dorsal lobes 7–9 × 4–6 mm, ventral lobe 9–11 × 6–7 mm. Androecium with four stamens, 4–5 mm, didynamous, included, filaments 3–5 mm, adnate to corolla, anthers 0.8–1.1 × 0.5–0.7 mm, connivent for up to 1 mm. Nectary usually absent, some flowers with small amounts of raised tissue at the base of the ovary. Gynoecium with ovary subinferior, to 1.6 mm wide, densely pilose with eglandular trichomes (mainly at the apex near the base of the style), style to 5.6 mm, glabrous, stigma stomatomorphic with a flap of tissue surrounding the dorsal surface. Fruits 13–25 × 2–2.5 mm, accrescent, dehiscing along dorsal surface, calyx persistent in fruit; seeds numerous, ovoid to ellipsoid, with many tube-shaped protuberances, 0.3–0.5 × 0.2–0.5 mm, dark brown to black.

Paratypes. PANAMA. Colón: Distrito Donoso. Área del proyecto minero Petaquilla, Valle Grande, Río Petaquilla, 7 Jun 2009, *B. Araúz, P. Moreno & J. I. González 1870* (MO).

Distribution and habitat. *Monopyle longicarpa* is endemic to Panama and is only known from two collections near the type locality in the Colón province. The lowland forests (i.e., below 500 m) of the Caribbean slope where *M. longicarpa* is abundant is classified by Holdridge (1978) as Tropical Wet Forest. *Monopyle longicarpa* grows in the shaded understory of mature forests along streams.

Phenology. Collected in flower and fruit in June and July.

Etymology. The specific epithet, *longicarpa*, refers to the elongate linear fruit (Fig. 12C).

Conservation and IUCN Red List Category. The only known populations of *Monopyle longicarpa* are located inside a region that will be developed for a copper mine by the Conseción de Minera Panama S.A. There are no known populations outside the copper mine concession and therefore significant efforts are being implemented by the Conseción de Minera Panama S.A. to cultivate and transplant *Monopyle longicarpa*. These conservation efforts are ongoing for *Monopyle longicarpa* and other species as a way to mitigate the impacts of losing biodiversity when the mine is implemented. According to the IUCN Red List criteria (IUCN 2001) for limited geographic range (B2a, less than 10 km² and known to exist at only a single location) and considering the uncertain future of the region, *Monopyle longicarpa* should be listed in the category CR (Critically Endangered).

Monopyle longicarpa is easily differentiated from all other congeners by the presence of elongate fruits that reach 2.5 cm in length (Fig. 12C). Most fruits of *Monopyle* are less than 1.5 cm in length. *Monopyle longicarpa* is vegetatively distinct by the presence of villous gold indument in contrast to the pilose and dark-brown to black indument in other species of *Monopyle*.

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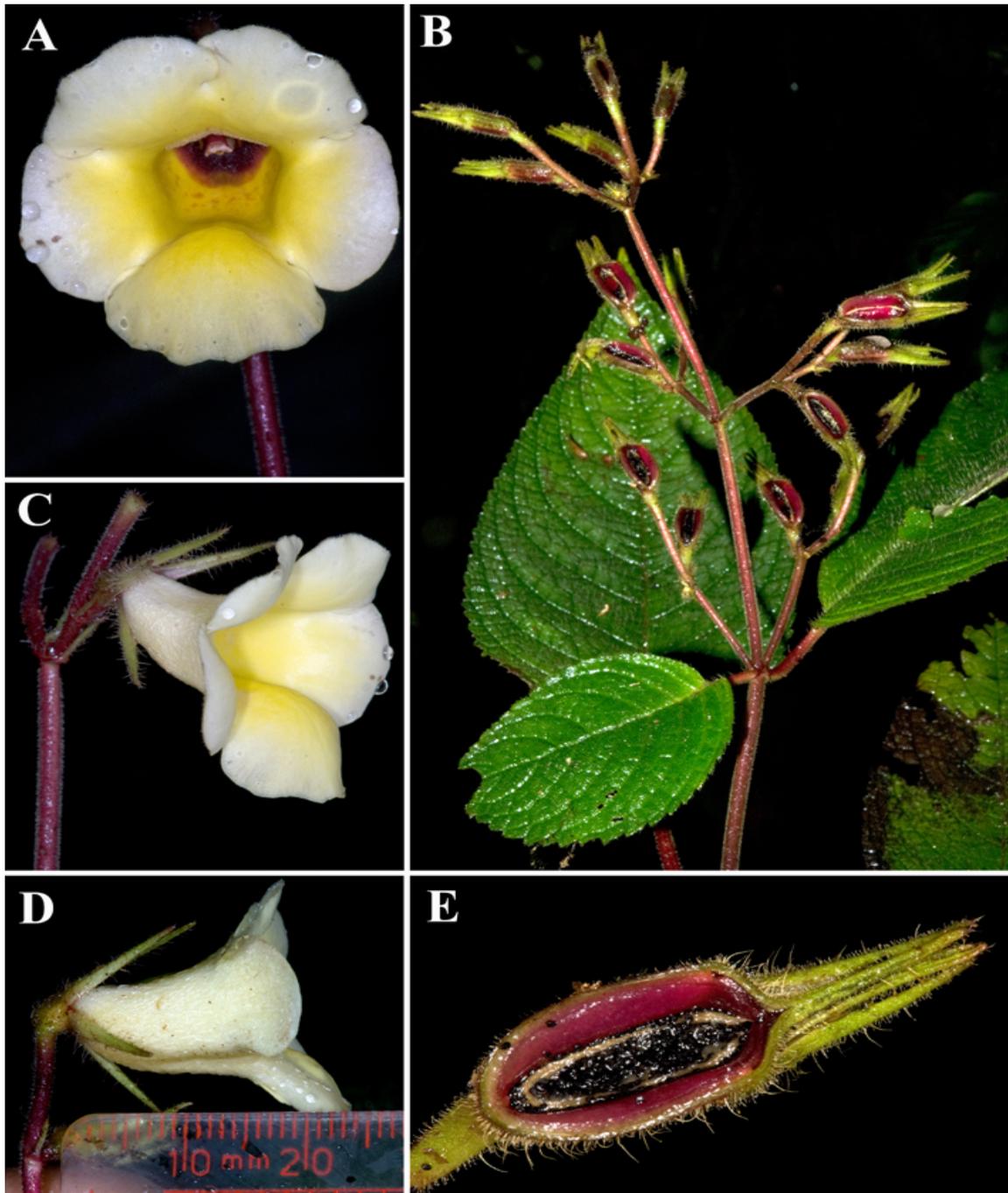


Figure 11. *Monopyle aurea*. A. Face view of flower showing maroon colored osmophore. B. Habit showing infructescence. C & D. Lateral view of flower. E. Mature fruit showing dorsal dehiscence. (Photos by J. L. Clark; voucher from the holotype, J. L. Clark & L. Martinez 12564 at US).



Figure 12. *Monopyle longicarpa*. A & B. Lateral view of flower. C. Mature fruit showing dorsal dehiscence. D. Immature fruit. E. Habit showing dorsiventral shoot and anisophyllous leaves. (Photos by J.L. Clark; voucher from the holotype: J. L. Clark & L. Martinez 12563 at US).

CHAPTER 6: TAXONOMIC SYNOPSIS OF MONOPYLE.

Monopyle Moritz ex Benth. is an assemblage of 101 species and an infraspecific taxon, and is the largest member of the Gloxinieae tribe. The genus has been studied to a limited extent, and species diversity up to this point has been grossly underestimated. The following treatment is based on the study of herbarium specimens and live material from many South and Central American collections that are housed around the world (see Chapter 2). Dichotomous keys and short descriptions of the species are included to provide a starting point for a systematic revision of the genus. With almost no taxonomic overlap between Central America and South America, separate keys address taxa in those regions. In addition, the diversity of species in the latter region is large and many taxa are endemic to an individual country, separate keys to particular South American countries have been developed to make identifying specimens easier and more efficient for the lay taxonomist. The new taxa described herein are not yet validly published; they are either in press or will be published in an upcoming revision of the genus.

Monopyle Moritz ex Benth.

Gen. Pl. 2. 997. 1876.

Scoliotheca Baill. Bull. Mens. Soc. Linn. Paris 1: 724.

Herbs or suffrutescent herbs, terrestrial or facultative epiphytes. Roots fibrous. Scaly rhizomes sometimes present, likely stress-induced. Indument of uncinata, septate, glandular, and/or simple trichomes. Stems erect to ascending (often dorsiventral), internodes swollen, subglabrous to densely pubescent, nodal ridge present between petiole bases. Leaves opposite, anisophyllous, lamina asymmetrical, base oblique to nearly equilateral, apex acute to acuminate, margins subentire to coarsely serrate with a

veinlet terminating in a gland in each tooth, adaxially green to red, abaxially green to dark red (purple), subglabrous to densely pubescent. Inflorescence axillary to terminal, composed of cymules, bracts persistent, opposite. Calyx of five sepals, variably fused at the base, lobes free, linear to suborbicular. Corolla of five petals, fused at the base, campanulate and variably gibbous ventrally, lobes free, white, yellow, or pink to purple (occasionally spotted); corolla tube glabrous to densely pubescent on the exterior, with glandular trichomes dorsally on the interior, lobes glabrous to sparsely pubescent on the margins, osmophore located at the base of the throat in the corolla (usually brightly colored). Androecium of four didynamous stamens, included, adnate to corolla. Gynoecium of two carpels, ovary subinferior, with partial rim of presumably nectariferous tissue adjacent to corolla insertion, style thin, glabrous to moderately pubescent, stigma stomatomorphic. Fruit a fleshy capsule, green to orange or red, linear to orbicular, dehiscing along a single dorsal suture to form a splash cup, calyx lobes persistent in fruit, usually accrescent. Seeds numerous, dark brown to black, ovoid to ellipsoid, with many tubercles.

Synopsis Notes

Specimen lists may only indicate exemplar specimens from each geographic area, especially if many specimens were available. All corolla pubescence characters refer to the external surfaces, unless noted otherwise; colored trichomes contribute to flower color reports (see *M. confusa* var. *mocoaensis*). Habitat and elevation information are compiled from all specimens seen. For specimens that are particularly difficult to distinguish, notes are provided to help identification.

Key to *Monopyle* of Central America.

Recent hybridization events between some species may decrease the utility of the key. This is especially true for some forms of *M. maxonii* C.V. Morton, which are putative hybrids with *M. longicarpa* J.L. Clark & Keene. These specimens typically have the indument and longer fruit of *M. longicarpa*. *Monopyle macrocarpa* as circumscribed here is excluded from this key, being geographically restricted to southern Ecuador and northern Peru.

1. Flowers yellow or cream, sometimes with red or purple markings in the throat.
 2. Flower white suffused with yellow in the throat and on the lobes, base of the throat maroon; glandular trichomes on the margins of the lobes; lateral shoots present.
 2. *M. aurea*
 - 2'. Flower yellow to cream with purple spots at the base of the throat; glandular trichomes absent; lateral shoots absent.
 4. *M. dichotoma*
- 1'. Flowers white with pink or purple markings on the lobes or in the throat.
 3. Plants without uncinata trichomes.
 4. Plants with a golden villous indument; glandular trichomes absent; fruits 21–30 mm long.
 9. *M. longicarpa*
 - 4'. Plants with golden strigose trichomes on the inflorescence only; glandular trichomes present throughout; fruits less than 20 mm long.
 12. *M. panamensis*
 - 3'. Plants with uncinata trichomes, on stem, leaves, and/or inflorescence.
 5. Leaves mammillate.
 6. Flowers white with yellow throat; plants densely pubescent; mammillation strongly pronounced.
 10. *M. mammillata*
 - 6'. Flowers white with purple markings on lobes; plants pubescent but not densely so; mammillation subtle, apparent with magnification.
 1. *M. attenuata*
 - 5'. Leaves not mammillate.
 7. Corolla large, 28–40 mm long, corolla tube abruptly deflexed then bending to horizontal.
 7. *M. grandiflora*
 - 7'. Corolla smaller, less than 28 mm long, corolla tube not abruptly deflexed.

