SYSTEMATICS AND BIOGEOGRAPHY OF THE NEOTROPICAL GENUS *PARADRYMONIA* AND CLOSE ALLIES

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A DISSERTATION

Submitted in partial fulfillment of the requirements
for the degree of Doctor of Philosophy
in the Department of Biological Sciences
in the Graduate School of
The University of Alabama

TUSCALOOSA, ALABAMA

2014

ABSTRACT

It is widely known that loss of biological diversity at different levels, such as genetic lineages, species, populations, communities and natural habitats, is imminent in many areas on Earth. That loss is exacerbated by the lack of taxonomic knowledge of many groups of organisms. Taxonomic knowledge is necessary to understand the ecology, biogeography and evolutionary history of organisms, as well to accurately implement management plans for the conservation of biodiversity. As with many other neotropical plant genera, *Paradrymonia* Hanst. (Gesneriaceae) was in need of a taxonomic revision. The genus, as traditionally circumscribed, includes a non-monophyletic assemblage of approximately 40 species of terrestrial and facultative epiphytic herbs that inhabit the understory of neotropical forests. The generic circumscription of *Paradrymonia* has been historically confusing and problematic due to the lack of unique diagnostic morphological characters. Molecular data of nuclear ribosomal and plastid DNA were used to reconstruct species relationships within the genus and closely related genera in subtribe Columneinae. *Paradrymonia*, as traditionally defined, is paraphyletic and includes taxa in three different clades. Phylogenetic results supported the re-circumscription of *Paradrymonia* and the resurrection of two previously recognized genera, *Centrosolenia* and *Trichodrymonia*, in order to accommodate the remaining ex-*Paradrymonia* species. New combinations, synonymies and further nomenclatural recommendations are made. A taxonomic revision of a re-circumscribed *Paradrymonia* is included. The revision includes a dichotomic key and a description for all the eight species. Furthermore, evolution of nine morphological and ecological characters was accessed using ancestral character reconstructions. Most of the characters for different lineages within the *Paradrymonia alliance* were homoplastic, suggesting convergent evolution as adaptation to similar ecological conditions and pollinators. Finally, ecological niche modeling (ENM) is used to assess the influence of Pleistocene climate in the Last Glacial Maximum (LMG; ~21,000 BP) on the current distribution of lowland species. Results are consistent with the existence of Pleistocene forest refugia as "museums" and not as drivers of speciation, which is inconsistent with the Pleistocene Refuge Hypothesis. Finally, descriptions for three species new to science, *Paradrymonia apicaudata*, *P. peltatifolia* and *Nautilocalyx erytranthus*, are provided.

DEDICATION

This dissertation is dedicated to my beloved mother, and father (in memoriam), who taught me to love learning and who always made my education one of their top priorities and gave me unconditional love and support to get here.

LIST OF ABBREVIATIONS AND SYMBOLS

BI	Bayesian inference
BP	Before present
C	Celsius
ca.	circa (Latin: approximately)
CCSM	Community Climate System Model
cm	centimeter
cpDNA	Chloroplast deoxyribonucleic acid
DNA	Deoxyribonucleic acid
e.g.	*Exempli gratia* (Latin: for example)
et al.	*Et alia* (Latin: and others)
ENM	Ecological Niche Model
ETS	External transcribed spacer region
GTR	General time reversible
I	portion of invariant sites
i.e.	*Id est* (Latin: that is)
ITS	Internal transcribed spacer region
LGM	Last Glacial Maximum
Km^2	Kilometers squared
m	Meter
MAXENT	Maximum Entropy

min	Minute
mm	Millimeter
MCMC	Markov Chain Monte Carlo
ML	Maximum likelihood
MP	Maximum parsimony
MCRA	Most common recent ancestor
N	North latitude
nrDNA	Nuclear ribosomal deoxyribonucleic acid
PMIP	Paleoclimate Modelling Intercomparison Project
PEG	Polyethylene glycol precipitation
PP	Posterior probabilities
PCR	Polymerase chain reaction
rDNA	Ribosomal deoxyribonucleic acid
sp.	Species (singular)
spp.	Species (plural)
s	Seconds
s.l.	*Sensu lato* (Latin: in a broad sense)
s.s.	*Sensu stricto* (Latin: in strict sense)
TBR	Tree bisection reconnection
USA	United States of America
W	West longitude
&	And
^{o}	Degrees

=	Equals
±	More or less
>	More than
~	Approximately
Γ	Gamma distribution
μL	Microliter(s)
‘	Minutes
%	Percent
“	Seconds

ACKNOWLEDGMENTS

Support for this project was provided by Sleeth scholarship Endowment fund (The Gesneriad Society, Inc.). I am deeply grateful to several source of founding during my years as a gradient student at the University of Alabama: The Department of Biological Sciences, The Graduate School, Capstone International, The Graduate Student Association and The Aquatic Biology Enhancement Research Fellowship.

I thank the curators and curatorial assistants from the Smithsonian Institution’s National Museum of Natural History – Department of Botany (US), the Missouri Botanical Garden (MO), the Field Museum of Natural History (F), the Marie Selby Botanical Gardens (SEL) and the University of Wisconsin (WIS) herbaria for made their collections available for my research.

I am grateful to my advisor, Dr. John Clark for his guidance and mentorship and for his contagious enthusiasm and passion for tropical plants. Special thanks to my committee members, Drs. Martha Powell, Juan Lopez-Bautista, Leslie Riessler and Larry Skog for their support, guidance and helpful suggestions to improve my project during my years of study at the University of Alabama. I am very grateful to Dr. Skog for sharing his expertise with me and for his feedback and methodic and insightful suggestions. I am grateful to Christian Feulliet who provided me with nomenclatural advice and for sharing his knowledge. Special thanks to Dr. Rissler and Sarah Duncan for providing guidance with niche modelling.

I want to express my appreciation for Steven Gingzbar for his genuinely good nature and continuous support and as well as for all the tremendous help with the herbarium loans, the

Gesneriad database, for watering my plants and for much more. I also thank all the other members of the Clark lab, both past and present, for their support and friendship, and the many undergraduates for their great help in the lab.

I thank Dr. Patricia Sobecky for her support and all the help that she provided me as Department Chair. Thanks to Debbie Eads and Karen Martin for all their assistance and kindness when dealing with paperwork and administrative tasks necessary for completing my Doctoral program.

I greatly appreciate the help of my mom, Elvia Pinto for being an amazing travel companion and enduring difficult conditions in the field in Colombia and Mexico, and for doing everything in her hands to help me to collect my plants. I also thank all the people who help me in the field, especially to Pedro Centeno, Cesar Grandez and Juan Perez (Peru) as well as to Don Fernando Toro (Colombia) for his help in the field and his hospitality. Thanks to Fundación Serraniagua for helping me with the logistics to visit San José del Palmar, Colombia.

I want to thank to Robbie Ward for his friendship, for his encouragement and for lovingly correcting my writing. Thanks to Patty Aguirre for taking good care of Vicktor, my furry unconditional companion, allowing me to focus in the writing stage of my dissertation.

Special thanks to my friends for their support and encouragement during the completion of my dissertation. Lorena Lopez, Laura Clavijo, Cassandra Coleman, Ana Tronholm, Gabriela Garcia, Sarah Duncan and Alvaro Baquero, thank you for making my graduate experience much better through your friendship. I am forever indebted to my mom and Diana and Alejandro, my siblings, for the support they provided throughout my whole life and during my Ph.D. program. My Ph.D. has been a long journey, with ups and downs and with many challenging moments that would have been impossible to overcome without their unconditional love.

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CHAPTER I

Molecular Phylogeny of the Neotropical Genus *Paradrymonia* (Gesneriaceae), Reexamination of Generic Concepts and the Resurrection of *Trichodrymonia* and *Centrosolenia*[1]

ABSTRACT

Paradrymonia Hanst. (Gesneriaceae) with 38 currently recognized species is a genus of facultative epiphytic herbs that inhabit the forest understory. The genus occurs throughout the Neotropics except for southeastern Brazil and the Caribbean. Monophyly of neotropical *Paradrymonia* and species relationships within the genus and closely related genera were evaluated based on molecular sequence data from the nuclear ribosomal (nrDNA) internal and external transcribed spacer regions (ITS and ETS), and the plastid (cpDNA) *psb*A-*trn*H intergenic spacer. Traditional *Paradrymonia* is clearly resolved as paraphyletic and includes taxa in three clades. The clade that contains the type species is recognized as *Paradrymonia* sensu stricto (s.s) and includes three species. The *Paradrymonia* s.s. clade is sister to a clade that includes species of *Nautilocalyx*, *Chrysothemis* and most of the species traditionally recognized as *Paradrymonia*. Morphological characters useful for circumscribing generic boundaries include bearded anthers, habit, presence of leaf anisophylly, and calyx lobe shape. Our results

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[1] Mora, M. and J.L.Clark. Molecular Phylogeny of the Neotropical Genus *Paradrymonia* (Gesneriaceae), reexamination of generic concepts and the resurrection of *Trichodrymonia* and *Centrosolenia*. *Systematic Botany.*(submitted)

support the re-circumscription of *Paradrymonia* and the resurrection of two previously recognized genera, *Centrosolenia* and *Trichodrymonia*, in order to accommodate the remaining ex-*Paradrymonia* species. The genus *Nautilocalyx* is paraphyletic and needs to be evaluated with broader taxon sampling.

Keywords: *Chrysothemis*; plastid DNA, Columneinae; Gesnerieae; *Nautilocalyx*; nuclear DNA, polyphyly.

INTRODUCTION

Gesneriaceae is a mostly tropical or subtropical plant family with 150-160 genera and ca. 3200 species (Burtt and Wiehler 1995; Weber 2004; Skog and Boggan 2006). Some classifications have divided the family into three subfamilies (Gesnerioideae, Cyrtandroideae, and Coronantheroideae) (Wiehler 1983; Burtt and Wiehler 1995), but most recognize only two subfamilies (Gesnerioideae and Cyrtandroideae) (e.g. Fritsch 1893-1894; Smith et al., 1997; Mayer et al. 2003; Weber 2004; Möller et al. 2009; Woo et al. 2011). Traditional classifications based on morphological data (e.g. Hanstein 1854; Fritsch 1893-1894; Wiehler 1983) have been shown to be artificial.

Recent molecular-based studies have redefined tribes to reflect monophyletic groups (Smith et al. 1997; Zimmer et al. 2002; Roalson et al. 2005; Woo et al. 2011; Weber et al. 2013). Weber et al. (2013) proposed a new comprehensive formal classification for the family based on molecular phylogenetic studies for New and Old world Gesneriaceae that resulted in a re-circumscription of the traditionally recognized tribes. For the Neotropical Gesneriaceae the number of tribes was reduced from nine to the following five: Besleriae, Coronanthereae, Gesnerieae, Napeantheae, and Titanotricheae (Weber et al. 2013). Gesnerieae, the largest tribe in the family, includes what was previously in the following tribes Gloxinieae, Gesnerieae, Episcieae and Sphaerorrhizeae (Weber et al. 2013). Sphaerorrhizeae (Gesnerieae sensu Weber et al. 2013), previously recognized as subfamily Coronantheroideae by Wiehler (1983) and Burtt and Wiehler (1995), is supported in Gesnerioideae based on recent phylogenetic studies that suggest that it is the sister clade to all other New World Gesneriaceae (Woo et al. 2011; Perret et al. 2012; Weber et al. 2013).

Columneinae (tribe Episcieae sensu Wiehler 1983) is the largest and most diverse subtribe in the Gesnerioideae and in the family with 26 genera and an over 700 species (Clark et al. 2006, 2012; Clark, 2009). The Columneinae is distinguished from the other subtribes of the tribe Gesnerieae by its nodal anatomy and chromosome number. All members of the Columneinae have a distinctive three-trace trilacunar nodal anatomy with split lateral bundles, as opposed to the conventional one-trace unilacunar nodal anatomy present in members of the other tribes of Gesnerioidae (Metcalfe 1950; Wiehler 1978). Most subtribes in the Gesnerieae have a base chromosome number of x= 13 or 14 (Wiehler 1983; Skog 1984; Burtt and Wiehler 1995; Smith et al. 2004). The Columneinae is unique in the tribe because it has a base chromosome number of x=9 (or x=8 in *Codonanthe* (Mart.) Hanst. and *Nemathanthus* Schrad.) (Wiehler 1978; Smith and Carroll 1997).

All genera in the Columneinae have been adequately evaluated in a phylogenetic context except for *Paradrymonia* Hanst., *Nautilocalyx* Linden ex Hanst., and *Chrysothemis* Decne. Recent phylogenetic studies have resulted in major shifts that have redefined most of the genera in the Columneinae so that they represent monophyletic groups (Clark et al. 2006; 2012). Although *Paradrymonia*, *Nautilocalyx*, and *Chrysothemis* form a clade within Columneinae (Clark et al. 2012; Perret et al. 2012), the relationships and generic delimitations within this clade have been problematic because material for generic type species was not available, and taxon sampling was mostly limited to Andean species. In this study we conducted field expeditions to Central and South America to increase taxon-sampling and include generic type species that were previously unavailable.

The species conventionally assigned to the genus *Paradrymonia* are widely distributed throughout the Neotropics, except southeastern Brazil and the Caribbean. The genus is especially diverse in northwestern South America with centers of diversity in Colombia and Ecuador. Unlike other genera in the Gesneriaceae that are abundant in mid-elevation montane forests (800-1500 m) (Perret et al. 2012), most species in *Paradrymonia* s.l. occur in lowland rainforests (< 800 m). One exception is *P. metamorphophylla*, which occurs in montane cloud forests up to 2500 m. Most species of *Paradrymonia* have narrow geographic ranges and grow in primary wet to moist forests on moss-covered rocks, wet logs, or edges of waterfalls and stream banks.

Many genera in the subtribe Columneinae (tribe Episcieae sensu Wiehler 1983) have at least one synapomorphy or distinctive morphological trait. For example, *Columnea* L. has an indehiscent fleshy berry; *Glossoloma* Hanst. has resupinate flowers; *Drymonia* Mart. has poricidal anther dehiscence; and *Episcia* has stolons. In contrast, *Paradrymonia,* has traditionally been defined by a combination of symplesiomorphic character states such as the epiphytic rosette forming habit, anisophyllous leaves, campanulate corollas, and semi-fleshy bivalved dehiscent capsules.

Paradrymonia is currently recognized with 38 species (Weber 2004; Skog and Boggan; 2007). It is the fourth largest genus in Columneinae after *Columnea* (200+ spp.), *Drymonia* (100+ spp.), and *Nautilocalyx* (ca. 60 spp.) (Clark 2009). The generic definition of *Paradrymonia* has been historically confusing because taxonomists have at some time recognized 17 (45%) of the described species as homotypic synonyms in other genera. *Paradrymonia* was first described by Hanstein (1854) with only one species, *P. glabra* (Benth.) Hanst. The concept of *Paradrymonia* as a genus was short-lived as Hanstein (1865) himself reduced it to a synonym of *Episcia* Mart. More than 100 years later, Wiehler (1973) re-established *Paradrymonia* by transferring four species that were previously recognized in *Episcia* (section *Paradrymonia* (Hanst.) Leeuwenbg.). Wiehler (1973) justified the re-circumscription and generic status by the presence of a rosette habit and long-lanceolate leaves.

The taxonomic challenges and non-monophyly of *Paradrymonia* are well-established in the literature (Smith and Carroll 1997; Clark and Zimmer 2003; Clark et al. 2006; Clark et al., 2012). *Paradrymonia* was recovered as monophyletic by Smith (2000); however, this study only included a limited sampling of three species. All other studies (Smith and Carroll 1997; Clark and Zimmer 2003; Clark et al. 2006; Clark et al. 2012) do not support the monophyly of *Paradrymonia*. The primary goal of this study was to use additional molecular sequence data from an expanded taxon sampling to: (1) re-circumscribe a monophyletic *Paradrymonia*; (2) identify well-supported clades among the *Paradrymonia* segregates; (3) increase taxon sampling relative to previous studies to resolve relationships between *Paradrymonia, Chrysothemis, Nautilocalyx* and closely related congeners; (4) to determine the placement of these genera within the subtribe Columneinae; and (5) evaluate diagnostic morphological characters of well-supported clades amongst currently recognized *Paradrymonia*.

MATERIALS AND METHODS

***Taxon sampling*—**A total of 80 ingroup and two outgroup taxa were sampled for the phylogenetic analyses. Fifteen out of 22 genera belonging to the subtribe Columneinae were included in the phylogeny. *Paradrymonia*, *Nautilocalyx*, and *Drymonia* were represented with 27, 23, and four species respectively. The remaining 13 genera were represented with one to three species each. *Sinningia cooperi* and *S. incarnata* were selected as outgroups based on previous phylogenies that strongly support subtribe Ligeriinae (tribe Sinningieae sensu Wiehler 1983) as the sister group to Columneinae (Perret et al. 2003; Zimmer et al. 2002).

DNA extraction, amplification and sequencing—DNA was isolated from fresh leaves dried in silica gel. Extractions of DNA were carried out using a Qiagen DNeasy Plant Mini Kit following the manufacturer's recommendations (Qiagen, Germantown, Maryland, USA).

Three markers used for this study were ITS and ETS (from nrDNA) and the *trnH- psbA* intergenic spacer (from cpDNA). The ITS region has been shown to be phylogenetically useful for analyses at the species level because it is variable and highly repeated in the plant genome allowing for easy detection, amplification and sequencing (Baldwin et al., 1995). The ETS region was chosen because it shares the same favorable features of ITS and it has been shown to provide more variable and parsimony informative characters than ITS (Baldwin and Markos 1998; Linder et al. 2000; Markos and Baldwin 2001, 2002; Vander Stappen 2003). Additionally, the combination of data from both regions have provided better resolved and increased support (Markos and Baldwin 2001; Vander Stappen 2003). The *psb*A-*trn*H intergenic spacer is considered among the most variable regions in the angiosperm plastid genome and it has been used in population genetic studies, in species-level phylogenies, and in DNA barcoding (Kress et al. 2005; Štorchová and Olson 2007; Yao et al. 2010).

The following primers were used to amplify the target DNA regions used in the study: (1) ITS4 and ITS 5 (Baldwin and Markos 1998); (2) 18S-ETS (Roalson et al. 2003) and ETS-B (Beardsley and Olmstead 2002); and (3) *psb*A-*trn*H (Sang et al. 1997). Promega Taq DNA polymerase kits were used to amplify DNA in accordance with the manufacturer's instructions (Promega, Madison, Wisconsin, USA).

The PCR reaction conditions for amplification of the ITS and ETS regions were as follows: (1) initial denaturizing at 95°C; (2) 34 cycles of 1 min at 95°C, 1 min at 48°C, 1 min at 72°C; and(3) a 7-min extension at 72°C. The PCR reaction conditions for amplification of the *psb*A-*trn*H spacer were as follows: (1) initial denaturizing at 95°C; (2) 30 cycles of 1 min at95°C, 30 s at 52°C, 30 s at 72°C; (3) followed by a 7-min extension.

PCR reactions were cleaned from unincorporated nucleotides and excess PCR primers using a PEG precipitation protocol prior to sequencing. Sequencing reactions were performed with ABI Prism BigDye Terminator Cycle Sequencing Ready Reaction Kits (PE Biosystems, Foster City, California) and were cleaned using EtOH/NaOAc precipitation. Sequencing was carried out at on an ABI 3731 genetic analyzer. Sequence chromatograms were examined and edited using Sequencher version 3.1.1 (Gene Codes Corporation 1998). GenBank accessions with their corresponding voucher information are provided in Appendix 1. Sequence alignments of all the data sets for the phylogenetic analyses are available from TreeBASE (study 14733).

***Sequence alignment*—**Sequences were initially aligned using ClustalW version 2.0

(Larkin et al. 2007) with default settings and subsequently manually adjusted using Se-Al version 2.0a11 (Rambaut 2002), a multiple sequence editor. Automated sequence alignments for the nuclear regions (ITS and ETS) required few manual adjustments. In contrast, alignments for the plastid marker, *psb*A-*trn*H, required extensive manual editing.

Inversions for six species were detected for the *psb*A-*trn*H dataset. Each inverted region was replaced with its reverse complement, such that sequence homology was maximized across the alignment (Whitlock et al. 2010). Additionally, inversions were scored as independent, single characters. A single region of approximately 42 characters from *psb*A-*trn*H was difficult to align and therefore excluded from the analyses.

***Phylogenetic Analyses*—**Data were analyzed separately (ITS, ETS, *psb*A-*trn*H) for parsimony analyses, and in combination under maximum parsimony, maximum likelihood (Felsenstein 1973) and Bayesian MCMC (Yang and Rannala 1997) methods.

No incongruence was detected from analyses of different matrices based on the evaluation of strongly supported nodes in the tree topologies. Incongruence among data partitions was evaluated by comparison of bootstrap support for clades (>75%) and posterior probability values greater than 0.95. The three datasets were combined in a total evidence approach (Kluge 1989) as suggested by Seelenan et al. (1997) and Wiens (1998), since there were no strongly supported nodes in conflict.

The maximum parsimony analyses were performed using the heuristic search option in PAUP* (Swofford 2003) with the following settings: 100 random addition replications with tree bisection reconstruction (TBR), branch swapping and MULTREES option in effect with a maximum of 10,000 trees being retained. Bootstrap analysis (Felsenstein 1985) with 1,000 replicates and 10 random sequenced additions per replicate were conducted to assess support values for the parsimony analysis.

The best-fitting model of DNA substitution was determined using the Akaike information criterion (Akaike 1974) under maximum likelihood settings as implemented by jModelTest (Posada, 2008). The best model of sequence evolution was the general time-reversible model (GTR+I+G) with some sites assumed invariant and with variable sites assumed to follow a gamma distribution. The following parameter estimates were obtained: base frequencies of 0.2569 (A), 0.2172 (C), 0.2298 (G), 0.2960 (T); substitution rates of 0.8679 (A–C), 2.5181 (A–G), 0.9418 (A–T), 0.7413 (C–G), 4.6177 (C–T), 1 (G–T); a gamma distribution shape parameter of 0.5030. Maximum likelihood (ML) heuristic bootstrapping search was performed using the default parameters in RAxML 7.2.6 (Randomized Axelerated Maximum Likelihood) through CIPRES portal (Stamatakis et al. 2008) for 100 replicates, repeated 10 times to generate 1000 replicates, starting from random trees.

Bayesian posterior probabilities (PP) were calculated with MrBayes 3.2 (Ronquist and Huelsenbeck 2003) for the combined dataset to further-investigate the impact of tree construction method on topology (Huelsenbeck and Ronquist 2001). The likelihood settings corresponded to the GTR+I+G + gamma model. A partitioned Bayesian analysis of the combined nuclear and plastid dataset was performed by applying the previously determined model to each data partition. Model parameters were independently optimized for the partitions of the combined nuclear and plastid datasets. One million generations were run for four Markov chains (MCMC) and sampled every 100th generation. The first 25% of trees were discarded as part of the burn-in phase and the remaining trees were used to calculate posterior probabilities in a 50% majority rule consensus tree. Trees were visualized in *FigTree* v1.3.1 (Rambaut 2009).

RESULTS

Phylogenetic analyses— The total evidence analyses (maximum parsimony, maximum likelihood and the Bayesian inference) resulted in trees with similar topology. Therefore, support values (Bootstrap/posterior probability values) are mapped onto the parsimony strict consensus tree (Fig. 1.1). The MP, ML and Bayesian analyses of the combined regions consistently revealed three highly supported main clades in the subtribe Columneinae (Fig. 1.1) : (1) the Guiana Shield clade (MP BS = 92%; ML BS = 97%; PP= 1.0); (2) the Core Columneinae clade (MP BS = 96%; ML BS = 98%; PP = 0.98); and (3) the *Paradrymonia* alliance clade (MP BS = 98%; ML BS = 98%; PP = 1.0).

The strict consensus trees of the MP and ML analyses and the majority-rule consensus Bayesian tree based on the plastid dataset (*psb*A-*trn*H) were mostly unresolved with no strongly supported clades (not shown). On the other hand, the single-nuclear marker analyses (ITS and ETS), as well as the combined analysis of all three markers with all of the phylogenetic approaches (MP, ML, and Bayesian inference) revealed the same three highly supported main clades (Fig. 1.1) and strongly support the non-monophyly of *Paradrymonia* (Fig 1.).

Maximum parsimony analyses—Table 1.1 presents a summary of statistics for the combined data set and individual partitions. Among the individual partitions, the percentage of informative characters was highest in the ETS region (51%), while *psb*A-*trn*H had the lowest percentage of informative characters (13%, Table 1.1).

The strict consensus trees from the maximum parsimony analyses of the individual ITS and ETS datasets as well as the combined data set (Fig. 1.1), were resolved, and strongly support the non-monophyly of *Paradrymonia* s. l. In contrast, the strict consensus tree for the cpDNA *psb*A-*trn*H region (tree not shown) was poorly resolved with only two pairs of species that were very strongly supported (BS MP> 95%) and congruent with the nrDNA datasets. Those species pairs are: *Roogeton cyclophyllus* + *R. viviparus* and *Nautilocalyx* sp. MM931 + *Nautilocalyx* sp. MM 949.

The MP strict consensus tree for the total evidence analysis (Fig. 1.1) strongly supports that traditionally recognized *Paradrymonia* is polyphyletic (i.e. *Paradrymonia* s.l.). Currently recognized *Paradrymonia* species were recovered as belonging to two clades in the Columneinae (Core Columneinae clade and three lineages in the *Paradrymonia* alliance clade; Fig. 1.1). The *Paradrymonia* alliance clade comprises seven strongly supported clades (herein referred to as clades I-VII in Fig. 1.1). Among these clades, three contain species of *Paradrymonia* (clades I, II and VII in Fig. 1.1). Clade I (MP BS = 98%; ML BS = 98%; PP = 1) includes the type species (*P. glabra*), and also includes *P. ciliosa* and *P. campostyla.* This small clade is strongly supported (MP BS = 98%; ML BS = 98%; PP = 1) as the sister group to the remaining species of the *Paradrymonia* alliance clade. Clade II is also strongly supported (MP BS = 95%; ML BS = 90%; PP = 1) and includes *Nautilocalyx cordatus* (=*Centrosolenia hirsuta*), *Nautilocalyx coccineus* (=*C. coccinea*) and *Paradrymonia densa* (=*C. densa*). Clade VI (*Trichodrymonia* clade) contains most of the traditionally recognized species of "*Paradrymonia*" and is strongly supported as the sister group to clade VI that contains the generic type species for *Nautilocalyx* (*N. bracteatus*).

The main difference between the topologies of the individual ITS and ETS consensus trees is the placement of the Core Columneinae and Guiana Shield clades. The individual analysis of ITS resulted in a poorly supported branch (BS < 50%) that subtends the Guiana

Shield and *Paradrymonia* alliance clades as sister groups. In contrast, the ETS and the total evidence analysis results in a strongly supported sister group relationship (BS = 100%) of the Guiana Shield clade and the Core Columneinae + *Paradrymonia* alliance clades (Fig. 1.1). In addition, a sister relationship between the Core Columneinae and the *Paradrymonia* alliance clades is strongly supported by the MP strict consensus of the ETS marker (BS = 90%); and moderately to strongly supported for the combined analysis (MP BS = 78%; ML BS = 84%; PP = 0.98, Fig. 1.1).

Maximum likelihood analysis**—**The topology of the maximum likelihood tree for the combined dataset (not shown) was highly congruent with results from the parsimony analysis. All of the major clades were recovered with strong support (Fig. 1.1). The support values for the ML analysis are mapped on the strict consensus tree (Fig. 1.1). In the ML tree (not shown), the *Paradrymonia* alliance clade (i.e. *Paradrymonia* s.l) also can be subdivided into seven subclades as in the MP tree. All of the seven subclades were strongly supported (Bootstrap value > 90%) except for clades II (*Centrosolenia* clade) and III (Pictus clade), which were not strongly supported (BS = 72 and 79% respectively, Fig.1). Subclades VI (*Nautilocalyx* s.s. clade) and VII (*Trichodrymonia* clade) also were recovered as sister taxa. One main difference between the ML and the MP analyses is that in the MP tree, subclade IV (*Chrysothemis* clade) appears as a basal clade sister to subclades V, VI, and VII (Amazonian "*Nautilocalyx*", *Nautilocalyx* s.s. and *Trichodrymonia* clades respectively; Fig. 1.1) whereas in the ML, the sister lineage to the clades VI (*Nautilocalyx* s.s. clade) and VII (*Trichodrymonia* clade) is not resolved (results not shown). Another difference is that in the ML analysis, *Nautilocalyx porphyrotrichus* is placed in subclade II (*Centrosolenia* clade; MP BS= 72%) whereas in the MP tree the relationship of this taxon with species in clade II, is unresolved (Fig. 1.1).

Bayesian analysis**—**The majority rule consensus tree resulting from the Bayesian analysis of the combined data set is congruent with the strict consensus tree of the parsimony and the majority rule likelihood analyses of the combined data sets (Fig. 1.1). At almost all nodes, posterior probability values were equal to or greater than bootstrap values in the parsimony and likelihood results.

The topology of the Bayesian tree is congruent with the MP and ML trees consisting of three major clades (Guiana Shield, Core Columneinae, and *Paradrymonia* alliance clades; Fig. 1.1) with posterior probability values equal to 1 (Fig.1). Relatively long branches (not shown) were found in *Cremersia patula* (Guiana Shield Clade) and *Codonanthopsis ulei* (Core Columneinae clade).

The results from the Bayesian analyses are congruent in regards to the seven subclades of the *Paradrymonia* alliance clade. All of the seven subclades were strongly supported (PP probabilities > 0.9) except for clade II (*Centrosolenia* clade, Fig.1). Subclade IV (*Chrysothemis* clade) appears as a basal clade sister to subclades V, VI, and VII (Amazonian "*Nautilocalyx*", *Nautilocalyx* s.s, *Trichodrymonia* clades respectively; Fig. 1.1) with low support (PP=0.57). Like the MP analysis, in the Bayesian analysis, Clade V (Amazonian "*Nautilocalyx*" clade) is sister to clades VI + VII (*Nautilocalyx* s.s + *Trichodrymonia* clades, respectively; PP=0.8)

Phylogenetic utility of ITS, ETS and* psb*A*-trn*H**—**ITS and ETS were the most informative regions among the three markers. The nuclear regions provided four times more parsimony informative characters than the *psb*A-*trn*H cpDNA marker (Table 1.1). Although both nuclear regions provided about the same number of informative characters (ITS=283; ETS=285), ETS yielded a greater number of phylogenetically informative characters per sequence length (Table 1.1). Most of the nodes in the resulting phylogenies of ETS and ITS combined were resolved. On the other hand, *psb*A-*trn*H resulted in the least number of variable and parsimony informative characters. The three main supported clades of subtribe Columneinae on the ITS and ETS trees received no support from the *psb*A-*trn*H sequences.

DISCUSSION

Combining the ITS, ETS and *psb*A-*trn*H data sets, which have no hard incongruences, resulted in a resolved and more highly supported phylogeny than any of the single-marker analyses (Fig. 1.1).

The trees based on the combined dataset for all the analytical methods (MP, ML and Bayesian analyses) revealed no strongly supported incongruent clades. The same strongly supported clades were recovered in each analysis, and differences in topology occurred only in clades with low bootstrap support (BS <50%). Consistently, Columneinae was divided into three following major clades: 1) Guiana Shield; 2) Core Columneinae; and 3) *Paradrymonia* alliance (Fig. 1.1). In all analyses of the combined dataset these clades were strongly supported (BS> 90% and PP =1).

***Comparison with other studies of Columneinae (Episcieae* sensu *Wiehler 1983) phylogeny*—**Nuclear markers (ITS and ETS) and the combined analyses are congruent in supporting the non-monophyly of *Paradrymonia*, as suggested by earlier studies with more limited taxon sampling (Smith and Carroll 1997; Clark and Zimmer 2003; Clark et al. 2006, Clark et al. 2012).

The basal placement of the Guiana Shield Clade within the subtribe Columneinae is strongly supported in all the phylogenetic analyses presented here (BS=100% PP=1.0, Fig. 1.1).

The placement of the Guiana Shield clade as basal to the Core Columneinae + *Paradrymonia* alliance clades is congruent with Clark et al. (2006), who used a total evidence analysis based on ITS, *psb*A-*trn*H and morphological data to produce a comprehensive phylogeny of the subtribe Columneinae (155 species and 21 out of the 22 genera). However, the statistical support for the basal placement of the Guiana Shield clade was low (BS<50%). Clark et al. (2006) included more taxa compared to the current study (151 vs. 82), but their focus was on the Core Columneinae clade. In contrast, we sampled 35 (18%) more species representing the *Paradrymonia* alliance clade and included an additional nrDNA molecular marker (i.e. ETS). The addition of ETS provided significant variation and parsimony informative characters (Table 1.1). Thus, the increased support in the present study is a result of the inclusion of ETS. The utility of ETS significantly increases support by adding 285 (51%) parsimony informative characters in contrast to 283 (37%) for ITS and 165 (31%) for *psb*A-*trn*H (Table 1.1).

In contrast, the placement of the *Paradrymonia* alliance and Guiana Shield clades in the present study are not congruent with Clark et al. (2012). The differences between these two studies could be attributed to different markers where the only marker that was used in the present study and Clark et al. (2012) is ITS. It should be noted that many of cpDNA markers in Clark et al. (2012) were limited in parsimony informative characters. For example, Clark et al. (2012) generated 8714 basepairs from 14 molecular markers for the Core Columneinae clade and only 383 (4.3%) were parsimony informative (Table 2 in Clark et al. 2012). In contrast, in the present study the utility of ETS alone accounted for 1300+ basepairs and resulted in 285 (51%) parsimony informative characters (Table 1.1). Other differences between the current study and Clark et al. (2012) could be attributed to differences in taxon sampling where there are only 20 species in common between the two studies. It should be noted that the sister group relationship of the Core Columneinae + Guiana Shield clades in Clark et al. (2012) lacks support in the MP analysis and is strongly supported in the ML analysis (MP BS=61; ML BS=100; PP=77). In contrast, the present study strongly supports the basal placement of the Guiana shield clade (MP BS=100; PP=100) and moderately to strongly supports the sister group relationship of the Core Columneinae and the *Paradrymonia* alliance clades (MP BS=78; MP BS= 84; PP=1.0). It is therefore highly recommended that future studies of the Columneinae include ETS because it provides significantly more parsimony informative characters relative to previous studies that depended on large quantities of cpDNA markers that provide relatively few parsimony informative characters.

Analyses by Perret et al. (2012) with a broader emphasis in the Gesnerioidae resulted in a basal placement of the *Paradrymonia* alliance clade. However, the study by Perret et al. (2012) lacked taxon sampling from the Guiana Shield and only four species from the *Paradrymonia* alliance clade (*Chrysothemis pulchella*, *Paradrymonia macrophylla*, *Nautilocalyx aeneus* and *N. melittifolius*). Thus, the lack of inclusion of species from the Guiana Shield and other differences in taxon sampling in Perret et al. (2012) makes comparisons at the level of Columneinae phylogeny to the present study of limited value.

Our results strongly support the placement of the Guiana Shield clade as basal within the Columneinae. The high number of endemic monotypic genera represented in the Guiana Shield clade could be a reflection that this clade has a relative older divergence compared with the Core Columneinae and *Paradrymonia* alliance clades. A combination of ancient divergence, vicariance and long distance dispersal have shaped the flora of the Guiana Shield (Givnish et al. 2004; Kelloff and Funk 2004; Rull 2005; Antonelli et al. 2009; Antonelli and Sanmartin 2011). The Guiana Shield flora has been described as a floristic region with ancient origins that has resulted in a high incidence of relict species (Maguire 1970; Steyermark 1986; Huber 1988, 1995). The restricted distribution and endemism of the Columneinae in the Guiana Shield clade could be the outcome of geology, topography, climatic factors (Kelloff and Funk 2004; Antonelli et al. 2009; Antonelli and Sanmartin 2011), geographic barriers to dispersal (Avise 2000) and low intrinsic dispersal ability (Croteau 2010) among others. Edaphic factors also appear to play and important role in the endemism of the Guiana flora as many unique floras of the Guiana Highlands are endemic to white sand and sandstone substrates (Kubitzki 1989, 1990; Clarke and Funk 2005).

Analyses presented here do not establish whether the *Paradrymonia* alliance clade is an older lineage than the Columneinae core clade but they do support the sister relationship between this two clades. These two clades are more diverse than the Guiana Shield clade and have centers of diversity in the Amazon, northern Andes and Central America.

The phylogenetic utility of plastid and nuclear DNA markers**—**As mentioned above, the external and internal transcribed spacers regions of nuclear ribosomal DNA (ETS and ITS respectively) compared to the plastid *psb*A-*trn*H intergenic spacer, provide significantly more parsimony informative characters and yielded results that were more robust and phylogenies that were better resolved. Among the nuclear markers, ETS produced a higher percentage of variability and was proportionally more informative than ITS despite its shorter sequence length (Table 1.1).

In contrast to the nuclear markers, the cpDNA marker *psb*A-*trn*H did not provide enough informative characters to resolve relationships among the taxa of interest. Alignments for the plastid marker, *psb*A-*trn*H, required extensive manual editing and the exclusion of an ambiguously aligned region. Automated alignment techniques were not feasible because of the following reasons: (1) the presence of inversions associated with palindromic sequences and (2) the presence of numerous indels that resulted in an ambiguous alignment. Inversions are known to be frequent for the *psb*A-*trn*H region (Sang et al. 1997; Tate and Simpson 2003; Clark et al. 2006; Kårehed et al. 2007; Borsch and Quandt 2009) and they appear to be common in non-coding plastid regions associated with stem-loops in the RNA secondary structures (Kelchner 2000; Storchova´ and Olson 2007). The most common explanation for these hairpin-associated inversions is a single mutational event (Kelchner 2000; Quandt et al. 2003; Kim and Lee 2005).

In addition to inversions, the *psb*A-*trn*H alignment presented numerous indels. One region of 42 characters was especially difficult to align and therefore excluded from the analyses. Many regions of indels were similar in unrelated taxa (i.e. species from different genera) indicating a high level of homoplasy. Sang et al. (1997) also noticed considerable homoplasy of indel characters for *psb*A-*trn*H within *Paeonia* (Paeoniaceae). In the present study, the remaining portion of the alignment included in the analysis was rather conserved and therefore of limited value in resolving relationships. Like Shaw et al. (2005) we conclude that *psb*A-*trn*H provides too little phylogenetic information to be recommended for future studies.

Likewise, the phylogenetic performance of *psb*A-*trn*H and other plastid markers has shown to be lower than nuclear non-coding sequences in other studies in the Gesneriaceae. For example, in Clark et al. (2012) ITS yielded at least five times the percentage of phylogenetically informative characters than any single non-coding plastid region used in the analysis. Some regions like the *trnL-F* spacer and the *trnL* intron had 2% or fewer parsimony informative characters per length of sequence (vs. 20% for ITS). Although Clark et al. (2012) included 14 markers, 10 of which were cpDNA non-coding regions, the combined regions yielded less than

5% informative characters. In contrast, the present study yielded 35% of parsimony informative characters using only three markers. The data presented here and in other studies clearly show that cpDNA noncoding sequences result in poorly supported phylogenies and limited resolution within the subtribe Columneinae. Although some relationships remain to be resolved, in the present study the combination of ITS and ETS provided sufficient characters for robust results and resolution amongst closely related taxa. The use of ETS for future analyses in the Gesneriaceae is encouraged.

***Phylogeny of* Paradrymonia *s.l. and taxonomic considerations*—*Guiana Shield Clade*—**The Guiana Shield Clade includes taxa that are endemic to that region in northeastern South America. This region is defined by the underlying geological formation known as the Guiana Shield and extends from western Colombia to eastern Brazil (States of Amapá Pará, Roraima and Amazonas), Venezuela (States of Delta Amacuro, Bolívar and Amazonas), Guyana, Suriname and French Guiana (Hollowell and Reynolds 2005). Interestingly, this region has a surprisingly large number of endemic genera of Gesneriaceae (Weber 2004). Out of the eight genera endemic to this region, seven belong to the Columneinae: *Lembocarpus* Leeuwenb., *Rhoogeton* Leeuwenb., *Lampadaria* Feuillet and L. E. Skog, *Cremersia* Feuillet and L. E. Skog (Feuillet and Skog 2003) and the recently described monotypic genera *Christopheria* and *Pagothyra* (Smith and Clark, 2013). The results presented here sampled all of the endemic genera except for *Lampadaria* and *Christopheria*. While the placement of *Lampadaria* remains uncertain, *Christopheria* (as *Episcia xantha* Leeuwenb. in Clark et al. 2012), was strongly supported as nesting in the Guiana Shield Clade. *Pagothyra* consists of a single species, *P. maculata*, a climbing vine with isophyllous leaves and bell–shaped yellow flowers mottled with bright red spots. This taxon was first placed in the genus *Episcia* by Hooker (1890) and then transferred to *Paradrymonia* by Wiehler (1978). Recently, this taxon was recognized as a monotypic genus, based on the unique apomorphy of the ventral corolla lobe occluding the throat like a trap door (Smith and Clark 2013). A recent analysis (Clark et al. 2012) supports a sister-taxon relationship between *Christopheria xantha* and *Pagothyra maculata*.

***Core Columneinae clade: Phylogenetic placement of* Drymonia longifolia *(ex-*Paradrymonia *species)*—**Among the three major clades within the subtribe Columneinae, the Core Columneinae clade is the largest and most diverse (Fig. 1.1). This clade includes *Drymonia longifolia* Poepp. *Drymonia longifolia* had been recognized as a member of *Paradrymonia* by Wiehler (1973), but it was originally described as a member of *Drymonia* by Poeppig (1840). Wiehler (1973) made the combination in *Paradrymonia* because he noted the presence of longitudinal slits instead of poricidal anther dehiscence. The presence of poricidal anther dehiscence in *Drymonia longifolia* was observed in early stage of anthesis that then developed into longitudinal slits as the flower matured (Clark pers. obs.) The shift between poricidal to longitudinal anther dehiscence has been observed for other species of *Drymonia* (Clark et al. 2006) and therefore makes it challenging to assign a definitive character state for anther dehiscence. Furthermore, the presence of isophyllous leaves, leafy calyx and succulent display capsule are further evidence that this taxon does not belong in *Paradrymonia.* Results presented here and in previous studies (Zimmer et al. 2002; Clark and Zimmer 2003; Clark et al. 2006; Clark et al. 2012) strongly support the placement of *Drymonia longifolia* as a member of *Drymonia*.

Paradrymonia *alliance clade -(subclades I thorugh VII)* —This study provides the most comprehensive taxon sampling for *Paradrymonia*, *Nautilocalyx* and *Chrysothemis*

(*Paradrymonia* alliance clade) to date. The *Paradrymonia* alliance clade is strongly supported (Fig.1) in this study as well as in previous analyses (Zimmer et al. 2002; Clark and Zimmer 2003; Clark et al. 2006; Clark et al. 2012). Our results show that this clade comprises seven moderately to strongly-supported lineages (clades I-VII in Fig. 1.1). Species relationships within these clades varied by analytical approach usually when the nodes were not strongly supported (BS values < 80% PP< 0.8) or were unresolved. Species traditionally recognized as *Paradrymonia* nest in three of the seven lineages within the *Paradrymonia* alliance clade: (1) *Paradrymonia* s.s. clade; (2) *Centrosolenia* clade; and (3) *Trichodrymonia* clade (Fig.1). Phylogenetic analyses also strongly support the genus *Nautilocalyx*, as currently circumscribed, to be paraphyletic. *Nautilocalyx* species nest in five subclades within the *Paradrymonia* alliance clade: (1) *Centrosolenia* clade; (2) Pictus clade*;* (3) *Chrysothemis* clade; (4) Amazonian "Nautilocalyx" clade; and (5) *Nautilocalyx* s.s. clade**.**

The placement of *Paradrymonia*, *Nautilocalyx* and *Chrysothemis* species within the main subclades is described below:

***Non-monophyly of* Paradrymonia**—Our results strongly support that *Paradrymonia* must be substantially re-circumscribed to reflect the phylogenetic results presented here (i.e. monophyletic genera). Clade I (as *Paradrymonia* s.s. in Fig. 1.1) is strongly supported as monophyletic (BS=98, PP=1). The *Paradrymonia* s.s. clade includes the generic type species, *Paradrymonia glabra* (Figs. 2A & B), *P. ciliosa* (Figs. 2C & D) and *P. campostyla*. Interestingly, *P. glabra* was recognized by Wiehler (1973) as a synonym of *P. ciliosa*. Extensive fieldwork and an ongoing monographic revision of *Paradrymonia* suggest that these two taxa are not conspecific based on morphological and geographical data. Both species have creeping stems, clustered leaves, elongate and coriaceous leaf blades, fimbriate corolla lobes and bearded anthers (Fig. 1.2). Characters that differentiate *Paradrymonia glabra* from *P. ciliosa* include the following: *P. glabra* has white, straight corollas covered with white trichomes (Fig. 1.2A) while *P. ciliosa* has cream-white, angulated corollas covered with red trichomes (Fig. 1.2C). Additionally, *P. glabra* is endemic to the Venezuelan Andes while *P. ciliosa* is a widespread taxon that is distributed from Nicaragua to northeastern Brazil.

***Bearded anthers and the* Paradrymonia *s.s. (subclade I)*—**As defined here, *Paradrymonia* s.s. includes species with anisophyllous leaves; succulent, large elliptic-oblanceolate leaf blades with decurrent bases (Fig. 1.2E); petioles longer than the inflorescence; flowers with calyx lobes linear to lanceolate (Fig. 1.2); corolla lobes crenate to fimbriate with elongate fimbriations on lower lobe (Figs. 2B & D); and anthers with an apical tuft of trichomes (i.e. "bearded anthers"; Fig. 1.2F). The presence of bearded anthers in *Paradrymonia* s.s. is a distinctive synapomorphy that has not been previously recognized at the generic level. Bearded anthers are not known to occur in other groups of Gesneriaceae. Although only two species included in the phylogeny have bearded anthers, other species such as *Paradrymonia buchtienii*, *P. lutea*, *P. yatua* and *P. tepui* also have this distinctive character. It is predicted that these species belong to the same clade because they present bearded anthers and are vegetatively similar to other members of *Paradrymonia* s.s.

The sister taxon to *Paradrymonia glabra* and *P. ciliosa* is *Paradrymonia campostyla* which lacks bearded anthers. In addition to lacking bearded anthers it also differs by the presence of elongate climbing stems with isophyllous leaves (vs. anisophyllous leaves and erect shoots); small oblong-elliptic to oblong-ovate leaf blades with subcordate bases (vs. oblanceolate with decurrent bases); and petioles shorter than the flowers (vs. petioles longer than the flowers). We refrain from recognizing *Paradrymonia campostyla* as a different genus even though is morphologically distinct from the core *Paradrymonia* clade based on the characters described above. Thus, *Paradrymonia campostyla* remains in *Paradrymonia*, but it is not considered a member of *Paradrymonia* s.s.

Centrosolenia (*subclade II)*—The *Centrosolenia* clade includes three species (Fig.1). *Centrosolenia* is an available name that includes *Centrosolenia hirsuta*, which is a synonym of *Nautilocalyx cordatus* and the generic type species for *Centrosolenia* Benth. The name *Centrosolenia* Benth. predates *Nautilocalyx* Linden ex Hanst., but the latter was conserved by Feuillet and Skog (1990).

Morphological characters that are shared among species in this clade include: (1) the presence of decumbent stems that root and branch at the nodes; (2) variegated leaf blades (especially along the midrib) (Fig. 1.3A) with asymmetrical bases and anastomosed tertiary venation; and (3) elongate narrow-tubular corollas (Fig. 1.3A). Some immature individuals of *Paradrymonia densa* have variegated leaves that lose their variegation at maturity. An important diagnostic character for *Centrosolenia* that distinguishes it from Clade V (Amazonian "*Nautilocalyx*") and Clade VI (*Nautilocalyx* s.s.) is the presence of oblong-lanceolate to oblong-spathulate calyx lobes. The other "*Nautilocalyx*" clades (V & VI) have calyx lobes that range from broadly ovate and leaf-like (Amazonian "*Nautilocalyx*", Fig. 4B) to linear-lanceolate (*Nautilocalyx* s.s. Figs. 3C & D). The ML and Bayesian analyses result in placing *Nautilocalyx porphyrotrichus* into *Centrosolenia*, but support is moderately low or weak (ML BS=72; PP=0.55). It is interesting to note that Leeuwenberg (1958) recognized six subsections in a classification of the genus *Episcia*, and included *Nautilocalyx porphyrotrichus* as *Episcia porphyrotricha* in section *Episcia*, subsection *Centrosolenia*. This species has bullate variegated leaves with white or yellow on the midrib, and red narrow-tubular corollas; characters common in other species in the *Centrosolenia* clade. Interestingly, all of the species represented in the phylogeny in this clade are from the Guiana Shield.

In addition to the species sampled here, it is predicted that other species that are not sampled will also belong to *Centrosolenia* because they share a suite of characters such as similar habit (terrestrial herb), obovate to oblanceolate leaf shape, membranous leaf texture, crenate margins, oblong calyx lobes and tubular corollas. These species are from the Venezuelan Guiana Shield (e.g. *Nautilocalyx chimantensis, N. crenatus, N. orinocensis* and *N. ruber*) and the Amazon basin (e.g. *N. paujiensis*, *N. pusillus*, *N. roseus* and *N. vestitus*). The present molecular analysis in conjunction with morphological characters and geographic distribution provide strong support for the *Centrosolenia* clade, therefore the genus *Centrosolenia* is re-established with 12 new combinations (see taxonomic treatment below).

Pictus clade (subclade III)— This clade includes *Nautilocalyx pictus* and a recently discovered species from Peru (*M.M. Mora 949*). Both species have in common the presence of flowers in axillary fascicles, acuminate linear-lanceolate bracts, elongate calyx lobes, creeping habit, elongate internodes, isophyllous leaves, and bullate leaf blades with crenate to crenulate margins. Taxonomic changes are not recommended for this clade until additional sampling includes more species of *Nautilocalyx*.

Chrysothemis *clade (subclade IV)—* This clade includes *Chrysothemis pulchella* (the generic type species of *Chrysothemis*), *C. friedrichsthaliana*, *Nautilocalyx mellitifolius* and *N.*

panamensis (Fig. 1.1). All members of this clade are obligate terrestrial herbs that occasionally form tubers.

Chrysothemis has been traditionally distinguished from other species in the subtribe Columneinae by the presence of connate calyx lobes, which make the calyx look like a cup with irregular or five-pointed rim (Fig. 1.3E). These calyces have been described as “water calyces” because they can retain water and often secrete liquid that allow the immature buds to develop under an aqueous solution that protects the buds from floral herbivores (Burtt and Woods 1975; Endress 1996; Carlson and Harms 2007). Studies of *C. friedrichsthaliana* by Carlson and Harms (2007) suggest that the water calyx helps protect immature flower buds from a small species of moth (*Alucita* sp.) that is a detrimental floral herbivore.

The present phylogenetic analysis suggests that the concept of the genus *Chrysothemis* should be expanded to include *Nautilocalyx adenosiphon, N. panamensis* and *N. mellitifolius*. Although these species have rather relatively free calyx lobes, they share with all other species an obligate terrestrial habit with underground tubers and succulent stems. Other diagnostic characters for the *Chrysothemis* clade include the following: (1) elliptic leaves with crenate-dentate to dentate-serrate margins; (2) slightly asymmetrical (oblique) leaf bases; (3) cross venulate to reticulate veins; and (4) semi-succulent fully reflexed capsules when opened.

***Amazonian* “Nautilocalyx” *clade (subclade VI)*—**This clade includes most of the species traditionally placed in *Nautilocalyx*. The species in this clade are obligate terrestrial herbs with similarities to members of the *Nautilocalyx* s.s. clade such as isophyllous leaves and succulent stems. An important distinction between the Amazon “*Nautilocalyx*” clade and the *Nautilocalyx* s.s. clade is that the calyx lobes are overlapping at the base or folded in a conduplicate manner such that each lobe is appressed to an adjacent lobe and folded lengthwise with the margin curved upward (Fig. 1.3B). The calyx lobes are also leaf-like and cover the basal gibbosity of the corolla tube. Most species in this clade have tubular white or cream corollas. The corolla tube is usually 3× or longer than the calyx lobes and is typically longitudinally sulcate with blunt ridges on both, the dorsal and ventral surface (Fig. 4B). The *Nautilocalyx* s.s. clade has calyx lobes that are nearly free, linear-lanceolate, and the corolla spur is exposed (Figs. 3C & D).

Nautilocalyx *s.s. clade*—This study is the first to include *Nautilocalyx bracteatus*, which is the type species for *Nautilocalyx*. This species is endemic to Colombia and occurs in the Departments of Antioquia, Chocó and Santander. The inclusion of this species in the analysis is crucial for a new taxonomic delimitation of *Nautilocalyx*. The genus was established by Hanstein in an introduction of genera (1854) and 11 years later, he reduced it to a synonym of *Episcia* (Hanstein 1865). Bentham (1876) then divided the genus *Episcia* into six sections including sect. *Nautilocalyx*. Sprague (1912) resurrected the genus on the basis of the position of the ovules on one or both surfaces of the placenta. However, Wiehler (1978) found Sprague’s character to be inconsistent and variable among some members of Episcieae.

The *Nautilocalyx* s.s. clade includes *N. antioquensis, N. bracteatus, N. colombianus* (Fig. 1.3C), and a recently discovered species that is new to science (Fig. 1.3D). This clade is defined by funnel or trumpet-shaped corolla with spreading corolla lobes, narrow lanceolate to linear-lanceolate calyx lobes with the dorsal lobe greatly reduced and recurved to accommodate the gibbosity at the base of the corolla, and a corolla tube that is less than 2× longer than the calyx (vs. 3× longer than the calyx in the Amazonian “*Nautilocalyx*” clade).

Most of the species in the *Nautilocalyx* s.s. clade are distributed in the Chocó Biogeographic region in Colombia and Ecuador, and at the Andes in Colombia. One species, *Nautilocalyx* sp. (*J.L.Clark 8268*; Fig. 1.3D), is east of the Andes in the Amazon basin of Colombia and northern Ecuador.

Trichodrymonia *clade*—The *Trichodrymonia* clade is comprised of most of the traditionally recognized species of *Paradrymonia* and includes the generic type species *Trichodrymonia congesta* Oerst. (= *Paradrymonia congesta* (Oerst.) Wiehler). The *Trichodrymonia* clade is a strongly supported monophyletic group (MP BS=88; ML BS=90; PP=0.94) and is the sister clade to *Nautilocalyx* s.s. (MP BS=72; ML BS=78 PP=1.0). A major challenge for this project was locating the generic type species of *Trichodrymonia* because it was only known from the type specimen collected by Liebmann in 1842 in Chinantla, Mexico. After more than a 150-year hiatus, the first author re-discovered this species on a 2010 collecting expedition to the type locality. The inclusion of *Trichodrymonia congesta* in the molecular phylogeny is necessary to unambiguously assign a genus name to this clade and to re-establish *Trichodrymonia*.

To account for the phylogenetic relationships and to accommodate this large segregate of *Paradrymonia* s.s., here we resurrect the genus *Trichodrymonia* and make 25 new combinations (see taxonomic treatment below). The species in this clade share many vegetative characters with those belonging to the *Paradrymonia* s.s. clade such as rosette habit (Fig. 1.3F), anisophyllous leaf pairs and elongated oblanceolate leaf blades. An important difference between *Trichodrymonia* and *Paradrymonia* is the absence of fimbriations on the corolla lobes in the former (Figs. 3G-I) and presence in the latter (Figs. 3A–F). Additionally, bearded anthers are present in *Paradrymonia* (Fig. 1.2) and absent in *Trichodrymonia*. The following characters define *Trichodrymonia*: (1) facultative epiphytic herbs; (2) leaves clustered in an apical rosette (Fig. 1.3F); (3) maroon sulcate petioles; (4) corollas salverform (Fig. 1.3G) to trumpet-shaped (Fig. 1.3H), occasionally hypocrytoid (Fig. 1.3I); (5) anthers glabrous with longitudinal dehiscence; (6) leaf pairs usually anisophyllous; and (7) fruits a semi-fleshy bivalved dehiscent capsule.

Conclusions—Analyses of relationships among the major *Paradrymonia* s.l. clades provide the most resolved phylogeny available for the genus. *Paradrymonia* s.l. as previously circumscribed is taxonomically reevaluated. Based on the present phylogeny and inferred morphological synapomorphies new combinations are provided that are consistent with the recognition of monophyletic genera. *Paradrymonia* is reduced to eight species (See taxonomic treatment), while the remaining ex-*Paradrymonia* species are placed in other genera. It is suggested that *Paradrymonia campostyla* remain in *Paradrymonia* until it is further evaluated at which time it may be circumscribed as a separate genus. *Chrysothemis* is monophyletic but the results presented here strongly support a broader circumscription that includes some species previously recognized in *Nautilocalyx*. *Nautilocalyx* is strongly supported as paraphyletic, but the recognition of additional new genera is not recommended until more comprehensive taxon sampling is included. The *Nautilocalyx* s.s. clade includes mostly species from Central America, northwestern South America (the Chocó Biogeographic region) and the northern Andes. *Nautilocalyx* s.s. is sister to *Trichodrymonia* and its species mainly differ from the ones comprising the Amazonian “*Nautilocalyx*” clade by the presence of infundibuliform or trumpet shape corollas (vs. tubular) and linear calyces (vs. leafy and ovate). Future studies with increased taxon sampling may support the segregation of the Amazonian "*Nautilocalyx*" as a genus. *Centrosolenia* is resurrected based on molecular and morphological evidence. Other species placed under *Nautilocalyx* need to be examined and sampled before a final taxonomic decision is made for this group.

TAXONOMIC TREATMENT

In the present treatment *Trichodrymonia* and *Centrosolenia* are resurrected to accommodate most of the ex-*Paradrymonia* species. Descriptions for *Paradrymonia* s.s. and for the resurrected genera *Trichodrymonia* and *Centrosolenia* are included. A list of species for each genus, including the new combinations, is provided.

Centrosolenia Benth., emend. M. M. Mora &J .L. Clark
Centrosolenia Benth. London J. Bot. 5: 362. 1846.—TYPE: *Centrosolenia hirsuta* Benth.

Terrestrial or saxicolous herbs; stems elongated, terete, decumbent, rooting and branching at the nodes. Leaves opposite, subequal to unequal in a pair; petioles usually hirsute or densely villous; leaf blades broadly oblong or ovate-oblong, apex broadly rounded, shortly acute or rarely subobtuse, base asymmetrical, rounded to subcordate, usually variegated and rugose or bullate above, scabrous or sparsely pubescent, hairs tending to be aggregated in the center of the vein-areoles; margin shallowly crenate-dentate to serrate, lateral nerves anastomosing near margin, conspicuously reticulated at least in the lower surface. Inflorescences axillary, cymose, 2--8-flowered; pedicels short, densely hirsute to villous. Flowers with calyx lobes almost free to the base, spathulate-oblong to lanceolate, apex obtuse or rounded, shallowly 2--3 repand-dentate in upper one-third; corolla oblique in calyx, narrowly tubular, villous throughout, white, violet or deep red, tube slender, gibbous at base, the spur ovate-oblong, lobes orbicular, upper three lobes slightly larger than the lower two lobes; stamens adnate just above the base of the corolla tube, filaments coiling after anthesis, anthers suborbicular or reniform, joined in two pairs; disc of a single dorsal nectariferous gland; ovary narrowly ovoid, pilose-sericeous, stigma stomatomorphic. Fruit a semi-succulent bivalved capsule. A genus with approximately 15 species distributed in the Amazon basin and the Guianas.

C. coccinea (Feuillet &L.E. Skog) M. M. Mora & J .L. Clark, comb. nov. *Nautilocalyx coccineus* Feuillet and L.E. Skog, Brittonia 54: 352–354, f. 1. 2003.**—**TYPE: GUYANA. Upper Potaro River region: upper slopes of Mt. Wokomung, 5°05’N. 59°50’W, 1540-1600 m, 11 Jul 1989, *B. M. Boom & G. J. Samuels 9186* (holotype: US!; isotype: NY!).

C. bryogeton (Leeuwenb.) M. M. Mora & J .L. Clark, comb. nov. *Episcia bryogeton* Leeuwenb., Acta Bot. Neerl. 7: 312. 1958. **—**TYPE: GUYANA. Kurupung R., near Makreba Falls, Upper Mazaruni dist., *Pinkus 12* (holotype: NY!; isotype: US!).

C. chimantense (L.E. Skog & Steyermark) M. M. Mora & J .L. Clark, comb. nov. *Nautilocalyx chimantensis* L.E. Skog & Steyermark, Novon 1: 217–219. 1991.**—**TYPE: VENEZUELA. Bolívar: Chimantá Massif, common along shaded wet bluffs and by waterfall along SW-facing sandstone bluffs and Chimantá-tepuí (Torono-tepuí), near southern corner, 1,700 m, 19-20 May 1953, *Steyermark 75473* (holotype: US!; isotypes: F!, VEN)

C. crenata (Feuillet) M. M. Mora & J .L. Clark, comb. nov. *Nautilocalyx crenatus* Feuillet, J. Bot. Res. Inst. Texas 2: 825–827. 2008.**—**TYPE: VENEZUELA. Amazonas: Cerro

Yapacana, alrededores del campamento a lo largo del río en las faldas en la parte suroeste, 3°45'N, 66°45'W, 825 m, 4 May 1970 (fl), *J.A. Steyermark & G. Bunting 103068* (holotype: US!; isotypes: NY!, VEN!).

C. hirsuta Benth., London J. Bot. 5: 362. 1846.—TYPE: GUYANA. Banks of the Rio Parama., *Schomburgk s.n.* (holotype: K!)

C. densa (C.H. Wright) M. M. Mora & J .L. Clark, comb. nov. *Episcia densa* C.H. Wright, Bulletin of Miscellaneous Information Kew 1895: 17. 1895.—TYPE: GUYANA. River Masouria *Jenman 2414* (holotype: K!)

C. orinocense (Feuillet) M. M. Mora & J .L. Clark, comb. nov. *Nautilocalyx orinocensis* Feuillet, J. Bot. Res. Inst. Texas 2: 833–834. 2008.—TYPE: VENEZUELA. Amazonas: Upper Orinoco river, Sierra Guaharibo, near Raudal de los Guaharibos, slopes of “Mt. Rimbaud,” light growth near the top, 30 Jul 1951 (fl), *L. Croizat 429* (holotype: NY!).

C. paujiensis (Feuillet) M. M. Mora & J .L. Clark, comb. nov. *Nautilocalyx paujiensis* Feuillet, J. Bot. Res. Inst. Texas 2: 827–828. 2008.—TYPE: VENEZUELA. Bolívar: 17 km E of El Paují by road and 64 kmW of Santa Elena by road, 4 km N of highway, Río Las Ahallas, ca. 4°30'N, 61°30'W, 850 m, 28 Oct 1985 (fl), *R.L. Liesner 19044* (holotype: US!; isotypes: MO!, VEN).

C. porphyrotricha (Leeuwenb.) M. M. Mora & J .L. Clark, *Episcia porphyrotricha* Leeuwenb. Acta Bot. Neerl. 7: 311, f. 26. 1958.—TYPE: GUYANA. Pakaraima Mts., Wenamu R., *Davenport 7* (holotype: K!).

C. pusilla (Feuillet) M. M. Mora & J .L. Clark, comb. nov. *Nautilocalyx pusillus* Feuillet, J. Bot. Res. Inst. Texas 2: 827–830. 2008.—TYPE: VENEZUELA. Bolívar: near El Paují, Río

Cabass, waterfall, 4°30'N, 61°35'W, 800–900 m, 3 Nov 1985 (fl), *R.L. Liesner 19429* (holotype: US!; isotypes: MO!, VEN!).

C. rosea (Feuillet) M. M. Mora & J .L. Clark, comb. nov. *Nautilocalyx roseus* Feuillet, J. Bot. Res. Inst. Texas 2: 830–833, fig. 4. 2008.—TYPE: VENEZUELA. Bolívar: N side of Auyan tepui, along banks of Quebrada Honda, Mar 1969 (fl), *G.C.K. Dunsterville & E. Dunsterville s.n.* (holotype: VEN!).

C. rubra (Feuillet) M. M. Mora & J .L. Clark, comb. Nov. *Nautilocalyx ruber* Feuillet, J. Bot. Res. Inst. Texas 2: 830–83. 2008.—TYPE: VENEZUELA. Amazonas: Dept. Atures, 4 km of Río Coro-Coro, W of Serranía de Yutajé, 9 km NW of settlement of Yutajé, along stream on plateau north of unnamed 1760 m peak, 5°41'N, 66°10'W, 1050–1300 m, 7 Mar 1987 (fl), *R.L. Liesner & B.K. Holst 21728* (holotype: US!; isotypes: MO!, VEN!).

C. vestita (Feuillet) M. M. Mora & J .L. Clark, comb. Nov. *Nautilocalyx vestitus* Feuillet, J. Bot. Res. Inst. Texas 2: 833–836. 2008.—TYPE: VENEZUELA. Bolívar: Cumbre del Cerro Guaiquinima, a lo largo del affluente del Río Carapo, 1 km río arriba del Salto Szczerbanari, 5°44'N, 63°41'W, 730–750 m, 23–24 May 1978 (fl), *J.A. Steyermark, P. Berry, G. C. K.Dunsterville & E. Dunsterville 117244* (holotype: VEN!).

PARADRYMONIA Hanst., emend. M. M. Mora & J .L. Clark

PARADRYMONIA Hanst., Linnaea 26: 207. 1854.—TYPE: *Paradrymonia glabra* (Benth.) Hanst. *Episcia* sect. *Paradrymonia* (Hanst.) Leeuwenb., Meded. Bot. Mus. Herb. Rijks Univ. Utrecht 146: 311. 1958.

Facultative epiphytes. Stems subwoody, elongate, creeping or ascending with many adventitious roots. Leaves of a pair equal to strongly unequal, usually, at least the longer one surpassing the stem; blade large, obovate to widely oblanceolate, acuminate at the apex, cuneate at the base or long decurrent into the petiole, coriaceous, somewhat succulent; serrulate at the margin. Inflorescences many-flowered in sessile or short-pedunculate umbels; bracts linear, pedicel hirsute; sepals free, linear to lanceolate, long acuminate, hirsute, unequal, the posterior one shorter, saccate at the base. Corolla oblique in the calyx, tubular with a broad limb, spurred at the base, all lobes or only the ventral one crenate or fimbriate; anthers oblong, coherent in pairs, barbate, longitudinally dehiscent; ovary villous with one or two disc glands; placentae ovuliferous on the inner surface only. A genus with approximately 10 species distributed in Central America, the Amazon basin and the Guianas.

P. BARBATA Feuillet & L.E. Skog

P. BUCHTIENII (Mansf.) Wiehler

P. CAMPOSTYLA (Leeuwenb.) Wiehler

P. CILIOSA (Mart.) Wiehler

P. GLABRA (Benth.) Hanst.

P. LUTEA Feuillet

P. TEPUI Feuillet

P. YATUA Feuillet

TRICHODRYMONIA Oerst. Emend. M. M. Mora & J .L. Clark

Trichodrymonia Oerst., Centralamer. Gesner. 38. 1858. Type Species: *Trichodrymonia congesta* Oerst.

Facultative epiphytes. Stems subwoody, usually short, with numerous adventitious roots. Leaves usually apically clustered, equal to strongly unequal in a pair, with at least the longer one surpassing the stem; petiole short or elongate but always shorter than the leaf-blade, usually marron and U-shaped in cross section; leaf blade large, obovate to widely oblanceolate, sometimes ovate, acuminate at the apex, usually cuneate at the base, or long decurrent into the petiole, sometimes subcordate, thin to coriaceous and dentate to serrulate at the margin. Inflorescences many-flowered in sessile or short-pedunculate umbels, usually close to the ground; bracts linear to ovate, pedicel glabrous or hirsute; sepals free or connate at the base, linear to lanceolate, long acuminate, glabrous to hirsute, subequal, saccate at the base; corolla oblique in the calyx, infundibuliform, trumpet-shaped or salverform, sometimes hypocyrtoid, spurred at the base; anthers oblong, coherent in pairs, glabrous, longitudinally dehiscent; ovary glabrous to sericeous with one disc gland; placentae ovuliferous on the inner surface only. Fruit a semi-fleshy bivalved dehiscent capsule, rarely a berry.

A neotropical genus of 40+ species, with at least 10 that are new to science. *Trichodrymonia* is distributed from southern Mexico to Central America, the Andes and the Amazon basin. Members of this genus grow predominantly in the understory of rainforests, on wet slopes, stream banks, or on moist rocks or logs.

T. alata (Kriebel) M. M. Mora & J .L. Clark, comb. nov. *Paradrymonia alata* Kriebel, Rhodora 106: 47. 2004.

T. alba (Wiehler) M. M. Mora & J .L. Clark, comb. nov. *Paradrymonia alba* Wiehler, Selbyana 5: 46. 1978

T. apicaudata (M. M. Mora & J. L. Clark) M. M. Mora & J .L. Clark, comb. nov. *Paradrymonia apicaudata* M. M. Mora & J. L. Clark, J. Bot. Res. Inst. Texas 6: 65-69. 2012.

T. aurea (Wiehler) M. M. Mora & J .L. Clark, comb. nov. *Paradrymonia aurea* Wiehler, Selbyana 5: 46-48. 1978.

T. congesta Oerst. Centralamericas Gesneraceer 38-39. 1858.

T. darienensis (Seem.) M. M. Mora & J .L. Clark, comb. nov. *Alloplectus darienensis* Seem., Botany of the Voyage of H.M.S. Herald 187. 1854.

T. erythropus (Hook.f.) M. M. Mora & J .L. Clark, comb. nov. *Episcia erythropus* Hook.f., Botanical Magazine 102: t. 6219. 1876

T. flava (Wiehler) M. M. Mora & J .L. Clark, comb. nov. *Paradrymonia flava* Wiehler, Selbyana 5: 51. 1978.

T. gibbosa (Wiehler) M. M. Mora & J .L. Clark, comb. nov. *Paradrymonia gibbosa* Wiehler, Selbyana 5: 52, pl. 12D.1978

T. gigantea (Wiehler) M. M. Mora & J .L. Clark, comb. nov. *Paradrymonia gigantea* Wiehler, Selbyana 5: 53.1978.

T. hirta (L.E. Skog) M. M. Mora & J .L. Clark, comb. nov. *Paradrymonia hirta* L.E. Skog, Ann. Missouri Bot. Gard. 65: 967. 1979

T. hypocyrta (Wiehler) M. M. Mora & J .L. Clark, comb. nov. *Paradrymonia hypocyrta* Wiehler**,** Selbyana 2: 82, pl. 25C. 1977.

T. lacera (Wiehler) M. M. Mora & J .L. Clark, comb. nov. *Paradrymonia lacera* Wiehler, Selbyana 7: 343, pl. 5A.1984

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T. longipetiolata (J.D. Sm.) M. M. Mora & J .L. Clark, comb. nov. *Paradrymonia longipetiolata* (J.D. Sm.) Wiehler, Selbyana 5:54.1978. *Episcia longipetiolata* J.D. Sm. Bot. Gaz. 25: 152-153. 1898.

T. macrophylla (Wiehler) M. M. Mora & J .L. Clark, comb. nov. *Paradrymonia macrophylla* Wiehler, Selbyana 5: 56. 1978.

T. maguirei (Feuillet) M. M. Mora & J .L. Clark, comb. nov *Paradrymonia maguirei* Feuillet, J. Bot. Res. Inst. Texas 3: 134, fig. 1. 2009.

T. metamorphophylla (J.D. Sm.) M. M. Mora & J .L. Clark, comb. nov. *Paradrymonia metamorphophylla* (J.D. Sm.) Wiehler, Phytologia 27: 327. 1973. *Alloplectus metamorphophyllus* J.D. Sm. Bot. Gaz. 52: 52. 1911.