8. Corolla pure white; large leaves generally 16–25 cm long, ovate to obovate.
9. Calyx lobes small, 3–5 mm long; inflorescence erect, open. 14. *M. sessilis*
- 9'. Calyx lobes large, 8–11 mm long; inflorescence lax. 6. *M. foliosa*
- 8'. Corolla with markings or colored lobes; leaves typically less than 16 cm long, not obovate, calyx lobes less than 8 mm long; inflorescence not lax.
10. Plants densely pilose; corolla tube exterior densely villous with long spreading trichomes. 5. *M. erecta*
- 10'. Plants glabrous or nearly so; corolla tube exterior variously pubescent with short and spreading or appressed trichomes.
11. Petioles with ciliate trichomes on the adaxial surface; calyx lobes spreading, apex recurved. 11. *M. maxonii*
- 11'. Petioles without ciliate trichomes on the adaxial surface; calyx lobes not spreading or recurved at the apex.
12. Leaves scarcely anisophyllous, similar in size.
13. Calyx lobes linear, 9–11 mm long at anthesis. 1. *M. attenuata*
- 13'. Calyx lobes ovate, 5–7 mm long at anthesis. 3. *M. ciliata*
- 12'. Leaves clearly anisophyllous.
14. Petiole of larger leaf 2.5–5 cm long; calyx lobes linear, apex acute. 8. *M. lilacina*
- 14'. Petiole of larger leaf 0.5–1.5 cm long; calyx lobes lanceolate, apex acuminate. 13. *M. puberula*

1. *Monopyle attenuata* Keene, *sp. nov.*—TYPE: *Nevers et al. 8018.*

Leaves mammillate, leaf bases nearly equilateral, peduncle to 15 cm, rachis to 6 cm, flowers nodding, white with purple spots, calyx lobes 2 to 3 times the length of the petals in bud.

Cloud forest. 100–800 m.

PANAMA. Comarca de San Blas: *Sytsma, Antonio, & Dressler 2755; Nevers, Herrera, & Gernado 8018.*

2. *Monopyle aurea* Keene & J.L. Clark, *sp. nov.*—TYPE: *J. L. Clark 12564.*

Lateral shoots present, inflorescence bracts up to 8 mm long, flowers yellow with dark maroon osmophore, with minute glandular trichomes on the margins of the corolla lobes, dark red fleshy fruit.

Tropical wet forest in the shady understory of mature forests along streams. 100–600 m.

PANAMA. Coclé: *C. Hamilton & G. Davidse 2710, 2816; B. Hammel 3378; G. Davidse & C. W. Hamilton 23544.* Colón: *J. L. Clark & L. Martinez 12564; G. McPherson 19902.*

3. *Monopyle ciliata* Keene, *sp. nov.*—TYPE: *B. Hammel 3195.*

Terrestrial herb or facultative epiphyte, leaf bases nearly equilateral, leaf margins ciliate, coarsely serrate to dentate, calyx lobes broadly lanceolate, scarcely longer than the petals in bud, buds nodding.

Tropical wet forest mostly in rocky soil along streams. 150–700 m.

PANAMA. Colón: *Hammel 3195; Antonio 3874, 3911, 3902; Sytsma, Andersson, & Dressler 4243.*

4. *Monopyle dichotoma* Keene, *sp. nov.*—TYPE: *Daniel et al. 5468.*

Lateral shoots absent, inflorescence paniculate, cymose, calyx lobes linear, twisted when dry, twice as long as petals in bud, corolla yellowish white with purple spotting in the base of throat.

Premontane to montane cloud forest. 600–1600 m.

PANAMA. Coclé: *Antonio 1127, 2091; Hammel 2577; J. P. Folsom & R. Robinson 2359; J. P. Folsom & A. Jaslon 2676; J. P. Folsom 3246; L. E. Skog, W. G. D'Arcy, & J. P. Folsom 4212; K. Sytsma & L. Andersson 4563; T. F. Daniel, F. Almeda, G. McPherson 5468; J. L. Clark 8621; J. L. Luteyn 14892.*

5. *Monopyle erecta* Keene, *sp. nov.*—TYPE: *T. B. Croat 22733.*

Lateral shoots present, calyx lobes linear, recurved at apex, corolla tube densely villous, flowers white with pink on lobes, calyx base typically red in fruit.

Premontane forest along slopes above river gorges. 500–850 m.

PANAMA. Panama: *S. Mori & J. Kallunki 4850, 4950; Nevers et al. 6297; T. B. Croat 22733; Wiehler & Dressler 71212.*

6. *Monopyle foliosa* Keene, *sp. nov.*—TYPE: *Herrera 1320.*

Leaves obovate, inflorescence lax, calyx lobes broadly elliptic, flowers white.

Habitat unknown. 500–560 m.

PANAMA. Comarca de San Blas: *Herrera 1320.*

7. *Monopyle grandiflora* Wiehler, *Selbyana* 5(1): 88–89 t. 4A. 1978.—TYPE: *H. Wiehler 5670.*

Inflorescence lax with a short peduncle, calyx lobes linear, up to 15 mm, 3–4 times longer than the petals in bud, corolla white to light purple, up to 35 mm long.

Premontane to montane forest. 700–1600 m.

PANAMA. Darién: *H. Herrera et al. 861; J. L. Reveal & J. A. Duke 4940; J. P. Folsom 4389B; W. G. D'Arcy & G. McPherson 16196.*

8. *Monopyle lilacina* (Lem.) Skog & Barrie, *comb. nov.*—TYPE: =*Chirita lilacina* Lem., *Ill. Hort.* 16: t. 608. 1869.

Leaves lanceolate to narrowly ovate, calyx lobes rounded at apex, corolla tube subglabrous, flowers white with pink on lobes.

Premontane forest. 1000–1200 m.

PANAMA. Chiriquí: *Valdespino et al. 673; B. Hammel 2186; H. W. Churchill, G. Nevers, & H. Stockwell 4735; S. Knapp 5039; T. Antonio 5104; S. Knapp & Vodicka 5572.*

9. *Monopyle longicarpa* J.L. Clark & Keene, *sp. nov.*—TYPE: *J. L. Clark & L. Martinez 12563.*

Indument villous, golden, minute glandular trichomes on the margins of the corolla lobes, flowers white with purple spotting at lobe margins, fruit elongate, linear.

Tropical wet forest in the shaded understory of mature forests along streams. 391 m.

PANAMA. Colón: *B. Araúz, P. Moreno & J. I. González 1870; J. L. Clark & L. Martinez 12563.*

10. *Monopyle mammillata* Keene, *sp. nov.*—TYPE: *J. L. Clark & I. Pizarro 12700.*

Indument densely villous, leaves mammillate, corolla white with bright yellow in the tube.

Wet forest, collected many times along the road. 300–600 m.

PANAMA. Comarca de San Blas: *G. de Nevers & C. Todzia 3533; J. L. Clark & I. Pizarro 12700.* Panama: *P. Busey 888; R. L. Liesner 1136.*

11. *Monopyle maxonii* C.V. Morton, *Publ. Field Mus. Nat. Hist. Bot. Ser. 18(4): 1183. 1938.*—TYPE: *Maxon & Harvey 7947.*

Leaves distinctly oblique with long ciliate trichomes on the adaxial surface of the petiole, calyx lobes short, triangular, recurved at the apex, flowers white to pink or purple.

Habitat. 800–1725 m.

COSTA RICA. Alajuela: *Martínez et al. 126; Herrera et al. 2028.* Cartago: *R. W. Lent 1081.* Guanacaste: *H. Wiehler et al. 9471.* Heredia: *P. C. Standley & J. Valerio 49701.* Puntarenas: *S. Koptur SK-126; W. C. Burger & J. L. Gentry, Jr. 262; W. R. Maxon 442.* PANAMA. Bocas del Toro: *G. McPherson 9549.* Chiriqui: *J. H. Kirkbride, Jr. & J. A. Duke 917.* Veraguas: *P. H. Allen 4350; K. Sytsma & L. Andersson 4600.*

12. *Monopyle panamensis* C.V. Morton, *Ann. Missouri Bot. Gard. 29(1): 58. 1942.*—TYPE: *P. H. Allen 2413.*

Internodes short, inflorescence with strigose golden trichomes, corolla white with dark purple lobes, flower deflexed.

Premontane forest. 600–1150 m.

PANAMA. Coclé: *P. H. Allen 1871; K. Sytsma & W. G. D'Arcy 3720; H. W. Churchill & G. de Nevers 4951; J. L. Clark 8756.*

Notes: This species lacks the uncinat trichomes typically found in the genus.

13. *Monopyle puberula* C.V. Morton, *Publ. Field Mus. Nat. Hist. Bot. Ser. 18(4): 1834. 1938.*—TYPE: *Maxon & Harvey 7990.*

= *Monopyle macrocarpa* var. *costaricana* Hemsl., *Biol. Cent.-Amer. Bot. 2(12): 472. 1882.*—TYPE: Endres 82.

Leaves mammillate (at low elevations), petioles very short, calyx lobes bright red (in dried material), base densely puberulent, flower white with purple lobes.

Cloud or montane forest. 200–1500 m.

COSTA RICA. Alajuela: *W. Burger & R. Baker* 9886; *A. Molina R. et al.* 17425.
 Cartago: *R. W. Lent* 1066, 1986. Guanacaste: *J. L. Chaves* 566. Limon: *G. Herrera & M. Solis* 2497. Puntarenas: *W. J. Kress & T. P. Prinzie* 94-4569; *J. R. Grant & J. R. Rundell* 92-01914. San Jose: *V. Ramírez et al.* 320; *H. Wiehler et al.* 9459.
 GUATEMALA. Alta Verapaz: *H. von Tuerckheim* 7929. PANAMA. Bocas del Toro: *H. Wiehler* W-2339. Coclé: *H. Wiehler & R. Dressler* 71258. Panama: *T. Antonio* 1113. Veraguas: *T. B. Croat* 27741.

14. *Monopyle sessilis* Keene, *sp. nov.*—TYPE: *G. de Nevers et al.* 5484.

Plants to 3 m, large leaves ~20 cm, inflorescence with 3–4 orders of branching, pedicels short, nearly sessile, flowers not deflexed in the calyx, corolla white, tube pubescent, constricted and forming a noticeable tube.

Tropical wet forest. 610–820 m.

PANAMA. Comarca de San Blas: *G. de Nevers et al.* 5484.

Key to *Monopyle* of Colombia

1. Inflorescence axillary.
 2. Corolla white, lobes densely spotted purple. 25. *M. simulans*
 - 2'. Corolla not spotted.
 3. Leaf bases often distinctly cordate; flowers small, 8–10 mm long; lower inflorescence bracts 5 mm or longer; fruit small, generally 1–1.5 cm long. 7. *M. cordata*
 - 3'. Leaf bases not distinctly cordate; flowers larger, 12 mm long or more; lower inflorescence bracts less than 5 mm; fruit larger, generally 1.5 cm or longer.
 4. Corolla white, throat yellow; calyx lobes short, ovate, ~2 mm long, blunt, apiculate, not accrescent in fruit. 1. *M. ambigua*
 - 4'. Corolla white to purple or pink; calyx lobes generally longer, lanceolate to ovate, acute to acuminate, usually accrescent in fruit.
5. Inflorescences nearly sessile in the leaf axil, with 1–3 flowers, peduncle less than 5 mm.
 6. Flowers pink, throat yellow, with maroon spots and osmophore; calyx lobes lanceolate to linear, 5 mm or less. 21. *M. mimuloides*
 - 6'. Flowers white to light blue or purple; calyx lobes lanceolate.
 7. Calyx lobes 7–11 mm long, if 7–8 mm long, flowers at least 25 mm long.
 8. Pedicels short, less than 1 cm; calyx with upper 3 lobes sometimes coherent, 10–11 mm long; flowers 10–20 mm. 16. *M. isophylla*
 - 8'. Pedicels long, (1–)1.5–3 cm; calyx without coherent lobes, 7–10 mm long; flowers 25–35 mm. 19. *M. macrantha*
 - 7'. Calyx lobes up to 7 mm long; flowers less than 25 mm long.
 9. Calyx lobes 6–7 mm long, glandular trichomes present; pedicels not elongating in fruit. 29. *M. uniflora*
 - 9'. Calyx lobes 3–6 mm long, glandular trichomes absent; pedicels elongating to 1 cm or more in fruit. 28. *M. turbinata*

5'. Inflorescences clearly pedunculate, with more than 3 flowers, peduncle 1 cm or more.

10. Peduncle generally 1 cm long; 3–6 flowers per inflorescence.

24. *M. rugosa*

10'. Peduncle usually at least 2 cm long; 3–20+ flowers per inflorescence.

11. Inflorescence with 1 order of branching.

28. *M. turbinata*

11'. Inflorescence with more than 1 order of branching.

12. Inflorescence strict, upright, usually 4–5 orders of branching; fruit constricted at the top of the ovary.

5. *M. candelabra*

12'. Inflorescences somewhat lax, usually 2–3 orders of branching; fruit not constricted at the top of the ovary.

13. Flowers white; fruit ovoid, 1(–1.5) cm long.

6a. *M. confusa* var. *confusa*

13'. Flowers purple on lobes; fruit cylindrical, (1.2–)1.5–2 cm long.

23. *M. pustulata*

1'. Inflorescence terminal.

14. Leaves clearly mammillate.

15. Petioles relatively short, generally less than 1.5 cm on larger leaf; calyx lobes lance-ovate, 1(–1.5) mm at the base; style 5 mm; corolla not seen.

3. *M. aspera*

15'. Petioles of larger leaves generally more than 3 cm; calyx lobes ovate, 2–3 mm wide at the base; flowers large, 2.5–3 cm long; style 10 mm long.

22. *M. ovata*

14'. Leaves not obviously mammillate.

16. Petioles of larger leaves generally more than 3 cm.

17. Lower inflorescence bracts ~1 cm long × 1–2 mm wide, lanceolate.

18. *M. longibractea*

17'. Lower inflorescence bracts usually < 6 mm long × < 1 mm wide, linear.

18. Calyx lobes linear, aristate, with spreading villous trichomes, 0.8–1.1 cm long at anthesis, not accrescent in fruit.

2. *M. aristata*

18'. Calyx lobes lanceolate to rounded, never aristate, without villous trichomes, generally not more than 6 mm long at anthesis, accrescent in fruit.

7. *M. cordata*

16'. Petioles shorter, generally less than 3 cm.

19. Calyx distinctly campanulate, lobes 4–5 mm across at the base, broadly deltoid.

4. *M. campanulata*

19'. Calyx not campanulate, lobes linear to ovate, but never broadly deltoid.

20. Inflorescences lax and open with 3–6 orders of branching.

21. Calyx lobes spreading or reflexed, linear; flowers white or pink, 1.5 cm long.

22. Flowers pink; plants of low elevation, 100 meters or less.

26. *M. stellata*

22'. Flowers white; plants of high elevation, 1350–1750 meters.

6a. *M. confusa* var. *confusa*

21'. Calyx lobes not spreading or reflexed; flowers lavender, 2 cm long.

23. Calyx lobes lanceolate, apex blunt to acute, never attenuate.

8. *M. cylindrica*

23'. Calyx lobes lanceolate-linear, apex attenuate.

12. *M. gracilis*

20'. Inflorescences often with less than 3 orders of branching, either upright and often appearing fascicled or pseudoverticillate, or reduced with relatively few flowers.

24. Inflorescences reduced with 1–2 flowers.

25. Upper leaf surface with septate and pilose uncinata trichomes.

26. Flowers with purple corolla lobes; fruit cylindrical, 1.5–2 cm long.

24. *M. rugosa*

26'. Flowers white; fruit ellipsoid, base strongly gibbous, 1–1.4 cm long.

6b. *M. confusa* var. *mocoensis*

25'. Upper leaf surface without uncinata trichomes.

27. Upper leaf surface with some glandular trichomes (often broken off); petioles of larger leaves usually more than 1 cm; flowers 1.0–1.5 cm long, not open campanulate.

23. *M. pustulata*

27'. Upper leaf surface without glandular trichomes; petiole of larger leaves rarely reaching 1 cm, usually less than 5 mm; flowers 1.5–2.5 cm long, open campanulate.

19. *M. macrantha*

24'. Inflorescences with more than 2 flowers, appearing fascicled or pseudoverticillate.

28. Lower inflorescence bracts ~1 cm long.

18. *M. longibractea*

28'. Lower inflorescence bracts < 5 mm long.

29. Calyx lobes linear, aristate, with spreading villous trichomes, 0.8–1.1 cm long at anthesis, not accrescent in fruit.

2. *M. aristata*

29'. Calyx lobes lanceolate to rounded, not aristate, with or without spreading trichomes, generally not more than 6 mm long at anthesis, accrescent or not in fruit.

30. Calyx lobes ovate, relatively short and broad, ≤ 2 times as long as wide, apex rounded to acute.

31. Flowers yellow; calyx lobes 3–4 mm long \times 2.5–4 mm wide.

11. *M. geniculata*

31'. Flowers white; calyx lobes 1–3 long \times 1–2 wide.

1. *M. ambigua*

30'. Calyx lobes lanceolate to ovate, more than twice as long as wide, apex acute to acuminate.

32. Stem, petiole, and peduncle with spreading villous trichomes.

33. Upper leaf surface with villous uncinata and long septate trichomes; petiole and calyx with long glandular trichomes.

27. *M. tenuis*

33'. Upper leaf surface with septate trichomes only, glandular trichomes absent.

34. Petioles short, less than 1 cm; lower leaf surface without uncinata trichomes.

13. *M. hirticalyx*

34'. Petioles longer, 1–4 cm long; lower leaf surface with uncinata trichomes.

20. *M. macrophylla*

32'. Stem, petiole, and peduncle without spreading villous trichomes.

35. Corolla lobes heavily spotted with purple. 25. *M. simulans*
- 35'. Corolla lobes white to violet, not spotted.
36. Leaves subsessile to short petiolate, petioles less than 1 cm long.
37. Stems with a mixture of pilose uncinata and long septate trichomes. 15. *M. incerta*
- 37'. Stems with pilose uncinata trichomes only or only a few septate trichomes.
38. Calyx lobes and corolla with septate, glandular trichomes.
39. Secondary peduncles short, less than 1 cm; inflorescences condensed, appearing fasciculate; corolla open campanulate, 1 cm wide or more at the base. 9. *M. fasciculata*
- 39'. Secondary peduncles more than 1 cm; inflorescence open, with 2 or more orders of branching; corolla narrow, campanulate, less than 1 cm wide at the base. 14. *M. inaequalis*
- 38'. Calyx lobes and corolla lacking septate, glandular trichomes.
40. Large leaves with short petioles, 1 cm or less; pedicels in fruit 1 cm or less; calyx lobes broad, ovate, acute. 10. *M. foreroi*
- 40'. Large leaves with long petioles, typically 2 cm or more; pedicels in fruit 1.5 cm or more; calyx lobes lanceolate to lance-ovate, attenuate. 8. *M. cuneata*
- 36'. Leaves with petioles of largest leaves more than 1 cm long.
41. Calyx pubescence of pilose uncinata trichomes only. 5. *M. candelabra*
- 41'. Calyx pubescence of pilose uncinata and long-septate glandular trichomes.
42. Corolla white, usually less than 1 cm long. 17. *M. leucantha*
- 42'. Corolla with purple lobes, usually at least 1 cm long. 28. *M. turbinata*

1. *Monopyle ambigua* Keene, *sp. nov.*—TYPE: *G. Davidse, A. Gentry, & F. Llanos 5628.*

Petioles up to 5 cm, inflorescences axillary and terminal, calyx lobes blunt, flowers white, trichomes with pustulate bases on the exterior of the corolla tube.

Forest edge along stream in montane forest. 1150–1900 m.

COLOMBIA. Caquetá: *X. Londono & L. P. Kvist 156; G. Davidse, A. Gentry, & F. Llanos 5628; J. Cuatrecasas 9154.*

2. *Monopyle aristata* Keene, *sp. nov.*—TYPE: *J. W. L. Robinson 341.*

Indument villous (especially pronounced on the calyces), calyx lobes long, narrow, corolla tube densely villous, white with pink to purple lobes.

Tropical wet forest along road banks. 100–220 m.

COLOMBIA. Chocó: *J. W. L. Robinson 341; E. Forero & A. Gentry 700; E. Forero et al. 5429, 5558, 5789; A. Gentry & M. Fallen 17448; A. Gentry & E. Renteria 24111.*

3. *Monopyle aspera* Keene, *sp. nov.*—TYPE: *O. de Benavides 10394.*

Leaves mammillate, petioles ~ 1 cm, inflorescence terminal with short secondary branches, calyx globose in bud, densely pubescent, flowers white with lavender lobes, fruit small, cylindrical.

Roadside. 320 m.

COLOMBIA. Nariño: *O. de Benavides 10394.*

4. *Monopyle campanulata* Keene, *sp. nov.*—TYPE: *A. Juncosa 1476.*

Inflorescence bracts broadly ovate, calyx campanulate, upper three lobes fused, broadly ovate to obovate, apex acute, corolla white, lobes magenta to purple, throat spotted purple in the base.

Wet forest along stream edges. 80–900 m.

COLOMBIA. Chocó: *A. Juncosa 1360, 1476.* Valle del Cauca: *S. Vogel 113; M. Amaya & J.F. Smith 610; H. Wiehler 7243; J. Cuatrecasas 13738.*

5. *Monopyle candelabra* Keene, *sp. nov.*—TYPE: *R. Fonnegra et al. 4185.*

Petioles up to 4 cm long, inflorescences axillary and terminal, with up to 5 orders of branching, calyx lobes lanceolate, dark red (in herbarium material), corolla tube white, lobes purple, style densely pubescent, fruit strongly gibbous, urceolate to turbinate.

Habitat unknown. 800–1150 m.

COLOMBIA. Antioquia: *D. Cadenas L. et al. 3095*; *R. Fonnegra et al. 4185*.

6a. *Monopyle confusa* Keene, *sp. nov.* var. *confusa*—TYPE: *J. A. Ewan 16691*.

Petioles ~2 cm, inflorescence axillary to terminal, 3–5 orders of branching, peduncles long, calyx lobes deltoid, flowers white.

Wet forest on steep slopes. 1420–1750 m.

COLOMBIA. Putumayo: *J. L. Fernández A. et al. 11042*; *J. A. Ewan 16691*; *F. R. Fosberg 20385*.

6b. *Monopyle confusa* var. *mocoaensis* Keene, *var. nov.*—TYPE: *R. E. Schultes & C. E. Smith 2017*.

Petioles ~2 cm, inflorescence axillary to terminal, two orders of branching, peduncles long, calyx lobes broad, deltoid, flowers white, tube exterior blush pink.

Wet forest on steep slopes. 600–850 m.

COLOMBIA. Putumayo: *R. E. Schultes & C. E. Smith 2017*; *J. Cuatrecasas 11398*.

7. *Monopyle cordata* Keene, *sp. nov.*—TYPE: *Callejas et al. 4586*.

Petioles ~4.5 cm, leaf bases subcordate, inflorescences terminal with up to 4 orders of branching, bracts large, leaf-like, glandular trichomes on the calyx, flowers white, lobes suffused with pink, fruit small, ovoid.

Humid tropical forest in damp streambeds. 310–700 m.

COLOMBIA. Antioquia: *Alverson et al. 268*; *D. D. Soejarto 2891*; *Callejas et al. 4586*.

8. *Monopyle cuneata* Keene, *sp. nov.*—TYPE: *M. Amaya & L. P. Kvist 460*.

Leaves with long petioles (> 2 cm); pedicels in fruit > 1.5 cm; calyx lobes lanceolate to lance-ovate, attenuate.

Habitat unknown. 1400 m.

COLOMBIA. Chocó: *M. Amaya & L. P. Kvist 460*.

9. *Monopyle cylindrica* Keene, *sp. nov.*—TYPE: *Cogollo et al. 4061*.

Plants glabrescent, petiole ~1 cm, inflorescence terminal with long peduncles, up to 4 orders of branching, bracts lanceolate, corolla white to pale purple, lobes with purple edges, fruit slightly gibbous, narrowly cylindrical.

Growing on and between rocks along a stream. 1460 m.

COLOMBIA. Antioquia: *Cogollo et al. 4061*; *Wiehler et al. 8764*.

10. *Monopyle fasciculata* Keene, *sp. nov.*—TYPE: *O. Haught 5213*.