T. ommata (L.E. Skog) M. M. Mora & J .L. Clark, comb. nov. *Paradrymonia ommata* L.E. Skog, Brittonia 30: 324. 1978.

T. peltata (C.V. Morton) M. M. Mora & J .L. Clark, comb. nov. *Episcia peltata* C.V. Morton, J. Wash. Acad. Sci. 35: 131. 1945

T. pedunculata (L.E. Skog) M. M. Mora & J .L. Clark, comb. nov. *Paradrymonia pedunculata* L.E. Skog, Brittonia 30: 325. 1978.

T. sastrei (Wiehler) M. M. Mora & J .L. Clark, comb. nov. *Paradrymonia sastrei* Wiehler, Gesneriana 1: 71. Fig. 21. 1995

T. sericea (Wiehler) M. M. Mora & J .L. Clark, comb. nov. *Paradrymonia sericea* Wiehler, Selbyana 5: 57. 1978.

T. splendens (Freiberg) M. M. Mora & J .L. Clark, comb. nov. *Paradrymonia splendens* Freiberg, Phyton (Horn, Austria) 37: 136.1997.

T. tylocalyx (Wiehler) M. M. Mora & J .L. Clark, comb. nov. *Paradrymonia tylocalyx* Wiehler, Selbyana 5: 58. 1978.

T. ulei (Wiehler) M. M. Mora & J .L. Clark, comb. nov. *Paradrymonia ulei* Wiehler, Gesneriana 1: 71, fig. 22. 1995.

ACKNOWLEDGMENTS. Support for this project was provided by The Gesneriad Society, Inc.and by the National Science Foundation (DEB-0841958 and DEB-0949169) to John L. Clark. We thank the Smithsonian Institution's National Museum of Natural History – Department of Botany (US), the Missouri Botanical Garden (MO), the Field Museum of Natural History (F), the Marie Selby Botanical Gardens (SEL) and the University of Wisconsin (WIS) herbaria for access to their collections.

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Table 1.1. Summary statistics derived from the parsimony analyses of nuclear and plastid markers

Statistic	**ITS**	**ETS**	**Combined nuclear data**	***Psb*A-*trn*H**	**Combined Nuclear and plastid data**
Total # of taxa	82	73	82	71	82
Basepairs in the alignment	1-758	759-1313	1-1313	1313-1886	1-1886
Total length (aligned)	758	555	1313	573	1886
Included characters	758	555	1313	525	1795
Number of MP trees	71	29	12	11	25
Tree length (steps)	1436	1193	2711	253	2977
Variable characters (%)	398 (52%)	373 (67%)	751 (57%)	165 (31%)	950 (53%)
Parsimony informative characters (%)	283 (37%)	285 (51%)	576 (44%)	67 (13%)	638 (35%)
Consistency Index	0.407	0.503	0.443	0.747	0.463
Retention index	0.700	0.735	0.706	0.723	0.704

APPENDIX 1. Taxa included in the analyses, voucher information, locality and GenBank accession numbers for ITS ETS and *trnH-psbA*. Unvouchered samples taken from live material growing at the U. S. Botany Research Greenhouses (USBRG) are designated by their accession number. Sequences not obtained are designated by ---; * indicate generic type species; herbarium acronyms follow Thiers (2013).

Taxon, Voucher, Locality, GenBank accessions: **ITS, ETS, *psbA*-trnH spacer**

Alloplectus hispidus (Kunth) Mart., *J. L. Clark 7720* (US), Ecuador, KF040174, KF040256, KF040101; ***Alloplectus weirii*** (Kuntze) Wiehler, *J.L. Clark 5788* (US), Ecuador, KF040175, KF040257, KF040102; ***Alsobia dianthiflora*** (H. E. Moore & R. G. Wilson) Wiehler, *J. Hall s. n.* (SEL), Cultivated (Costa Rica), KF040176, KF040258, KF040103; ***Alsobia puntata*** (Lindl.) Hanst. *, *J. L. Clark 8851* (US), Cultivated (Mexico), KF040177, KF040259, KF040104; ***Chrysothemis friedrichstaliana*** (Hanst.) H. E. Moore, *J.L. Clark 10018* (US), Colombia, KF040179, KF040261, KF040106; ***Chrysothemis pulchella*** (Donn ex Sims) Decne. *, *J.L. Clark 8864* (US), Cultivated (unknown), KF040180, KF040262, KF040107; ***Cobananthus calochlamys*** (Donn.Sm.) Wiehler *, *J.L. Clark 5613* (US), Cultivated (Guatemala), KF040181, KF040263, KF040108; ***Codonanthe carnosa*** (Gardner) Hanst., *J.L. Clark 6268* (US), Cultivated (Brazil), KF040182, KF040264, KF040109; ***Codonanthe gracilis*** (Mart.) Hanst., *J. F. Smith 3721* (US), Cultivated (Brazil), KF040183, KF040265, KF040110; ***Codonanthopsis ulei*** Mansf., *J.L. Clark 8868* (US), Cultivated (Brazil), KF040178, KF040260, KF040105; ***Columnea dressleri*** Wiehler, *J.L. Clark 8559* (US), Panama, KF040184, KF040266, KF040111; ***Columnea linearis*** Oerst., *J.L. Clark 6274* (US), Cultivated (Costa Rica), KF040185, KF040267, KF040112; ***Columnea scandens*** L., *J. L. Clark 8879* (US), Cultivated (unknown), KF040186, KF040268, KF040113; ***Crantzia cristata*** (L.) Scop., *J.L. Clark 6546* (US), Martinique, KF040187, KF040269, KF040114; ***Cremersia platula*** Feuillet & L.E. Skog *, *J.J. de Granville 14868* (CAY), French Guiana, KF040188, ---, --- ; ***Drymonia killipii*** Wiehler, *J.L. Clark 7521* (US), Ecuador, KF040189, KF040270, KF040115; ***Drymonia lanceolata*** (Hanst.) C.V.Morton, *J.L. Clark 8553* (US), Panama, KF040190, KF040271, KF040116; ***Drymonia longifolia*** Poepp., *J.L. Clark 6262* (US), Ecuador, KF040191, KF040272, KF040117; ***Drymonia urceolata*** Wiehler, *J.L. Clark 5225* (US), Ecuador, KF040192, KF040273, KF040118; ***Episcia cupreata*** (Hook.) Hanst., *J.L. Clark 8844* (US), Cultivated (Colombia), KF040193, KF040274, KF040119; ***Episcia lilacina*** Hanst., *J.L. Clark 8881* (US), Costa Rica, KF040194, KF040275, KF040120; ***Glossoloma medusaeum*** (L.E. Skog) J.L.Clark, *J.L. Clark 4973* (US), Ecuador, KF040195, KF040276, KF040121; ***Glossoloma tetragonum*** Hanst., *J.L. Clark 8547* (US), Panama, KF040196, KF040277, KF040122; ***Lembocarpus amoenus*** Leeuwenb. *, *J.L. Clark 8841* (US), Cultivated (French Guiana), KF040197, ---, KF040123; ***Nautilocalyx antioquensis*** Wiehler, *M.M. Mora 806* (US), Colombia, KF040205, KF040285, --- ; ***Nautilocalyx bracteatus*** (Planch.) Sprague, *M.M. Mora 800* (US), Colombia, KF040206, KF040286, KF040131; ***Nautilocalyx bullatus*** (Lem.) Sprague, *M.M. Mora 971* (UNA), Cultivated (Peru), KF040207, KF040287, KF040132; ***Nautilocalyx coccineus*** Feuillet & L.E. Skog, *D. Clarke 10295* (US), Guyana, KF040208, KF040288, KF040133; ***Nautilocalyx colombianus*** Wiehler, *J.L. Clark 12454* (US), Panama, KF040209, KF040289, KF040134; ***Nautilocalyx cordatus*** (Gleason) L.E. Skog, *K. Redden 2359* (US), Guyana, KF040210, KF040290, KF040135; ***Nautilocalyx forgetii*** (Sprague) Sprague, *J.L. Clark 8847* (US), Cultivated (Peru), KF040212, KF040292, KF040137; ***Nautilocalyx glandulifer*** Wiehler, *J.L. Clark 10012* (US), Ecuador, KF040211, KF040291, KF040136; ***Nautilocalyx hirsutus*** (Sprague) Sprague, *M.M. Mora 950* (US), Peru, KF040204, KF040284, KF040130; ***Nautilocalyx melittifolius*** (L.) Wiehler, *J.L. Clark 6540* (US), Martinique, KF040213, KF040293, KF040138; ***Nautilocalyx pallidus*** (Sprague) Sprague, *J.L. Clark 9352* (US), Ecuador, KF040214, KF040294, KF040139; ***Nautilocalyx panamensis*** (Seem.) Seem., *J.L. Clark 12735* (US), Panama, KF040215, KF040295, KF040140; ***Nautilocalyx pemphidius*** L.E. Skog, *D. Bell 324* (US), Venezuela, KF040216, KF040296, --- ; ***Nautilocalyx pictus*** (W. Hook.) Sprague, *D. Clarke 9974* (US), Guyana, KF040217, ---, KF040141; ***Nautilocalyx porphyrotrichus*** (Leeuwenb.) Wiehler, *J.L. Clark 10449* (UNA), Cultivated (unknown), KF040218, KF040297, KF040142; ***Nautilocalyx punctatus*** Wiehler, *K. Redden 3407* (US), Venezuela, KF040219, KF040298, --- ; ***Nautilocalyx whitei*** Rusby, *J.L. Clark 6793* (US), Bolivia, KF040220, KF040299, KF040143; ***Nautilocalyx* sp. Clark 8268,** *J.L. Clark 8268* (US), Ecuador, KF040199, KF040279, KF040125; ***Nautilocalyx* sp. Mora 931,** *M.M. Mora 931* (US), Peru, KF040200, KF040280, KF040126; ***Nautilocalyx* sp. Mora 933,** *M.M. Mora 933* (US), Peru, KF040201, KF040281, KF040127; ***Nautilocalyx* sp. Mora 939,** *M.M. Mora 939* (US), Peru, KF040202, KF040282, KF040128; ***Nautilocalyx* sp. Mora 949,** *M.M. Mora 949* (US), Peru, KF040203, KF040283, KF040129; ***Nautilocalyx* sp. Mora 970,** *M.M. Mora 970* (UNA), Ecuador, KF040198, KF040278, KF040124; ***Nematanthus albus*** *Chautems*, *J.L. Clark 6266* (US), Cultivated (Brazil), KF040221, KF040300, KF040144; ***Nematanthus corticola*** Schrad. *, *J.L. Clark 6271* (US), Cultivated (Brazil), KF040222, KF040301, KF040145; ***Pagothyra maculata*** (Hook. f.) J.F. Sm. & J. L. Clark, *K. Redden 2231* (US), French Guiana, KF040245, KF040321, --- ; ***Codonanthopsis anisophylla*** (Feuillet & L.E.Skog) Chautems & Mat. Perret, *D. Clarke 10413* (US), Guyana, KF040227, KF040305, KF040149; ***Paradrymonia aurea*** Wiehler, *J.L. Clark 5409* (US), Ecuador, KF040228, KF040306, KF040150; ***Paradrymonia binata*** Wiehler , *J.L. Clark 8848* (US), Ecuador, KF040229, ---, KF040151; ***Paradrymonia campostyla*** (Leeuwenb.) Wiehler, *J.L. Clark 8855*

(US), Cultivated (French Guiana), KF040230, KF040307, KF040152; ***Paradrymonia ciliosa*** (Mansf.) Wiehler, *D. Clarke 10239* (US), Guyana, KF040231, KF040308, KF040153; ***Paradrymonia congesta*** (Oerst.) Wiehler, *M.M. Mora 969* (US), Mexico, KF040232, KF040309, KF040154; ***Paradrymonia densa*** (C.H.Wright) Wiehler, *K. Redden 1060* (US), Guyana, KF040233, KF040310, --- ; ***Paradrymonia erythropus*** (Hook. f.) Wiehler, *M.M. Mora 805* (US), Colombia, KF040234, KF040311, KF040155; ***Paradrymonia flava*** Wiehler, *J.L. Clark 12547* (US), Panama, KF040223, ---, KF040146; ***Paradrymonia flava*** Wiehler, *J.L. Clark 8846* (US), Panama, KF040235, ---, KF040156; ***Paradrymonia gibbosa*** Wiehler, *M.M. Mora 833* (US), Colombia, KF040236, KF040312, KF040157; ***Paradrymonia gigantea*** Wiehler, *M.M. Mora 846* (US), Colombia, KF040237, KF040313, KF040158; ***Paradrymonia glabra*** (Benth.) Hanst, *J.L. Clark 10075* (UNA), Cultivated (Venezuela), KF040238, KF040314, KF040159; ***Paradrymonia hypocyrta*** Wiehler, *J.L. Clark 10010* (US), Ecuador, KF040240, KF040316, KF040160; ***Paradrymonia lacera*** Wiehler, *J.L. Clark 11942* (UNA), Cultivated (Ecuador), KF040241, KF040317, KF040161; ***Paradrymonia macrophylla*** Wiehler, *J.L. Clark 8545* (US), Panama, KF040243, KF040319, KF040163; ***Paradrymonia macrophylla*** Wiehler, *M.M. Mora 811* (US), Ecuador, KF040244, KF040320, KF040164; ***Paradrymonia metamorphophylla*** (Donn.Sm.) Wiehler, *J.L. Clark 6028* (US), Ecuador, KF040246, KF040322, KF040165; ***Paradrymonia pedunculata*** L.E. Skog, *USBRG 1994-184*(US), Cultivated (Costa Rica & Panama), KF040247, KF040323, KF040166; ***Paradrymonia sericea*** Wiehler, *M.M. Mora 838* (US), Colombia, KF040249, KF040325, KF040168; ***Paradrymonia splendens*** M. Freiberg, *J.L. Clark 7351* (US), Ecuador, KF040250, ---, --- ; ***Paradrymonia ulei*** Wiehler, *M.M. Mora 877* (US), Peru, KF040251, KF040326, KF040169; ***Paradrymonia* sp. Clark 12550,** *J. L. Clark 12550* (US), Panama, KF040248, KF040324, KF040167; ***Paradrymonia* sp. Mora 816,** *M.M.*

Mora 816 (US), Colombia, KF040224, KF040302, KF040147; ***Paradrymonia* sp. Mora 823,** *M.M. Mora 823* (US), Colombia, KF040242, KF040318, KF040162; ***Paradrymonia* sp. Mora 842,** *M.M. Mora 842* (US), Colombia, KF040225, KF040303, KF040148; ***Paradrymonia* sp. Mora 845,** *M.M. Mora 845* (US), Colombia, KF040239, KF040315, --- ; ***Paradrymonia* sp. Mora 895,** *M.M. Mora 895* (US), Colombia, KF040226, KF040304, --- ; ***Rhoogeton cyclophyllus*** Leeuwenb. *, *D. Clarke 10350* (US), Guyana, KF040252, KF040327, KF040170; ***Rhoogeton viviparus*** Leeuwenb., *D. Clarke 9255* (US), Guyana, KF040253, KF040328, KF040171.

Outgroup: ***Sinningia cooperi*** (Paxt.) Wiehler, *J.L. Clark 8857* (US), Cultivated (Brazil), KF040254, KF040329, KF040172; ***Sinningia incarnata*** (Aubl.) D.L. Denham, *J.L. Clark 8849* (US), Cultivated (Colombia), KF040255, KF040330, KF040173.

FIG. 1.1. Parsimony strict consensus tree from the total evidence analysis of three datasets (nrDNA ITS, nrDNA ETS and cpDNA *trnH-psbA*) showing the three main clades within tribe Episcieae and the principal monophyletic subclades within the *Paradrymonia* alliance clade. Maximum parsimony bootstrap values are above the branches, and those derived from maximum likelihood (when nodes are shared) are below the branches. Only bootstrap values ≥ 50% are shown. Thickened branches indicate ≥ 0.9 Bayesian posterior probability values. An asterisk (*) following the species name indicates the species is the type species of the genus.

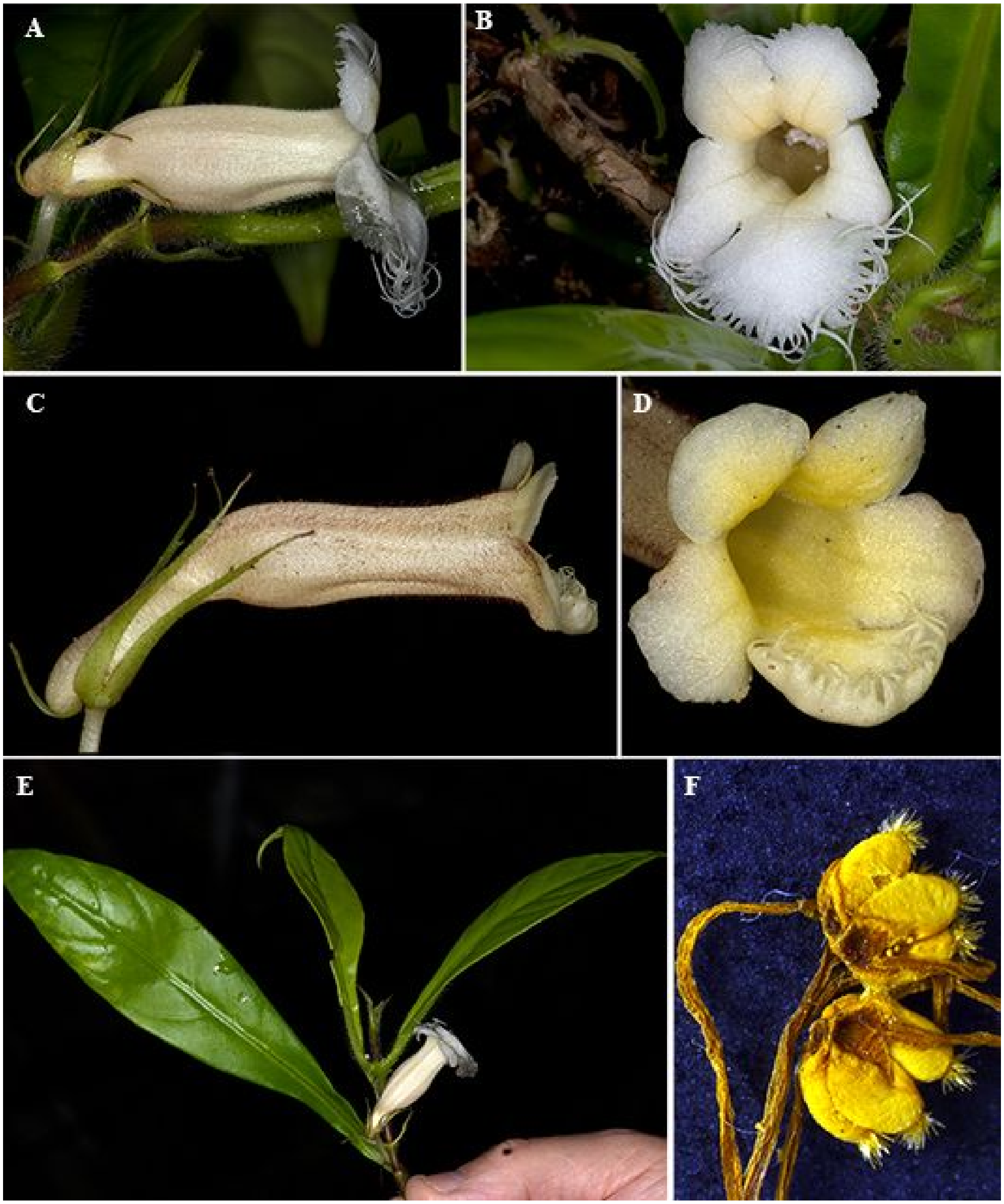

FIG. 1.2. Morphological characters in *Paradrymonia glabra* and *P. ciliosa* (*Paradrymonia* s.s. clade from Fig. 1). A. Lateral flower of *Paradrymonia glabra* showing straight (non-angulate corolla). B. Front view of *P. glabra* showing fimbriations on lower corolla lobe. C. Lateral flower of *P. ciliosa* showing angulate corolla. D. Flower of *P. ciliosa* showing fimbriations on lower corolla lobe. E. Leaves of *P. glabra*. F. Bearded anthers of *P. glabra*. Images by John L. Clark; A. B. and D. from *J. L. Clark et al. 11331*. B. and C. from *J. L. Clark et al. 12490.*

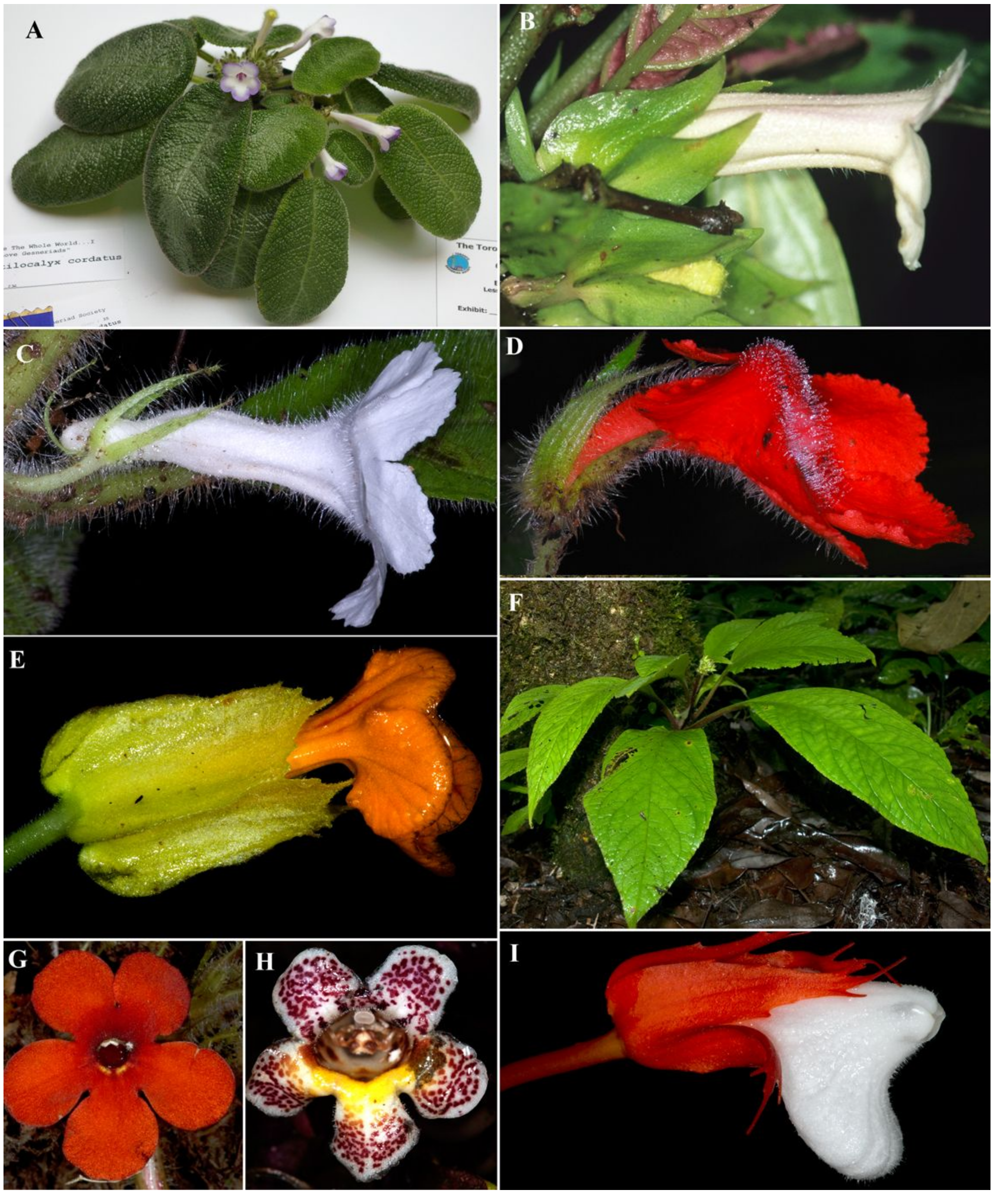

FIG. 1.3. Morphological characters in selected species from the *Paradrymonia* alliance clade (from Fig. 1). A. *Centrosolenia hirsuta* (=*Nautilocalyx cordatus, Centrosolenia* clade) showing variegated leaves and elongate tubular corollas. B. Front view of *Nautilocalyx ecuadorensis* (Amazonian "*Nautilocalyx*" clade in Fig.1) showing ovate calyx lobes and corolla tube longitudinally sulcate with blunt ridges on both, the dorsal and ventral sides. C. *Nautilocalyx colombianus* (*Nautilocalyx* s.s. clade in Fig. 1) showing trumpet-shaped corolla and lanceolate calyx lobes. D. *Nautilocalyx erytranthus* showing trumpet-shaped corolla with reflexed lobes and lanceolate calyx lobes (*Nautilocalyx* s.s. clade in Fig. 1). E. *Chrysothemis friedrichsthaliana* (*Chrysothemis* clade) showing flower with fused calyx lobes. F. *Trichodrymonia pedunculata* (=*Paradrymonia pedunculata*; *Trichodrymonia* clade) showing rosette habit and elongated leaves with decurrent base. G-H. Flowers showing absence of fimbrations in corolla lobes: G. Frontal view of the salverform corolla in *Trichodrymonia ulei* (=*P. ulei*). H. Frontal view of the trumpet-shaped corolla in *Trichodrymonia aurea* (=*P. aurea*). I. Lateral view of the hypocyrtoid corolla of *T. hypocyrta* (=*P. hypocyrta*). Images by Ron Myrh (A) and John L. Clark (B-I).

CHAPTER II

Revision of the Neotropical Genus *Paradrymonia* (Gesneriaceae)

ABSTRACT

The recently re-circumscribed neotropical genus *Paradrymonia* (Gesneriaceae) is reviewed. Most species of *Paradrymonia* are facultative epiphytes that form apical rosettes and have anisophyllous leaves. Leaf blades are coriaceous, lanceolate to oblanceolate with the base decurrent into the petiole. Flowers usually have crenate or fimbriate corolla lobes and anthers with a distal tuft of hairs. The genus has a complex taxonomic history including misidentification of species. Eight species are recognized in this revision: *P. barbata*, *P buchtienii, P. campostyla*, *P. ciliosa*, *P. glabra, P. lutea*, *P. tepui* and *P. yatua*. The genus is distributed in Central America, the Amazon basin and the Guiana Shield. The center of diversity is the Guiana Shield where seven of the eight species occur. A nomenclator of all excluded or uncertain species names attributed to *Paradrymonia* is included with currently accepted names. All species are described and mapped and a key for the species is provided.

INTRODUCTION

The neotropical Gesneriaceae have been entangled with taxonomic confusion for 150+ years after the publication of the first major treatment for the family by Hanstein (1854, 1856, 1859, 1865). Taxonomic confusion is attributed to the emphasis given to floral characters that are the result of convergence (Wiehler, 1983; Clark and Zimmer; Clark et al., 2006, Clark et al., 2012).

Another factor that has added confusion to the circumscription of Neotropical genera in the Gesneriaceae is that many new genera were established based on limited dried specimens sent to Europe from the Neotropics. As more species in these groups were introduced, the older concepts overlapped and generic delimitation become blurred. Consequently, many recent additions to vaguely established genera have created discordant elements within these genera (Wiehler, 1983).

The use of molecular phylogenies in the last 10 years has significantly transformed the systematics of the family (Weber et al. 2013) subtribe Columneinae (tribe Episciae sensu Wiehler, 1983) to the extent that several taxonomic groups defined by traditional taxonomic approaches have been rejected by molecular data. For example, many species traditionally recognized as *Alloplectus* were transferred to *Columnea*, *Nematanthus*, *Drymonia*, *Glossoloma* and *Crantzia* (Clark and Zimmer, 2003). Likewise, molecular phylogenetic analyses have revealed new monospecific genera in the subtribe Columneinae (Smith and Clark, 2013). Mora and Clark (in review) using molecular data have recently re-circumscribed the genus *Paradrymonia* resurrecting *Centrosoleni*a and *Trichodrymonia*.

The interest in providing a revision of *Paradrymonia* has arisen largely because the taxonomy of this genus has been particularly problematic. The generic concept of *Paradrymonia* has been historically confusing as is evidenced by the fact that 45 % of the described species have been placed under other genera (Skog and Boggan, 2007). Another major reason that prevented to attain a satisfactory generic concept is the morphological similarity of *Paradrymonia* with other related genera within the subtribe Columneinae (tribe Episcieae sensu Wiehler, 1983), such as *Episcia, Alsobia, Nautilocalyx, Chrysothemis* and *Drymonia*.

Recent molecular phylogenetic analyses (Clark et al., 2006; 2012; Mora and Clark, in review) showed that *Paradrymonia* as traditionally circumscribed was paraphyletic indicating that characters used to distinguish the genus such as anisophyllous leaves, epiphytic-rosette forming habit, and funnel-shaped corollas were homoplastic. Consequently, the circumscription of *Paradrymonia* has been amended in order to account for evolutionary relatedness between species. Most of the ex–*Paradrymonia* species are now in *Trichodrymonia*. *Paradrymonia* currently includes only eight described species: *Paradrymonia barbata*, *P. buchtienii P. campostyla*, *P. ciliosa*, *P. glabra* (the type species), *P. lutea*, *P. tepui* and *P. yatua* (Mora & Clark, in review).

Most of the species of *Paradrymonia* and *Trichodrymonia* share the epiphytic-rosette forming habit and the presence of anisophyllous, large, coriaceous, lanceolate to oblanceolate leaves with decurrent bases on the petiole. The main difference to distinguish among these taxa is the presence of bearded anthers and fimbriate corolla lobes in *Paradrymoni*a (with the exception of *P. campostyla* and *P. barbata* where bearded anthers are absent). Characters that are helpful for differenciating *Paradrymoni*a from *Trichodrymonia* and *Centrosolenia* are listed in Table 2.1

As *Paradrymonia* has a complex taxonomic story including misidentification of species, a description of the genus and species, as well as a key to the species is provided.

PHYLOGENY

The generic circumscription for *Paradrymonia* has been historically confusing and problematic due to the inconsistency of diagnostic morphological characters and the lack of monophyly. A phylogenetic framework was important for understanding the taxonomy of this assemblage of facultative epiphytic herbs that inhabit the understory of neotropical rainforests.

The taxonomic revision presented here is based on recent phylogenetic analyses of molecular data (Mora & Clark in review). In the analyses Mora and Clark (in review) tested the monophyly of *Paradrymonia* and evaluated the species relationships within the genus and closely related genera based on molecular sequence data from the nuclear ribosomal (nrDNA) internal and external transcribed spacer regions (ITS and ETS), and the plastid (cpDNA) *psbA-trnH* intergenic spacer. The phylogeny indicated that traditionally recognized *Paradrymonia* was paraphyletic and included taxa in four of the nine clades illustrated in Fig. 2.1: (1) Core Columneinae clade; (2) *Paradymonia* s.s clade (3); *Centrosolenia* clade; and (4) *Trichodrymonia* clade. As a major result of the phylogeny, Mora and Clark (in review) re-circumscribed *Paradrymonia* and resurrected *Centrosolenia* and *Trichodrymonia*, in order to accommodate the ex-*Paradrymonia* species.

The recircumscribed genus *Paradrymoni*a is basal and sister to *Centrosolenia*, *Trichodrymonia*, *Chrysothemis* and a paraphyletic *Nautilocalyx. Nautilocalyx* sensu lato contains species in four clades shown in Fig 1. (Pictus clade, Amazonian "*Nautilocalyx*" clade, *Chrysothemis* and *Nautilocalyx* s.s.). In the *Paradrymonia* clade, *P. campostyla* was recovered as sister to *P. ciliosa and P. glabra*. Although not included in the phylogeny, *P. barbata* is predicted to be closely related to *P. campostyla* based on the similarity of characters, such as elongate climbing stems with isophyllous leaves with small, oblong-elliptic to oblong-ovate leaf blades with subcordate bases. Likewise, the remaining species not included in the phylogeny, are predicted to belong to the crown clade of *Paradrymonia* together with *P. glabra* and *P.ciliosa* based on morphological similarities such as presence of anisophyllous leaves, rosette-forming habit, presence of fimbriations in the margin of the corolla lobes and bearded anthers (Mora and Clark, in review).

TAXONOMIC HISTORY

Paradrymonia (Gesneriaceae) was first erected by Hanstein in 1854 with only one species, *P. glabra* (Benth.) Hanst. The species was originally described by Bentham (1850) based on a living collection with white flowers and ciliate corolla lobes that arrived at the Royal Botanic Gardens at Kew collected by Wagener from La Guayra [La Guiara], Venezuela. Bentham, who was a gesneriad expert, placed the species in *Centrosolenia*, a genus established by him in 1846 with *Centrosolenia hirsuta* as the type species. Years later, Hanstein (1865) synonymized under *Episcia* his own genera (*Alsobia Nautilocalyx, Paradrymonia*), Oersted's *Trichodrymonia* and Bentham's *Centrosolenia*, due to the lack of clear floral morphological synapomorphies to distinguish these genera.

Bentham in his Genera Plantarum (Bentham, 1876) divided *Episcia* into six sections, including section *Centrosolenia* that contained the species previously placed in *Centrosolenia, Paradrymonia and Trichodrymonia.* The same system was adopted by Fritsch (1893–1894), an Austrian botanist and professor of botany at Graz (Stafleu and Cowan, 1976).

Sprague (1912) was the next botanist at the Royal Botanical Gardens, Kew who studied the *Episcia* complex, and resurrected the genus *Nautilocalyx* on the basis of the position of the ovules on one or both surfaces of the placenta. He suggested the resurrection of *Centrosolenia* and *Paradrymonia*, but he did not publish any additional transfers from *Episcia* sensu lato (Sprague, 1912; Wiehler, 1978). Wiehler (1978) found Sprague's character to be inconsistent and variable among some members of tribe Episcieae (subtribeColumneinae sensu Weber et al. 2013).

Morton (1938) reinstated *Centrosolenia* and described *Centrosolenia decurrens*, a species here referred as a synonym of *Paradrymonia ciliosa* (see taxonomic treatment below).

Leeuwenberg (1958) proposed a different subdivision of *Episcia*, dividing the genus in seven sections. One of the sections corresponded with section *Paradrymonia* including species that today correspond to the genera *Paradrymonia* and *Trichodrymonia*.

Over a century later after the establishment of *Paradrymonia* by Hanstein, Wiehler (1973) resurrected the genus by transferring four species from *Episcia*. Additionaly, he placed *Centrosolenia glabra* as a synonym of *Paradrymonia ciliosa* (= *Hypocyrta ciliosa* Martius), a species from Amazonian Brazil that was collected and described by Martius (1829). Wiehler (1978) distinguished *Paradrymonia* from *Episcia*, *Alsobia* and *Nautilocalyx* by vegetative characters and habit. *Episcia* was defined as a terrestrial genus of small herbs with two stolons per node, *Alsobia* as an epiphytic taxon with one stolon per node, *Nautilocalyx* as terrestrial herb with soft or succulent stems and *Paradrymonia* as terrestrial or epiphytic rosettes or vines with large leathery lanceolate leaves (Wiehler, 1978).

More recently, Mora and Clark (in review) re-circumscribed *Paradrymonia*. Changes in the generic circumscription drastically reduced the number of species from 38 species to eight. *Centrosolenia* and *Trichodrymonia* were resurrected in order to accommodate the remaining ex-*Paradrymonia* species (Mora & Clark, in review). Most of the ex–*Paradrymonia* species are now in *Trichodrymonia. Centrosolenia* was reestablished by transferring 10 species from *Nautilocalyx* and only one species from *Paradrymonia* (Mora & Clark, in review). Likewise, *Pagothyra maculata*, a climbing vine with isophyllous leaves and bell–shaped yellow flowers mottled with bright red spots was previously included in the genus *Paradrymonia*. Recently, this taxon was recognized as a monotypic genus, based on the unique apomorphy of the ventral corolla lobe occluding the throat like a trap door (Smith and Clark, 2013). *Paradrymonia* sensu stricto is a small genus with eight described species distributed from southern Nicaragua to northern Brazil and Bolivia (Fig. 2.2). Most of the species that today belong to *Paradrymonia* have been described from the Guiana Shield and the Amazon Basin (Feuillet, 2009a, b).

MORPHOLOGY

Habit. Species of *Paradrymonia* are herbs or subshrubs, without stolons and with a single main stem producing leaves and flowers (monopodial shoot pattern). Most species are terrestrial or facultative epiphytes on low trunks. The facultative epiphytes are usually found on moss–covered trunks and usually have a rosette habit with short internodes towards the apex (Fig. 2.3A). It is likely that the leaf rosettes serve as a trap where organic matter accumulates. Epiphytes from several other families have adapted a rosette form which facilitates water accumulation and litter-trapping (Benzing, 1990). The compressed internodes are in close contact with the substrate and produce numerous and long adventitious roots. The stems are usually decumbent and the internodes are much longer in juvenile plants. Only *Paradrymonia campostyla* (Fig. 2.3C) and *P. barbata* do not form rosettes. These species are climbers with adventitious roots developing from their elongate stems to support them.

Leaves. The leaves of all species are opposite and decussate. Most species have strongly anisophyllous leaves, with one of the leaves in a pair noticeably reduced. Sometimes the reduced leaf is linear and stipule-like so that the leaves appear alternate rather than opposite. The degree of anisophylly seems to be variable and dependent on the light conditions. Plants growing in shaded conditions have strong anisophylly relative to those exposed to higher levels of light (Wiehler, 1978; Dengler and Sanchez-Burgos, 1988). *Paradrymonia barbata* and *P. campostyla* are the only species in the genus that have isophyllous to sub-isophyllous leaves (Fig. 2.3C). The shape of the large leaf blade of anisophyllous species is commonly oblanceolate but also may be obovate, ovate and elliptic, or with the base decurrent into the petiole. The petiole in this species is stout, sulcate with acute margins (U-shaped) in cross-section and usually wine-red. Species with isophyllous leaves (i.e., *P. barbata* and *P. campostyla*) have relatively small leaves with elliptic leaf blades with rounded to subcordate bases and tender petioles. In all species the upper leaf surface is flat (i.e.,, rugose or bullate surfaces absent) and the secondary venation is mostly inconspicuous in living plants. Most species have coriaceous and glabrescent leaves, but young leaves are conspicuously pubescent. Leaves of *Paradrymonia campostyla* are hirsute on both sides of the leaf blade.

Inflorescence. The inflorescences are axillary sometimes exceeding the length of the petiole, and are pair-flowered cymes, similar to many other Gesneriaceae (Weber, 1982; Wiehler 1983). The cymes are usually congested, many-flowered (up to 10), epedunculate and subtended by linear bracts. The flowers are often in compact clusters close to the ground or substrate and hidden by the leaves. *Paradrymonia barbata* and *P. campostyla* have considerably fewer flowers (1--4) than the rosette-forming-habit species.

Calyx. The calyx consists of five lobes that are connate for 3-5 mm at the base. The dorsal calyx lobe that surrounds the corolla spur is slightly reduced and appears recurved to accomodate the corolla gibbosity (Fig. 2.3D). The lateral calyx lobes are directed upwards in contrast to the ventral lobes that are directed forward. The shape of the calyx lobes are mostly linear-lanceolate in *Paradrymonia barbata*, *P. buchtienii*, *P. ciliosa* (Fig. 2.3D, E), and *P. glabra* (Fig. 2.2B, F); in *P.campostyla* (Fig. 2.2H).

The corolla is sympetalous with an elongate tube and five spreading lobes. Most species have fimbriate margins on the lobes (Fig. 2.3B-F), but the lobes are almost entire in *P. campostyla* (Fig. 2.3H). *Paradrymonia buchtenii* has a distinctive bright yellow, trumpet to salver-shaped corolla with a wide limb, fimbriate lobes and narrow throat. orolla colors vary within populations of some species. For instance, populations of *P. ciliosa* highly exposed to light have light yellow corollas in contrast to populations growing in shady areas that have white corollas.

Androecium. *Paradrymonia* has four stamens that are adnate to the base of the corolla tube. The filaments are glabrous and curved. Anthers are coherent and dehisce by longitudinal slits. The stamens are protandrous, with the anthers releasing pollen before the stigma of the same flower is receptive. After anthesis, filaments coil, pulling the anthers back toward the base of the corolla tube. A distinctive characteristic of most of species in the genus (except for *P. barbata* and *P. campostyla*) is the presence of bearded anthers with an apical tuft of hairs (Fig. 2.3G)**.**

Gynoecium and nectary. The ovary is usually covered with green or red hairs pressed close to the surface. The style is terete and glabrous and the stigma is stomatomorphic. The stigma, like the anthers, never extends beyond the corolla throat. The nectary consists of a glabrous posterior gland at the base of the ovary.

Pollination. The shape of *Paradrymonia* species conforms to the “euglossophilous” pollination syndrome discussed by Wiehler (1978, 1983). Euglossophilous species are putatively pollinated by Euglossine bees, and characterized by flowers with white, cream white or light yellow corollas. Although no formal pollination studies have been made for *Paradrymonia*, individuals of *Euglossa decorata* and *Euglossa* sp. have been reported visiting *Paradrymonia campostyla*, foraging for nectar (Hentrich, 2008).

Fruit. The fruit is a subglobose, semi-fleshy, bivalve capsule that splits loculicidally exposing a mass of numerous oblong seeds with prominent fleshy white funicles.

TAXONOMIC TREATMENT

Paradrymonia Hanst. Linnaea 26: 207. 1854. *Episcia* sect. *Paradrymonia* (Hanst.) Leeuwenb. Meded. Bot. Mus. Herb. Rijks Univ. Utrech 146: 311. 1958. TYPE: *Paradrymonia glabra* (Benth.) Hanst [=*Centrosolenia glabra* Benth].

Creeping herbs or facultative epiphytes. Stems subwoody, elongate, creeping or ascending with many adventitious roots. Leaves of a pair equal to strongly unequal, usually, at least the longer one surpassing the stem; often rather long–petiolate; leaf blade small to large, obovate to widely oblanceolate, sometimes oblong, acuminate at the apex, cuneate at the base or long decurrent into the petiole, rarely rounded at base, coriaceous, glabrous to hirsute, somewhat succulent; obscurely to conspicuously serrulate at the margin, sometimes the margin with glandular teeth. Inflorescences axillary, usually many–flowered in sessile or short–pedunculate umbels, rarely solitary; bracts linear, pedicel hirsute; calyx lobes free, linear to lanceolate, long acuminate, hirsute, unequal, the posterior one shorter, saccate at the base. Corolla oblique in the calyx, amply tubular with a broad limb or widely salverform to trumpet-shaped, spurred at the base, all lobes or only the ventral one crenate or fimbriate, sometimes all lobes entire; stamens 4, dydynamous, included; anthers oblong, coherent in pairs, usually barbate with a distal tuft of hairs or sometimes glabrous, longitudinally dehiscent; ovary superior, villous; style included, with one or two disc glands; placentae ovuliferous on the inner surface only. Fruit a bivalve capsule; valves thin, semi–fleshy, seeds brown, striate. A genus with eight described species distributed in Central America, the Amazon basin and the Guianas (Fig. 2.2).

KEY TO THE SPECIES OF *PARADRYMONIA*

1. Climbing plants with isophyllous leaves; leaf blade less than 12 cm long, oblong to oblong elliptic or ovate-lanceolate with base rounded or subcordate, never decurrent into the petiole; inflorescence with 1–4 flowers; anthers glabrous, lacking a distal tuft of hairs
    2. Stem herbaceous; adventitious roots at the nodes and internodes, leaves glabrescent, pubescent on the midrib and veins only; corolla tube less than 2.5 cm long, ventral corolla lobe fimbriate with filiform fimbriae…………………………………………….……1. *Paradrymonia barbata*
    2. Stem suffrutescent; adventitious roots scattered throughout the stem, mainly at the nodes; leaves hirsute on both sides; corolla tube 3.5 cm or longer; ventral corolla lobe entire….…..……………………………3. *Paradrymonia campostyla*
1. Erect herbs or rosette-forming low epiphytes with facultative anisophyllous leaves; larger leaf blade in a pair more than 15 cm long, oblanceolate to lanceolate-elliptic with base decurrent into the petiole, glabrescent to moderately pilose; inflorescence with 4–25 flowers; anthers bearded with a distal tuft of hairs
    3. Calyx lobes subulate or linear-lanceolate

4. Leaf blade broadly lanceolate-elliptic to ovate-elliptic; tertiary veins moderately conspicuous; flowers bright yellow.………………………………………2. *Paradrymonia buchtienii*

4. Leaf blade frequently lanceolate to oblanceolate; tertiary veins inconspicuous, flowers white, creamy-white or pale yellow

   5. Corolla creamy-white to yellowish covered with reddish indument, corolla tube angulate. Widespread in the Neotropics………………………………..4. *Paradrymonia ciliosa*

   5. Corolla white to creamy-white covered with white indument; corolla tube straight. Venezuela (Carabobo, Miranda). ……………………………………….5. *Paradrymonia glabra*

3. Calyx lobes broadly lanceolate to elliptic-lanceolate

   6. Corolla white or creamy-white.

      7. Leaf blades obovate to broadly elliptic; calyx tinged with red. …….……………………………………..7. *Paradrymonia tepui*

      7. Leaf blades elliptic-lanceolate; calyx green. ……………………………….…………8. *Paradrymonia yatua*

   6. Corolla bright yellow……………………………..…6. *Paradrymonia lutea*

1. ***Paradrymonia barbata*** Feuillet & L.E. Skog, Brittonia 54: 356, 2003, fig. 3.—TYPE: GUYANA. Cuyuni-Mazaruni Region: Permanent miner's campsite near Eping River, E of several diamond pits, 6°00'N, 60°10'W, 122 m, 2 Feb 1991(fl), *Mc Dowell & Stobey 3810* (holotype: BRG; isotypes; K! US!).

Herbaceous epiphytic climber. **Stems** 20 cm long or more, succulent, terete, hirsute, branched, appressed or pendent, with spreading adventitious roots on the side attaching to the substrate. **Leaves** isophyllous or equal in a pair; **petiole** short, 0.5–1 cm long, hirsute; **leaf blade** ovate-lanceolate, coriaceous, usually asymetrical, acute at the apex, rounded or subcordate at the base, 4–5 × 2–2.5 cm; margin crenate and ciliate, appressed-pubescent to glabrescent with few short rigid hairs on the veins above, glabrescent between the veins and appressed-pubescent on the midrib and veins below; primary lateral veins 5–6 pairs. **Inflorescence** axillary with 1–4 flowers; **flowers** with peduncle very short; bracts linear, 4 × 1 mm, rounded at apex, entire, hirsute; **pedicels** 0.5–1 cm long, hirsute; **calyx lobes** free, erect, subequal, narrow-lanceolate, 6–10 × 2–2.6 cm, acute at the apex,with 1–4 inconspicuous teeth at the margin, hirsute outside, strigose inside, the dorsal lobe slightly curved around the corolla spur; **corolla** somewhat funnel-shaped, spurred at the base, cream; tube short, 10–13 mm long, 5–6 mm at throat, hirsute outside, glabrous inside; lobes spreading, rounded, glabrous; lateral lobes 2 × 1.5 mm, dorsal lobes 2 × 3 mm; ventral lobe 4 × 4 mm, long-fimbriate; the fimbria filiform, wider at the base and gradually tapering at the apex, flexuous, 3–7 mm long, stamens slightly excerted, inserted near the corolla base; **stamens** 4, filaments glabrous, anthers orbicular, coherent into a tetrad, dehiscing by longitudinal slits; staminode filiform ca. 3 mm long, without anther; **ovary** ellipsoid, sericeous; style 7–9 mm long; nectary a large double connate dorsal gland; style 7–9 mm long, glabrous. **Fruit** not seen.

Distribution and habitat (Fig. 2.4). —*Paradrymonia barbata is* known only from the type locality in the Cuyuni-Mazaruni region of Guyana. It occurs in lowland rainforests, near diamond pits at ca. 120 m (Feuillet and Skog, 2003).

Phenology. —*Paradrymonia barbata* is only known from the type specimens. Flowering observed in February.

Paradrymonia barbata appears most similar to *P. campostyla* from Surinam and French Guiana. Both species are climbing species with small, isophyllous leaves. However, *P. barbata* has a much smaller corolla and the ventral lobe is fimbriate with filiform fimbria (vs. entire corolla lobes in *P. campostyla*).

2. *Paradrymonia buchtienii* (Mansf.) Wiehler, Selbyana 5:49. 1978. *Episcia buchtienii* Mansf. Repert. Spec. Nov. Regni Veg. 38: 25. 1935. —TYPE: BOLIVIA. La Paz: Mapiri. *Buchtien 1344* (holotype: B, destroyed; lectotype designated by Wiehler, 1978: NY!; isolectotypes: HBG! NY! SEL! US!).

Terrestrial or facultative epiphyte. **Stem** subwoody, terete, reddish brown, hirsute (with white trichomes). **Leaves** strongly unequal in a pair, the smaller one subulate (slender tapering to a point) and acuminate, ca. 1.5 × 0.1 cm, densely pilose; large blade: **petiole** elongate 8–25 cm long, succulent, slightly pilose, mostly glabrescent; large **leaf blade** lanceolate-elliptic to ovate-elliptic, abruptly decurrent into the petiole, long-acuminate at the apex, 6–15 × 18–38, the margin sparsely short-serrated, glabrescent above, laxly pilose beneath, densely pilose on the midrib and veins below. **Inflorescence** axillary, fasciculate, peduncle very short or obsolete; **flower**s with **pedicels** 1–3.5 cm long, green to reddish wine, densely pilose, trichomes long, reddish to purpureous; **calyx lobes** free, linear-lanceolate, acuminate at the apex, 13–30 × 3–4 mm, green to reddish wine, covered with reddish to purplish trichomes, margins with 1–2(–3) subulate teeth in the upper third; **corolla** widely salverform to trumpet-shaped, spurred at the base, enlarged upwards, bright yellow, corolla tube 2.7–3 cm; moderately pubescent outside, the limb divided into five broad lobes, the lobes variable, crenate or fringed, the lower lobe fringed with short laciniae, glabrous; throat narrowing at the base of the corolla lobes, forming a constricted opening; **stamens** 4, inserted near the base of the corolla, filaments glabrous, ca. 7 mm long, anthers coherent into a square, bearded with a tuft of hairs at the base; **ovary** ellipsoid,densely pilose; nectary a large double connate dorsal gland; style glabrescent, ca. 1.7 cm long. **Fruit** not seen.

Distribution and habitat (Fig. 2.5). —*Paradrymonia buchtienii* is only known from Cochabamba and La Paz provinces in Bolivia. It occurs in lowland moist forests on the foothills of the eastern slope of the Andes at 600–1020 m.

Phenology. —Collections of *Paradrymonia buchtienii* are rare. Flowering collections are only known from May and November.

Paradrymonia buchtienii is vegetatively similar to *P. ciliosa*. It differs from *P. ciliosa* by having a more broadly elliptic leaf blade with more conspicuous secondary veins and generally longer petioles. *Paradrymonia buchtienii* is also superficially similar to *P. lutea.* Both species share the bright yellow flowers but the later species differ by having a tubular corolla shape (vs.widely salverform to trumpet-shaped).

REPRESENTATIVE SPECIMENS. **Bolivia.**—COCHABAMBA: Carrasco, campamento Guacharos en el Parque Nacional Carrasco, 17°04'16"S, 65°39'04"W, 16 May 2004, *Altamirano & Terán 542* (MO!).—LA PAZ: Bautista Saavedra, Area Natural de Manejo Integrado Apolobamba, Florida, ladera exposición SW al lado de carretera. Bosque subandino interior pluvial. 15°9’59”S, 68°32’30”W, 1020 m, 3 May 2005. *Fuentes 7870 (*LPB, MO!, US!).

3. *Paradrymonia campostyla* (Leeuwenb.) Wiehler, Selbyana 5: 49. 1978. *Drymonia campostyla* Leeuwenb., Acta Botanica Neerlandica, 7: 305, 393. 1958. —TYPE: SURINAM. *Jonker & Jonker 625* (holotype: U!; isotype: US!).

Creeping or climbing suffrutescent herb. **Stem** about 50 cm long, branched with spreading adventitious roots, hirsute, especially near the apex; young stems green, older stems brownish. Leaves isophyllous; petiole 0.6–5 cm long, hirsute; leaf blade oblong–ovate or oblong, 2.5–10 ×1.2–5 cm, acute to acuminate at the apex, rounded or subcordate at the base, subentire or obscurely repand–serrate, hirsute or densely pilose on both sides, especially on the midrib and veins beneath, dark green above, paler beneath. **Inflorescence** with 1–3 flowers; **flowers** with peduncle very short or obsolete, with some bracts; bracts lanceolate, 5–10 ×1–2 mm, acuminate at the apex, entire, hirsute on both sides; **pedicels** hirsute, 5–20 mm long; **calyx lobes** mostly free, four 20–35 ×5–11 mm, the fifth (dorsal) about half as long as the others, ovate–lanceolate, long acuminate at the apex, rounded at the base, 12–21 × 2.5–5 mm, repand–serrate at the margin, hirsute on both sides, especially outside; **corolla** white outside, yellow and with purple lines (nectar guides) inside partially pubescent with glandular hairs inside, hirsute outside; amply tubular, slightly contracted above the spur, 3.5–6 cm long, 3–5 mm wide at base, 10–15 mm wide at the throat, tube 3–5 cm long; spur obtuse, about as long as wide,3–5 mm long, limb 2—3.5 cm wide; lobes subequal, rounded, entire; **stamens** 4, included, anthers coherent, 2.5 × 2 mm; staminode very small, 1 mm long, glabrous with a triangular acuminate sterile anther; **ovary** ovoid, hirsute, 4–5 ×2.5–3 mm; style shortly hirsute with often obscurely aggregated hairs; stigma bilobed; nectary a large double connate dorsal gland, glabrous. **Fruit** a globose bivalve capsule included in the calyx, 9–10 mm in diameter, pale green, hirsute. **Seeds** ellipsoid, 1–1.2 × 0.25–0.3 mm, dark brown. (Fig. 2.3C, H)

Distribution and habitat (Fig. 2.4).—*Paradrymonia campostyla* occurs in Surinam, French Guiana and Brazil (Amapá) at 80–550 m in lowland rainforests.

Phenology.—Flowering collections of *Paradrymonia campostyla* are from all the months except January and October and November suggesting flowering period is relatively broad. Fruits are known only from March, April and July.

Paradrymonia campostyla does not resemble any other species of *Paradrymonia*. We include it in *Paradrymonia* s.s. based only in molecular analysis (Mora and Clark, in review). This is the only species in the genus with isophyllous leaves, comparatively much smaller, oblong to oblong–ovate or leaves (vs. large oblanceolate and long decurrent into the petiole), and its corolla lobes lack fimbriations and the anthers are not bearded as in other species of *Paradrymonia*. *Paradrymonia campostyla* was originally placed under the genus *Drymonia* by Leeuwenberg in 1958 showing the uncertainty of its phylogenetic affinities.

REPRESENTATIVE SPECIMENS. **French Guiana**.—CAYENNE. A proximité du village Zidock, haut Oyapock, *Prévost & Grenand 1988* (P, US!); Environs de Lodebert, *Wachenheim 162* (US!); Crique Fromager - Bassin de l'Approuague, PK 11,2 après Régina sur la RN2, *Blanc 207* (CAY, P, US!); Montagne de Kaw, *Deroin 159* (P); Chemin des Emerillons, 10.7 km de Dégrad Claude, à son intersection avec le petit Tamouri, *Granville 2258* (CAY, US!); D.Z. du Haut-Kourcibo, bassin du Sinnamary, *Granville et al. 11270* (CAY, US!); Mts. Bakra, entre Pic Ardent et Pic Coudreau, *Granville & Cremers 11837* (CAY, NY P, U, US!).—SAINT-LAURENT-DU-MARONI: Route de l'Acarouany, bassin de la Mana, Piste forestière vers Les Roches, *Cremers & Hoff*

11342 (B, CAY, COL, G, HAMAB, NY, P, STR, US, USM, VEN); Route de L'Acarouany - Basse Mana, *Fleury 395* (CAY, P, US); Rivière Petite Ouaqui = Rive gauche, à 3.5 km en amont de "Saut Baille Nom", *Granville 1858* (CAY, US); Mont Galbao, Secteur Est, *Granville et al. 8733* (CAY, NY US); Fleuve Lawa, Papaichton, layon de la source, *Sastre et al. 8140* (P, US, U); summit, Mt. Galbao, *Tay 104* (MPU, MPU). **Surinam**.—BROKOPONDO. Brownsberg, *Kock s.n.* (U); 3 km zo van basiskamp, 2 km beneden Blanche Marievallen, Nickeririvier, *Maas & Tawjoeran 10909* (BBS); Nature Park Brownsberg, *Koster LBB13025* (BBS, US); Rock bank of Irene fall ub spatterzone, slope 70° W, *Tjon-Lim-Sang & Wiel 9* (BBS); Near Brownsberg, *Wessels-Boer 634* (US).—MAROWIJNE: Marowijne Distr., Nassau Mts., Plateau C, *Jansen-Jacobs et al. 6266* (US).—SIPALIWINI: Vicinity of Ulemari River, 13 km upstream from its confluence with Litani River, *Hammel & Koemar 21373* (US); Krammaman, road to Kadjoe, near Kabel, Upper Surinam River; Emmaketen, *Stahel 42*[B.W. no. 5642] (US).

4. *Paradrymonia ciliosa* (Mart.) Wiehler, Phytologia 27: 308. 1973. *Hypocyrta ciliosa* Mart. Nov. Gen. Sp. Pl. 3: 53. 1829. *Episcia ciliosa* (Mart.) Hanst., Flora Brasiliensis 8(1): 403. 1864. *Columnea ciliosa* (Mart.) Kuntze, Revis. Gen. Plantarum 2: 472. 1891.—TYPE: BRAZIL: Amazonas. *Martius, Obs. 3117 s.n.*; (holotype: M!, photos: U, US, WAG).

Episcia hansteiniana Mansf., Repert. Spec. Nov. Regni Veg. 38: 25. 1935. *Paradrymonia hansteiniana* (Mansf.) Wiehler, Selbyana 5: 54. 1978.—TYPE: PERU. Loreto, Iquitos. *Tessmann 5088* (holotype: B [destroyed]).—PERU. Loreto. Carretera Oleoducto Secundario entre los Campamentos Bartra 1 y Bartra 4, *Diaz 1401* (neotype, here designated: US!; isoneotypes: MO!, SEL!)

Centrosolenia decurrens C.V. Morton, Publ. Field Mus. Nat. Hist., Bot. Ser. 18(4): 1158. 1938.

Episcia decurrens (C.V. Morton) Leeuwenb., Acta Bot. Neerl. 8: 53. 1959.

Paradrymonia decurrens (C.V. Morton) Wiehler, Phytologia 27:308. 1973. —TYPE: COSTA RICA: Finca Montecristo, on Río Reventazón, below El Cairo, Prov. Limón, alt. 25 m, 18–19 Feb 1926. *Standley & Valerio 48589* (holotype: US!)

Paradrymonia prististoma Wiehler Phytologia 73: 233. 1992. —TYPE: ECUADOR. Napo: unfinished road from Tena to Latacunga, along Río Pano, 16–18 km from Tena, terrestrial and epiphytic, 23 Apr 1986, *Wiehler & GRF Expedition 86184* (holotype: SEL!: isotype: QCA!)

Paradrymonia glandulosa Feuillet, TYPE: VENEZUELA. Amazonas. Depto. Atabapo: Cerro Marahuaca,"Sima Camp", south–central portion of forested slopes along eastern branch of Caño Negro, 3°43'N, 65°31'W, 1140 m, 21–24 Feb 1985, fl., *Steyermark & Holst 130443* (holotype: US!; isotypes: MO!, VEN!)

Paradrymonia hamata Feuillet, TYPE: VENEZUELA. Amazonas. Depto. Río Negro: Cerro de la Neblina, Río Yatúa, 140–1700 m, 31 Dec 1957, fl., *Maguire, Wurdack &. Maguire 42563* (holotype: NY!).

Terrestrial, saxicolous, or rosette forming herb. **Stem** somewhat succulent becoming subwoody at base covered with a light tan rhytidome, procumbent, sometimes erect, the erect shoots 10–25 cm long, ca. 0.5–1 cm diameter, hirsute (with white or reddish trichomes), glabrescent towards base; the internodes 1–3 cm long, with adventitious roots and internodes. **Leaves** strongly unequal in a pair, sometimes the smaller one early deciduous; larger leaf: **petiole** 4–15 cm long, ca. 8 mm in diameter, adaxially winged, succulent, green to reddish wine, densely to slightly appressed–pilose; leaf blade coriaceous, succulent, chartaceous when dry, 18–30 × 7–13 cm or elliptic–lanceolate to oblanceolate, rarely broadly ovate to widely elliptic, orbicular acuminate to long acuminate at apex, strongly decurrent at base. margin glandular–serrate or serrulate, dark green, appressed–pilose to glabrous above, paler green or flushed with green and minutely pubescent to glabrous below (sericeous along the green veins), the lateral pair of veins 8–13. **Inflorescence** axillary cymes of 4–10 flowers, epedunculate, bracts small, lanceolate linear ca. 15 × 2 mm; pedicels 0.1–1.5 (–3.5) cm long, green,densely pilose, trichomes red. **Flowers** with **calyx lobes** free, subequal, pale green bordered with maroon, long-lanceolate, 8–20 × 1–2 mm, apex long linear–acuminate about half the total length, margin with a few obscure teeth or loosely glandular serrate, pilose with reddish hairs; **corolla** oblique in the calyx, tubular–infundibular, ca. 4.5—5.0 cm long, the spur 5 mm long, tube 2.5 cm long, proximally narrowed for 1.8 cm, ca. 4 mm in diameter, then bending downward and expanding to a diameter of 10 mm, dorsally and ventrally with 2 longitudinal furrows, creamy white to yellowish (when plants are in open areas exposed to light) with red trichomes, lobes shallow, the 2 dorsal and 2 lateral lobes subequal, ca. 5 × 8 mm, entire to crenate, the lower lobe ca. 8 × 10 mm long with prominent teeth curved upward or fimbriate, the inside of the tube glabrous with purple lines; stamens 4, included, the filaments ca. 3 cm long, fused and adnate to the base of the corolla tube for 2.5 cm, cream–white, glabrous, the anthers coherent into a square, each anther ca. 2 × 2 mm, the anther cells bearded; **ovary** turbinate, 4–5 mm long at anthesis. covered with long red trichomes, nectary a large double connate dorsal gland, ca. 3 × 2 mm; the style ca. 3 cm long, white, pilose, (trichomes red), stigma stomatomorphic. **Fruit** a semi–succulent bivalve capsule, greenish. (Fig. 2.3A, D, E).

Distribution and habitat (Fig. 2.5).—*Paradrymonia ciliosa* is the most widely distributed species in the genus. It is distributed throughout the neotropics south of Mexico, in South America to the east of the Andes in the Amazon basin and the Guiana Shield. It grows as a terrestrial rosette forming herb or as a creeping lower epiphyte in the Tropical wet forest life zone at sea level to 1400 m.

Phenology.—*Paradrymonia ciliosa* has been collected in flower all year around and in fruit in January to February and in May to October.

Paradrymonia ciliosa resembles *P. glabra* by the presence of thick stems with usually short internodes, terrestrial or creeping on rocks or climbing on lower tree trunks, large coriaceous, semi–succulent leaves with the base decurrent into the petiole, and short inflorescences in the leaf axils. *Paradrymonia ciliosa* differs from *P. glabra* by the following characters: (1) leaf blade wider with a more conspicuous glandular–serrate margin; (2) longer petioles (>4 cm); and (3) cream to yellowish corolla (vs. white) with the distal portion of the corolla tube elongated and angulated (vs. short and straight). *Paradrymonia ciliosa* can also be distinguished from *P. glabra* by the presence of red trichomes (vs. white) on the corolla. Although an angulate corolla is usually common in *P. ciliosa*, some populations (e.g., Guyana) have rather straight corollas.

Wiehler (1973) treated *Paradrymonia glabra* and *P. ciliosa* as conspecific based on their morphological similarities such as white flowers with fringed corolla lobes. *Paradrymonia glabra* was a species name that has been placed for a long time in synonymy under *Paradrymonia ciliosa*. We consider these two taxa as heterospecific and should therefore be recognized as separate species based on examination of morphological characters outlined above and differences in geographic distribution

The first author has noticed morphological variability between populations of *Paradrymonia ciliosa*. For example, plants growing in open areas tend to have a darker yellowish corolla. The width of the leaves can be also quite variable as well as the degree of angulation of the corolla.

Mansfeld (1935) described a species from Iquitos, Peru, as *Episcia hansteniana* which Wiehler (1978), transferred to the genus *Paradrymonia*. The type specimen was not seen by Wiehler since it was destroyed in Berlin in WWII. Based on the vague description in the protologue and its distribution, we consider that the name *P. hansteniana* is a synonym of *Paradrymonia ciliosa*.

The species concept applied here includes a broad geographic range. The specimens from Central America that are recognized here as *Paradrymonia ciliosa* were traditionally recognized as *Paradrymonia decurrens.* The specimens from Venezuela, in the State of Amazonas that are recognized here as *Paradrymonia ciliosa* were traditionally recognized as *Paradrymonia hamata.* The specimens from northwestern Amazonia (i.e., Ecuador, Peru and Brazil) that are recognized here as *Paradrymonia ciliosa* were traditionally recognized as *Paradrymonia pististoma.*

REPRESENTATIVE SPECIMENS.**Bolivia**.—COCHABAMBA: Prov. Chapare, ca. 30 km north of Villa Tunari, *Besse et al. 508* (SEL); hotel el Puente near villa Tunari, *Wood 16122* (K); Mpio. Chapare, Parque Nacional Carrasco. Old road to Comunidad El Palmar, *Clark & Rodriguez 6791* (AAU, E, K,US LPB, MO, NY SEL, UNA, US). **Brazil.**—ACRE: Mpio. Cruzeiro do Sul, Cruzerio do Sul, Río Jurua & Río Moa, slopes of Serra da Moa, *Prance et al. 12152* (US).—AMAPÁ: Río Oiapoque, Río Pontanari, *Irwin et al. 47294* (NY). AMAZONAS: Río Lajes, 6 km beyond of Presidente Figueiredo, *Hutchison et al.* 8732 (US). **Colombia**.—AMAZONAS. Río

Apaporis, Cachivera of Jirijirimo and environs, *Schultes & Cabrera 12496* (US), *14086* (GH, MO, US); Río Igara-Parana, corr. La Chorrera, territoire des indiens Witoto Jitomagaro.—CAQUETÁ: 28 km SE of Morelia along road to Río Pescado (SE of Florencia), *Davidse et al. 5665* (MO).—PUTUMAYO: Valle del Guamués; Reserva indígena El Afilador, Camp Alegre, Comunidad Kofán, *Cogollo et al. 6771* (MO).—VAUPÉS: Mitu, bosque orilla Vaupés, *Pérez Arbeláez & Cuatrecasas 6787* (US), *6789* (F, US); Río Kananari, Cerro Isibukuri, *Schultes & Cabrera 13332* (US), *13472* (GH); Mitú and vicinity, *Zarucchi 1617* (GH, MO, US). **Costa Rica**.—ALAJUELA. Near Río San Rafael, 2 km W of La Marina, Llanura de San Carlos, *Molina R. et al. 17394* (GH, NY US). La Concepción, Llanuras de Santa Clara, *Donnell Smith 6732* (GH, US); ca. 3 km NNE of Bijagua along the new road to Upala, *Burger & Baker 9800* (MO, PMA).—GUANACASTE: Near Volcán Arenal, in rain forest area, past forded river, *Wiehler & GRF Expedition 94104* (SEL).—HEREDIA: *Anderson et al. 132* (BH, WIS); Parque Nacional Braulio Carrillo, *Chacón 592* (INB, MO, US); Forest between Río Peje and Río Sardinalito, *Grayum & Herrera 7904* (INB, MO); En borde del río afluente del Sarapiqui, en el lindero Norte de Puerto Viejo, *Jiménez M. 3435* (US), *3598* (GH, BM, DS, WIS); La Selva, *Koptur 306* (MO).—LIMÓN: Hills 2 airline km SSE of Islas Buena Vista in the Río Colorado, 14 airline km SW of Barra del Colorado, *Davidse & Herrera 31024* (MO, US); Hacienda Tapezco-Hda La Suerte, 29 air km W of Tortuguero, *Davidson & Donahue 8537* (US).—SAN JOSÉ: Parque Nacional Braulio Carrillo. Sendero Las Palmeras, *Araúz 875* (UNA, USJ); Cantón Acosta, Dist. Sabanillas, Hda. Tiquires. cima de la Fila Zoncuano, por sendero a Tiquiritos, *Morales 4586* (INB, MO). **Ecuador**.—MORONA-SANTIAGO: Cantón Palora, Palora. Parroquia. Main road from Macas-Puyo highway towards the town of Palora. *Clark & Katzenstein 8361* (QCNE, US).—NAPO: Río Wai Si Aya, a northern tributary to Río Aguarico, small path going E-SE, path about

6 km upriver from San Pablo, *Brandbyge & Asanza 32712* (AAU, US); Río Wai Si Aya, 1 km upstream from the outlet in Río Aguarico, *Brandbyge et al.* 33242 (AAU, US); Cantón Tena, Reserva Biologica Jatun Sacha, 8 km from Puerto Misahualli *Cerón et al. 2000* (US); Parroquia: Talag. Comunidad Cando, north of Río Jatunyacu, *Clark et al. 5686* (US); 4 km sur de Puerto Napo en el Río Napo, *Dodson et al. 14949* (MO); *Foster 3680* (F); Cantón Tena, Cerro Antisana,Talag, 15 km SSW of Tena, *Grubb et al. 127* (BH, K NY); Baeza to Lago Agrio, about 45 km out of Baeza, *Wiehler & GRF Expedition 86200* (SEL).—ORELLANA: Cantón Aguarico, Yasuní Forest Reserve, E of Pontificia, *Acevedo & Cedeno 7395* (NY US); lagoons of Garza Cocha. Río Garza, *Cerón & Gallo 4944* (MO, QAP, US); Cantón Orellana, Yasuní Biosphere Reserve. Tiputini Biodiversity Station. Sendero Chichico to sendero Parahuaco, *Clark et al. 9573* (QCNE, SEL, UNA, US).—PASTAZA: Trail to Copataza, 10 km S of Sarayacu, *Lugo S. 5542* (US).—SUCUMBÍOS: "Napo." Lagunas de Cuyabeno, *Brandbyge et al. 36130* (AAU, US). **French Guiana**: *Granville 962* (CAY, US). **Guatemala.**—IZABAL: Montañas del Mico, 7-8 km W of Santo Tomás de Castilla on road to microwave tower, *Stevens et al. 25563* (MO). **Guyana**.—CUYUNI-MAZARUNI: Pakaraima Mts, Kurupung River, Makreba Falls, trail from E base of falls, *Hoffman et al. 2065* (US); Pakaraima Mountains, Kurupung-Membaru trail, 2.75 km from Kumarau Falls, *Hoffman & Marco 2138* (US), 2317 (US); Membaru - Kurupung trail, *Maguire & Fanshawe 32368* (US); N bank, W branch of Eping River, *McDowell & Stobey 3917* (NY, US); Upper Mazaruni River basin, Partang River, Merume Mountains; 2nd falls of Partang River, about 12 mi above mouth, *Tillett et al. 43920* (US).—POTARO-SIPARUNI: Upper Potaro R., near new Ayanganna airstrip, *Clarke et al. 9905* (US), *10239* (US); [Mazaruni-Potaro] Kaieteur plateau, along Mure-Mure Creek ca. 3 miles upstream from creek mouth, *Cowan & Soderstrom 2208* (US); Amatuk Falls, Potaro R, *Kelloff et al. 1402* (NY, US); Line from Kaieteur to Tukeit,

Lance & Bird 21 (US); Amatuk Portage, *Maguire & Fanshawe 23019* (US). **Honduras**.—GRACIAS A DIOS: Camp Tiro, 2 mi. NW of Bulebar on third northern branch of Quebrada Tiro, tributary of Río Platano; along walk 1 km S of camp, *Saunders 1088* (MO, NY, UNAH). **Nicaragua**. Wanke Río, *Schramm s.n.* (F); Mpio. de Bonanza, Territorio Mayangna Sauni - As - Musawas, alrededor de Atipak, *Aker et al. 726* (MO). ATLÁNTICO SUR: Mpio. Zelaya, Municipio de Nueva Guinea, Reserva Indio-Maiz, colinas de piedra fina, *Rueda et al. 9806* (MO), *10155* (MO).—JINOTEGA: Municipio de Wiwili, zona de amortigüamiento de Bosawas, comunidad de San Andrés; Transecto 12, ubicado en zona agrícola (Uran tingni), *Coronado et al. 3176* (MO); Salto Kayaska, Río Bocay, SW of falls, *Stevens et al. 16466* (MO, US). MATAGALPA: Al NW of Cerro Musun, *Araquistain & Moreno 2590* (MO).—RÍO SAN JUAN: Río Indio, Cano Negro, *Araquistain 3430* (US); *Bunting et al. 809* (F); "La Gloria", 3.5 km al NE del poblado de Boca de Sábalo, *Moreno 25444* (US).—ZELAYA: 5 mi w of Bonanza, *Atwood & Neill 7018* (MO); Municipality of Sinua, Cooperativa El Hormiguero, *Ortiz 815* (MO, US), *930* (MO); Bluefields, *Proctor et al. 26998* (EAP, F, NY); Río Punta Gorda, E of Corriente la Guitarrona, *Rueda et al. 3525* (MO). **Panama**.—CHIRIQUÍ: Cerro Colorado, area surrounding the stream that flows by Escopeta, new works, *Folsom 4937* (MO, US).—COCLÉ: Area between Cano Blanco del Norte, Cano Sucio and Chorro del Río Tife, *Davidse & Hamilton 23611* (US); La Mesa, 4 km N of El Valle, *Dwyer 11863* (MO); *Nee & Dwyer 9160* (MO); *Skog & Butcher 4118* (MO, P, US); Alto Calvario, 7 km N of El Copé, collections made on Atlantic slope, *Folsom 2881* (US); 7 km N of Llano Grande on road to Coclesito, *Hammel 1938* (MO), *2538* (MO).—COLÓN: Distr. Donoso, Concesión de Minera Panama S.A. Helipad LIMO03 (Zona Este), *Clark & Zapata 12487* (UNA, US), *12490* (UNA, US); ca. 2-3 mi up the Río Guanche, *Kennedy & Foster 2126* (MO).—PANAMÁ: San Blas Nusagandi, along trail to Quebrada de Nusagandi, *Werff 7048* (MO); Cerro

Bonyic, above Quebrada Huron, *Kirkbride & Duke 599* (MO), *627* (MO); Along road past Fortuna dam towards Chiriquí Grande, *McPherson 8539* (MO); Vicinity of Chiriqui Lagoon, Fish Creek Mts, *Wedel 2238* (MO), *2270* (MO), *2279* (MO, US) El Llano-Carti road in vic of Gorgas Lab Mosquite control Project site at km 12, *Croat 26074* (MO), *33745* (MO, NY); El Llano-Carti highway, ca. 19 km N of El Llano, *Dressler 4552* (MO, PMA, SEL).—VERAGUAS: Río Primero Braso, 2.5 km beyond agriculture school Alto Piedra near Santa Fé, *Croat 25489B* (MO), *49137* (MO); Near 2nd branch of Río Santa Maria, road from Santa Fé, *Witherspoon & Dressler 8897* (MO, US). **Surinam**.—SIPALIWINI: Haut Litany - Bassin du Litany; forêt sur flat; rive droite, layon vers le Talouakem; *Stahel s.n.* (US, U). **Venezuela**.—AMAZONAS: Depto. Atabapo: in saddle between Duida and Marahuaca near base of Duida, *Liesner 25365* (SEL); Depto. Atabapo: Cerro Yapacana, Río Orinoco, *Maguire et al. 30621* (NY), *42563* (NY).—DISTRITO FEDERAL: Cerro Naiguata, slopes sloping toward the sea facing north, above Naiguata, vicinity of Quebasenilla, 6 km SW of Cocuizal, *Steyermark 91913* (US).