Leaves nearly sessile, petioles very short, inflorescence with cymules reduced to short fascicles, calyx lobes lanceolate, corolla white or pale violet, large, ~25 mm long, Habitat unknown. 1000 m.

COLOMBIA. Valle del Cauca: *O. Haught 5213*.

11. *Monopyle foreroi* Keene, *sp. nov.*—TYPE: *E. Forero et al. 6053*.

Leaf lamina distinctly asymmetrical, petioles ~1 cm, inflorescence terminal with little branching, calyx lobes obovate to elliptic, corolla white, lobes purple.

Growing near streams. 520–1400 m.

COLOMBIA. Chocó: *M. Amaya & L.P. Kvist 460; Forero et al. 6053*.

12. *Monopyle geniculata* Keene, *sp. nov.*—TYPE: *Croat & Watt 70453*.

Leaves broadly ovate to elliptic, calyx lobes orbicular to broadly ovate, apex blunt, corolla yellow, fruit base geniculate.

Steep rocky cliff or road banks. 100–400 m.

COLOMBIA. Valle del Cauca: *Vogel 114; Devia 576; M. Amaya & Smith 607; Smith et al. 1412; Haught 5330; Wiehler et al. 7245; Croat & Watt 70453*.

13. *Monopyle gracilis* Keene, *sp. nov.*—TYPE: *Betancur et al. 2613*.

Petioles ~2 cm long, inflorescence terminal, up to 3 orders of branching, branches very thin, bracts short, ovate, calyx lobes linear, margins somewhat recurved, enclosing corolla until flowers open, corolla white, lobes white to purple.

Primary forest. 1500 m.

COLOMBIA. Nariño: *Betancur et al. 2613; B. R. Ramírez P. 3381*.

14. *Monopyle hirticalyx* Keene, *sp. nov.*—TYPE: *Forero et al. 3125*.

Plants densely villous, inflorescence terminal, peduncle very short, calyx base globose, lobes rounded, corolla white, lobes clear lavender, throat spotted in the base, corolla up to 20 mm long.

Forest. 600–900 m.

COLOMBIA. Chocó: *Forero et al. 3125*.

15. *Monopyle inaequalis* C.V. Morton, –TYPE: *G. Klug 1900*. *Revista Universitaria* [Cuzco] 33(87): 115. 1945.

Stems thin, weak, petioles short, adaxially verrucose, corolla spotted in the base, fruit small (< 1 cm).

Forest. 325 m.

COLOMBIA. Putumayo: *G. Klug 1900*.

Notes: This species is only known from the type specimen.

16. *Monopyle incerta* Keene, *sp. nov.* –TYPE: *Forero et al. 3338*.

Petioles short, inflorescence with two orders of branching, corolla white, lobes pale purple.

Roadside. 200–400 m.

Notes: very similar to *M. macrophylla*, but petioles much shorter, nearly sessile, inflorescence with few glandular trichomes, corolla tube white, lobes pale purple.

COLOMBIA. Chocó: *Forero et al. 3035, 3338*.

17. *Monopyle isophylla* (Benth.) Keene, comb. and stat. nov. –TYPE: *Spruce s.n.* = *Monopyle macrocarpa* var. *isophylla* Benth. *Icones Plantarum* 12: 85, t. 1198. 1876.

Inflorescence terminal or axillary (predominantly axillary), calyx lobes at least 2 times longer than the petals in bud, and equal in length to the fruit, corolla white, lobes light to dark purple.

Forest. 0–793 m.

COLOMBIA. Nariño: *A. H. G. Alston 8494*.

18. *Monopyle leucantha* Moritz ex Benth. *Icones Plantarum* 12: 87. 1876. –TYPE: Moritz 868.

Leaves distinctly petiolate, primary peduncle long (up to 12 cm), flowers in fascicles on the secondary peduncle, calyx lobes short, ovate, apex blunt, flowers small, 1–2 cm long, corolla white with pink, lobes white.

Dense woods, along streams. 1800–2600 m.

COLOMBIA. Boyacá: *Grubb et al. 655*. Norte de Santander: *Schlim 22; Cuatrecasas et al. 12529; Cuatrecasas 12854*. Santander: *E. P. Killip & A. C. Smith 15553, 17098, 19273*.

19. *Monopyle longibractea* Keene, *sp. nov.*—TYPE: *Lellinger & de la Sota 94*.

Bracts long and leaf-like, calyx lobes reflexed, lanceolate, base densely pubescent in flower, corolla white, lobes sometimes with purple, fruit slightly gibbous.

Along streams in lowland rainforest. 0–50 m.

COLOMBIA. Chocó: *Lellinger & de la Sota 94*; *Haught 5520*.

20. *Monopyle macrantha* Keene, *sp. nov.*—TYPE: *E. Forero & R. Jaramillo 2460*.

Petioles short (typically < 1 cm), inflorescence short, terminal, sparse, calyx lobes long, lanceolate, flowers large (~ 3 cm), corolla white to blue, lobes light purple.

Humid premontane forest. 1050–1900 m.

COLOMBIA. Antioquia: *A. Cogollo, D. Cárdenas, & O. Alvarez 3973*; *R. Fonnegra et al. 5514*; *J. P. Folsom 10617*; *J. Pipoly, W. Rodríguez, & O. Alvarez 17783*. Caldas: *K. von Sneidern 5479*. Chocó: *J. E. Ramos, P. A. Silverstone, L. H. Ramos et al. 1535*; *Forero et al. 3396*. Risaralda: *J. L. Fernández Alonzo, C. Orozco, P. Franco, J. Betancur et al. 9093*; *J. L. Fernández Alonzo et al. 10182*.

21. *Monopyle macrophylla* Benth., *Icones Plantarum* 12: 86. 1876.—TYPE: *Lobb 94*. =*M. pilosula* C.V. Morton, *Revista Universitaria [Cuzco]* 33(87): 112. 1945.—TYPE: *W.A. Archer 1802*.

Lamina of large leaf strongly asymmetrical, petioles and inflorescence with abundant long, septate, glandular trichomes, flowers purple, nearly ventricose, fruit short (< 1.5 cm), geniculate.

Very wet primary forest, along streams, typically on inclined terrain. 150–1000 m.

COLOMBIA. Chocó: *Forero et al. 3035, 3338*. Nariño: *S. Vogel 21*; *S. Bellow & J. Parra 134*. Unknown: *Lobb 94*.

22. *Monopyle mimuloides* Keene, *sp. nov.*—TYPE: *T. B. Croat & J. Watt 70414*.

Stems densely puberulent, inflorescences reduced, axillary, with 1–3 flowers, corolla pink, throat yellow with maroon spots and osmophore, calyx lobes short, 5 mm or less.

Wet slopes or cliffs. 145–900 m.

COLOMBIA. Valle del Cauca: *M. Amaya & J. F. Smith 608*; *E. P. Killip 5363, 5383*; *T. B. Croat & J. Watt 70414*.

23. *Monopyle ovata* Keene, *sp. nov.*—TYPE: *F. J. Roldán et al. 744.*

Leaves mammillate, petioles long on larger leaf up to 6 cm, calyx lobes ovate, 2–3 mm wide, flowers large, up to 3 cm, corolla lavender with yellow in throat spotted or not, style up to 10 mm long.

Cloud forest on slopes. 1600–1800 m.

COLOMBIA. Antioquia: *F. J. Roldán et al. 744; Cogollo et al. 3981; A. Gentry & E. Renteria A. 24549, 24550; Gentry et al. 76144.*

24. *Monopyle pustulata* Keene, *sp. nov.*—TYPE: *R. Callejas et al. 4262.*

Corolla tube pubescent, trichomes with pustulate base, peduncles long, up to 12.5 cm, calyx lobes spreading, typically dark red outside to light tan inside, corolla white, lobes dark purple.

Secondary forest and pasture. 1200–1980 m.

COLOMBIA. Antioquia: *Kalbreyer 1309; A. Juncosa 1385; B. Daniel 1495; R. Fonnegra et al. 4136; R. Callejas et al. 4262; B. Daniel 4496; G. Gutierrez 35566.*

25. *Monopyle rugosa* Keene, *sp. nov.*—TYPE: *D.L. Hugh-Jones 438.*

Lamina adaxially rugose, inflorescence axillary, peduncle ~2 cm, calyx lobes equaling length of petals in bud, corolla spotted red/pink, lobes purple.

Along roadsides on banks and rocky cliffs. 300–1000 m.

COLOMBIA. Antioquia: *E. P. Killip 11453, 35607.* Valle del Cauca: *A. R. Bridgeman 195; D. L. Hugh-Jones 438; J. F. Smith, R. Bernal, X. Londono, W. Devia 1453; E. André 2506; F. C. Lehmann 5838.*

26. *Monopyle simulans* Keene, *sp. nov.*—TYPE: *J. Cuatrecasas 11399.*

Lamina adaxial surface pubescent with minute uncinata trichomes intermixed with intermediate septate trichomes, corolla white, lobes spotted purple, tube with pustular based trichomes.

Roadsides and disturbed mountain forest along ravines. 560–700 m.

COLOMBIA. Caquetá: *Londono & Kvist 135; A. Gentry, G. Davidse, & F. Llanos 9156.* Putumayo: *J. M. Idrobo & M. Ospina-Hernández 2382; J. Cuatrecasas 11399.*

27. *Monopyle stellata* Keene, *sp. nov.*—TYPE: *F. García C. & E. D. Agualimpia 330.*

Inflorescence open, with 3 or more orders of branching, calyx lobes spreading, linear, flowers small, pink, up to 1.5 cm.

Primary forest. 0–100 m.

COLOMBIA. Choco: *Warner 285; F. García C. & E. D. Agualimpia 330.*

28. *Monopyle tenuis* Keene, *sp. nov.*—TYPE: *M. Amaya & L. P. Kvist 429.*

Indument villous, leaves bullate, without minute uncinata trichomes on abaxial surface, inflorescence terminal, lax with thin pedicels, flowers purple, tube white, fruit small, gibbous at the base.

Humid forest. 400 m.

COLOMBIA. Antioquia: *W. Johnson & F. A. Barkley 18C538A.* Chocó: *M. Amaya & L. P. Kvist 429.*

29. *Monopyle turbinata* Keene, *sp. nov.*—TYPE: *J. Cuatrecasas 15554.*

Lower leaves nearly isophyllous, inflorescences terminal (occasionally appearing axillary), flowers tube white, lobes light purple, fruit strongly gibbous, turbinate.

High forested fronts growing on moss cover boulders in streams. 100–1400 m.

COLOMBIA. Bolivar: *J. Cuatrecasas 15554.* Boyacá: *A. E. Lawrance 701.* Santander: *O. Haught 1942.*

30. *Monopyle uniflora* J.L. Clark & Keene, *J. Bot. Res. Inst. Texas* 5(2): 517–520, f. 2A, 3, 4A–C. 2011.—TYPE: *J. L. Clark & Gesneriad Research Expedition Participants 11162.*

Inflorescences axillary with few flowers (1–2 per cyme), bracts basally appressed, flowers white to light lavender with yellow in the throat.

Flat forest and humid tropical primary forest. 87–300 m.

COLOMBIA. *M. Amaya & J. F. Smith 599; E. P. Killip 34854.*

Key to *Monopyle* of Ecuador

1. Flowers yellow. 14. *M. flava*
- 1'. Flowers not yellow.
2. Leaves mammillate.
3. Inflorescences axillary, flowers solitary. 35. *M. trachyphylla*
- 3'. Inflorescences terminal, flowers more than one.
4. Calyx lobes fimbriate, upper three partially connate. 16. *M. inopinata*
- 4'. Calyx lobes not fimbriate, not partially connate.
5. Calyx lobes ovate; flowers white with purple lobes. 22. *M. mexiae*
- 5'. Calyx lobes lanceolate; flowers white. 30. *M. rubicunda*
- 2'. Leaves not mammillate.
6. Inflorescences axillary.
7. Stems pubescent with longer trichomes to 1 mm or more.
8. Stems and calyx lobes densely pubescent with red trichomes, more than 1 mm long. 12. *M. erythrochaete*
- 8'. Stems and calyx lobes moderately pubescent, pubescence not red, usually not more than 1 mm.
9. Flowers white, heavily spotted purple. 6. *M. chrysotricha*
- 9'. Flowers white, not spotted. 23. *M. multiflora*
- 7'. Stems glabrescent or pubescent with short trichomes, less than 1 mm.
10. Calyx without glandular trichomes; flowers white with purple spots. 4. *M. axillaris*
- 10'. Calyx with glandular trichomes; flower white with purplish lobes, but lacking spots.
11. Peduncles short, up to 2 mm in flower. 36. *M. uniflora*
- 11'. Peduncles longer, up to 5 mm or more in flower. 26. *M. parviflora*
- 6'. Inflorescences terminal.