5. *Paradrymonia glabra* (Benth.) Hanst. Linnaea 26: 207. 1854. *Centrosolenia glabra* Benth. Bot. Mag. 76: t. 4552. 1850. *Episcia glabra* (Benth.) Hanst., Linnaea 34(3): 349. 1865. *Episcia glabra* (Benth.) Hanst., Linnaea 34(3): 349. 1865. —TYPE: Cult. Kew Gardens. Orig. from La Guayra, Venezuela. *Wagener s.n.* (holotype: K!; isotype: K!)

Erect herb. **Stem** terete, 30 cm long or more, succulent, reddish brown, hirsute (with white trichomes), glabrescent towards base becoming subwoody covered with a light tan rhytidome. **Leaves** strongly unequal in a pair, the smaller one lanceolate and acuminate; petiole short, widely winged by decurrent leaf tissue, succulent, green, hirsute with white hairs; large leaf blade ovate to oblanceolate tapering at the base into a stout petiole, 15–35 × 4–12 cm, acuminate at the apex, the margin obscurely serrate. **Inflorescences** axillary, fasciculate, **pedicel** 1–4.5 cm long, green to reddish wine, long–hirsute, trichomes white; **flowers** with **calyx lobes** free, 15–20 × 2–3 mm, the four longer lobes linear–lanceolate, acuminate at the apex, the upper lobe shorter and deflected by the spur, margins with 1–3 teeth in the upper third, sometimes entire, with long, hirsute, white trichomes; **corolla** tubular–urceolate, enlarged upwards, inflated toward the middle, projected below into a short obtuse spur, white to creamy white, pubescent with white trichomes, the limb divided into five broad short lobes of with the lower one fringed with long thread–like laciniae, and the upper lobes variable crenate to fringed with shorter laciniae than the lower lobe; **stamens** 4, inserted near the base of the corolla, filaments glabrous, anthers coherent into a square, bearded with a tuft of hairs at the apex; ovary conical, hairy with two lammeliform bipartite, parietal placenta; nectary a large double connate dorsal gland; style glabrescent. **Fruit** a semi–succulent bivalve capsule. (Fig. 2.3B, F,G).

Distribution and habitat (Fig. 2.5).—The species is only known from Venezuela. The protologue for *Paradrymonia glabra* indicates that the specimen was collected in La Guayra [La Guaira], Venezuela. However, no recent collections are from that locality. Most of the collections are from the Guatopo National Park, southeast of Caracas near the border of the state of Miranda. The park is on the Coastal range (Cordillera de la Costa) between the towns of Santa Teresa del Tuy and Altagracia de Orituco. Other collections are from the Moron River basin in the Carabobo state. *Paradrymonia glabra* occurs in the tropical wet forests and pre–mountain wet forests at 20–1100 m (Feuillet, 2009b).

Phenology.—Flowering collections of *Paradrymonia glabra* are from August to January suggesting that the flowering occurs during the rainy season. Fruits are known only from April, at the end of the dry season.

Paradrymonia glabra and *P. ciliosa* are similar in their habit and general appearance. Both species are terrestrial or facultative epiphytes on low tree trunks, they have thick stems with short internodes, large coriaceous, semi–succulent leaves with the base decurrent into the petiole forming an apical rosette, and very short inflorescences in the leaf axils. *Paradrymonia glabra* differs from *P. ciliosa* by a more narrow leaf blade, shorter petioles, white corolla (vs. cream to yellowish corolla), presence of basal gibbosity on corolla tube (vs. absence of corolla gibbosity), and red trichomes on the corolla (vs. white trichomes on the corolla) (Fig. 2.3).

REPRESENTATIVE SPECIMENS.**Venezuela.**—CARABOBO: Mpio. Autonomo Mora, Cuenca hidrográfica del río Morón, parte alta, *Díaz & Niño 186* (MO, US); About 18-20 km S of Puerto Cabello, about 9-14 km S of San Esteban on old trail to Valencia ca. 4 km S of Col bridge, *Liesner & Medina 13755* (MO, US); 5-6 km S Borburata, río San Gian, *Steyermark 94338* (NY, US). MIRANDA: Parque National Guatopo, *Wiehler 72407* (SEL, US), *Bernardi 5688* (NY), *5831*; along S end of La Macanilla trail, 32 km NW of Altagracia de Oriuco, *Nee 17829* (NY); 32 mi (51 km) NNW of Altagracia de Orituco, 21 mi (33 km) SE of Santa Teresa, *Steyermark 87108* (US); Carretera Sta. Teresa- Altagracia de Orituco, *Aristeguieta 1750* (NY); environs of La Toma de Agua Macanillas, Río Chico, *Aristeguieta 3808* (US, VEN); Cerros del Bachiller, western sector, between base and summit, above Quebrada Bachiller, south of Cano Rico and Bachiller, 11 km (by air) SSE of El Guapo, *Steyermark & Davidse 116564* (MO, SEL).

6. *Paradrymonia lutea* Feuillet, J. Bot. Res. Inst. Texas 3: 585–588. 2009.—TYPE: VENEZUELA. Amazonas. Depto. Río Negro: Neblina Massif, Canyon Grande, along Río Mawarinuma, ca. 7 km ENE of Puerto Chimo, 0°50–51'N, 66°02–06'W, 300 m, 9–14 Jul 1984, fl., *Davidse & Miller 27212* (holotype: US!; isotypes: MO!, NY! VEN!).

Herbaceous epiphyte or lithophyte. **Stem** densely pilose with reddish trichomes. **Leaves** opposite, markedly unequal in a pair, the small one scale-like, promptly deciduous; larger leaf: **petiole** 15–40 cm long, wine-red, glabrous to appressed pubescent; leaf blade broadly-ovate to ovate-elliptic, 12–33 × 5–22 cm, cuneate and shortly decurrent at base, abruptly acuminate at apex, inconspicuously glandular-serrate and sparcely ciliate at the margins, glabrescent, sometimes the veins sparsely appressed–pubescent above, primary lateral veins 9–13 pairs, sunken above, raised below, tertiary venation not evident. **Inflorescences** 12–25 per axil; peduncle 3–5 mm long, appressed–pubescent, bracts oblanceolate to elliptic-lanceolate, acute at apex, 9–13 × 1.5–4 mm; **flowers** with **pedicels** sericeous, 2–3.5 cm long; **calyx lobes** free, 15–25 × 3–6 mm, broadly lanceolate or elliptic–lanceolate, long acuminate at the apex, sparsely ciliate in the upper half, entire in the basal half, with a few hardened blunt teeth toward the apex; **corolla** bright yellow, tubular, 4–4.5 cm long, glabrous inside except for the verrucose throat, slightly pubescent outside except toward the base, spur 3.5 × 5 mm, ovate–oblong, glabrous; corolla lobes suborbicular, 6 × 7 mm, glabrous inside, ventral lobe pilose outside, the others glabrescent throughout or pilose only toward base outside; **stamens** 4, inserted on the corolla, anthers 2 × 2 mm, bearded; nectary a large double connate dorsal gland, glabrous; **ovary** densely sericeous, style 25 mm long, glabrous at base, sparsely pilose toward apex, stigma stomatomorphic. **Fruits** and seeds not seen.

Distribution and habitat (Fig. 2.4). —*Paradrymonia lutea* grows as a terrestrial or facultative epiphyte on the base of tree trunks or on rocks in rainforests at 150–1250 m on the Neblina Massif, Amazonas (Venezuela).

Paradrymonia lutea is most similar to *Paradrymonia tepui*. Both species have broadly lanceolate or lanceolate–elliptic calyx lobes. The two species differ by the following characters: presence of white-creamy corollas in *P. tepui* (vs. bright yellow in *P. lutea*); leaf blades that are broadly ovate to ovate elliptic with cuneate base in *P. lutea* (vs. oblanceolate and long-attenuate base in *P. tepui*); and bracts and calyx lobes that are elliptic-lanceolate in *P. lutea* (vs. linear-lanceolate). Original descriptions of the flowers were made by Steyermark and included in the protologue by Feulliet (2009b).

REPRESENTATIVE SPECIMENS.**Venezuela**.—AMAZONAS: Río Negro Dept., foot hills of S slope of N arm of Cerro de la Neblina above Puerto Chimo camp on Río Mawarinuma, *Liesner 15896* (MO, US, VEN); Río Negro Dept., Cerro de la Neblina camp V, valley N base of Pico Cardona, *Liesner & Stannard 16895* (MO, US, VEN)

7. *Paradrymonia tepui* Feuillet, J. Bot. Res. Inst. Texas 3: 588–589. 2009.—TYPE: VENEZUELA. Amazonas: Depto. Río Negro: Cerro Aracamuni, summit, Proa Camp, in ravines and near edge of tepui, 01°32'N, 65°49'W, 1400 m, 31 Oct 1987, fl. & fr., *Liesner & Carnevali 22679* (holotype: US!; isotype: MO!).

Terrestrial herb, epiphyte or lithophyte. **Stems** densely pilose with reddish trichomes. **Leaves** opposite, strongly unequal in a pair, the small one scale–like, mostly persistent; larger leaf: **petiole** 13–24 cm long, glabrescent, green, U-shaped in cross section; **leaf blade** obovate to broadly elliptic, 14–30 × 6–14, cuneate and briefly decurrent at base, obtuse to acuminate at apex, margin minutely and sparcely serrate and ciliate, glabrous except abaxially on veins, midrib flatten to raised above, prominently raised below, 7–10 pairs of primary lateral veins, impressed on both surfaces. **Inflorescences** axillary, densely fasciculate on short peduncle; peduncles 1–1.5 cm long; bracts similar to the calyx lobes; **pedicels** sparsely appressed pilose. **Flowers** with **calyx lobes** greenish-tan tinged with red, oblanceolate to lancelate–elliptic, long-acuminate at apex, 1.7 × 0.4 cm, sparsely pilose, few glandular teeth limited to the apex; corolla (seen only in bud) white, hyaline–pilose, spur 5 × 3 mm, tube 2 cm long, ventral lobe undulate to slightly fimbriate; **stamens** 4, inserted on the corolla, anthers bearded. **Fruit** subglobose, greenish tan, tinged with red.

Distribution and habitat (Fig. 2.4). —*Paradrymonia tepui* has been collected on slopes and summit of a tepui, Cerro Aracamuni, in the Dept. Río Negro (Amazonas, Venezuela) between 600 and 1400 m. It also occurs in French Guiana (Feuillet 2009b)

Phenology. —Records of flowering for *P. tepui* are from March to April and October.

Paradrymonia tepui resembles *P. ciliosa* by its general appearance: thick stem with usually short internodes, creeping on the substrate, strongly unequal leaves in a pair, the larger ones with long petioles, short inflorescence peduncles in the leaf axils, and creamy white corollas. *Paradrymonia tepui* differs from *P. ciliosa* by the broadly lanceolate or lanceolate-eliptic calyx lobes in the fomer (vs. linear–acuminate in *P.ciliosa*). *Paradrymonia tepui* is most similar to

Paradrymonia lutea. Both species have broadly lanceolate or lanceolate–elliptic calyx lobes but *P. tepui* has white-creamy corollas (vs. bright yellow).

REPRESENTATIVE SPECIMENS. **French Guiana**.—CAYENNE. Grand Saut sur l'Armontabo affluent de l'Oyapock, *Prévost 1903* (P, US); Crique Gabaret - Bassin de l'Oyapock, *Cremers 9951* (CAY, NY, P, U, US); Route Régina, St. Georges D.Z. 5, P.K. 43, *Cremers & Gautier 12030* (US); Kaw Mountains, secondary forest across road from Trésor Voluntary Natural Reserve, *Smith et al. 4114* (US). **Venezuela.**—AMAZONAS: Depto. Río Negro: Cerro Aracamuni summit, Proa Camp, near edge of tepui, 1°32'N, 65°49'W, 1400 m, 27 Oct 1987, *Liesner & Carnevali 22530* (MO, US); Dept. Río Negro, slopes of Cerro Aracamuni, Quebrada Camp, Laja area, 1°24'N, 65°38'W, 600 m, 22 Oct 1987, fr., *Liesner & Carnevali 22324* (MO, US), *22530* (MO, US).

8. *Paradrymonia yatua* Feulliet, J. Bot. Res. Inst. Texas 3: 588–591. 2009.—TYPE: VENEZUELA. Amazonas. Depto. Río Negro: Río Yatúa, at base of Piedra Arauicaua, 100–140 m, 3 Feb 1954, fl., *Maguire, Wurdack & Bunting 37466* (holotype: US!; isotype: NY!).

Saxicolous herb. **Stem** short pilose, trichomes hyaline. **Leaves** very unequal in a pair, the small one scale-like, often early deciduous; the larger one: **petiole** 13–30 cm long, 1 cm wide (life-measurement), glabrous; **leaf blade** broadly obovate to elliptic or lanceolate, cuneate and then long decurrent into the petiole, acuminate at apex, margin entire or serrulate toward apex, glabrous both sides, 40–55 × 13–18 cm, midrib strikingly raised below, 12–13 main veins on each side of the midrib. **Inflorescence** axillary, densely fasciculate; bracts similar to the sepals;

pedicels 1.5–3 cm, sparsely pilose; **flowers** with **calyx lobes** green, oblanceolate to lance-elliptic, long linear at apex, 2.5–2.8 × 0.9–1.1 cm, margin entire loosely ciliate, sparsely pilose; **corolla** creamy-white, 6–6.5 mm long, spur 8 × 3 mm, curved, tube 2–2.8 cm long, pilose outside with hyaline trichomes, lobes rounded, entire, 10 × 10 mm, ventral lobe undulate to crenate at margin, pilose at base outside with hyaline trichomes, otherwise glabrous; dorsal gland, entire, rounded, 2 mm long, 1 mm wide; **stamens** 4, inserted on the corolla; anthers reniform-suborbicular, bearded; **ovary** slender ovoid, densely short strigose, trichomes reddish-purple, style 2.5 cm long, conspicuously short-hirsute, trichomes dark. **Fruit** and seeds not seen.

Distribution and habitat (Fig. 2.4). —*Paradrymonia yatua* is only known from the type locality at the base of Cerro Arauicaua, near Río Yatúa (Amazonas, Venezuela), between 100 and 150 m elevation. (Feulliet 2009b).

Phenology. —Records of flowering for *P. tepui* are from February and April.

Paradrymonia yatua is similar to *P. ciliosa*, *P. lutea* and *P. tepui* by its general appearance. *P. yatua* resembles *P.ciliosa* by having creeping thick stems with short internodes, strongly anisophyllous leaves with long petiolate leaves and axillary inflorescences with creamy-white corollas. *Paradrymonia yatua* differs from *P. ciliosa* and *P. glabra* by the oblanceolate to elliptic-lanceolate calyx lobes in *P. yatua* (vs. linear-lanceolate) and by having the ventral corolla lobe with undulate to crenate margins (vs. fimbriate). *Paradrymonia yatua* differs from *P. lutea* by its white corolla (vs.yellow) and from *P. tepui* by its green calyx (vs. tinged with red).

REPRESENTATIVE SPECIMENS: VENEZUELA. Amazonas: Depto. Río Negro: Cerro Arauicaua, al pie y en las faldas inferiores, Río Yatúa, 1°35’N, 66°10’W,125–150 m, 11 Apr 1970, fl., *Steyermark & Bunting 102546* (MO, NY, US, VEN).

A PARADRYMONIA NOMENCLATOR

Excluded or uncertain species

Below there is a list of published names of *Paradrymonia* and their present taxonomic placement. An equal sign (=) precedes the currently accepted name (Bold type). Combinations by previous authors are noted with place of publication.

Paradrymonia alata Kriebel, Rhodora 106: 47. 2004.—TYPE: COSTA RICA. Limón: Cordillera de Talamanca, 200 m aguas abajo de la confluencia de Quebrada Cañabral con Río Barbilla, 10º00'10"N, 83º25'30"W, 100 m, 5 Nov 1988. *Herrera 2287* (holotype: INB; isotype: MO!). =***Trichodrymonia alata* (Kriebel) M.M. Mora and J.L. Clark**, comb. nov.

Paradrymonia alba Wiehler, Selbyana 5: 46.1978. —TYPE: PANAMA. Bocas del Toro: Filo de Almirante, valley beyond ridge when approaching from Almirante, 22 May 1972. *Wiehler &Dressler 72303* (holotype: SEL!). **=*Trichodrymonia alba* (Wiehler) M.M. Mora and J.L. Clark**, comb. nov.

Paradrymonia apicaudata M.M. Mora & J.L. Clark, J. Bot. Res. Inst. Texas 6: 65-69. 2012.—TYPE: COLOMBIA. Valle: From Campoalegre into area controlled by Corporación Valle del Cauca, trail uphill behind last camp (El Chanco), 04°00'N 076°40'W, 400-610 m, 17

Feb 1989, *Smith*, *Bernal*, *Londoño and Devia 1357* (holotype*:* SEL!*;* isotypes: F!, MO!, US!, WIS!).= ***Trichodrymonia apicaudata* (M.M. Mora & J.L. Clark) M.M. Mora and J.L. Clark**, J. Bot. Res. Inst. Texas 6: 66–68. 2012.

Paradrymonia aurea Wiehler, Selbyana 5: 46-48.1978.—TYPE: ECUADOR. Pastaza: Road Puyo to Canelos, 8 km E of Puyo, 21 Apr. 1986, *Wiehler & GRF Expedition 86129* (neotype, designated by Clark et al., 2003: SEL!; isoneotype: US!). **=*Trichodrymonia aurea* (Wiehler) M.M. Mora and J.L. Clark**, comb. nov.

Paradrymonia anisophylla Feuillet & L.E. Skog, Brittonia 54: 354, fig. 2. 2003.—TYPE: GUYANA. Cuyuni-Mazaruni region, Partang riv., top of Merume Mtn. 1140 m, 1 jul 1960 (fl), Tillett, Tillett & Boyan 43948 (holotype: US!; isotype: NY!).= ***Codonanthopsis anisophylla* (Feuillet & L.E. Skog) Chautems & Mat. Perret**, *Selbyana* 31: 65-253. 2013.

Paradrymonia binata Wiehler, Phytologia 73: 2311. 1992.—TYPE: ECUADOR. Esmeraldas; Km 5-18 on road Lita to Alto Tambo, 18 Jan. 1987, *Dodson, Hirtz, Benzing, Luer & Luer 16833*; (neotype designated by Clark et al. 2003. SEL!; isoneotype: MO!) **=*Trichodrymonia binata* (Wiehler) M.M. Mora and J.L. Clark**, comb. nov.

Paradrymonia bullata Gómez-Laurito & Chavarría, Brenesia 33: 145. 1991. —TYPE: COSTA RICA: San José: Tarrazú, 1 km al norte de Esquipulas, a ca. 50 m al oeste del camino, a la orilla de una quebrada ignominada afluente del Río Naranjo, a 16 km por aire de Quepos, 9º30'10"N, 84º03'10"W, 300 m. *Gómez-Laurito 11686* (holotype: CR; isotypes: F!, USJ). Notes: Kriebel (2004) transferred this species to the genus *Nautilocalyx*, but since the specific epithet in this genus was already occupied by *Nautilocalyx bullatus* (Lem.) Sprague, he renamed the species *N. biserrulatus*. **=*Nautilocalyx biserrulatus* Kriebel**, Rhodora 106: 46. 2004.

Paradrymonia conferta (C.V. Morton) Wiehler, Selbyana 5: 50. 1978. *Centrosolenia conferta* C.V. Morton, J. Wash. Acad. Sci. 35: 126. 1945.—TYPE: PERU. Huanuco. *Poeppig 1671* (holotype: C; isotypes: F, K!, M, US!). *Episcia conferta* (C.V. Morton) Leeuwenb., Acta Bot. Neerl. 8: 52. 1959. =***Trichodrymonia conferta* (C.V. Morton) M.M. Mora and J.L. Clark**, comb. nov.

Paradrymonia congesta (Oerst.) Wiehler, Selbyana 5: 50. 1978.

Trichodrymonia congesta Oerst., Centralamericas Gesneraceer 38-39. 1858.—TYPE: MEXICO. Oaxaca. Chinantla, *Liebmann 9214*. (holotype: W; isotype: W). *Episcia congesta* (Oerst.) Hanst., Linnaea 34: 347. 1865. *Centrosolenia congesta* (Oerst.) C.V. Morton, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1159. 1938. =***Trichodrymonia congesta* Oerst.**, Centralamericas Gesneraceer 38-39. 1858.

Paradrymonia darienensis (Seem.) Wiehler, ("dariensis"), Selbyana 5: 56. 1978.

Alloplectus darienensis Seem. The Botany of the Voyage of H.M.S. ~Herald~ 187. 1854. *Episcia darienensis* (Seem.) Leeuwenb., Acta Bot. Neerl.8: 52. 1959. —TYPE: PANAMA: Darién: Cape Corrientes, dark woods. *Seemann 1058*; (holotype: K!; isotypes: BM!, MO!, U (photo), US! (photo)). **=*Trichodrymonia darienensis* (Seem.) M.M. Mora and J.L. Clark**, comb. nov.

Paradrymonia decurrens (C.V. Morton) Wiehler**,** Phytologia 27: 308. 1973.

Centrosolenia decurrens C.V. Morton, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1158. 1938. *Episcia decurrens* (C.V. Morton) Leeuwenb., Acta Bot. Neerl. 8: 53. 1959.**—**TYPE: COSTA RICA. Limón: Finca Montecristo, on Río Reventazón, below El Cairo, alt. 25 m, 18-19 Feb 1926. *Standley & Valerio 48589* (holotype: US!-1305619. =***Paradrymonia ciliosa* (Mart.) Wiehler**, Phytologia 27: 308. 1973.

Paradrymonia densa (C.H. Wright) Wiehler, Selbyana 5: 50. 1978. *Episcia densa* C.H. Wright, Bull. Misc. Inform. Kew. 1895: 17. 1895.—TYPE: GUYANA: River Masouria, *Jenman 2414* (holotype:K!). *Centrosolenia densa* (C.H. Wright) Sprague, Bull. Misc. Inform. Kew. 1912: 87. **=*Centrosolenia densa* (C.H. Wright) M.M. Mora and J.L. Clark**, comb. nov.

Paradrymonia erythropus (Hook.f.) Wiehler, Selbyana 5: 50. 1978.

Episcia erythropus Hook.f., Botanical Magazine 102: t. 6219. 1876.—TYPE: Cult. Hort. Kew, ex Hort. Veitch s.n.; Colombia (holotype: K!). **=*Trichodrymonia erythropus* (Hook.f.) M.M. Mora and J.L. Clark**, comb. nov.

Paradrymonia flava Wiehler, Selbyana 5: 51. 1978.—TYPE: PANAMA: Colón: Río Guanche, near Portobelo,10 Aug 1971. *Wiehler & Dressler 71158.* (holotype: SEL!; isotypes: BH, F, GH, K!, MO!,. NY!, PMA, US!). ***=Trichodrymonia flava* (Wiehler) M.M. Mora and J.L. Clark**, comb. nov.

Paradrymonia fuquaiana Wiehler, Phytologia 73: 232. 1992.—TYPE: ECUADOR. Napo: road Hollin-Loreto, 27 Apr. 1995, *Wiehler & GRF Expedition 95116. (*neotype designated by Clark et al. 2003: SEL!; isotype: MO!). After close examination of specimens throughout its geographic range, we conclude that *P. fuquiana* and *T. aurea* are conspecific and are therefore synonymized here. ***=Trichodrymonia aurea* (Wiehler) M.M. Mora and J.L. Clark**, comb. nov.

Paradrymonia gibbosa Wiehler, Selbyana 5: 52, 12D. 1978.—TYPE: COLOMBIA.Valle: Old road from Cali to Buenaventura near La Elsa, 30 Apr. 1972, *Wiehler & Dressler 7278* (lectotype designated by J.R. Clark et al. 2003: SEL!). ***=Trichodrymonia gibbosa* (Wiehler) M.M. Mora and J.L. Clark**, comb. nov.

Paradrymonia gigantea Wiehler, Selbyana 5: 53. 1978.—TYPE: Cult. Hort. Selby from Valle, Colombia. *Wiehler et al. 76247*; (holotype: SEL!; isotype: US!). Origin of cultivated material: Colombia. Valle: Old road from Cali to Buenaventura near La Elsa, 30 Apr. 1972, *Wiehler et al. 7236*. ***= Trichodrymonia gigantea* (Wiehler) M.M. Mora and J.L. Clark**, comb. nov.

Paradrymonia glandulosa Feuillet, J. Bot. Res. Inst. Texas 3583–585. 2009. —TYPE: VENEZUELA. Amazonas. Depto. Atabapo: Cerro Marahuaca,“Sima Camp”, south–central portion of forested slopes along eastern branch of Caño Negro, 3°43'N, 65°31'W, 1140 m, 21–24 Feb 1985, fl., *Steyermark & Holst 130443* (holotype: US!; isotypes: MO!, VEN). =***Paradrymonia ciliosa* (Mart.) Wiehler**, Phytologia 27: 308. 1973.

Paradrymonia hamata Feuillet, J. Bot. Res. Inst. Texas 3: 585–591, fig. 2. 2009.—TYPE: VENEZUELA. Amazonas. Depto. Río Negro: Cerro de la Neblina, Río Yatúa, 140–1700 m, 31 Dec. 1957, fl., *Maguire, Wurdack & Maguire 42563* (holotype: NY!). =***Paradrymonia ciliosa* (Mart.) Wiehler**, Phytologia 27: 308. 1973.

Paradrymonia hansteiniana (Mansf.) Wiehler, Selbyana 5: 54. 1978. *Episcia hansteiniana* Mansf. Repert.Spec. Nov. Regni Veg. 38: 25. 1935.—TYPE: PERU. Loreto, Iquitos. *Tessmann 5088* (holotype: B (destroyed)).—PERU. Loreto. Carretera Oleoducto Secundario entre los Campamentos Bartra 1 y Bartra 4, *Diaz 1401* (neotype, here designated: US!; isoneotypes: MO!, SEL!): =***Paradrymonia ciliosa* (Mart.) Wiehler**, Phytologia 27: 308. 1973.

Paradrymonia hirta L.E. Skog, Ann. Missouri Bot. Gard. 65:967. 1979.—TYPE: PANAMA: Darién: Cuasí-Caná trail between Cerro Campamiento and La Escalera to Páramo, east of Tres Bocas, *Kirkbride & Duke 1293* (holotype: MO!). **=*Trichodrymonia hirta* (L.E. Skog) M.M. Mora and J.L. Clark**, comb. nov.

Paradrymonia hypocyrta Wiehler, Selbyana 2: 82, pl. 25C. 1977.—TYPE: ECUADOR: Los Ríos: Montaña de Ila, km 12, road from Patricia Pilar to 24 de Mayo, 540 m alt., 30 May 1976, *Dodson 6092* (holotype: SEL!). **=*Trichodrymonia hypocyrta* (Wiehler) M.M. Mora and J.L. Clark**, comb. nov.

Paradrymonia lacera Wiehler, Selbyana 7: 343, pl. 5A. 1984. — TYPE. ECUADOR: Cotopaxi: 3 km E of El Palmar, on road from Quevedo to Latacunga, 800 m, 5 Apr. 1980, *Dodson & Gentry 10194* (holotype: SEL!; isotypes: QCA!, QCNE!). **= *Trichodrymonia lacera* (Wiehler) M.M. Mora and J.L. Clark**, comb. nov.

Paradrymonia lineata (C.V. Morton) Wiehler, Phytologia 27: 308.1973. *Centrosolenia lineata* C.V. Morton, Ann. Missouri Bot. Gard. 29: 41-42. 1942.—TYPE: PANAMA. Coclé: hills on trail to La Mesa, north of El Valle de Anton, alt. 1000 m, 31 Aug 1941, *Allen 2717* (holotype: US!). *Episcia lineata* (C.V. Morton) Leeuwenb., Acta Bot. Neerl. 8: 53. 1959. **=*Trichodrymonia lineata* (C.V. Morton) M.M. Mora and J.L. Clark**, comb. nov.

Paradrymonia longifolia (Poepp.) Wiehler, Selbyana 5: 54.1978. *Drymonia longifolia* Poepp., Nov. Gen. Sp. Pl. 3: 4. 1840. —TYPE. PERU: Huanuco. *Poeppig 1671* (holotype: W; isotypes: W(2)). *Besleria longifolia* Poepp. ex Hanst., nom. nud. pro syn. Linnaea 34 : 348.1865. **=*Drymonia longifolia* Poepp.,** Nov. Gen. Sp. Pl. 3: 4. 1840.

Paradrymonia longipetiolata (J.D. Sm.) Wiehler, ("longipedunculata") Selbyana 5: 54. 1978. *Episcia longipetiolata* J.D. Sm. Bot. Gaz. 25: 152-153. 1898. —TYPE. COSTA RICA : borders of the road to Carrillo, alt. 300 m, Jun 1890, *Tonduz 2493* (holotype: US!;

isotype: CR). **=*Trichodrymonia longipetiolata* (J.D. Sm.) M.M. Mora and J.L. Clark**, comb. nov.

Paradrymonia lurida (C.V. Morton & Raymond) Wiehler, Phytologia 27: 308.1973. *Episcia lurida* C.V. Morton & Raymond, Baileya 18: 9-11, fig. 2. 1971.—TYPE. Collected in the Jardin Botanique de Montreal, August, 1966, culture number 2209-60; grown from cuttings received from the Bailey Hortorium, Ithaca, New York, through Dr. H.E. Moore, Jr., where grown from material originally collected near Cariblanco, Sarapiqui Valley, Prov. Alajuela, Costa Rica, by Clarence Horich. *Raymond s.n.* (holotype: US!; isotype: MTJB). After close examination of specimens throughout its geographic range, it is concluded that *P. lurida and T. lineata* are conspecific. **=*Trichodrymonia lineata* (C.V. Morton) M.M. Mora and J.L. Clark**, comb. nov.

Paradrymonia macrophylla Wiehler, Selbyana 5: 56.1978. —TYPE. PANAMA. Coclé: hills N of El Valle de Anton, 15 Aug 1971, *Wiehler & Dressler 71286* (holotype: SEL!). **=*Trichodrymonia macrophylla* (Wiehler) M.M. Mora and J.L. Clark**, comb. nov.

Paradrymonia maculata (Hook.f.) Wiehler Selbyana 5: 57. 1978. *Episcia maculata* Hook.f. Bot., Mag. 116: t. 7131. 1890.—TYPE: Cult. Hort. Kew. Originally from Guyana, collector unknown *s.n.* (holotype: K! (photos BH, NY!, U, US!, WAG); isotype: K!). =***Pagothyra maculata* (Hook.f.) J.F. Sm. & J.L. Clark**, Syst. Bot. 38: 462. 2013.

Paradrymonia maguirei Feuillet. J. Bot. Res. Inst. Texas 3: 134, fig. 1. 2009.—TYPE: VENEZUELA. Amazonas. Depto. Alto Orinoco: Cerro Marahuaca, 1000 m, 3 May 1949, *Maguire & Maguire, Jr. 29185* (holotype: NY!, pro parte: specimen A and material in pocket). =***Trichodrymonia maguirei* (Feuillet) M.M. Mora and J.L. Clark**, comb. nov.

Paradrymonia metamorphophylla (J.D. Sm.) Wiehler, Phytologia 27: 327. 1973.

Alloplectus metamorphophyllus J.D. Sm. Bot. Gaz. 52: 52. 1911. **—**TYPE: COSTA RICA: San José: La Palma, alt. 1500-1600 m., Sept 1896, *Tonduz 10884*; (lectotype designated by Morton, 1938: US!).=***Trichodrymonia metamorphophylla* (J.D. Sm.) M.M. Mora and J.L. Clark**, comb. nov

Paradrymonia ommata L.E. Skog, Brittonia 30: 324.1978. —TYPE. PANAMA: Bocas del Toro: Quebrada Huron, rapid stream through Evergreen Seasonal Forest, 90-120 m, 11 Apr 1968, *Kirkbride & Duke 437* (holotype: MO!; isotypes: REED, SCZ). **=*Trichodrymonia ommata* (L.E. Skog) M.M. Mora and J.L. Clark**, comb. nov.