12. Calyx lobes fimbriate.
13. Bracts small, narrow; calyx lobes not connate. 13. *M. fimbriicalyx*
- 13'. Bracts broadly ovate; upper calyx lobes connate.
14. Stems pubescent with long, spreading trichomes. 9. *M. connata*
- 14'. Stems pubescent with short, appressed trichomes. 24. *M. obscura*
- 12'. Calyx not fimbriate.
15. Calyx lobes ovate.
16. Flowers white, heavily spotted purple. 21. *M. maculata*
- 16'. Flowers white to purple, but not heavily spotted.
17. Calyx lobes abruptly acuminate; style pubescent.
18. Large leaves subsessile, petioles < 5 mm long. 34. *M. subsessilis*
- 18'. Large leaves petiolate, petioles generally 1 cm or longer. 11. *M. ecuadorensis*
- 17'. Calyx lobes acuminate, but not abruptly so; style glabrous.
19. Leaf edge pubescent with long septate (4-10 septae) trichomes. 29. *M. robusta*
- 19'. Leaf edge pubescent but trichomes with few or no septae (0-1).
20. Indument moderately to densely puberulent with uncinata trichomes. 34. *M. subsessilis*
- 20'. Indument not as above.
21. Upper surface with regularly distributed bulbous based and uncinata trichomes; petioles of mature large leaves short, up to 5 mm; some leaf bases rounded to acute; bracts ovate; glandular trichomes absent on corolla margin. 18. *M. iserniana*

21'. Upper surface glabrescent, very sparsely pubescent with bulbous based and uncinata trichomes; petioles of mature large leaves longer, typically 10 mm or more; leaf bases very strongly oblique and attenuate to cuneate; short glandular trichomes at the corolla margin.

2. *M. archidonaensis*

15'. Calyx lobes lanceolate to linear, not ovate.

22. Flowers less than 1 cm long.

23. Upper leaf surface glabrescent, occasionally with long, septate trichomes; flower urceolate, lobes not spreading or recurved.

37. *M. urceolata*

23'. Upper leaf surface pubescent, with intermixed small uncinata and long septate trichomes; flower campanulate, lobes spreading, recurved.

1. *M. albiflora*

22'. Flowers more than 1 cm long.

24. Calyx lobes short, 2–3 mm long.

25. Larger leaves 10 cm wide, leaf base only slightly oblique, both sides cordate.

27. *M. pedunculata*

25'. Larger leaves 8 cm wide, most leaf bases strongly oblique, typically only one side cordate.

26. *M. parviflora*

24'. Calyx lobes more than 3 mm long.

26. Calyx lobes linear, more than 1 cm long.

27. Lower leaf surface with short, uncinata trichomes.

19. *M. linearis*

27'. Lower leaf surface with long, septate trichomes.

33. *M. subintegerrima*

26'. Calyx lobes various, less than 1 cm long.

28. Inflorescences pseudoverticillate.

29. Plants of low elevation (400–600 m); calyx lobes narrowly lanceolate, calyx strongly verrucose in fruit.

38. *M. verrucosa*

29'. Plants of mid elevation (1500 m); calyx lobes lanceolate to lanceovate, calyx not verrucose in fruit.

3. *M. awaensis*

28'. Inflorescences not pseudoverticillate.

30. Corolla lobes heavily spotted with irregular large blotches, red to purple.

31. Leaves densely pubescent adaxially with uncinata and long septate trichomes; inflorescence an open paniculate cyme, lower secondary peduncles generally more than 2 cm long; fruit not verrucose.

25. *M. paniculata*

31'. Leaves glabrescent with a few scattered septate trichomes; inflorescence with congested, reduced paniculate cymes at each node, lower secondary peduncles less than or equal to 1 cm; fruit verrucose.

7. *M. clarkii*

30'. Corolla lobes not heavily spotted with irregular large blotches, smaller spots or lines present in some species.

32. Plants densely villous with long, septate trichomes; pubescence on corolla septate, 1.8–2.0 mm long.

10. *M. dolichothrix*

32'. Plants not densely villous; pubescence on corolla generally less than 1 mm long.

33. Upper leaf surface of mature leaves with a mixture of uncinata and septate trichomes.

34. Calyx with uncinata and long, septate trichomes.

35. Calyx with glandular trichomes.

15. *M. glandulosa*

35'. Calyx lacking glandular trichomes.

29. *M. robusta*

34'. Calyx with uncinata trichomes only.

36. Upper leaf surface of mature leaves sparsely pubescent, typically with only septate (glandular) trichomes on margin; calyx lobes lance-elliptic, acute, scarcely exceeding the corolla in bud; style densely pubescent.

5. *M. bilsaensis*

36'. Upper leaf surface of mature leaves sparsely to moderately pubescent, typically with intermixed pilose uncinata and long septate trichomes lacking glands; calyx lobes lance-linear, long attenuate, up to twice as long as the corolla in bud; style glabrous.

M. communis hyb.

33'. Upper leaf of mature leaves glabrescent to sparsely pubescent with septate trichomes, uncinata trichomes absent.

37. Stem glabrescent or essentially glabrous.

8. *M. communis*

37'. Stem sparsely to densely pubescent with uncinata trichomes.

38. Calyx and fruit with glandular trichomes. 32. *M. stenoloba*
- 38'. Calyx and fruit lacking glandular trichomes.
39. Corolla tube white, only lower lobes with purple markings or markings absent. 31. *M. sodiroana*
- 39'. Corolla tube white with all lobes purple to violet.
40. Calyx lobes lanceolate, even in bud, 6–8 mm long; stems and leaves not trapping dirt. 28. *M. pubescens*
- 40'. Calyx lobes lanceolate, lance-ovate in bud, 4–6 mm long; stems and leaves trapping dirt (plants appear muddy or dirty). 17. *M. inquinata*

1. *Monopyle albiflora* Keene, *sp. nov.*—TYPE: *J. L. Clark & C. Morocho 5872*.

Peduncle short (< 4 cm), calyx lobes lanceolate, densely puberulent, exceeding the ovary apex at anthesis, flowers white, tubular, nodding.

Premontane wet to moist forest. 1200–1800 m.

ECUADOR. Morona-Santiago: *J. L. Clark & C. Morocho 5872*; *J. L. Clark et al. 9887, 9892, 9896, 9916*; *Wiehler et al. 88182*.

2. *Monopyle archidonaensis* Keene, *sp. nov.*—TYPE: *J. L. Clark et al. 7216*.

Leaves glabrescent adaxially, leaf base attenuate, inflorescence terminal, 2–4 orders of branching, bracts broad ovate to elliptic, corolla white, lobes purple, small glandular trichomes on at the margins.

Premontane wet forest. 650–1690 m.

ECUADOR. Napo: *D. Cuamacás 107*; *D. Neill et al. 14284*.

3. *Monopyle awaensis* Keene, *sp. nov.*—TYPE: *Rubio et al. 893*.

Inflorescence with 2 orders of branching, calyx lobes broadly ovate, dark red maroon, corolla white, lobes purple or with purple spots.

Pluvial premontane forest. 1500 m.

ECUADOR. Carchi: *Rubio et al. 893*.

4. *Monopyle axillaris* Keene, *sp. nov.*—TYPE: *J. L. Clark et al. 7555*.

Leaves bicolorous, veins prominent, inflorescences axillary, peduncles long (~ 4 cm), corolla white, lobes heavily spotted purple to maroon, fruit linear with a gibbous base.

Steep shaded roadside embankment. 450–600 m.

ECUADOR. Esmeraldas: *J. L. Clark et al. 7091, 7555*; *H. Wiehler et al. 9008, 9063, 9526, 9548*.

5. *Monopyle bilsaensis* Keene, *sp. nov.*—TYPE: *J. L. Clark 9619*.

Leaves adaxially pilose uncinatae intermixed with long septate trichomes, inflorescence terminal (sometimes appearing axillary), 1–3 orders of branching, flowers nodding, corolla white, lobes blue to purple, throat yellow, fruit cylindrical, slightly gibbous at the base.

Premontane wet forest. 400–1150 m.

Notes: This species appears to be hybridizing with *M. communis*. The hybrids have sparsely pubescent styles or intermediate leaf pubescence. Some of the hybrids also have broadly turbinate fruit with intermediate uncinata trichomes.

ECUADOR. Esmeraldas: *N. Pitman 721; H. Wiehler et al. 9582; J. L. Clark 9619.*

6. *Monopyle chrysotricha* Keene, *sp. nov.*—TYPE: *L. P. Kvist & E. Asanza 40316.*

Indument golden, inflorescences axillary, calyx lobes green to red or red, corolla white, lobes purple or white with purple spots.

Very wet primary forest with abundant epiphytes. 50–250 m.

ECUADOR. Esmeraldas: *Yáñez et al. 1410, 1586; J. L. Clark 7190; L. P. Kvist & E. Asanza 40316, 40877.*

7. *Monopyle clarkii* Keene, *sp. nov.*—TYPE: *J. L. Clark et al. 7398.*

Inflorescence a terminal, paniculate cyme, up to 4 orders of branching, 2° branches short (≤ 1 cm), corolla white, lobes spotted blue, throat spotted purple in the base.

Premontane to montane forest. 1300–1600 m.

ECUADOR. Imbabura: *J. L. Clark et al. 7353, 7398.*

8. *Monopyle communis* Keene, *sp. nov.*—TYPE: *J. L. Clark 7122.*

Leaves with long, septate trichomes at maturity, inflorescences terminal, 3–9 orders of branching, pedicels accrescent in fruit, flowers erect, corolla white, lobes purple.

Premontane wet forest along streams. 300–1800 m.

Notes: This taxon is hybridizing along its geographic range. *Monopyle bilsaensis* and *M. communis* appear to hybridizing readily in northern Ecuador. It may also be coming into contact with *M. ecuadorensis*, as some specimens have broader calyx lobes. Specimens from above 1000 meters are much more robust (nearly 2 meters high) and have inflorescences with many orders of branching (*M. ramifera*).

ECUADOR. Carchi: *W. S. Hoover et al. 2451, 2591, 2967; J. L. Clark et al. 6368.*
Esmeraldas: *H. Wiehler et al. 9570; D. Neill et al. 13891.* Guayas: *J. L. Clark et al. 3862.* Imbabura: *J. L. Clark et al. 7517.* Manabí: *T. Delinks 4; J. L. Clark et al. 2729.*
Pichincha: *P. Mendoza-T. et al. 518, 538; A. Hirtz & X. Hirtz 4292; G. L. Webster 32875; H. Wiehler et al. 90124.*

9. *Monopyle connata* J.L. Clark & Keene, *sp. nov.*—TYPE: *X. Cornejo & C. Bonifaz 5287.*

Indument long spreading, inflorescence bracts ovate to obovate, serrate, calyx with the three dorsal lobes fused, serrate, corolla white, lobes spotted purple, throat yellow.

Humid premontane forest. 600 m.

ECUADOR. Esmeraldas: *X. Cornejo & C. Bonifaz 5287.*

10. *Monopyle dolichothrix* Keene, *sp. nov.*—TYPE: *S. Trogisch et al. 90.*

Indument of long, spreading villous trichomes, corolla white, lobes purple, throat white, with dark purple spots, trichomes 1.8–2 mm.

Premontane tropical forest. 1000 m.

ECUADOR. Napo: *S. Trogisch et al. 90.*

11. *Monopyle ecuadorensis* C.V. Morton, *Revista Universitaria [Cuzco] 33(87): 106. 1945.*—TYPE: *Y. Mexia 6693.*

Indument moderately to densely puberulent, petiole adaxially verrucose, calyx lobes deltoid, large, broad at the base (~5 mm), acuminate, completely covering flowers in bud, corolla white, lobes purple to edged in purple, style pubescent.

Dense primary or secondary forest. 150–1000 m.