Paradrymonia pedunculata L.E. Skog, Brittonia 30: 325.1978. — TYPE. PANAMA: Darién: Puerto St. Dorothea, 21 Jul 1962, *Dwyer 2268* (holotype: MO!; isotype: US!)

Rhoogeton panamensis Wiehler, Phytologia 73: 239. 1992. — TYPE. COSTA RICA: Jul. 1980, *Pittier& Durand 2654*[Biolley 343] Neotype: US!; Isoneotype: BR). Neotype designated by Clark et al. 2003.

Paradrymonia picta (Hook.) Hanst., Linnaea 26: 180. 1854. *Centrosolenia picta* Hook., Bot. Mag. 77: pl. 4611. 1851.—TYPE: BRAZIL. *Spruce s.n.*; (holotype: K!). *Collandra picta* (Hook.) Lem., non Kl. & Hanst, 1854. *Columnea picta* sensu Lem. ex Hanst. in Mart., non H.Karst. Fl. Brasil. 8: 422. 1864. *Columnea picta* (Lem. ex Hanst.) Voss, in Siebert & Voss, Vilmorin's Blumengärt. (ed. 3) 1: 798. 1894. *Episcia picta* (Hook.) Hanst., in Mart. Fl. Brasil. 8: 403. 1864. *Nautilocalyx lacteus* Sandw., Bull. Misc. Inform. Kew 1931: 489. 1931.—TYPE: GUYANA. *Sandwith 3* (holotype: K!). = ***Nautilocalyx pictus* (Hook.) Sprague**, Bull. Misc. Inform. Kew 1912: 88. 1912.

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Paradrymonia sastrei Wiehler, Gesneriana 1: 71. Fig 21. 1995.—TYPE: COLOMBIA: Amazonas: Río Igareparaná (tributary of Río Putumayo), corregimiento: La Chorrera: San Antonio (ca. 72 °W, 2 °S), 9 July 1974, *Sastre 3608* (holotype: P). **=*Trichodrymonia sastrei* (Wiehler) M.M. Mora and J.L. Clark**, comb. nov

Paradrymonia sericea Wiehler, Selbyana 5: 57. 1978. — TYPE: Specimen from cultivated material, originally from Valle, Colombia, *Wiehler 75270* (holotype: SEL!). **=*Trichodrymonia sericea* (Wiehler) M.M. Mora and J.L. Clark**, comb. nov.

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Paradrymonia tylocalyx Wiehler, Selbyana 5: 58. 1978.—TYPE: Specimen from cultivated material originally from Colombia, Valle: Old road from Cali to Buenaventura below La Elsa, 30 Apr. 1972,, 13 May 1975, *Wiehler 75271* (holotype: SEL!).**=*Trichodrymonia tylocalyx* (Wiehler) M.M. Mora and J.L. Clark**, comb. nov.

Paradrymonia ulei Wiehler, Gesneriana 1: 71, fig. 22. 1995.—TYPE: PERU: Loreto. Pongo de Cainarachi (below Yurimaguas), Sept. 1902, *Ule 6328* (holotype: HBG). **= *Trichodrymonia ulei* (Wiehler) M.M. Mora and J.L. Clark**, comb. nov.

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Table 2.1. Comparison of *Paradrymonia*, *Centrosolenia* and *Trichodrymonia*

	Paradrymonia	*Centrosolenia*	*Trichodrymonia*
Habit	terrestrial, climber or facultative epiphyte, usually forming rosettes	Terrestrial or lithophyte	terrestrial, facultative epiphyte, lithophyte, usually forming rosettes
Tuber	Absent	Absent	Present in *T. pedunculata*
Anisophylly	Usually strongly anisophyllous with one leaf in a pair reduced except in *P. barbata* and *P. campostyla*	Isophyllous or anisophyllous	Usually strongly anisophyllous with one leaf in a pair reduced
Leaf margin	Serrate to double serrate	Crenate	Serrate to double serrate
Leaf base	Usually attenuate, or decurrent into the petiole, sometimes subcordate	Usually subcordate or markedly asymmetrical	Usually attenuate, or decurrent into the petiole, sometimes subcordate or peltate
Flowers	Usually many (more than ten) congested in leaf axils. 1-4 in. *barbata* and *P. campostyla*	2-4 in leaf axils	Usually many (more than ten) congested in leaf axils
Calyx lobe shape	linear-lanceolate to elliptic-lanceolate	narrowly-lanceolate, or oblong-spatulate	Lanceolate to linear-lanceolate
Calyx lobe margin	frequently with subulate teeth with hardened tip	subentire, frequently with subulate teeth with hardened tip	Serrate to lacerate, frequently with subulate teeth with hardened tip
Corolla shape	Funnel-shaped to trumpet-shaped	Elongate and tubular	Salverform, trumpet shaped, hypocyrtoid
Corolla color	White to yellow, without spots	Lilac, red, white	White (sometimes purple-spotted), orange, red, yellow
Corolla lobe margin	Usually with fimbriations	Entire or crenate, never fimbriate	Entire or crenate, never fimbriate
Bearded anthers	Present, except in (*P. barbata* and *P. campostyla*)	Absent	Absent
Fruit	Semi-fleshy bivalved capsule	Semi-fleshy bivalved capsule	Semi-fleshy bivalved capsule, berries in *T. metamorphophylla*

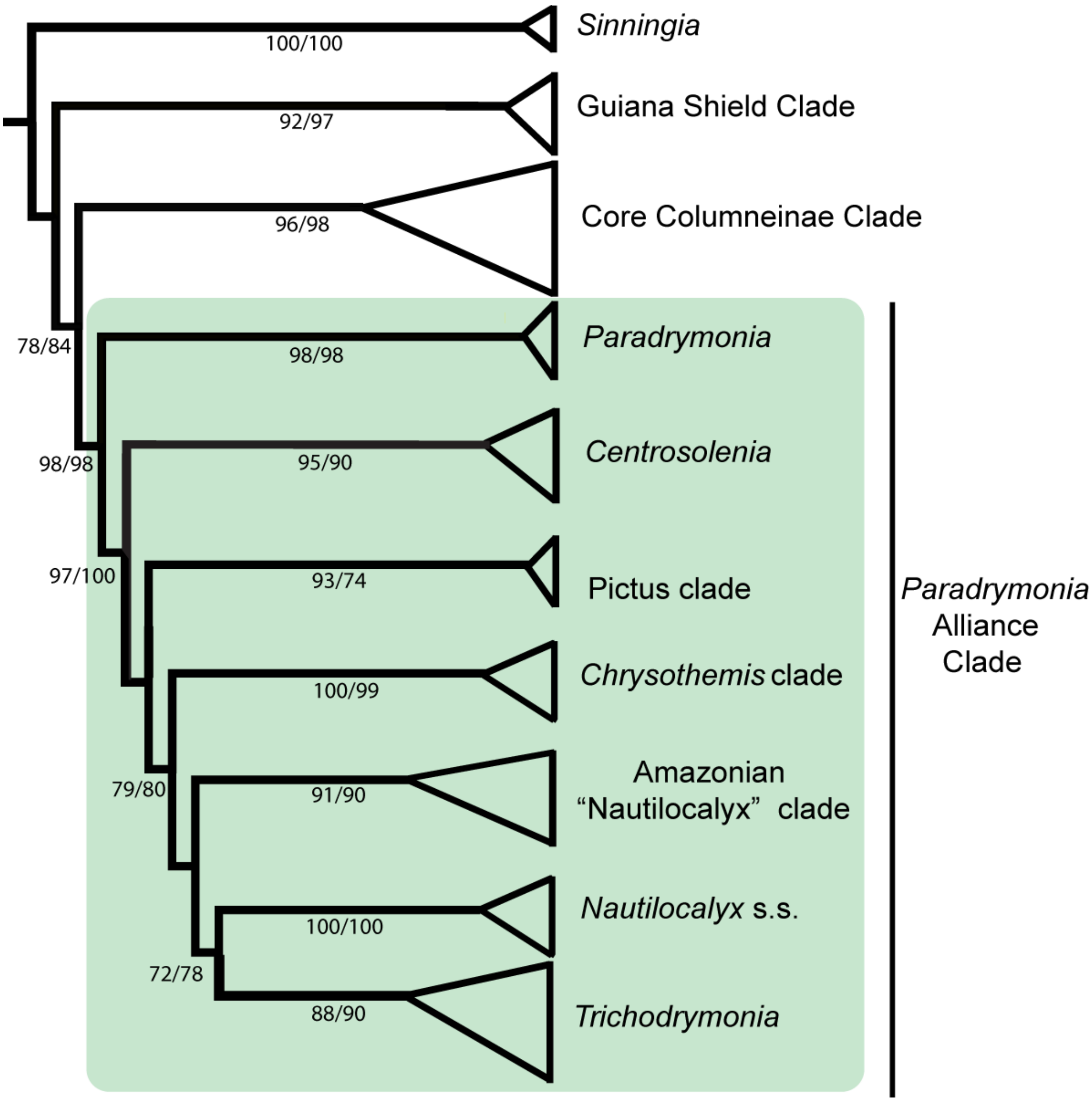

Fig. 2.1. Summary of the strict consensus tree from total evidence analysis of three molecular markers analysis (ETS, ITS and *psb*A- *trn*H) showing the relationships within the main monophyletic clades within the subtribe Columneinae. The strict consensus tree is from 25 most parsimonious trees of 2977 steps. Maximum parsimony and maximum likelihood bootstrap values are above and below the branches respectively. Only bootstrap values ≥50% are shown. Complete phylogenetic analysis is provided in Mora and Clark (in review).

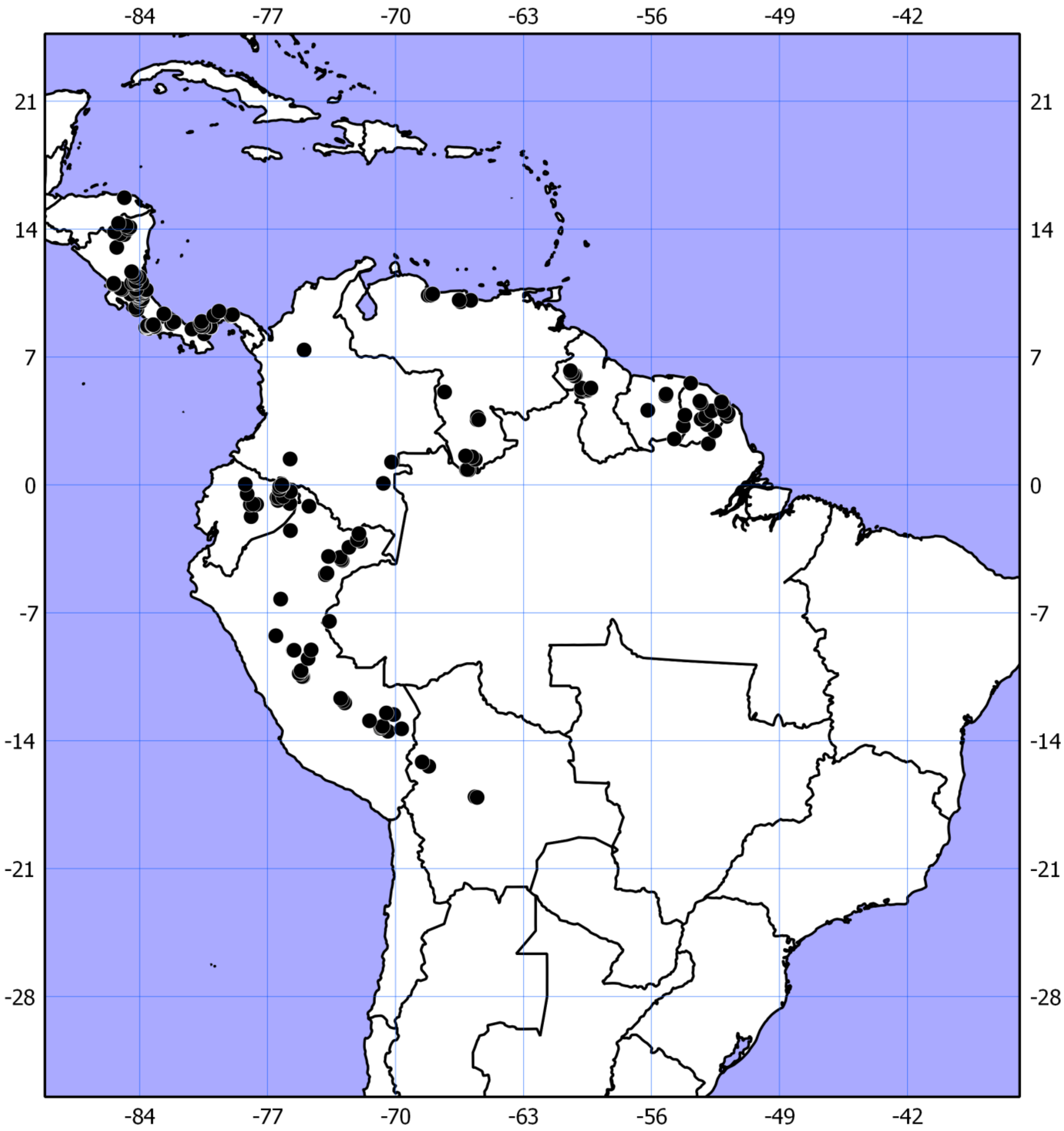

FIG. 2.2. Geographic distribution of *Paradrymonia*.

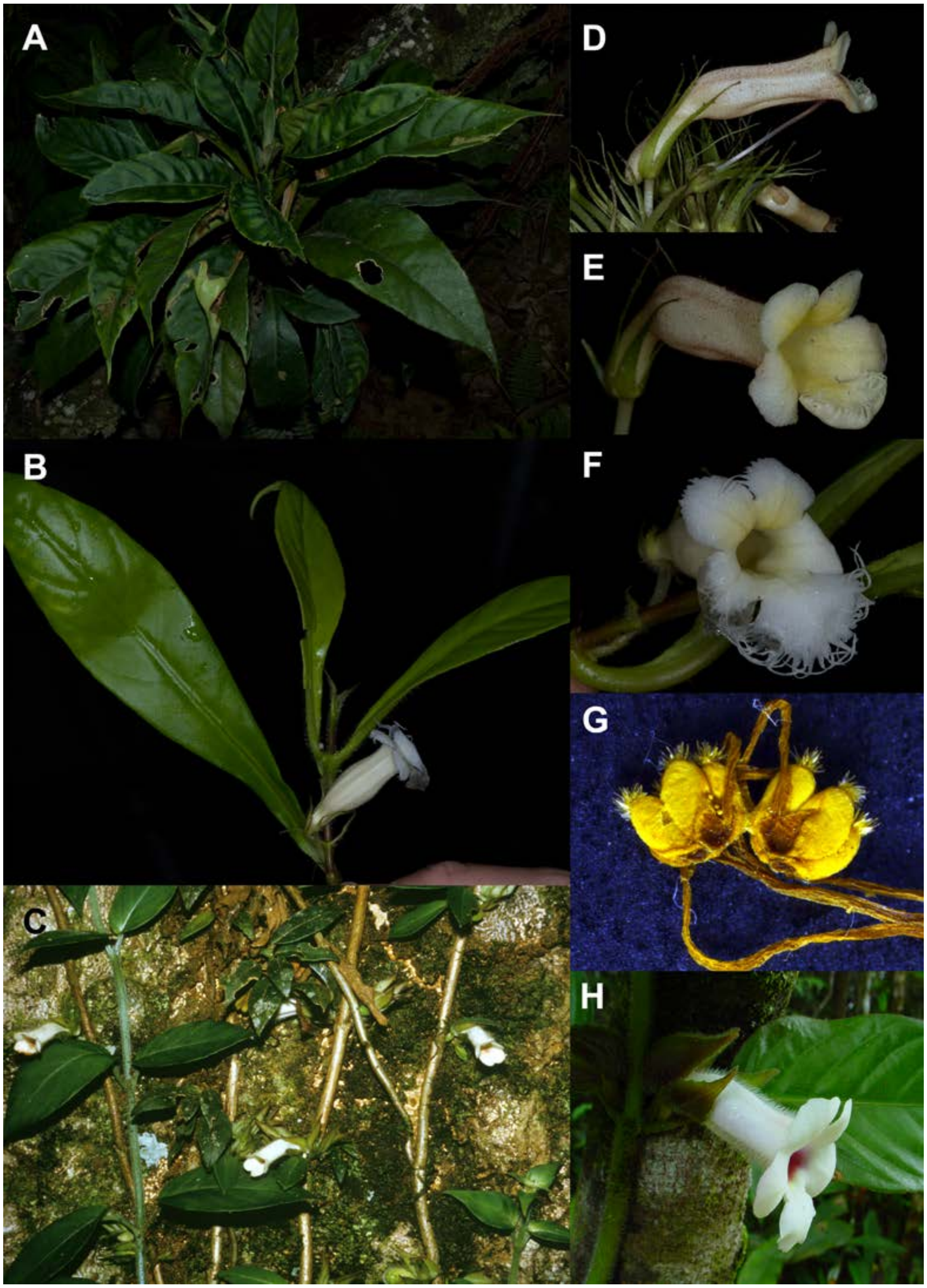

FIG. 2.3. Habit and morphological features in *Paradrymonia ciliosa, P. glabra* and *P. campostyla*. A. Habit of *P. ciliosa* showing leaves forming a rosette. B. Leaves and lateral view of flower of *P. glabra* showing straight (no-angulate corolla). C. Habit of *P. campostyla* showing long internodes and isophyllous leaves. D–E. Flower of *P. ciliosa* showing angulate corolla and fimbriations on lower corolla lobe F. Front view of *P. glabra* showing fimbriations on lower corolla lobe. D. Bearded anthers of *P. glabra*. H. Lateral view of flower of *P. campostyla* without fimbrations.

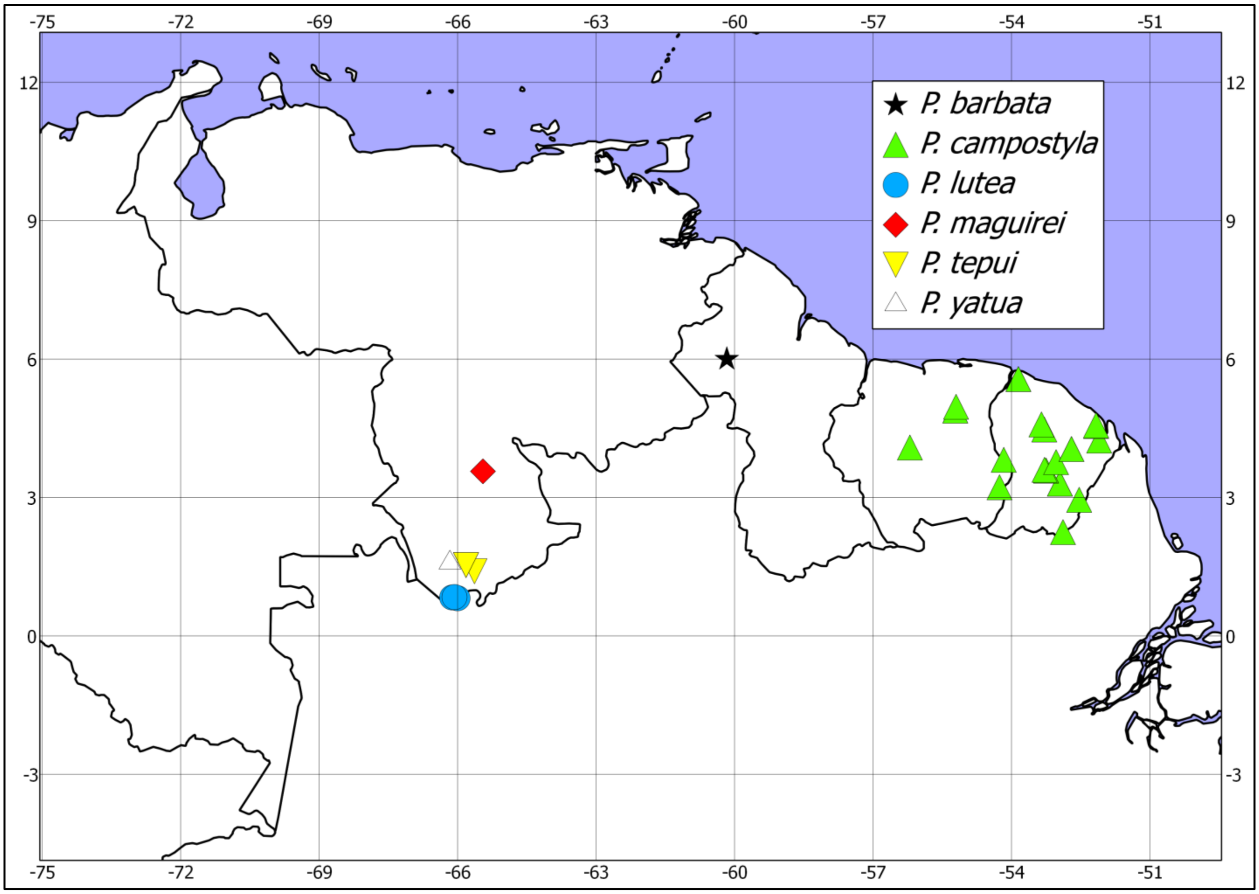

FIG. 2.4. Geographic distribution of *Paradrymonia barbata, P. campostyla, P. lutea, P. maguirei*, *P. tepui*, and *P. yatua.* All of these species are endemic to the Guiana Shield.

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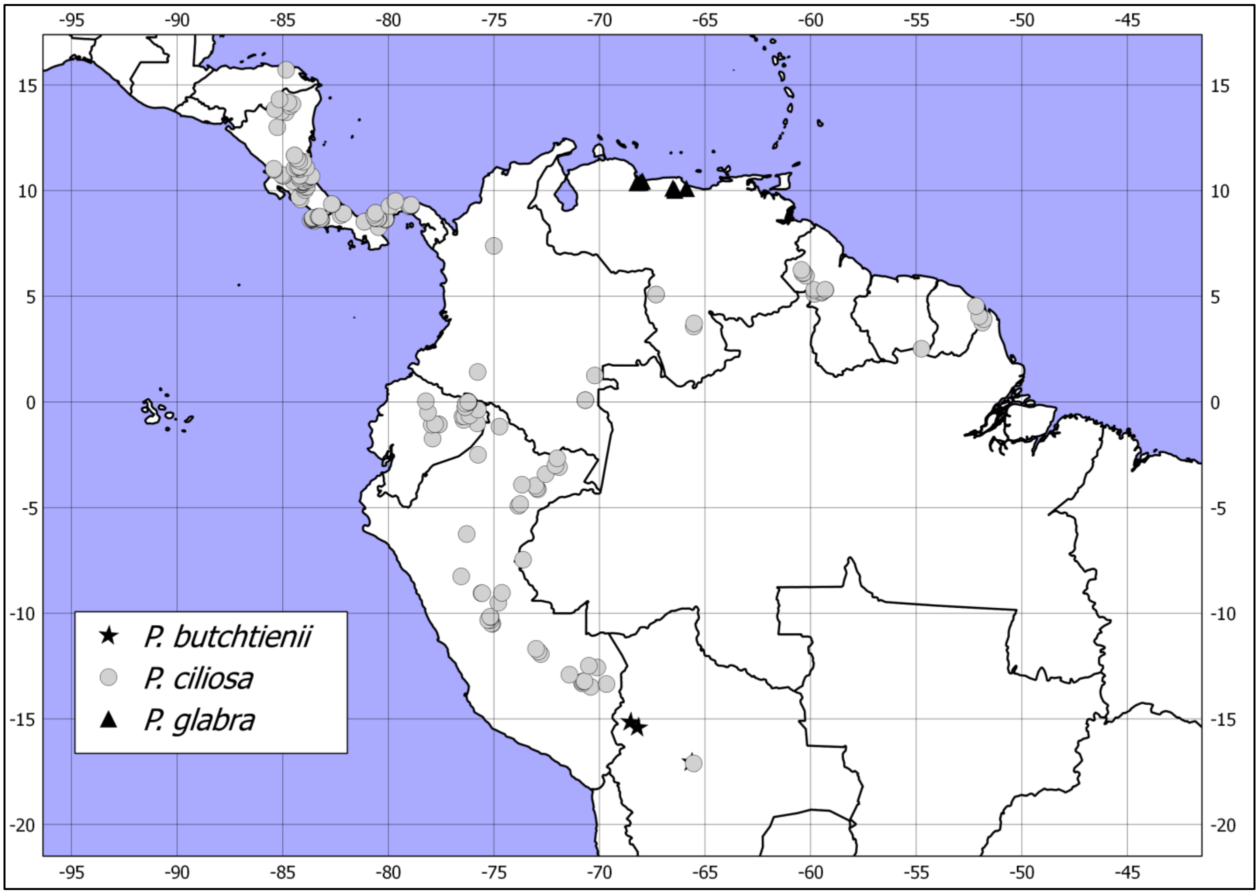

FIG. 2.5. Geographic distribution of *Paradrymonia buchtienii*, *P. ciliosa* and *P. glabra*.

CHAPTER III

Character Evolution and Biogeography in the *Paradrymonia* Alliance, Subtribe Columneinae, Tribe Gesnerieae

ABSTRACT

A recent phylogeny of the *Paradrymonia* alliance identified seven well-supported clades. We assessed the taxonomic utility and evolution of the following nine morphological and ecological characters: habit, growth form, leaf dimorphism, calyx fusion, calyx lobe shape, pollination syndrome, presence of bearded anthers and corolla shape. Characters were optimized on a parsimony consensus tree of a total evidence analysis from three molecular markers (nrDNA ITS, nrDNA ETS, and cpDNA *psb*A-*trn*H). Additionally, ancestral areas were reconstructed by mapping current geographic distributions on the same tree. The analyses suggest that the most recent common ancestor of the *Paradrymonia* alliance originated in the Guiana Shield roughly 10 Mya with the following characters: terrestrial caulescent herb, leaves isophyllous; non-fused linear-lanceolate calyx lobes; and white funnel-shaped corollas that are typical of bee pollination. Unidirectional shifts from entomophily to ornithophily have occurred multiple times in the *Paradrymonia* alliance while the evolution of hypocyrtoid corolla has a single origin. Most of evaluated characters for genera/clades within the *Paradrymonia* alliance were homoplasic suggesting convergent evolution as adaptation to shady understory environments, nutrient-poor habitats, and similar pollinators among others.

Keywords—homoplasy, convergent evolution, morphology, pollination syndromes, Neotropics, understory.

INTRODUCTION

Molecular phylogenies have provided an essential framework for new taxonomic classifications of a myriad of organisms and have brought new light on evolutionary events that have shaped current biodiversity. Molecular phylogenies have also allowed plant systematists to gain insight on the evolution of morphological characters, and to identify homoplasious characters previously recognized as homologous and vice versa. Across different group of plants high levels of morphological homoplasy have been reported (e.g. Arecaceae, Norup et al. 2006; Orobanchaceae, Yang et al. 2003; Sapotaceae, Swenson et al. 2008; Malvaceae, Escobar-García et al. 2009; Gesneriaceae, Clark et al. 2012).

In the Gesneriaceae, for example, various molecular phylogenies have proved to be strongly inconsistent with the traditional, morphology-based classification across different taxonomic ranks (e.g. Clark and Zimmer 2003; Smith et al. 2004; Roalson et al. 2005; Weber 2004; Chautems and Perret 2013; Weber et al. 2013). The last classification for the whole family based on essentially morphological data was that of Burtt and Wiehler (1995). Recently, Weber et al. (2013) proposed a new comprehensive formal classification for the family based on molecular phylogenetic studies for New and Old World Gesneriaceae that resulted in a re-circumscription of the traditionally recognized tribes. For the Neotropical Gesneriaceae the number of tribes was reduced from nine to the following five: Beslerieae, Coronanthereae, Gesnerieae, Napeantheae, and Titanotricheae (Weber et al. 2013). Gesnerieae, the largest tribe in the family, includes what was previously in the following tribes Gloxinieae, Gesnerieae, Episcieae and Sphaerorrhizeae (Weber et al. 2013).

Extremely high levels of morphological homoplasy are frequently responsible for problems in generic delimitation (Norup et al. 2006). Good examples of taxonomic problems caused by homoplasy of morphological characters can be found in the Neotropical subtribe Columneinae, tribe Gesnerieae (tribe Episcieae *sensu* Wiehler1983). This subtribe is morphologically diverse with 26 genera and over 700 species and it is characterized by having superior ovaries, a three-trace trilacunar node with split lateral bundles, flowers derived from a pair-flowered cyme inflorescence, and a haploid chromosome number of x=8 or 9 (Wiehler 1978; Wiehler 1983; Weber 2004; Weber et al. 2013). Among the genera in the subtribe that have previously been recovered as non-monophyletic are *Alloplectus* (Clark and Zimmer 2003; Clark et al. 2006), *Neomortonia* (Smith and Carroll 1997; Smith 2000), *Nautilocalyx* and *Paradrymonia* (Smith 2000; Clark et al. 2006; Clark et al 2012; Mora and Clark in review). Discordance between molecular and traditional classifications in the genera of Columneinae is attributed to convergence of floral characters such as corolla shape (Wiehler 1978, 1983). Although molecular data is not exempted from homoplasy, it represents a more objective criteria for evaluating taxon boundaries. In the last few years it has become increasingly common to reexamine morphological characters once well-supported monophyletic groups have been identified (Clark et al. 2012). This method has facilitated the discovery of unique morphological synapomorphies that had not been recognized before or, in the absence of unique synapomorphies, the discovery of combinations of meaningful homoplasious character states to circumscribe monophyletic groups (e.g. Hughes et al. 2004; Norup et al. 2006; Escobar-Garcia 2009).

In a recent phylogeny Mora and Clark (in review) sampled the subtribe Columneinae with an emphasis on a clade recognized as the “*Paradrymonia* alliance” which includes species of *Paradrymonia* and closely related genera such as *Chrysothemis*, and *Nautilocalyx* and the recently resurrected genera *Trichodrymonia* and *Centrosolenia*. The *Paradrymonia* alliance clade was strongly supported as monophyletic and was recovered as sister to the "Core Columneinae" clade *sensu* Mora and Clark (in review), which includes large genera such as *Columnea*, *Drymonia*, and *Glossoloma*. These two clades are sister to the most basal clade, the Guiana Shield Clade that includes endemic genera to the Guiana Shield such as *Lembocarpus*, *Rhoogeton* and *Cremersia* (Clark et al. 2006; Mora and Clark in review). Up to now, potentially diagnostic characters for the clades within the *Paradrymonia* alliance have not been formally evaluated within a phylogenetic framework based on molecular data. Thus, the aim of the current study is to examine the evolution of traits that might be proven important to help circumscribe those clades. To this end, the distribution of these traits was mapped on a tree built according to recent phylogenetic analyses of the Subtribe Columneinae with an emphasis on the *Paradrymonia* alliance (Mora and Clark in review). The objectives of the current study are: (1) to assess potentially useful ecological or phenotypic traits to help circumscribe the main clades within the *Paradrymonia* alliance; (2) to evaluate biogeographic regions and corresponding clade-based groups to help circumscribe the main clades within the *Paradrymonia* alliance; (3) to examine transformation patterns and evolution of those traits; and (4) to provide insights into the biogeographic history of well supported clades in the *Paradrymonia* alliance.

MATERIALS AND METHODS

A recent phylogeny for the *Paradrymonia* alliance (subtribe Columneinae) using a combined analysis of three molecular markers (nrDNA ETS, nrDNA ITS and plastid non-coding *psb*A- *trn*H), is provided in Mora and Clark (in review). A summary of this evolutionary hypothesis for the subtribe Columneinae with emphasis in the *Paradrymonia* alliance is shown in Figure 1. This phylogenetic hypothesis, which is by far the most comprehensive for the *Paradrymonia* alliance, forms the basis for the ancestral reconstructions presented here. The methods used to generate the sequences and the phylogenetic analyses as well as the species names, vouchers and GenBank numbers for all species used in the phylogenetic analyses are listed in Mora & Clark (in review).

ANCESTRAL STATE RECONSTRUCTIONS

Morphological and ecological character states were scored and mapped onto the Maximum Parsimony (MP) strict consensus tree obtained in the phylogenetic analyses by Mora and Clark (in review) from the combined data set using parsimony ancestral states reconstruction implemented in Mesquite v. 2.75 (Maddison and Maddison 2011). The MP method was chosen over the Maximum Likelihood (ML) method, also implemented in this software, based on its capability to include polymorphisms, which is lacking in the latter. Morphological and ecological information were primarily obtained from field work, observations of herbarium material and complemented with literature (mainly from protologues). These characters were scored at the species level across the entire taxon sample (Table 3.1) but only species in the *Paradrymonia* alliance are illustrated (Figs. 2-5). The following six individual characters were mapped: (1) habit; (2) growth form; (3) presence of tubers; (4) leaf dimorphism; (5) calyx connation; (6) calyx lobe shape; (7) corolla shape; and (8) presence of bearded anthers. Additionally, putative pollination syndromes were scored based on the combination of corolla shape and color.

Habit, growth form, and presence of tubers—Each species included in the phylogeny was scored as having one of five ecological habits: strictly epiphytic (0); facultative epiphytic (1); strictly terrestrial (2); epipetric (3); and climber (4). Strictly epiphytic species spend their entire life on another plant. Facultative epiphytic species can grow either as terrestrial or as epiphytes. Strictly terrestrial species are always rooted in the ground. Epipetric species grow on rocks. Climbers climb on trees but maintain contact with the ground. Likewise, each taxon included in the phylogeny was scored as having acaulescent (0); or rosulate (1) growth form. Caulescent species have a well-developed stem above-ground, usually with elongate internodes (longer than broad). Rosulate species have short above ground stems with short internodes, and clustered leaves towards the apex forming a rosette. Similarly, presence of tubers was coded as absent or present.

Leaf dimorphism—Species were coded as isophyllous (0) if they had a pair of leaves of equal or subequal size at a node; as strongly anisophyllous (1) if they had nodes in which the pairs of leaves were always different in size, with one leaf in a pair of regular size, and the other considerable smaller, sometimes reduced to a stipule-like structure.

Calyx architecture and calyx lobe shape—Four states for calyx architecture were scored based on the degree of fusion of the calyx lobes: calyx lobes mostly free or connate only at the base (0); connate into a cup (1); partially fused with four lobes connate for 1/3 their length (2); partially fused with four lobes connate for 1/2 their length (3). Species with the two lateral and the two lower lobes connate and the dorsal lobe free were scored as having partially connate calyx lobes. Additionally, we plotted onto the phylogenetic tree calyx lobe shape for species with free calyx lobes. Calyx lobe shape states were: ovate (0); linear-lanceolate (1); spathulate (2); and oblanceolate (3).

Corolla shape and presence of bearded anthers**—**Corolla shape was coded as a binary character: hypocyrtoid corolla vs. any other shape (tubular, funnel-shaped or salverform). Hypocyrtoid flowers are defined here as corollas with an inflated ventral pouch that protrudes beyond the throat. Additionally, presence of bearded anthers was also mapped. Bearded anthers are defined as having an apical tuft of hairs.

Evolution of pollination syndrome**—**Pollination syndromes are suites of floral traits that are thought to reflect adaptation for particular pollinators (Stebbins, 1974; Fægri and van der Pijl, 1979; Fenster et al. 2004). The use of pollination syndromes has led to criticisms mainly based on some evidence that flowers attract a broader range of visitors than expected (Waser et al. 1996; Smith et al. 2008; Ollerton et al. 2009). Nevertheless, there is ample evidence supporting a strong association between certain floral traits and functional groups of pollinators that exert similar selective pressures (Fenster et al. 2004; Martén-Rodríguez et al. 2009; Rosas-Guerrero et al. 2014). Although we are aware that pollinator observations exist only for a very few species in the *Paradrymonia* alliance, previous observations (Wiehler 1978, 1983) and ongoing field observations support these associations. Following the pollination concept we assigned each species included in the phylogeny to a pollination syndrome mostly on the basis of their floral traits (floral shape and color). Floral traits were associated with hummingbird-pollinated flowers and insect-pollinated flowers (ornithophily vs. entomophily) as defined in Faegri & van der Pijl (1979). Flowers with tubular or hypocyrtoid corollas with bright yellow, orange or red corollas and/or calyces were considered floral characteristics compatible to bird-pollination syndrome, and therefore scored as ornithophilous while flowers with trumpet-shaped or tubular corollas with predominantly white or cream colors and nectar guides were recorded as entomophilous.