ECUADOR. Azuay: *J. L. Clark et al. 2517.* Bolivar: *X. Cornejo & C. Bonifaz 4315.* Cañar: *H. Vargas & W. Defas 5832; J. L. Clark et al. 6206.* Cotopaxi: *Y. Mexia 6693; C. H. Dodson et al. 9209; C. Dodson et al. 14436.* El Oro: *L. A. de Escobar 889.* Guayas: *O. Haught 2870; J. L. Clark et al. 3862a.* Los Rios: *C. & T. Dodson 15862.* Pichincha: *P. Mendoza-T. et al. 604.*

12. *Monopyle erythrochaete* Keene, *sp. nov.*—TYPE: *W. Palacios 11423.*

Indument red to reddish brown, leaves lanceolate, veinlets terminating each serration with black glands, peduncles short, nearly sessile, corolla white to cream, lobes white to pale purple.

Humid montane forest. 850–1600 m.

ECUADOR. Morona-Santiago: *H. Lugo S. 3651; W. Palacios 11423.* Pastaza: *H. Wiehler & D. Masterson 79232.* Zamora-Chinchiipe: *H. van der Werff & W. Quizhpe 21645.*

13. *Monopyle fimbricalyx* Keene, *sp. nov.*—TYPE: *H. Wiehler 9091*.

Inflorescence with 3–7 orders of branching, calyx lobes fimbriate, flowers large (2–2.5 cm), corolla white to cream, lobes pale purple, throat yellow.

Sub-cloud forest with exposure towards the Pacific. 1100–1300 m.

ECUADOR. Pichincha: *A. Hirtz 4523*; *H. Wiehler et al. 9091*.

14. *Monopyle flava* L.E. Skog, *Phytologia* 28: 233, f. 1. 1974.—TYPE: *Wurdack 2104*.

Leaves large, up to 18 cm long, inflorescences large, open with 4–10 orders of branching, peduncles long, calyx lobes small, ovate, corolla yellow, throat with red spotting, fruit short (< 1 cm), cylindrical, strongly gibbous at the base.

Humid premontane forest along streams. 380–1200 m.

ECUADOR. Morona-Santiago: *Morales et al. 1448*; *A. Hirtz & X. Hirtz 4378*; *H. van der Werff & W. Palacios 10326*. Zamora-Chinchipec: *H. van der Werff & E. Freire 13349*; *Cerón et al. 16917*.

15. *Monopyle glandulosa* Keene, *sp. nov.*—TYPE: *J. L. Clark et al. 5638*.

Inflorescence with 1–2 orders of branching, calyx lobes with long, septate glandular trichomes, flowers large (2–3 cm), corolla white to slightly blue, lobes purple.

Clay cliffs and primary forest. 750 m.

ECUADOR. Napo: *E. W. Davis 377*; *H. Wiehler et al. 86198, 93221, 95108*.

16. *Monopyle inopinata* Keene, *sp. nov.*—TYPE: *T. B. Croat et al. 83459*.

Indument of intermixed short, appressed, uncinat and long septate trichomes, leaves mammillate, opposing leaf small, orbicular, inflorescence terminal, bracts large, fimbriate, secondary peduncle subsessile, upper 3 calyx lobes partially fused, corolla white, lobes spotted purple.

Primary forest along the roadside or streams. 250–1300 m.

ECUADOR. Carchi: *W. S. Hoover 1272*. Esmeraldas: *J. C. Valenzuela et al. 660*; *H. Wiehler et al. 9004*; *R. W. Dunn DN 95-04-043*.

17. *Monopyle inquinata* Keene, *sp. nov.*—TYPE: *H. Lugo S. 3441*.

Leaf strongly asymmetrical, bullate, margins scarcely revolute, peduncles short (2–4 cm), calyx densely pubescent with long, uncinat trichomes, corolla violet.

Roadside and disturbed forest. 985 m.

ECUADOR. Napo: *H. Lugo S. 3065, 3089, 3441*; *H. Wiehler et al. 9599*; *Croat et al. 87816*.

18. *Monopyle iserniana* Cuatrec., Anales. Ciencias. Universidad de Madrid 4(2): 254. 1935.—TYPE: *J. Isern 498*.

Stem glabrescent, petioles short, inflorescence terminal, 1–3 orders of branching, often with a pair of leaf-like bracts at apex of the peduncle, bracts ovate, calyx lobes broad at the base, corolla white to lavender, lobes purple, fruits typically small, not exceeding the length of the calyx lobes.

Premontane wet forest. 200–250 m.

ECUADOR. Orellana: *L. Carrillo & D. Reyes 410*. Sucumbios: *E. Freire & I. Suárez 5106*.

19. *Monopyle linearis* Keene, *sp. nov.*—TYPE: *X. Cornejo & C. Bonifaz 7781*.

Inflorescence with 1 order of branching, calyx lobes long (~1.5 cm), linear, 2–3 times longer than the petals in bud, flowers small, equaling to slightly exceeding the calyx lobes, corolla white, lobes purple, throat white.

Primary or secondary humid to wet cloud forest. 150–750 m.

ECUADOR. Esmeraldas: *X. Cornejo & C. Bonifaz 7781*. Manabí: *T. Delinks 11*; *J. L. Clark 4302*.

20. *Monopyle macrophylla* Benth., Icones Plantarum 12: 86. 1876.—TYPE: *Lobb 94*. =*M. pilosula* C.V. Morton, Revista Universitaria [Cuzco] 33(87): 112. 1945.—TYPE: *W.A. Archer 1802*.

Lamina of large leaf strongly asymmetrical, petioles and inflorescence with abundant long, septate, glandular trichomes, flowers purple, nearly ventricose, fruit short (< 1.5 cm), geniculate.

Very wet primary forest, along streams, typically on inclined terrain. 150–1000 m.

ECUADOR. Esmeraldas: *W. S. Hoover et al. 3111*; *J. L. Clark 7164*; *D. Neill et al. 12465, 13895*.

21. *Monopyle maculata* Keene, *sp. nov.*—TYPE: *T. B. Croat 94529*.

Plants glabrescent, inflorescence with 1–2 orders of branching, bracts ovate, calyx broadly ovate, corolla white, lobes heavily spotted purple.

Habitat unknown.

ECUADOR. Pichincha: *T. B. Croat 94529*.

22. *Monopyle mexiae* C.V. Morton, Revista Universitaria [Cuzco] 33(87): 107. 1945.—TYPE: *Y. Mexia 7077*.

Plants branching, leaves distinctly mammillate, internodes short, small leaves typically orbicular, sessile, inflorescence with 1–2 orders of branching, calyx ovate to broadly ovate, acuminate, corolla white, lobes blue to purple, fruit not exceeding the length of the calyx lobes.

Dense wet forest or streamside. 500–1000 m.

ECUADOR. Napo: *J. Hudson* 833; *A. F. Skutch* 4455; *Y. Mexia* 7077. Pastaza: *H. Lugo S.* 4875.

23. *Monopyle multiflora* Keene & J.L. Clark, *J. Bot. Res. Inst. Texas* 5(2): 514–517, f. 1A–F, 2. 2011. –TYPE: *J. L. Clark et al.* 10407.

Stems dorsiventral, indument villous intermixed with intermediate uncinata trichomes, inflorescence axillary, bracts spreading at the base, corolla white.

Transitional montane/premontane to lowland forest. 31 m.

ECUADOR. Esmeraldas: *J. L. Clark et al.* 10407; *J. Jaramillo et al.* 13811.

24. *Monopyle obscura* Keene, *sp. nov.*–TYPE: *H. T. Beck et al.* 3051.

Indument of appressed, uncinata trichomes, occasionally with longer septate trichomes, leaves small, inflorescence terminal, bracts reduced, not serrate, typically pedunculate, corolla white, lobes spotted purple, throat yellow.

Montane cloud forest along the roadside and streams. 1080 m.

ECUADOR. Carchi: *H. T. Beck et al.* 3051. Esmeraldas: *H. Wiehler et al.* 9003.

25. *Monopyle paniculata* Benth., *Icones Plantarum* 12: 86. 1876.–TYPE: *Spruce* 5071.

Leaves abaxially dark purple or red, inflorescence a terminal, paniculate cyme, 3–5 orders of branching, corolla white, lobes heavily spotted purple, throat spotted purple, fruit small, orbicular.

Premontane wet forest. 800–2016 m.

ECUADOR. Pastaza: *H. Lugo S.* 409; *J. Hudson* 820; *J. L. Clark et al.* 9114. Tungurahua: *H. Lugo S.* 794.

26. *Monopyle parviflora* Keene, *sp. nov.*–TYPE: *W. Palacios* 5612.

Indument villous to densely villous, most trichomes with uncinata glands, leaves oblique, inflorescence terminal (sometimes appearing axillary), 1–2 orders of branching, flowers small (1–1.5 cm), corolla white, lobes purple.

Pluvial premontane forest. 650–1300 m.

ECUADOR. Napo: *W. Palacios 5729A*; *H. Wiehler et al. 86225*. Sucumbios: *H. Wiehler et al. 98136*.

27. *Monopyle pedunculata* Keene, *sp. nov.*—TYPE: *H. Wiehler et al. 88120*.

Leaves large (~15 cm long), inflorescence terminal with many septate, glandular trichomes, peduncles long (~11 cm), calyx lobes short, up to 2 mm, acute, corolla blue, throat with spots in the base.

On damp rocks by waterfall. ~ 1000 m.

ECUADOR. Morona-Santiago: *H. Wiehler et al. 88120*.

28. *Monopyle pubescens* Keene, *sp. nov.*—TYPE: *O. Haught 3486*.

Indument villous to densely villous, leaves large (~20 cm), inflorescences terminal, 1–2 orders of branching, calyx lobes long, lanceolate, flowers large, up to 2.5 cm, corolla white, lobes deep blue to purple.

Damp shady forest. 100 m.

ECUADOR. Manabí: *O. Haught 3486*.

29. *Monopyle robusta* Keene, *sp. nov.*—TYPE: *Y. Mexia 6845*.

Indument densely pilose to villous with uncinata trichomes, leaves with distinctly oblique bases, calyx lobes ovate to broadly ovate, corolla white, lobes light to dark purple, fruit equaling the calyx lobes.

Dense forest. 325–375 m.

ECUADOR. Pastaza: *Y. Mexia 6845*.

30. *Monopyle rubicunda* Keene, *sp. nov.*—TYPE: *J. L. Clark 7050*.

Indument of red trichomes, leaves distinctly mammillate, inflorescence terminal, calyx lobes long, lanceolate, green abaxially, white adaxially, corolla white.

Premontane wet forest. 500–1200 m.

ECUADOR. Morona-Santiago: *F. Nicolalde et al. 1110*; *J. L. Clark 6912, 7050*.

31. *Monopyle sodiroana* Fritsch, *Bot. Jahrb. Syst.* 50(4): 394. 1914 [1913].—TYPE: *Sodiro 119/1 (P!)*.

Leaves bullate, inflorescence terminal, occasionally reverting to vegetative growth at apex, flowers large, up to 3 cm, corolla white, ventral lobe white or with purple spotting, throat with bright yellow stripe.

Wet premontane to montane forest along streams and in pasture. 1200–2400 m.

ECUADOR. Carchi: *W. S. Hoover & S. Wormley 1502; L. J. Dorr & L. C. Barnett 6089; J. L. Clark & O. Mejia 6298*. Pichincha: *E. André K48, K49*.

32. *Monopyle stenoloba* C.V. Morton, *Revista Univ. (Cuzco)* 33(87): 110. 1945.—TYPE: *Y. Mexia 6897*.

Leaves petiolate, adaxially green, abaxially red to maroon, slightly oblique, calyx lobes lanceolate to spatulate, corolla white, lobes light blue to purple, throat white or with dark spots.

Primary or disturbed rainforest. 320–1000 m.

Notes: There are several collections from Sucumbíos that may represent another species, but more material is needed to confirm a separate taxon. These specimens have broad, spatulate calyx lobes and tend to be somewhat glabrescent.

ECUADOR. Napo: *C. Cerón 601, 628; J. L. Clark et al. 9378; L. B. Holm-Nielsen et al. 19690*. Pastaza: *F. Hurtado & D. Neill 1490; H. Lugo S. 4253, 4271*. Sucumbios: *H. Wiehler et al. 9886, 9887, 9891; T. Croat & L. Hannon 93477*.