Historical Biogeography—To assess ancestral biogeographic areas, geographic distributions of the terminal taxa on the Columneinae phylogeny were traced using Parsimony Ancestral States as implemented in Mesquite v. 2.75 (Maddison and Maddison 2011). Geographic ranges of the terminal taxa were divided into seven biogeographic areas of endemism: Andes (0); Central America (1); Chocó region [Chocó-Darién-Western Ecuador, including the foothills of the Western Andes] (2); Amazon Basin [including the foothills of the Eastern Andes] (3); Guiana Shield [including contiguous eastern Amazonia] (4); Eastern Brazil (5); and the Caribbean [including the adjacent littoral of northern South America] (6).

RESULTS

Habit and vegetative characters—Parsimony reconstruction of ecological and vegetative morphological characters such as habit, growth form, presence of tubers and leaf dimorphism is shown in Fig. 3.2. All of the vegetative characters used in our analysis represent plesiomorphies for the *Paradrymonia* alliance (Fig. 3.2). The reconstruction of ancestral character states using maximum parsimony (MP) indicates that the hypothetical ancestor of subtribe Columneinae and each of the clades within the *Paradrymonia* alliance were strictly terrestrial. Climbing, epiphytic, facultative epiphytic and epipetric habits are derived from a terrestrial habit (Fig. 3.2). There was at least one reversal to a strictly terrestrial habit in the genus *Trichodrymonia* (i.e. *Trichodrymonia* sp. Mora 816). Facultative epiphytism has at least three independent origins in the *Paradrymonia* alliance in subtribe Columneinae. The climbing habit has evolved at least twice while the evolution of an epipetric habit evolved in at least three clades within the *Paradrymonia* alliance (Fig. 3.2.)

Tubers are present in *Sinningia incarnata* and *S. cooperi*, the outgroup taxa, and in all members of *Lembocarpus* and *Rhoogeton* which belong to the Guiana Shield Clade (Table 1). In the *Paradrymonia* alliance tubers appear to have evolved independently at least two times. All species in the *Chrysothemis* clade produce tubers while only one species of *Trichodrymonia* (i.e. *T. pedunculata*) has evolved tubers (Fig. 3.2).

As inferred from the MP reconstruction the ancestor of Columneinae was a caulescent herb with a well-developed underground stem. This suggests that the rosulate growth form in Columneinae is derived. From the ancestral condition the rosulate habit originated at least four times in the *Paradrymonia* alliance; once in *Paradrymonia*, one time in *Centrosolenia* and *Trichodrymonia* and at least once in the Amazonian "*Nautilocalyx*" clade. In *Trichodrymonia* there are at least two independent reversals to a caulescent growth form in *Trichodrymonia* sp. (*Mora 816*) and *T. metamorphophylla* (Fig. 3.2). Like the rosulate habit, results suggest that anisophylly is a derived character and has evolved independently at least two times from isophylly in the *Paradrymonia* alliance (Fig. 3.2). In *Trichodrymonia* there are at least two independent reversals to isophylly from an anisophyllous state that correspond with the species of *Trichodrymonia* with caulescent stems mentioned above.

Floral characters and pollination syndrome —Ancestral reconstruction of calyx lobe architecture suggests that the ancestral flower of subtribe Columneinae had a calyx with nearly free calyx lobes or connate only at the base (Fig. 3.3). The same is true for the most recent common ancestor of the *Paradrymonia* alliance (Fig. 3.3). Although the species used in the phylogeny as outgroups (*Sinningia incarnata* and *S. cooperi*, Table 1), have nearly free calyx lobes, connate calyx lobes occur in other species in the genus. All calyx lobes connate into a cup are only encountered in the core clade of *Chrysothemis,* while partially connate calyx lobes (lateral and lower lobes connate, dorsal free), have evolved at least three times independently; once in *Centrosolenia densa,* once in *Trichodrymonia hypocyrta* and one time in a group of species herein defined as the "*T. macrophylla* complex" which include *T. macrophylla* and *T. gigantea* among others (Fig. 3.3). This complex is characterized by having relatively large calyx lobes (>3 cm) which are fused more than half its length and large (30-70cm long), semi-coriaceous, elliptic leaf-blades with a marginal collective vein (a continuation of a primary lateral vein, often the lowermost one) similar to the venation in the genus *Anthurium* (Araceae). Both connate and partially connate calyx lobes have evolved from ancestors with free calyx lobes (Fig. 3.3). Among the partially connate calyx lobes the degree of connation is variable. For example in *Centrosolenia densa*, and *Trichodrymonia hypocyrta* lobes are connate for 1/3 of their length while calyx lobes in the "*T. macrophylla* complex" are connate for more than 1/2 theirlength.

Calyx lobe shapes varied among species with nearly free calyx lobes (Fig. 3.3). Linear-lanceolate shape often precedes the evolution of all other calyx lobe shapes, with ovate, spathulate and narrowly-oblanceolate calyx lobes always evolving from ancestors with linear-lanceolate calyx lobes. Ovate calyx lobes have evolved at least four times in the *Paradrymonia* alliance. All species in the Amazonian "*Nautilocalyx*" clade, except *Nautilocalyx pemphidius*, have ovate calyx lobes. Ovate calyx lobes have an independent origin in *Trichodrymonia*. Likewise, oblanceolate calyx lobes have evolved once in the Pictus clade and spatulate calyx lobes evolved once in *Centrosolenia* (Fig. 3.3).

Most of species in the *Paradrymonia* alliance exhibit flowers with floral traits compatible with an entomophilous syndrome such as light colored corollas which are funnel-shaped with broad tubes and limbs (Fig. 3.4). Floral characteristics that are compatible with bird-pollination syndrome such as bright colors and narrow tubular corollas have evolved at least eight times in the *Paradrymonia* alliance. Although the outgroup taxa display characteristics compatible with ornithophilous syndrome, ornithophily appears to be derived, relative to entomophily, with no evidence of reversals in the *Paradrymonia* alliance (Fig. 3.4). The ornithophilous flowers in the *Paradrymonia* alliance exhibit more morphological diversity as compared with entomophilous flowers. Flowers presumed to be pollinated by birds were tubular, salverform and hypocyrtoid. The hypocyrtoid shape has only evolved once in the *Paradrymonia* alliance from an entomophilous ancestor and it is present in *Trichodrymonia binata*, *T. hypocyrta* and *T. splendens* (Fig. 3.4).

Bearded anthers are only known to occur in the core *Paradrymonia* clade, here represented with *P. ciliosa* and *P. glabra*. This character appears to be a putative synapomorphy for the core clade of *Paradrymonia*.

Historical biogeography—The ancestral reconstruction based on the current distribution of terminal taxa predicts that the Guiana Shield is the ancestral area for the tribe Columneinae and for two of the three major clades in the tribe: the Guiana Shield clade and the *Paradrymonia* alliance (Fig. 5). The Guiana Shield clade is basal in the tribe and consists of taxa endemic to the lowlands of the Guiana Shield region. This clade is sister to the Core Columneinae clade and to the *Paradrymonia* alliance. The ancestral area for the core Columneinae clade, which includes large genera such as *Columnea* L., *Drymonia* Mart. and *Glossoloma* Hanst., is equivocal (Fig. 5).

The earliest diverging genus within the *Paradrymonia* alliance is *Paradrymonia*. The most recent common ancestor for the genus is also predicted to have originated in the Guiana Shield (Fig. 5). *Paradrymonia* consists of eight species (Mora and Clark, in review) distributed in the lowlands of the Amazon basin and the Guiana Shield, northern Colombia and Venezuela, and Central America. The center of diversity is in the Guiana Shield where most of the species occur. *Paradrymonia campostyla* is basalmost and sister to *Paradrymonia ciliosa* and

Paradrymonia glabra. *Paradrymonia ciliosa* is the only species in the genus to occur west of the Andes. This is the most widespread species and is distributed in northern South America and Central America. *Paradrymonia glabra* occurs in northern Venezuela in the Cordillera de la Costa (Coastal Range) in the Caribbean region. The rest of the species in the genera (not included in the phylogeny) have restricted geographic distributions in the rainforests of the Guiana shield and in the foothills of the table-top mountains of the region, commonly known as *tepuis.*

The second divergent clade is *Centrosolenia,* a recently resurrected genus with 12 species endemic to the Guiana Shield region and contiguous Amazonia (Mora and Clark, in review). The eastern Amazonia and the Guiana Shield is indicated as an unequivocal ancestral area for *Centrosolenia* (Fig. 5). The third clade in the *Paradrymonia* alliance corresponds with the Pictus clade and includes "*Nautilocalyx*" *pictus* and a new species from Amazonian Peru. The ancestral reconstruction suggests that the most recent common ancestor for the members of this small clade originated in the Amazon Basin (Fig. 5).

The ancestral area for *Chrysothemis* is equivocal (Fig. 5). This genus with nine species is distributed throughout the Neotropics, but most of the species occur in the Amazon region. One species, *Chrysothemis pulchella,* is the most widespread species and is present throughout the Neotropics except southern Brazil.

Each of the most recent common ancestors for the Amazonian "*Nautilocalyx"* clade, *Nautilocalyx* s.s. and *Trichodrymonia* were inferred to have originated in the Amazon region (Fig. 5). Species in the Amazonian "*Nautilocalyx"* clade occur predominantly in the Amazon Basin and in the foothills of the eastern Andes. Few species (not represented in the phylogeny) occur in the foothills of the Central Cordillera in Colombia and in Central America.

There is a basal split in *Nautilocalyx*, between species occurring on the east side of the Andes (Amazonian taxa) and species occurring to the west of the Andes (Fig. 5). Almost half of species of *Nautilocalyx* (*N. aeneus*, *N. antioquensis*, *N. colombianus* and *N. bracteatus*) occur in the Magdalena Valley River in the foothills of the Central Cordillera in Colombia. Only *N. erytranthus* is known to occur in the foothills of the eastern Andes and in the Amazon Basin. *Nautilocalyx* s.s. is absent in the Guiana Shield.

Trichodrymonia, the sister taxon of *Nautilocalyx*, occurs throughout the Neotropics, except southeastern Brazil and the Caribbean. Almost 70% of species (19 out of 26) occur in Colombia. Most are from the Chocó region and occur in low and middle elevations (200-1000 m). One exception is *T. metamorphophylla*, which grows in montane cloud forests up to 2500 m. This species is widely distributed throughout the Andes and the mountain ranges in Central America.

Some earlier divergent taxa in *Trichodrymonia* are from the Amazon basin and the Andes, but most of them are on the western slopes of the Andes. Interestingly, later divergent taxa such as *T. aurea* and *T. ulei* occur in the Amazon region but the maximum parsimony analyses indicate that the ancestral area for these taxa is along the western slopes of the Andes (Fig. 5).

DISCUSSION

Ancestral reconstructions of morphological and ecological traits indicated that the most recent common ancestor of the *Paradrymonia* alliance was terrestrial, lacked tubers and had caulescent stems with isophyllous leaves. Its flowers had free or mostly free calyx lobes which were linear-lanceolate in shape and had predominantly white funnel-shaped corollas that are often associated with bee pollination.

With the exception of two character states (connate calyx lobes in to a cup and presence of bearded anthers), all morphological and ecological traits explored here were homoplasious within the subtribe Columneinae. High levels of homoplasy has been reported for several other neotropical plant groups (e.g., Moylan et al. 2004; Tam et al. 2004; Norup et al. 2006; Swenson et al. 2008). Important biological causes of homoplasy include convergent/parallel evolution and reticulation (Escobar-Garcia et al. 2009). Convergent evolution appears to be widespread in Columneinae (Tribe Episcieae sensu Wiehler (1983); Clark et al. 2012). Since no natural hybrid origin of species has been reported for any members of the *Paradrymonia* alliance, much of the homoplasy across taxa in the clade is likely the result of convergence.

Evolution of habit, growth form and anisophylly—Neotropical Gesneriaceae are remarkable in having several strikingly different ecological habits, ranging from terrestrial, climbing, facultatively epiphytic or epipetric, and strictly epiphytic species (Wiehler 1978, 1983). A terrestrial habit was reconstructed unequivocally as the ancestral condition for the three main clades in the subtribe Columneinae and for the seven main clades within the *Paradrymonia* alliance except for the *Paradrymonia* clade in which the ancestral habit was reconstructed as equivocal (Fig. 3.2). Most of the *Paradrymonia* species are facultative epiphytes, with species growing on trees or on the ground, while *P*. *campostyla* and *P*. *barbata* (latter species not included in the phylogeny) are root climbers and rely on other plants for support. Interestingly, no obligate epiphytes exist in the *Paradrymonia* alliance. Taxa readily recognized as epiphytic also grow as terrestrial where they are often found growing along trunks less than 2 meters above the ground. Most species of *Trichodrymonia* are facultative epiphytes with only one species reversing to an obligate terrestrial habit (Fig. 3.2). Interestingly, most species in the *Paradrymonia* alliance that are obligate terrestrial or climbers have a caulescent growth form with isophyllous leaves. Conversely, all of the species in *Paradrymonia* and *Trichodymonia* with a rosulate growth form are facultative epiphytes or epipetric and have anisophyllous leaves (Fig. 3.2). Epiphytic and epipetric habits have generally been considered nutrient poor environments for plant development (Benzing 1990). Many epiphytic species have evolved adaptations that provide efficient access to and retention of water and nutrients such as a rosette form which usually facilitates water accumulation and litter-trapping (Benzing 1990).

In most genera of Gesneriaceae isophylly and anisophylly are fixed traits in mature individuals (Wiehler 1978). Remarkably, facultative epiphytes in *Paradrymonia* and *Trichodrymonia* also exhibit facultative anisophylly. Many individuals of species in these two genera exhibit plasticity in the expression of anisophylly depending on the light conditions and availability of growing space (Wiehler, 1978; Dengler and Sanchez-Burgos 1988, Dengler 1999). Anisophylly is suggested to be an adaptation to shady habitats such as the understory, since s light capture is maximized by reducing mutual shading of leaves (Givnish 1984). Many species of *Paradrymonia* and *Trichodrymonia* are inhabitants of the understory, where only about 1–3% of sunlight reaches this layer (Chazdon 1988, Clark et al. 1996). Field observations suggest that individuals of *Paradrymonia* and *Trichodrymonia* in shady understory habitats tend to have a more marked expression of anisophylly (Wiehler 1978, and personal observations). When anisophylly is extreme, the opposite-decussate leaf pairs of *Paradrymonia* and *Trichodrymonia* resemble an alternate phyllotaxy. Rosette-forming species with short internodes have leaves that are much more congested and have more potential for leaf overlapping than their caulescent, long-internode counterparts. Anisophylly may be also an adaptation to the rosette growth form to minimize self-shading (Dengler 1999).

It is not surprising then that epiphytism, rosulate growth form and anisophylly are convergent characters. Homoplasy is common in characters that are ecologically significant (Armbruster 1996). However, the facultative nature of epiphytism and anisophylly is not that common across the subtribe Columneinae and is only present in *Paradrymonia* and *Trichodrymonia* within the *Paradrymonia* alliance. The plasticity of these ecological traits could be an adaptation to environmental heterogeneous habitats (Alpert and Simms 2002; Valladares et al. 2007), especially to heterogeneous light and microhabitat conditions. From the taxonomic standpoint, plasticity in habit and/or leaf dimorphism might also be a useful character to distinguish taxa belonging to *Paradrymonia* and *Trichodrymonia* from other phenotypically similar gesneriad genera with fixed traits.

Evolution of tubers—Acquisition of tubers has evolved many times in the Neotropical Gesneriaceae. In *Sinningia*, for example, it is believed that acquisition of tubers has occurred independently several times from a non-tuberous ancestor as an adaptation to colonize rocky habitats in open or forested areas (Perret et al. 2003). Tubers have also arisen independently in subtribe Columneinae in the genera *Lembocarpus* and *Rhoogeton* (Clark et al. 2012) and in *Drymonia* (Smith 2000). In the *Paradrymoni*a alliance presence of tubers has evolved independently at least two times (Fig. 3.2). Tubers are present in all members of the *Chrysothemis* clade and in *Trichodrymonia pedunculata* (Fig. 3.2). Some species of *Chrysothemis* are common in areas with a periodic change of wet and dry seasons (Leeuwenberg, 1958). Tubers allow species such as *C. friedricshthaliana* to stay dormant when water is scarce until the next rainy season (Skutch, 1992; Carlson 2007). Despite the homoplastic nature of this character, presence of underground tubers is an important taxonomic character defining *Chrysothemis* in combination with the strictly terrestrial habit, isophyllous leaves, caulescent growth form and succulent stems. The presence of tubers in *Trichodrymonia* is an autapomorphic character since no other species in the genus besides *T. pedunculata* is known to have it.

Calyx architecture and calyx lobe shape—Calyx lobes connate into a cup are synapomorphic for the core clade of *Chrysothemis* (Mora and Clark in review). The high degree of connation of calyx lobes has traditionally been used to circumscribe *Chrysothemis* (Leeuwenberg 1958). Calyces that are completely fused into a "cup" have been described as "water calyces" because they can retain water and produce an aqueous solution that possibly protects the buds from floral herbivores (Skutch 1992; Burtt and Woods 1975; Endress 1996; Carlson and Harms 2007). Studies of *C. friedrichsthaliana* by Carlson and Harms (2007) suggest that the "water calyces" helps protect flower buds from a floral herbivore (i.e. *Alucita* sp.). The presence of a water calyx is present in the core clade of *Chrysothemis*, but absent in basal taxa such as "*Nautilocalyx" mellitifolius* and "*N*". *panamense*, which have mostly free calyx lobes (Fig. 3.3). These basal taxa are more difficult to recognize at a generic rank because they are not defined by synapomorphies. However, the molecular evidence in combination with morphological similarities such as succulent caulescent stems, underground tubers, isophyllous leaves with cross-venulate venation strongly supports the inclusion of "*Nautilocalyx" mellitifolius* and "*N*". *panamense* in *Chrysothemis* (Mora and Clark in review).

Wiehler (1978) described an informal section that included *Trichodrymonia macrophylla*, *T. gibbosa* and *T. gigantea* based on their large leaves. Since no other sections in *Trichodrymonia* have been identified so far, here we refer to this group of species, as well as other undescribed species in the same clade as the "*Trichodrymonia macrophylla* complex." This complex appears to be a distinct morphologically homogeneus group, easily recognizable by the high degree of connation of four of its five calyx lobes and by the combination of the following symplesiomorphic characters: presence of markedly anisophyllous leaves, with the larger leaf blade semi-coriaceous, elliptic, and with a marginal collective vein. Although partially connate calyx lobes (four lobes connate, dorsal one free) have evolved at least three times in the *Paradrymonia* alliance, they only appear to have the ventral and lateral calyx lobes connate for more than half of their length. The highly connate calyx lobe is a synapomorphy for this clade.

On the other hand, spathulate calyx lobes are only known to occur in *Centrosolenia* within the *Paradrymonia* alliance. Some species in the genus *Episcia* in the Core Columneinae clade also have this type of calyx lobes, but species in that genus can be easily distinguished from those in *Centrosolenia*, by the presence of stolons.

Although calyx lobe shape is symplesiomorphic (Fig. 3.3), the character appears to be a taxonomically useful when used in combination with other homoplasious characters to identify the main clades/genera within the *Paradrymonia* alliance. For example, it is very useful to distinguish Nautilocalyx s.s., the Amazonian "*Nautilocalyx*" clade and Pictus clade. All of the species in these clades are caulescent and have isophyllous leaves, however *Nautilocalyx* s.s., usually has plagiotropous stems which are somewhat creeping, as well as lanceolate calyx lobes, and trumpet-shaped corollas while species in the Amazonian "*Nautilocalyx*" clade usually have erect free-standing stems, ovate calyx lobes and broadly tubular corollas. On the other hand, species in the Pictus clade have relatively long creeping stems with long internodes, oblanceolate calyx lobes which are usually 5× times longer than wide and campanulate corollas.

Presence of bearded anthers— Wiehler (unpublished manuscript) suggested that the presence of bearded anthers in *Paradrymonia* might increase the pollen transfer efficiency by the plant's pollinator. However no formal detailed studies of plant-animal interactions have been performed and further investigation is needed to elucidate the function of these trichomes.

The presence of bearded anthers is the only morphological synapomorphy known as a useful diagnostic character for the core *Paradrymonia* clade (Mora and Clark in review). This character is especially important to distinguish the core species in *Paradrymonia* from *Trichodrymonia*. Although these two genera seem to be relatively distantly related within the *Paradrymonia* alliance, they are phenotypically similar due to convergent evolution. Many species in *Trichodrymonia* and all species belonging to the core *Paradrymonia* clade are facultative epiphytes with a rosulate growth form (Fig. 3.2), and have funnel-form to trumpet-shaped corollas (Fig. 3.4). Bearded anthers are absent in *P. campostyla* (Fig. 3.4) and *P. barbata* (not included in the phylogeny), which suggests that the origins of anther trichomes evolved from a recent common ancestor that does not include the basal taxa. The inclusion of *P. campostyla* and *P. barbata* as members of *Paradrymonia* makes it necessary to use a combination of symplesiomorphic traits for defining generic limits within the *Paradrymonia* alliance. The use of symplesiomorphies is common practice in other groups that have high levels of homoplasy (e.g., palms, Norup et al. 2006; legumes, Hughes et al. 2004).

Pollination shifts—Entomophily, or floral traits related to insect pollination, was recovered as the ancestral condition in the *Paradrymonia* alliance. Many species within the *Paradrymonia* alliance (Fig. 3.4) and other genera in other clades in the Columneinae such as *Alsobia*, *Drymonia* and *Episcia*, present the same basic corolla shape and color i.e. funnel-form to trumpet-shape with white as the predominant color. This floral phenotype has been commonly associated with pollination by euglossine bees in the neotropical subtribe Columneinae (Wiehler 1978, 1983; Steiner 1985). Similarity in floral characters caused substantial confusion in the early taxonomy of the subtribe (tribe Episcieae sensu Wiehler 1983, Clark et al. 2012), when these characters were believed to be homologous instead of the result of selection pressures exerted by shared pollinators (Wiehler 1983, Weber 2004, Weber and Skog 2007).

Brightly colored tubular corollas and hypocyrtoid flowers have been associated with pollination by hummingbirds in neotropical Gesneriaceae (Wiehler 1983, Skog and Kvist 2000, Marten-Rodriguez et al. 2009). Our ancestral reconstructions indicate that suits of traits that conform to hummingbird -pollination are derived, relative to those associated with bee-pollination in the *Paradrymonia* alliance (Fig. 3.4). Shifts to ornithophily (usually from bee-pollination) have occurred repeatedly and independently in different lineages of angiosperms (Cronk and Ojeda 2008). A directional bias that favors bee to bird-pollination shifts has been suggested in other groups (Fægri and van der Pijl 1979; Thomson and Wilson 2008). This bias in pollination shifts has been explained by a: (1) higher pollination efficiency by hummingbirds as compared with bee-pollination; (2) changes in biochemical pathways that produce floral pigments that attract hummingbirds and deter bees and (3) mutations with large effects on floral phenotypes that favors frequency of bird pollination (Thomson and Wilson 2008). Regardless of the intrinsic changes that causes shifts in pollination syndromes, ecological changes such as pollinator visitation rates are necessary before genetics of floral traits become fixed (Thomson and Wilson 2008).

Even though there are more cases of convergence in pollination syndromes within the *Paradrymonia* alliance, some sister or closely related species have evolved different pollination syndromes from each other (Fig. 3.4). In a quantitative study of pollination syndromes, Rosas-Guerrero et al. (2014) found that while floral traits predict effective pollinators they do not exclude other secondary pollinators, supporting Stebbins's hypothesis (1970). Interestingly, the authors also found that important secondary pollinators may correspond to ancestral pollinator groups. This means that although ornithophilous flowers in the *Paradrymonia* alliance are visited more frequently and effectively by birds, they can also be visited by less efficient floral visitors such as bees. Conversely, plants predominantly adapted to bee pollination might be secondarily pollinated by birds. This also suggest that current floral traits in many plants have the potential for adapting to different pollinators if environmental conditions changeand affect the frequency of visitation of a given pollinator (Kay et al. 2005; Whittall and Hodges 2007).

Hypocyrtoid corollas**—**Extreme ornithophily can be observed in hypocyrtoid flowers in the Gesneriaceae (Fig. 3.4). The hypocyrtoid corolla shape was the basis for the previous artificially defined genus *Hypocyrta* Mart., which is now understood to include species from different lineages havinga similar distinctive spurred, urceolate corolla with an inflated ventral pouch and reduced corolla lobes (Fig. 3.4). Although hypocyrtoid corollas have evolved many times in other neotropical Gesneriaceae (e.g. *Gasteranthus*, *Nematanthus*, *Drymonia*) it has evolved just once in the *Paradrymoni*a alliance in a small clade within *Trichodrymonia* (Fig. 3.4). The restricted neck of the corolla may serve to form of sympatric isolation to avoid hybridization with closely related species that are pollinated by bees (Wiehler 1983; Skog and Kvist 2000).

Historical biogeography—Results of the ancestral reconstruction suggest that the subtribe Columneinae arose in the Guiana Shield in northern South America. This is supported by the basal placement of the Guiana Shield clade in the phylogeny by Mora & Clark (in review). Perret et al. (2012) in a dated phylogeny suggested that the Columneinae originated in the Amazon region and that the earliest divergent clade in the tribe is formed by the genera *Chrysothemis*, *Nautilocalyx* and *Paradrymonia* (in the *Paradrymonia* alliance, fig 1). The disparities in outcomes between their analyses and our studies can be mainly attributed to different taxonomic sampling (Mora & Clark, in review). Their analyses had a broader emphasis in the subfamily Gesnerioidae. However, the study by Perret et al. (2012) included only four species from the *Paradrymonia* alliance (*Nautilocalyx mellitifolious*, *Chrysothemis pulchella*, *Nautilocalyx aeneus* and *Paradrymonia macrophylla*) and did not take into account taxa from the Guiana Shield. Furthermore, they considered the Guiana Shield as part of the Amazon region, while we consider the Amazon basin and the Guiana Shield as two different biogeographical units.

Based on the dated phylogeny by Perret et al. (2012) the stem age for the subtribe Columneinae (tribe Episcieae *sensu* Wiehler 1983) was ca. 30 Mya. Since these authors did not include the Guiana shield clade and other basal taxa that belong *Paradrymonia* alliance, the exact age for the most recent common ancestor (MRCA) of Columneinae remains to be resolved and warrants further evaluation including these taxa in a time-calibrated phylogeny.

At least five genera in the Columneinae are endemic to the Guiana shield (*Lembocarpus*, *Rhoogeton*, *Cremersia*, *Christopheria* and *Pagothyra*). The ancestral reconstruction for the MRCA of this clade together with the present-day restricted geographic distribution of its terminal taxa, suggests that this lineage originated and diversified in situ. Most of the genera in this clade are monospecific, except for *Rhoogeton* (two species). The high number of genera and low species per genus is an interesting taxonomic pattern. Among widely known biological factors that have been suggested in other organisms as being linked to relative small taxonomic size are dispersal ability (e.g. Myer 1963) and competitive exclusion (Hardin 1960). The competitive exclusion principle states that taxa having species that compete for the same resources cannot coexist and, as a consequence, the better-adapted species will ultimately displace its competitor (Hardin 1960). Darwin (1859) was one of the earliest to propose that competition is greater between congeneric species than between distantly related species. This idea, congruent with the niche conservatism concept (Wiens & Graham 2005; Losos 2008; Wiens et al. 2010) assumes that close relatives are likely to have similar niches and therefore a more frequent competitive exclusion (Viollé et al. 2011). Viollé et al. (2011) experimentally tested this hypothesis using protists as model organisms. This hypothesis, coined the phylogenetic limiting similarity hypothesis by Viollé et al. (2011), is a feasible explanation for the low species diversity in the Guianan endemic genera. Some similar closely related species in the Guiana Shield clade may have gone extinct due to the combination of low vagility and competitive exclusion. Consequently, sister taxa growing in the same area may have evolved distinguishing characteristics to be able to coexist. These morphological or physiological differences might have been associated with differentiation of the genera.

The split between the Core Columneinae clade and the *Paradrymonia* alliance clade is estimated to have occurred ca. 28 Mya (Perret et al. 2012). Our ancestral area reconstruction for the Core Columneinae clade was uncertain (Fig. 5). This clade is the most speciose in the tribe and its genera have different centers of diversity. Most of the species of large genera such as *Columnea*, *Drymonia* and *Glossoloma* occur in the Andes and in Central America (Clark et al. 2006) while most of the diversity for *Codonanthe* (Mart.) Hanst., *Codonanthopsis* and *Nematanthus* is in eastern Brazil (Perret et al. 2012). On the other hand, our reconstruction shows unequivocally the Guiana Shield as the ancestral area for the most recent common ancestor

(MRCA) of the *Paradrymonia* alliance. Perret et al. (2012) estimated that the most common recent ancestor of the *Paradrymonia* alliance originated approximately 10 Mya in the Miocene and that the genera such as *Nautilocalyx* and *Tricodrymonia* diversified mainly after the beginning of the Pliocene (ca. 5 Mya).

The ancestral reconstruction suggests that the MRCA of the *Paradrymonia* alliance originated in the Guiana Shield, diversified there and new taxa subsequently spread radially throughout the Amazon Basin and northern Venezuela and Colombia. Gentry (1982) found that many neotropical plant groups, especially those that occur in the lowlands have a disjunct distribution in the northern Andes and Central America (trans-Andean) and on the eastern side of the Andes (cis-Andean). This suggests that the Andes are an important barrier for the dispersal of lowland taxa. *Paradrymonia ciliosa* is the only known species in the *Paradrymonia* alliance to be widespread on both sides of the Andes. This distribution suggests that this species colonized Central America from the Amazon region before the end of the final uplift of the eastern cordillera Andes.

Concluding remarks—This study indicates that most of the characters explored here are homoplasious. It is interesting that in spite of all the extensive morphological homoplasy, the main clades/genera within the *Paradrymonia* alliance are strongly supported by molecular data. The remarkable morphological similarity of species in different clades might be the result of convergent evolution as adaptation to, for instance, shady understory environments, nutrient-poor habitats, and similar pollinators. Although there were synapomorphic characters that defined clades within the *Paradrymonia* alliance, these characters were lacking in the basal species rendering them of limited suitability for generic diagnoses. These genera can be diagnosed by a combination of characters that, although homoplasious within the neotropical Gesneriaceae, are taxonomically diagnostic within the *Paradrymonia* alliance.

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Table 3.1. Matrix of morphological or ecological character states for species in subtribe Columneinae and outgroups (*Sinningia incarnata* and *S. cooperi*). Description of characters and states are given in Materials and Methods. Numbers surrounded by brackets signify polymorphic states. Voucher numbers are provided for taxa represented by multiple accessions or if there is more than one collection per species or if the species is new or unidentified.