33. *Monopyle subintegerrima* Keene, *sp. nov.*—TYPE: *P. J. Grubb et al. 1475*.

Leaves subentire, calyx lobes long (≥ 1 cm), linear to lanceolate, flowers large (~3 cm), corolla white, lobes purple.

Rainforest beside streams. 610 m.

ECUADOR. Napo: *P. J. Grubb et al. 1475*.

34. *Monopyle subsessilis* Benth., *Icon. Pl.* 12: 86. 1876.—TYPE: *Spruce 4151 (K!)*.

Stems ridged or verrucose, indument sparsely to densely pilose with uncinat trichomes, petioles subsessile, inflorescence terminal, 1–3 orders of branching, calyx lobes broad ovate, attenuate to acuminate, corolla white to violet, lobes pale to dark purple.

Primary rain forest. 700–900.

Notes: The plants in Ecuador have very broad, angular calyx lobes and much larger fruit. They cannot currently be separated as another taxon, but may prove to be one with more investigation.

ECUADOR. Morona-Santiago: *G. Harling & L. Andersson 12870; H. Wiehler et al. 88116*.

35. *Monopyle trachyphylla* Keene, *sp. nov.*—TYPE: *C. H. Dodson 6110*.

Leaves distinctly mammillate, inflorescence axillary, 1–2 flowered, bracts long (~3 mm), corolla white, lobes blue to purple.

Cloud forest. 300–1000 m.

ECUADOR. Pichincha: *P. C. D. Cazalet & T. D. Pennington 5227.*

36. *Monopyle uniflora* J.L. Clark & Keene, *J. Bot. Res. Inst. Texas* 5(2): 517–520, f. 2A, 3, 4A–C. 2011.–TYPE: *J. L. Clark & Gesneriad Research Expedition Participants 11162.*

Inflorescences axillary with few flowers (1–2 per cyme), bracts basally appressed, flowers white to light lavender with yellow in the throat.

Flat forest and humid tropical primary forest. 87–300 m.

ECUADOR. Esmeraldas: *Tipaz et al. 2218.*

37. *Monopyle urceolata* Keene, *sp. nov.*–TYPE: *J. L. Clark et al. 9001.*

Leaf margins and petioles with long, septate trichomes, flowers small, urceolate (~ 1 cm), corolla cream to white, lobes white or with a blue spot on ventral and lateral lobes, throat white to slightly yellow, fruit small (< 1 cm), strongly gibbous at the base.

Premontane to montane forest along streambeds. 1000–2200 m.

ECUADOR. Zamora-Chinchiipe: *W. H. Camp E-1396; J. L. Clark et al. 3167, 6499, 9001, 9999.*

38. *Monopyle verrucosa* Keene, *sp. nov.*–TYPE: *J. L. Clark 3676.*

Inflorescence with cymes in fascicles, corolla white, lobes blue with purple lines or dots, throat yellow, fruit verrucose.

Premontane wet forest. 400–650 m.

ECUADOR. Esmeraldas: *N. Pitman & M. Bass 1050; J. L. Clark et al. 8814, 9615.*

Key to *Monopyle* of Peru

Monopyle angustifolia Fritsch likely belongs to a species complex that includes *M. peruviana* Keene, but the protologue does not match any collections that were available for this study.

1. Flowers yellow.
 2. Stem densely pubescent with spreading trichomes; leaves strongly rugose.
 4. *M. citrina*
 - 2'. Stem sparsely pubescent; leaves not distinctly rugose.
 3. Leaves up to 12 cm wide; inflorescences with 4–10 orders of branching; fruit short and broad, < 1 cm long.
 7. *M. flava*
 - 3'. Leaves generally < 6 cm wide; inflorescences with 1–3 orders of branching; fruit narrowly cylindrical, 2–2.5 cm long.
 12. *M. luteola*
- 1'. Flowers white to purple or pink.
 4. Leaves mammillate.
 5. Pubescence dark red with longest trichomes more than 1 mm long; calyx lobes lance-elliptic to oblanceolate, widest at or above the middle, recurved at the apex.
 20. *M. setosa*
 - 5'. Pubescence red or not, if red then longest trichomes less than 1 mm long; calyx lobes lanceolate to ovate, widest at the base, not recurved at the apex.
 6. Leaves strongly mammillate; calyx lobes acuminate, 5–6 mm long.
 14. *M. mexiae*
 - 6'. Leaves not strongly mammillate.
 7. Calyx lobes long attenuate, 9–14 mm long.
 11. *M. lanceolata*
 - 7'. Calyx lobes short, 2–4 mm long.
 16. *M. parvisepala*
 - 4'. Leaves not mammillate.
 8. Stems pubescent with long, spreading trichomes, longest trichomes to 1 mm or longer.
 9. Trichomes dark reddish purple, extremely dense on calyx lobes, nearly obscuring their shape.
 6. *M. erythrochaete*
 - 9'. Trichomes various but never dark reddish purple, calyx lobe shape clearly evident despite pubescence.

10. Calyx lobes short and broad, 2 mm wide, 5–6 mm long, obtuse to acute.
15. *M. nitida*
- 10'. Calyx lobes narrower, < 2 mm wide, acute to attenuate.
11. Calyx lobes lanceolate to linear, 10–24 mm long; flowers large, 25–30 mm long.
9. *M. gigantea*
- 11'. Calyx lobes lanceolate to oblanceolate, generally < 10 mm long; flowers up to 20 mm long.
12. Larger leaves broad, 5–14 cm wide; calyx lobes lanceolate to oblanceolate; fruit narrowly cylindrical, ~ 2 mm wide.
24. *M. villosa*
- 12'. Larger leaves narrower, 3–4.5(–5) cm wide; calyx lobes lanceolate; fruit short and broad, ~ 4 mm wide.
13. Leaves densely villous with uncinata trichomes; inflorescence branched with 3 or more flowers.
23. *M. vestita*
- 13'. Leaves moderately villous, lacking uncinata trichomes, appearing ciliate; inflorescence with 1–2 flowers.
5. *M. crinita*
- 8'. Stems pubescent to glabrous, longest trichomes < 1 mm long.
14. Flowers small, 10 mm or less.
15. Larger leaves 7–12 cm wide.
16. *M. parvisepala*
- 15'. Larger leaves 5 cm or less.
16. Flower buds with short, uncinata trichomes, septate trichomes lacking.
10. *M. granularis*
- 16'. Flower buds with septate trichomes.
17. Inflorescences strict (racemose cyme), secondary peduncles absent, with 1 order of branching.
22. *M. tenuifolia*
- 17'. Inflorescences open, secondary peduncles more than 1 cm long, 3 or more orders of branching.
18. *M. rosea*
- 14'. Flower larger, more than 10 mm.
18. Lowest inflorescence bracts large, leaf-like.
1. *M. alba*
- 18'. Lowest inflorescence bracts small, not leaf-like.

19. Inflorescences of open paniculate cymes, secondary peduncles generally 2 cm or longer.

20. Larger leaves 8–10 cm wide; calyx lobes lanceolate, 4–6 mm long; fruit cylindrical, 20–24 mm long.

19. *M. rosimaculata*

20'. Larger leaves narrower, generally less than 8 cm wide; combination of calyx and fruit characters differing from above.

21. Calyx lobes less than 8 mm; fruit short, less than 1 cm long.

3. *M. anomala*

21'. Calyx lobes more than 1 cm long; fruit cylindrical, 3.5–4 cm long.

8. *M. fulvida*

19'. Inflorescences not paniculate, often few flowered with long pedicels more than 2 cm long, or if paniculate then secondary peduncles less than 2 cm.

22. Leaves persistently pubescent adaxially.

23. Leaves sessile, petioles generally 5 mm long or less.

21. *M. subsessilis*

23'. Larger leaves petiolate, petioles more than 5 mm long.

13. *M. macrocarpa*

22'. Leaves nearly glabrous adaxially.

24. Larger leaves 7–16 cm wide; flowers purple; calyx lobes less than 5 mm long.

25. *M. violacea*

24'. Larger leaves narrower, generally 6 cm wide or less; flowers white with purple lobes; calyx lobes more than 1 cm long.

25. Stems glabrescent; flowers generally 5 or fewer per inflorescence; fruit not verrucose.

17. *M. peruviana**

25'. Stems moderately to densely pubescent with uncinata trichomes; flowers generally more than 5 per inflorescence; fruit verrucose.

8. *M. fulvida**

* hybrids are intermediate

1. *Monopyle alba* Keene, *sp. nov.*—TYPE: *R. Vásquez & Flores 26256*.

Leaves adaxially septate, abaxially puberulent, inflorescence terminal, secondary peduncles long (~ 3 cm), bracts often leaf-like, calyx lobes long, lanceolate, reflexed in flower, corolla white.

Primary forest. 1950–2200 m.

PERU. Cajamarca: *V. Quipuscoa S. 393*; *E. Rodríguez 687*.

2. *Monopyle angustifolia* Fritsch, *Bot. Jahrb. Syst.* 50(4): 394. 1914 [1913].—TYPE: *Ule 33/2*.

Notes: Known only from the type collection, which was destroyed at Berlin.

PERU.

3. *Monopyle anomala* Keene, *sp. nov.*—TYPE: *C. Díaz et al. 4351*.

Plants glabrous to glabrescent, inflorescence terminal, open, secondary peduncles long, 2.5–3 cm, calyx lobes lanceolate, corolla translucent green (white?), ovary apex swollen, broad, fruit short, < 1 cm long.

Habitat unknown. 1920–2300 m.

PERU. Amazonas: *C. Díaz et al. 4351*.

4. *Monopyle citrina* Keene, *sp. nov.*—TYPE: *J. Schunke-Vigo 11810*.

Leaves distinctly bullate, petioles short, inflorescence terminal, 2–4 flowers per node, corolla brilliant yellow to green.

Dense cloud forest. 900–1610 m.

PERU. Huánuco: *Skog et al. 5123*; *A. Gentry et al. 16063*.

4. *Monopyle crinita* Keene, *sp. nov.*—TYPE: *H. van der Werff et al. 16241*.

Indument villous with many glandular trichomes, inflorescence axillary, calyx lobes nearly glabrous, corolla white to purple, lobes purple, throat white.

Intact forest. 800 m.

PERU. Amazonas: *H. Ellenberg 3496*.

5. *Monopyle erythrochaete* Keene, *sp. nov.*—TYPE: *W. Palacios 11423*.

Indument red to reddish brown, leaves lanceolate, veinlets terminating each serration with black glands, peduncles short, nearly sessile, corolla white to cream, lobes white to pale purple.

Humid montane forest. 850–1600 m.

PERU. Amazonas: *H. Beltran & R. Foster 1098, 1113.*

6. *Monopyle flava* L.E. Skog, *Phytologia* 28: 233, f. 1. 1974.—TYPE: *Wurdack 2104* (US!).

Leaves large, up to 18 cm long, inflorescences large, open with 4–10 orders of branching, peduncles long, calyx lobes small, ovate, corolla yellow, throat with red spotting, fruit short (< 1 cm), cylindrical, strongly gibbous at the base.

Humid premontane forest along streams. 200–1300 m.

PERU. Amazonas: *V. Hodges & J. Gorham 122; B. Berlin 311; G. Tessmann 4170.*

7. *Monopyle fulvida* Keene, *sp. nov.*—TYPE: *J. Schunke V. 7312.*

Stems densely pubescent with uncinat trichomes, inflorescence terminal, bracts dark red, flowers generally more than 5 per inflorescence, corolla light pink to purple, lobes light purple, fruit verrucose, dark orange to yellow.

Humid forest. 450–700 m.

Notes: This species seems to be hybridizing with other sympatric species (*M. macrocarpa* and *M. peruviana*). It is very closely related to *M. peruviana* morphologically and hybrid zones make identification very difficult.

PERU. San Martín: *J. Schunke V. 7575, 12026.*

8. *Monopyle gigantea* Keene, *sp. nov.*—TYPE: *R. Vásquez et al. 27459.*

Leaves strongly anisophyllous, inflorescence axillary (sometimes appearing terminal), calyx lobes long, up to 2 cm, flowers large, up to 3.5 cm, corolla white to light blue, lobes white to light blue, throat yellow.

Primary high montane rainforest. 1350–2300 m.

PERU. Amazonas: *K. Young & M. Eisenberg 337; D. N. Smith & S. Vasquez S. 4903.*

9. *Monopyle granularis* Keene, *sp. nov.*—TYPE: *E. Rodríguez R. 1977.*

Leaves adaxially nearly glabrous, abaxially puberulent with uncinat trichomes, inflorescence terminal, 2–4 orders of branching, peduncle and rachis glabrous, flowers small (< 1.5 cm), corolla white.

Primary forest. 1700–1800 m.

PERU. Cajamarca: *E. Rodríguez R. & M. Núñez 1927; J. Campos & S. Nuñez 4599.*

10. *Monopyle lanceolata* Keene, *sp. nov.*—TYPE: *D. C. Wasshausen & F. Encarnación 900.*

Indument red, leaves rugose, small leaf orbicular, inflorescence terminal, secondary branches short (< 1 cm), bracts large (occasionally leaf-like), calyx lobes broadly lanceolate, corolla white, throat yellow.

Edge of secondary growth in lowland rainforest. 850 m.

PERU. Loreto: *D. C. Wasshausen & F. Encarnación 900.*

11. *Monopyle luteola* Keene, *sp. nov.*—TYPE: *D. N. Smith 8462.*

Leaves adaxially nearly glabrous, abaxially puberulent, inflorescence terminal, 1–3 orders of branching, calyx lobes lanceolate, corolla white to pale yellow, lobes yellow, throat yellow with red lines near the base, fruit thinly cylindrical, ~ 2 cm long.

Forest and stream edges. 300–450 m.

PERU. Pasco: *R. B. Foster 8587.*

12. *Monopyle macrocarpa* Benth., *Icones Plantarum* 12: 85–86, t. 1198, f. 1–5. 1876.—TYPE: *Spruce 4151 (K!).*

Leaves abaxially pilose uncinata, typically asymmetric, falcate, inflorescence terminal, few flowered, calyx lobes long (~ 1 cm), lanceolate, corolla white, lobes white to light purple at the margin, throat yellow with purple spots at the base, fruit long (>2.5 cm), cylindrical, curved near the middle.

Forest growing near streams or waterfalls. 900–1300 m.

PERU. San Martín: *J. Halton & L. Besse 58; L. Besse et al. 786; A. Gentry et al. 37877.*

13. *Monopyle mexiae* C.V. Morton, *Revista Universitaria [Cuzco]* 33(87): 107. 1945.—TYPE: *Y. Mexia 7077 (US!).*

Plants branching, leaves distinctly mammillate, internodes short, small leaves typically orbicular, sessile, inflorescence with 1–2 orders of branching, calyx ovate to broadly ovate, acuminate, corolla white, lobes blue to purple, fruit not exceeding the length of the calyx lobes.

Dense wet forest or streamside. 500–1000 m.

PERU. Amazonas: *B. Berlin 1805; H. van der Werff et al. 14494; R. Vásquez et al. 27412, 27414.*

14. *Monopyle nitida* Keene, *sp. nov.*—TYPE: *E. P. Killip & A. C. Smith 26087.*

Plants small, indument densely villous, inflorescences terminal and axillary, calyx lobes round at the apex, corolla white, fruit globose.

Dense forest. 650–900 m.

PERU. Junín: *E. P. Killip & A. C. Smith 26087*.

15. *Monopyle parvisepala* Keene, *sp. nov.*—TYPE: *R. Vásquez et al. 2329*.

Large leaves up to 12 cm wide, scarcely mammillate, inflorescence terminal, 8–10 orders of branching, calyx lobes lanceolate, blunt to acute, short, 2–4 mm, corolla green (likely white in flower).

Inundated secondary forest. 160 m.

PERU. Loreto: *R. Vásquez et al. 2329*.

16. *Monopyle peruviana* Keene, *sp. nov.*—TYPE: *J. Schunke Vigo & J. G. Graham 15850*.

Stems glabrescent, larger leaves narrow, generally 6 cm wide or less, inflorescence terminal, bracts yellowish green, calyx lobes more than 1 cm long, flowers generally 5 or fewer per inflorescence, corolla white, lobes white to purple, fruit not verrucose.

Humid primary forest. 300–550 m.

Notes: This species hybridizes readily with sympatric species and is difficult to identify. The smooth fruit and typically very narrow leaves are distinguishing features.

PERU. Loreto: *P. J. M. Maas et al. 4575*; *L. E. Skog et al. 5135*. Ucayali: *J. Schunke Vigo & J. G. Graham 15779*.

17. *Monopyle rosea* Keene, *sp. nov.*—TYPE: *J. Campos et al. 3019*.

Leaves glabrous adaxially, puberulent abaxially, inflorescence terminal, open, secondary peduncles long (2–3 cm), calyx densely pilose with uncinatate trichomes, reflexed in flower, corolla pink.

Habitat unknown. 1700–2000 m.

PERU. Amazonas: *J. Campos et al. 3019*.

18. *Monopyle rosimaculata* Keene, *sp. nov.*—TYPE: *J. Schunke V. 11697*.

Leaves sparsely pilose to glabrous adaxially, puberulent abaxially, inflorescence terminal, open, 3–5 orders of branching, calyx broadly lanceolate, corolla white, lobes purple, villous.

High forest near steam edges. 400–800 m.

PERU. San Martín: *J. Schunke V. 5607, 10888, 11697*.

19. *Monopyle setosa* Keene, *sp. nov.*—TYPE: *E. Rodríguez* 289.

Indument pilose to villous, trichomes dark red, leaves distinctly mammillate, calyx lobes long ovate to lanceolate, recurved apex, corolla white, lobes purple.

Primary forest along streams. 300–600 m.

PERU. Amazonas: *V. Hodges & J. Gorham* 49; *N. Jaramillo et al.* 1076.

20. *Monopyle subsessilis* Benth., *Icon. Pl.* 12: 86. 1876.—TYPE: *Spruce* 4151.

Stems ridged or verrucose, indument sparsely to densely pilose with uncinata trichomes, petioles subsessile, inflorescence terminal, 1–3 orders of branching, calyx lobes broad ovate, attenuate to acuminate, corolla white to violet, lobes pale to dark purple.

Primary rain forest along embankments or streams. 200–1400 m.

PERU. Amazonas: *S. Tunqui* 450; *B. Berlin* 598. Cuzco: *M. Timaná* 1061; *R. B. Foster* 10625. Huánuco: *R. B. Foster* 9354; *B. Wallnöfer & M. Henzel* 112-16388. Junín: *E. P. Killip & A. C. Smith* 26091, 26114, 26216. Loreto: *D. C. Wasshausen & F. Encarnación* 907; *Y. Mexia* 6253a. Madre de Dios: *T. S. Wachter* 6; *R. Foster & T. Wachter* 7405. Pasco: *R. Foster et al.* 7871; *R. Vásquez et al.* 29716. San Martín: *J. Schunke* V. 4502.

21. *Monopyle tenuifolia* Keene, *sp. nov.*—TYPE: *R. Foster et al.* 7730.

Plants glabrescent, leaves narrow, inflorescence terminal, lax, calyx lobes short, lanceolate, corolla white, lobes purple, fruit small, ≤ 1 cm long.

Wet shaded banks along streams, dense cloud forest. 1600–1800 m.

PERU. Loreto: *L. E. Skog et al.* 5162 p.p. Pasco: *L. E. Skog et al.* 5047.

22. *Monopyle vestita* Keene, *sp. nov.*—TYPE: *H. A. Allard* 22105.

Indument dense pilose to villous, inflorescence terminal, calyx lobes long, lanceolate, corolla pinkish purple, lobes pink to purple.

Humid forest. 350–400 m.

PERU. Loreto: *R. Scholnik* 1133. San Martín: *J. Schunke* V. 4669; *C. A. Ridoutt* 12980.

23. *Monopyle villosa* Keene, *sp. nov.*—TYPE: *E. Rodríguez et al.* 1141.

Indument evenly villous (ciliate), inflorescence terminal, constricted, with few branches, corolla white, lobes purple.

Primary forest. 320–680 m.

PERU. Amazonas: *E. Rodríguez et al.* 980; *N. Jaramillo et al.* 1205.

24. *Monopyle violacea* Keene, *sp. nov.*—TYPE: *H. van der Werff et al. 16250.*

Large mature leaves 7–15 cm wide, inflorescence terminal, constricted, corolla purple, lobes purple, fruit thin, cylindrical.

Intact forest. 800 m.

PERU. Amazonas: *H. van der Werff et al. 16252.*

Monopyle of Venezuela

1. *Monopyle leucantha* Moritz ex Benth., *Icones Plantarum* 12: 87. 1876.—TYPE: *Moritz 868*.

Leaves distinctly petiolate, primary peduncle long (up to 12 cm), flowers in fascicles on the secondary peduncle, calyx lobes short, ovate, apex blunt, flowers small, 1–2 cm long, corolla white with pink, lobes white.

Dense woods, along streams. 800–2600 m.

Notes: The plants of low elevation are quite different in inflorescence structure and flower size. These populations are diverging from the high elevation populations and may merit recognition.

VENEZUELA. Aragua: *A. Fendler 794*. Falcón: *R. Wingfield 8104*. Merida: *L. R. Terán 13191*. Tachira: *C. E. B. de Rojas 1238*; *J. Steyermark et al. 98290*.

CHAPTER 7: FINAL CONCLUSIONS

Monopyle is significantly more diverse than previous studies have recognized and includes 101 species and an infraspecific taxon. Many of the species are endemic, but there are a few widespread species that are quite morphologically diverse. This pattern is potentially due to the tendency of species to hybridize when they are sympatric and is especially evident in Ecuador and northern Peru. The widespread species include: *Monopyle puberula* and *M. maxonii* in Central American, as well as *M. communis*, *ecuadorensis*, and *subsessilis* in South America. This hybridization has misled many taxonomists and erroneous determinations of species are the norm. A large proportion of the herbarium specimens from South America, deposited in herbaria throughout the world, are identified as *Monopyle macrocarpa*. This problem is corrected (see Chapter 6) with detailed keys and a synopsis of the known species within *Monopyle*. The species can easily be separated based on a suite of characters. The most informative of these tends to be a combination of indument, inflorescence structure, calyx shape, and fruit morphology (see Chapter 2).

The confirmation of effective morphological characters for *Monopyle*, at the genus level, allowed for comparison to other genera in the Gloxinieae tribe. Many related genera (i.e., *Gloxinella*, *Gloxiniopsis*, and *Nomopyle*) were separated based on morphology. This morphological separation permitted a more comprehensive molecular study of the genus with a stricter comparison of other genera. The molecular study showed that there are several complex evolutionary processes acting in concert on the genera in Gloxinieae. *Monopyle* as a genus is monophyletic, but has come into contact multiple times with other genera (i.e., *Diastema*, *Gloxinella*, *Nomopyle*, and *Phinaea*) or

their ancestors. The nuclear tree also showed that there have also been ancient and recent gene duplication events within Gloxinieae. All of the genera tested have two or more copies of *GFLO*. The potential hybridization and polyploidization make the delineation of groups very difficult without comparison between trees from chloroplast and nuclear genes. *Monopyle* also appears to be autogamous or apomictic and will produce seeds without cross-pollination. Although, there is so much discord in the phylogenetic trees there are clearly four new genera not shown in previous studies.

Resolving relationships within *Monopyle* and the Gloxinieae will require more sampling in the future. This will need to be two-pronged attempt including more taxa and phylogenetically informative nuclear genes. Chromosome mapping and counts will be necessary to determine whether *GFLO* is effective for examining inheritance patterns and ploidy levels, respectively. Field studies will also be imperative to sample multiple populations in hybrid zones to compare the genetic diversity among and between samples. Many useful morphological characters are lost on herbarium sheets and field research would greatly improve dichotomous keys and descriptions of species. The four new species that were described from Ecuador and Panama (see Chapters 4 and 5) were known from few or no previous collections. This result shows that even with extensive collection many species are poorly understood or rarely collected endemic species. Many of these species grow in areas that are difficult to reach, along steep embankments or rock faces. Future research will show even more species diversity in the genus and the tribe. This will improve the effectiveness of conservation efforts in the Neotropics allowing species to be identified and protected.



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