Taxon	**Habit**	**Growth form**	**Leaf dimorphism**	**Tubers**	**Calyx lobe fusion**	**Calyx lobe shape**	**Pollination syndrome**	**Bearded anthers**	**Geography**
Alloplectus hispidus	0	0	0	0	0	0	1	0	[0, 3]
Alloplectus weirii	0	0	0	0	0	0	1	0	[0, 1, 3]
Alsobia dianthiflora	0	0	0	0	0	1	0	0	1
Alsobia punctata	0	0	0	0	0	1	0	0	1
Chrysothemis friedrichstaliana	2	0	0	1	1	3	1	0	[1, 2]
Chrysothemis pulchella	2	0	0	1	1	3	1	0	[1, 2, 3, 6]
Cobananthus calochlamys	1	0	0	0	0	0	0	0	1
Codonanthe carnosa	0	0	0	0	0	1	0	0	5
Codonanthe gracilis	0	0	0	0	0	1	0	0	5
Codonanthopsis ulei	0	0	1	0	0	1	0	0	3
Columnea dressleri	0	0	1	0	0	1	1	0	1
Columnea linearis	0	0	1	0	0	0	1	0	1
Columnea scandens	0	0	1	0	0	1	1	0	[1, 2, 3]
Crantzia cristata	1	0	0	0	0	0	0	0	6
Cremersia platula	2	1	0	0	0	1	0	0	4
Drymonia killipii	0	0	0	0	0	0	0	0	2
Drymonia lanceolata	2	0	0	0	0	0	0	0	2
Drymonia longifolia	2	0	0	0	0	0	0	0	3
Drymonia urceolata	2	0	0	0	0	0	1	0	[0, 3]
Episcia cupreata	2	0	0	0	0	1	1	0	[0, 1, 2, 3, 6]
Episcia lilacina	2	0	0	0	0	1	1	0	[1, 2]

Taxon	**Habit**	**Growth form**	**Leaf dimorphism**	**Tubers**	**Calyx lobe fusion**	**Calyx lobe shape**	**Pollination syndrome**	**Bearded anthers**	**Geography**
Glossoloma medusaeum	0	0	0	0	0	1	1	0	1
Glossoloma tetragonum	0	0	0	0	0	0	1	0	2
Lembocarpus amoenus	2	1	0	1	0	1	0	0	4
Nautilocalyx antioquensis	3	0	0	0	0	1	0	0	2
Nautilocalyx bracteatus	1	0	0	0	0	1	0	0	2
Nautilocalyx bullatus	2	0	0	0	0	0	0	0	3
Nautilocalyx coccineus	3	0	1	0	0	2	1	0	4
Nautilocalyx colombianus	2	0	0	0	0	1	0	0	2
Nautilocalyx cordatus	2	1	0	0	0	2	0	0	4
Nautilocalyx erytranthus	2	0	0	0	0	1	1	0	3
Nautilocalyx forgetii	2	0	0	0	0	0	0	0	3
Nautilocalyx glandulifer	2	0	0	0	0	0	0	0	3
Nautilocalyx hirsutus	2	0	0	0	0	0	0	0	3
Nautilocalyx melittifolius	2	0	0	1	0	0	0	0	6
Nautilocalyx pallidus	2	0	0	0	0	0	0	0	3
Nautilocalyx panamensis	2	0	0	1	0	0	0	0	[0, 1, 2]
Nautilocalyx pemphidius	2	1	0	0	0	1	0	0	3
Nautilocalyx pictus	2	0	0	0	0	3	0	0	[3, 4]
Nautilocalyx porphyrotrichus	4	0	0	0	0	1	1	0	[3, 4]
Nautilocalyx punctatus	2	0	0	0	0	0	0	0	[3, 4]
Nautilocalyx sp. Mora 931	2	0	0	0	0	0	0	0	3
Nautilocalyx sp. Mora 933	2	1	0	0	0	0	0	0	3
Nautilocalyx sp. Mora 939	2	0	0	0	0	0	0	0	3
Nautilocalyx sp. Mora 949	1	0	0	0	0	3	0	0	3
Nautilocalyx sp. Mora 970	2	0	0	0	0	0	0	0	3
Nautilocalyx whitei	2	0	0	0	0	1	1	0	3
Nematanthus albus	0	0	0	0	0	1	0	0	5
Nematanthus corticola	0	0	0	0	0	1	1	0	5

Taxon	**Habit**	**Growth form**	**Leaf dimorphism**	**Tubers**	**Calyx lobe fusion**	**Calyx lobe shape**	**Pollination syndrome**	**Bearded anthers**	**Geography**
Paradrymonia anisophylla	0	0	1	0	0	1	0	0	4
Paradrymonia aurea	1	1	1	0	0	1	0	0	3
Paradrymonia binata	1	1	1	0	0	1	1	0	2
Paradrymonia campostyla	4	0	0	0	0	0	0	0	4
Paradrymonia ciliosa	1	1	1	0	0	1	0	1	[1, 2, 3, 4]
Paradrymonia congesta	1	1	1	0	0	1	0	0	1
Paradrymonia densa	2	1	0	0	0	3	0	0	4
Paradrymonia erythropus	3	1	1	0	0	1	0	0	2
Paradrymonia flava (JLC 12547)	1	1	1	0	0	1	0	0	[1, 2]
Paradrymonia flava (JLC 8846)	1	1	1	0	0	1	0	0	[1, 2]
Paradrymonia gibbosa	1	1	1	0	2	3	0	0	2
Paradrymonia gigantea	1	1	1	0	2	3	0	0	2
Paradrymonia glabra	1	1	1	0	0	1	0	1	0
Paradrymonia hypocyrta	1	1	1	0	2	3	0	0	2
Paradrymonia lacera	1	1	1	0	0	3	1	0	2
Paradrymonia macrophylla	1	1	1	0	0	1	0	0	0
Paradrymonia sp. Mora 811	1	1	1	0	2	3	0	0	2
Paradrymonia maculata	1	1	1	0	2	3	0	0	2
Paradrymonia metamorphophylla	1	1	1	0	2	3	0	0	2
Paradrymonia pedunculata	4	0	0	0	0	1	0	0	4
Paradrymonia peltatifolia	1	1	1	0	0	1	0	0	2
Paradrymonia sericea Wiehler	1	0	1	0	0	1	1	0	[0, 1, 2, 3]
Paradrymonia sp. Mora 816	2	0	1	0	0	0	1	0	2
Paradrymonia sp. Mora 821	1	1	1	0	2	3	0	0	2
Paradrymonia sp. Mora 830	1	1	1	0	0	1	0	0	3
Paradrymonia sp. Mora 842	1	1	1	0	0	1	1	0	2
Paradrymonia sp. Mora 895	1	1	1	0	0	1	1	0	3
Paradrymonia splendens	1	1	1	1	0	1	0	0	2

Taxon	**Habit**	**Growth form**	**Leaf dimorphism**	**Tubers**	**Calyx lobe fusion**	**Calyx lobe shape**	**Pollination syndrome**	**Bearded anthers**	**Geography**
Paradrymonia ulei	1	1	1	0	0	0	0	0	2
Rhoogeton cyclophyllus	2	1	0	1	0	1	0	0	4
Rhoogeton viviparus	2	1	0	1	0	1	0	0	4
Sinningia cooperi	2	0	0	1	0	1	1	0	5
Sinningia incarnata	2	0	0	1	0	0	1	0	[0, 1, 2, 3, 5]

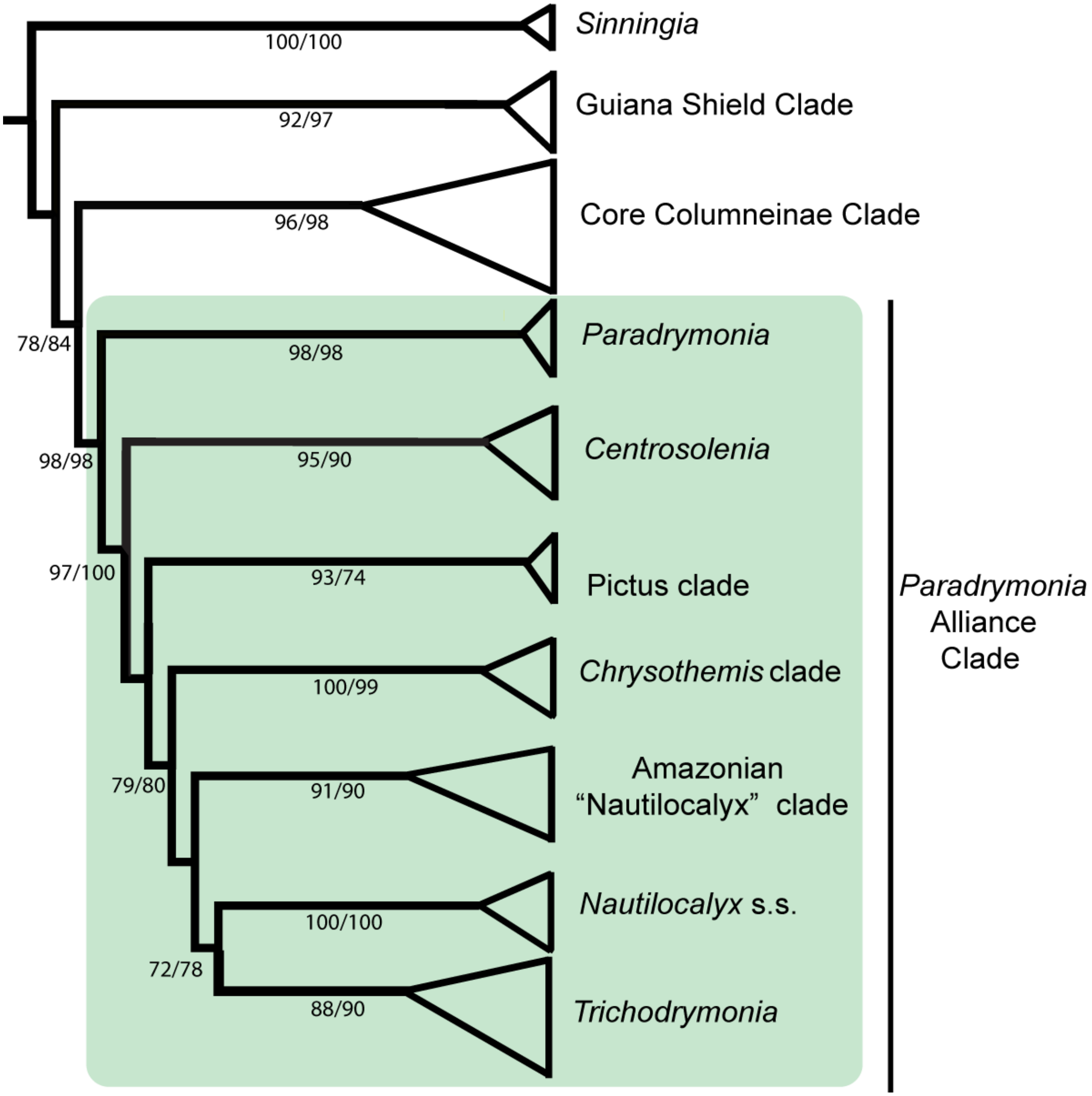

Fig. 3.1. Summary of the strict consensus tree from total evidence analysis of three molecular markers analysis (ETS, ITS and *psb*A- *trn*H) showing the relationships within the main monophyletic clades within the subtribe Columneinae. The strict consensus tree is from 25 most parsimonious trees of 2977 steps. Maximum parsimony and maximum likelihood bootstrap values are above and below the branches respectively. Only bootstrap values ≥50% are shown. Phylogenetic hypothesis based on Mora and Clark (in review).

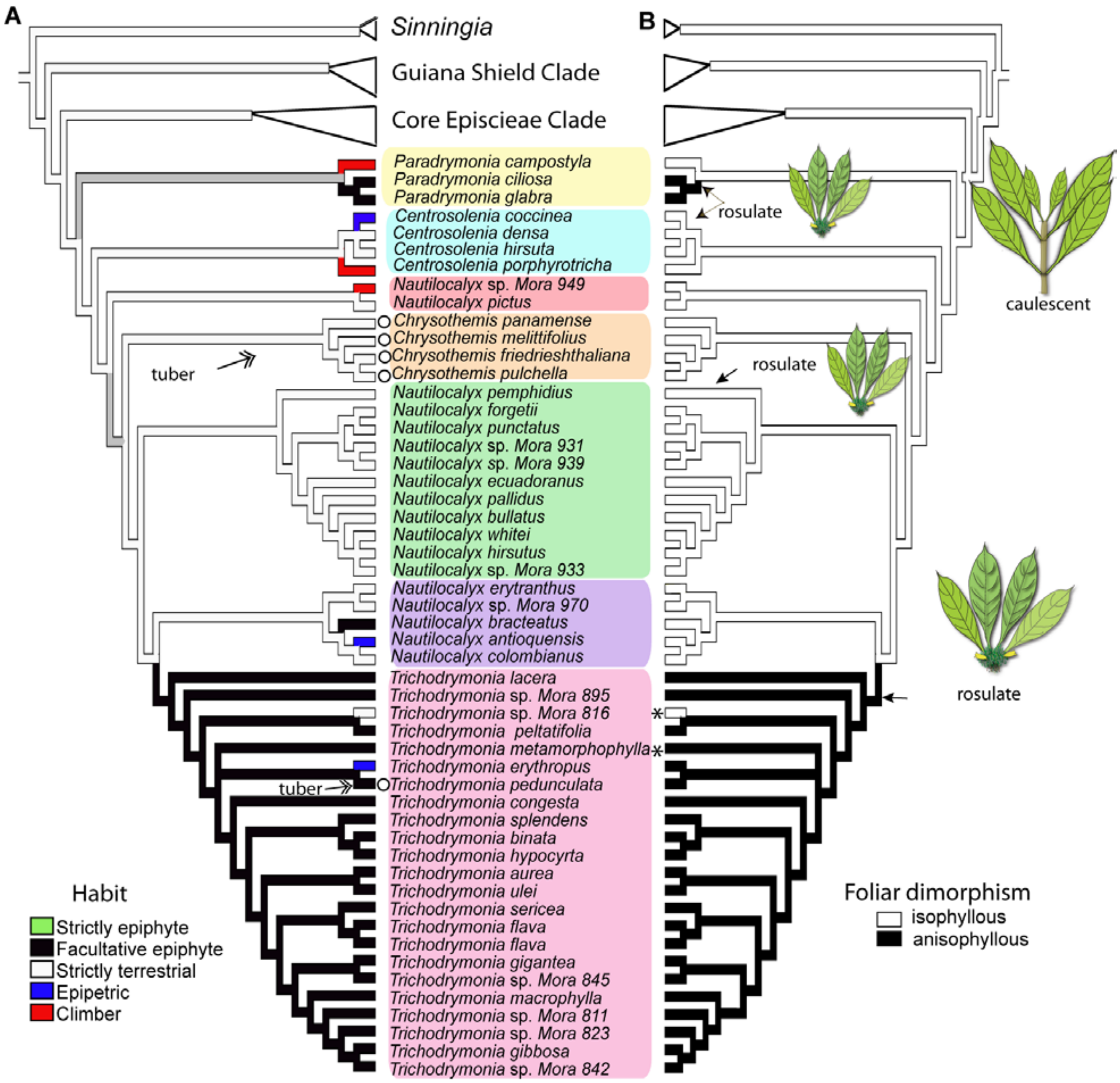

Fig. 3.2. Mirror trees showing the inferred evolution of habit (tree A) and leaf dimorphism (tree B) based on parsimony character mapping onto the strict consensus from Mora and Clark (in review). Gray branches correspond to unresolved ancestral character states. Each main clade within the *Paradrymonia* alliance (illustrated in Fig. 1) is colored differently. Presence of tubers are represented with a circle and its acquisition is indicated with a double arrow head on tree A. Acquisition of a rosulate form from an ancestral caulescent form is illustrated to the right and indicated with a single arrow head on tree B.

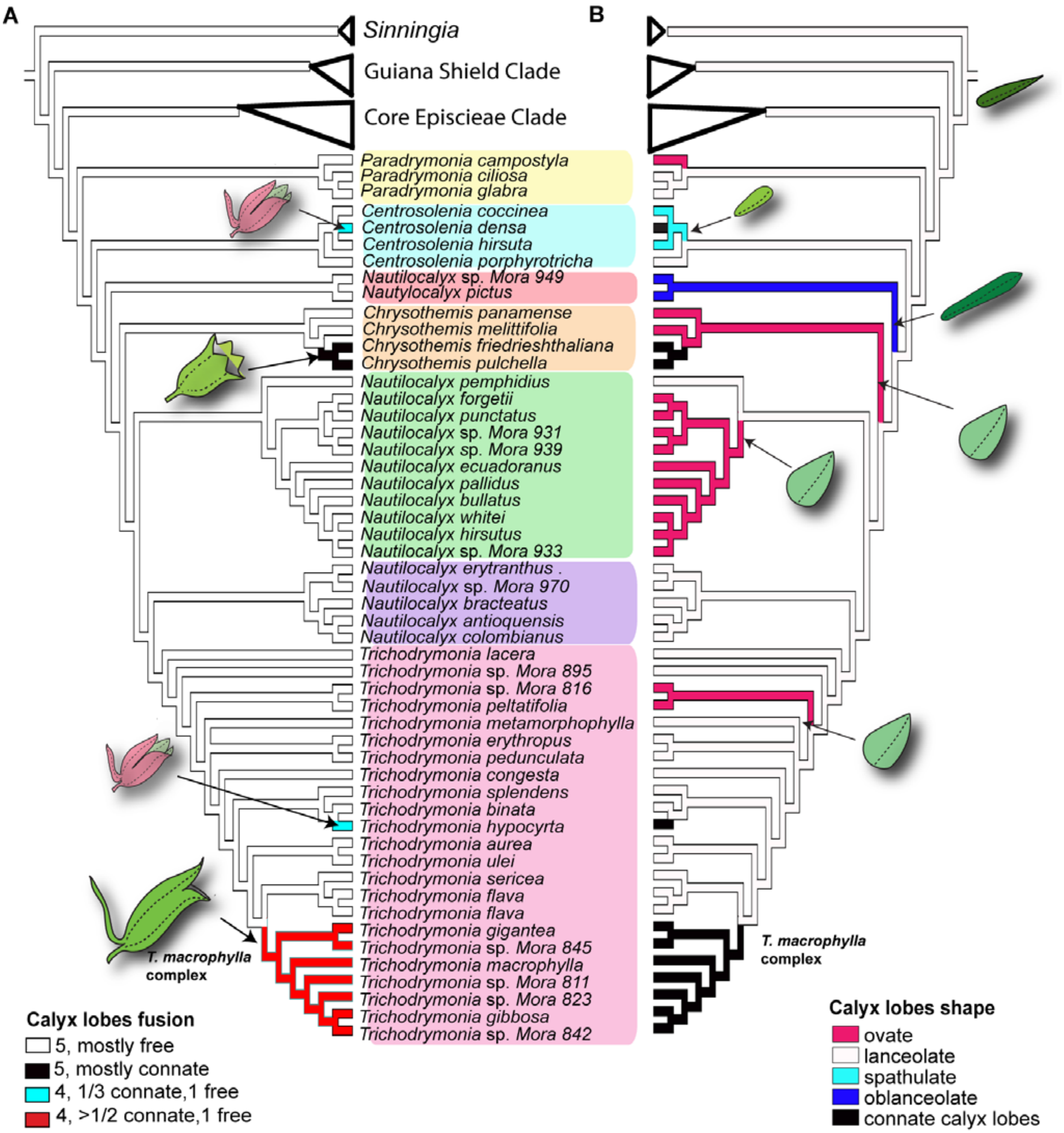

Fig. 3.3. Mirror trees showing the inferred evolution of calyx fusion (tree A) and calyx lobe shape (tree B) based on parsimony character mapping onto the strict consensus from Mora and Clark (in review). (tree A Calyx lobes architecture: mostly free (0); connate into a cup (1); partially fused with four lobes connate for 1/3 their length and the dorsal lobe free (2); partially fused with four lobes connate for 1/2 their length and the dorsal lobe free (3). Each main clade within the *Paradrymonia* alliance (illustrated in Fig. 1) is colored differently.

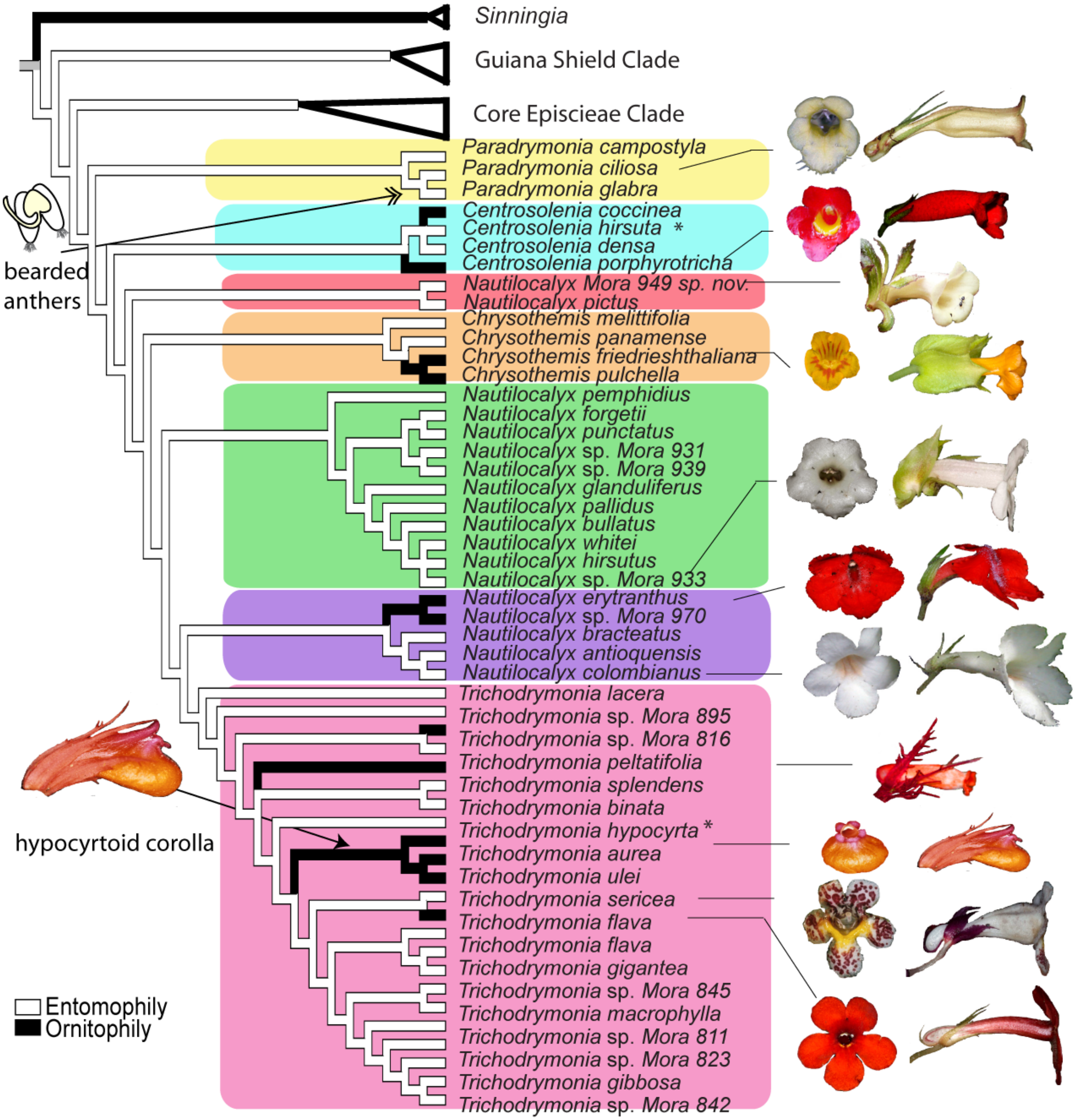

Fig. 3.4. Inferred evolution of pollination syndrome based on parsimony character mapping onto the strict consensus from Mora and Clark (in review). Acquisition of bearded anthers and hypocyrtoid corolla is illustrated on the left. Each main clade within the *Paradrymonia* alliance (illustrated in Fig. 1) is colored differently. Some flowers are illustrated to show diversity in corolla morphology.

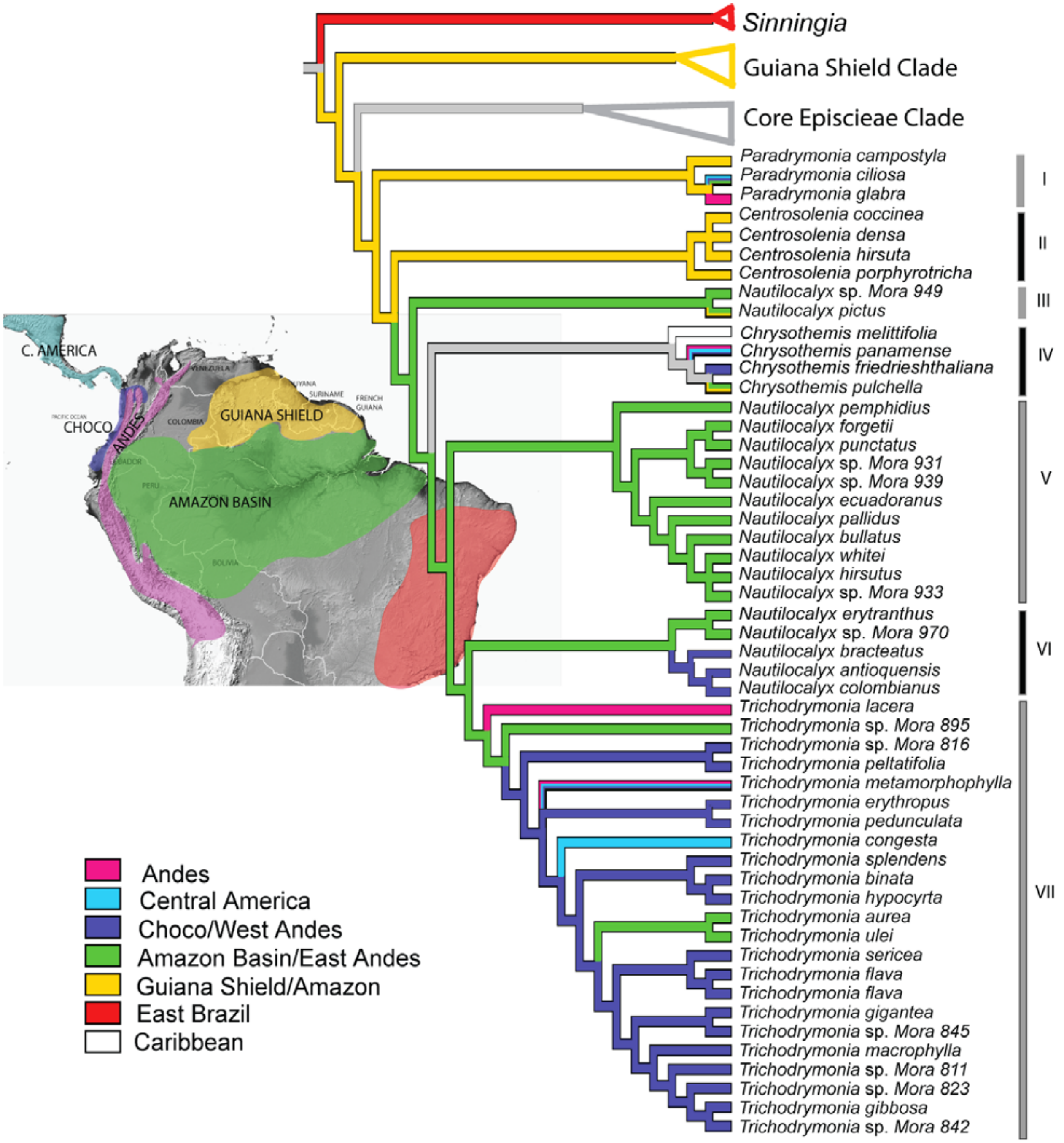

Fig. 3.5. Ancestral reconstruction of geographic diversification in tribe Columneinae with emphasis in the Paradrymonia alliance, based on based on parsimony character mapping of the modern distributions of terminal taxa onto the strict consensus from Mora and Clark (in review). Gray branches indicate uncertainty in the reconstruction of ancestral distributions. I. *Paradrymonia*. II. *Centrosolenia*. III. Pictus clade. IV. *Chrysothemis*. V. Amazonian "*Nautilocalyx*" Clade. VI. *Nautilocalyx* s.s. clade. VI. *Trichodrymonia*.

CHAPTER IV

Neotropical Lowland Gesneriads: Biogeographic Insights From Paleodistribution Reconstructions

ABSTRACT

The Neotropics are well known for harboring extraordinary plant diversity. Different hypotheses have tried to explain this neotropical richness. Among the most contentious has been the "Pleistoscene refuge theory" which invokes speciation by vicariance caused by Pleistocene climate dynamics (Haffer, 1969). I used ecological niche modeling (ENM) as an independent approach to assess the extent to which present-day and Pleistocene climate in the Last Glacial Maximum (LMG; 21000 yrs. BP) has influenced the current distribution of ten lowland forest gesneriad species. My results support the hypothesis that the Andean Mountains together with the presence of the llanos savannas of Colombia and Venezuela have created a vicariant barrier between trans-Andean (west of the Andes) and cis-Andean (east of the Andes) lowland forest taxa. Reconstructed distributions of taxa within trans-andean and cis-Andean lowlands during the LGM corresponded to a certain extent with the locations postulated as rainforest refugia. The fact that common areas of prediction were spatially coincident with some refugia suggests that these areas are indeed reservoirs of diversity and they are not an artifact of sampling as suggested by some authors. However, these reservoirs of diversity acted more as "museums" rather than drivers of speciation during the Pleistoscene which is inconsistent with the refugia hypothesis.

***Keywords*—**Andes Mountains, Amazonia, biogeography, ecological niche models, Gesneriaceae, LGM, lowland forest, MaxEnt, Pleistocene.

INTRODUCTION

The neotropics are well known for harboring an extraordinary diversity of fauna and flora. For instance, of all the flowering plant species (ca. 250,000) about one-third exist in the neotropics (Myers, 1980; Smith 2004). The high plant species richness in the region has been explained in terms of environmental factors (e.g., Gentry, 1982a, b; Kreft et al., 2004, 2007) or by historical and evolutionary hypotheses (e.g., Pennington and Dick, 2004; Donoghue 2008; Antonelli et al., 2009, Antonelli and Sanmartin, 2011). These various hypotheses range from a gradual accumulation and/or maintenance of species over time through low extinction rates (Fischer 1960, Stebbins 1974) to a recent diversification and radiation of lineages through rapid speciation rates (Haffer, 1969; Prance, 1973; Gentry, 1982a; Hughes and Eastwood, 2006).

Within the neotropics, plant diversity is not equally distributed. Gentry (1982a) identified two common patterns of plant distribution, which he defined as “Amazonian-centered” and “Andean-centered”. The first pattern is presented by taxa with center of diversity in the Amazon region, and the second one, with taxa especially diverse in the lowlands near the base of the mountains and in middle elevation forest of the northwestern Andes and the Chocó biogeographic region, which as currently defined, stretches from the western slopes of the Andes of Colombia and Ecuador to the Pacific Ocean and from eastern Panama to central coastal Ecuador (Gentry, 1982b). This distributional pattern was first pointed out for lowland forest birds (Chapman, 1917; Haffer, 1967). More recent studies that have analyzed phylogenies of lowland organisms from this region (arachnids, birds, primates, reptiles and trees), have found a basal divide between the lowland tropical forest at the east and west of the Andes (Miller, 2008). One plausible hypothesis postulated to explain this particular distribution is that the final uplift on the northern Andes in the late Pliocene divided the distribution of lowland forest organisms (Chapman, 1917; Miller, 2008; Antonelli et al., 2009).

Although a plethora of hypotheses for the diversity in the lowland neotropical forest abound, the most popular and controversial one is likely the Pleistocene refugia hypothesis (Solomon et al., 2008). This hypothesis has been both supported, (Prance, 1973, 1982; Brown et al. 1974; Mayr and O'hara, 1986; Fjeldsa, 1994) and challenged (e.g., Colinvaux et al., 2001; Knapp and Mallet, 2003; Wilf et al., 2003). The forest refuge hypothesis, first proposed formally by Haffer (1969), is based on the idea that the climatic changes during the Pleistocene (i.e. diminution in temperature and humidity during the glacial period) led to fragmented and isolated tropical forest surrounded by dry habitats. Although this hypothesis was originally formulated to explain the significant diversity and endemicity in the Amazon lowland forests, Haffer (1967) suggested that Pleistocene climatic oscillations resulted in different isolated refuges at the west of the Andes. These western (trans-Andean) refuges were isolated from one another and from the great "Amazonian Refuge" east of the Andes (Haffer, 1967).

Paleodistribution reconstruction has been possible with the advent of ecological niche models (ENM). These models predict potential geographical distributions of a species based on its ecological and environmental requirements by using point occurrences and Geographic Information Systems (GIS) technology (Anderson et al., 2002a; Raxworthy et al., 2003; Martínez-Meyer, 2004). ENM's have been also used to predict species' future ranges due to climate change (e.g., Anciaes and Peterson, 2006) and to infer past ranges (e.g., Peterson, 2006; Bonaccorso et al., 2006; Walker et al., 2009). Most of the paleodistributions of neotropical organisms have been devoted to the reconstruction of vertebrate taxa in the Pleistocene for the Amazon region (Solomon et al., 2008) and has not yet utilized to test the hypothesis of Pleistocene refugia at the west side of the Andes in South America.

Since much of the diversity and endemicity of the neotropical lowland forest have been attributed to the uplift of the Andes and Pleistocene climatic shifts, here I use ENMs as an independent approach to assess the extent to which the Andes and the Pleistocene climate in the Last Glacial Maximum (LMG; ~21000 yrs. BP) has influenced the geographic ranges of ten species of lowland Gesneriaceae. Here I specifically test the Pleistocene refuge hypothesis not only for the Amazonian region but also for the lowland region west of the Andes in South America. Gesneriads are ideally suited to test the hypothesis in question because they have similar environmental tolerances and may have occupied similar forest refugia as a response to Pleistocene climate changes. The 10 species of Gesneriaceae belong to the closely related genera in the Neotropical *Paradrymonia* alliance and have either trans-Andean or Amazonian distribution or both.

Study group**—**The family Gesneriaceae comprises ca. 3500 species of herbs, shrubs, small trees and epiphytes and climbers, found predominantly in the tropics and subtropics. Gentry (1982a) described the neotropical Gesneriaceae as a typical Andean-centered taxa with most species in lowland and pre-montane forest of the northern Andes. Within the tribe Columneinae, the largest tribe in the subfamily Gesnerioideae, *Paradrymonia*, *Nautilocalyx* and *Chrysothemis* are genera that are part of one of the most recently derived major clades in the tribe, named the *Paradrymonia* alliance (Mora & Clark in review) and are found predominantly in lowland tropical forest. we selected ten species with different distribution patterns (Table 4.1) in order to test our hypothesis. Although approximate distributions of these taxa have been recognized (Wiehler, 1983), geographic ranges of the species have not been formally defined in part because many of the species are poorly known and they are underrepresented in herbarium collections. Fortunately, with the advent of the ENMs and improved modeling algorithms (e.g., MaxEnt), we can estimate the distribution of species with as few as five point localities (Hernandez et.al 2008).

MATERIALS AND METHODS

Species distribution in current and past Climate**—**We obtained locality information from a compiled database of herbaria collections maintained by the United States Herbarium at the Smithsonian Institution. This database was complemented with more recent geospatial data extracted from the Missouri Botanical Garden's W3TROPICOS database (www.tropicos**.**org). Additionally, we used GEOlocate to obtain geographic coordinates of specimens whose locality information was available but was not georeferenced. Finally, the environmental niche models (ENMs) of 10 species belonging to the *Paradrymonia* alliance were constructed. Here, we selected for the analysis the species with fifteen or more point localities. All the set of species contained a total of 629 occurrence points (Table 4.1). For each species, a distribution model was generated using the 19 bioclimatic layers (Appendix 1) for the present climate and the point occurrence data. Climatic layers represent a subset of the Worldclim global climate layers (Hijmans et al., 2005; available at http://www.worldclim.org) thought to be among the most biologically relevant to construct ENM (Warren et al., 2008). These bioclimatic variables were produced by interpolating monthly mean temperature and precipitation data onto a digital elevation model and were downloaded at spatial resolution of ≈2.5 arc-minutes (5×5 km grid cell) for current and LGM conditions. All the layers were in the geodetic coordinate system (i.e., latitude and longitude) using the World Geodetic System 1984 (WGS84).

ENMs were generated using the maximum entropy machine-learning algorithm in MAXENT 3.3.3e (Phillips et al., 2006). MaxEnt (Phillips et al., 2006, 2009) uses known occurrences and environmental layers to make inferences about probability of distribution of a species in a given geographic area. High probability indicates that the area is predicted to have suitable environmental conditions for this species (Elith et al., 2006). We ran MaxEnt using the "default" settings mode as suggested by Phillips and Dudik (2008). After running MaxEnt, the resulting ASCII files were placed into raster format using ArcGIS 9.1 and viewed. The predicted potential distribution (ecological niche) of each species was rendered in five distinct categories using the natural breaks method of classification (Jenks' method) in ArcGIS 9.1. This method assigns the data to classes using an iterative algorithm that minimizes the variance within classes and maximizes variance between classes (Rissler and Apodaca, 2007).

Species distribution in the Last Glacial Maximum (LGM)**—**To estimate the geographic distribution and extent of suitable climate for each species during the LGM (~21,000 yrs. BP), we used the Community Climate System Model [CCSM1], http://www.ncdc.noaa.gov/paleo/modelvis.html/] (Kutzbach et al., 1998) with data from the Paleoclimate Modelling Intercomparison Project (PMIP) website [http://pmip.lsce.ipsl.fr/pmip/].

Additionally, we used the measuring area tool in ArcGis to measure areas of potential suitable habitat to compare changes in distributional area at present day and LGM climatic conditions. Areas were measured in square kilometers (km^2).

RESULTS

Western Amazonian-centered species—*Nautilocalyx erytranthus* is known to occur in the lowlands on the western side of the Amazonian basin in Colombia, Ecuador, and Peru (Mora and Clark, in press). Fig.4.1 shows maps comparing the current estimated distributions and during the LGM. The species was predicted to occur in the northwestern section of the Amazon basin in Colombia, Ecuador, Brazil, Peru, and in the wet lowland areas of the Guiana Shield in Venezuela (Figs.4.1, 4.2). Another area predicted as suitable habitat for *N. erytranthus* under current environmental conditions is the narrow tropical forest belt along the eastern flank of the eastern cordillera in Colombia and Ecuador as well as in some small areas in the foothills of the eastern Andes in Peru. The forest at the eastern flank of the eastern Andes in Colombia is separated from the upper Amazon forests by a matrix of unsuitable habitat. This matrix corresponds to the *Llanos* savanna of Colombia and Venezuela at the upper part of the Amazon forest. This species was predicted to be absent from the Guianas. *Nautilocalyx erytranthus* is also predicted to occur in the trans-Andean forest of the Pacific lowlands of Colombia and adjacent lowlands in Ecuador at the western side of the Andes, on the western slopes of the Cordillera Occidental and northern end of the Central and Western Cordilleras of Colombia and in the humid middle Magdalena Valley as well as on the Caribbean coast of Costa Rica (Figs. 4.1, 4.2). This pattern was observed for the estimated distribution of the species at the LGM (Fig. 4.2).

The cis-Andean LGM estimated distribution for *Nautilocalyx erytranthus* was predicted to be about seven percent less than the estimated distribution under current environmental conditions (Table 4.1). Interestingly, the area of suitability in the trans-Andean region was estimated to be larger and more continuous at the LGM than under present-day conditions (Fig. 4.2).

Trichodrymonia aurea, a species known to occur in moist pre-montane forest at 800-1700 m in Ecuador, is predicted to occur along the northern Andes in Peru, Ecuador and in the three main Andean ranges in Colombia–Cordillera Occidental, Central and Oriental (Fig. 4.1). The predicted area of suitable conditions for *T. aurea* was about 47% larger than at present-day (Table 4.1). This species would have found suitable climatic conditions during the LGM across the narrow tropical forest belt along the eastern flank of the eastern cordillera in Colombia and would have thrived in the lowlands in the western Amazon basin and in the lowlands surrounding the *tepuis* (table-like mountains) of the Guianan highlands (Fig. 4.3).

Central Amazonian-centered species—*Nautilocalyx arenarius* is only known to occur in Amazonian low caatinga on the northern basin of the Rio Negro in the Amazon Territory of Venezuela near eastern Colombia and northwestern Brazil (Fig. 4.4). The low caatinga is a distinctive type of tropical rain forest of low stature which grows on seasonally water-logged, white, nutrient-poor sand soils, drained by black water (Coomes and Grubb, 1996). This type of vegetation occurs within a mosaic of forests grading from an evergreen forest to herbaceous savannas and is characterized by relatively open vegetation with few short trees (5-15 m), abundant shrubs and small climbers and epiphytes with some open areas and grasses (Coomes and Grubb, 1996).

Under current environmental conditions *N. arenarius* is predicted to occur in the State of Amazonas in Venezuela in the upper portions of the Orinoco, Casiquiare and Rio Negro river basins, and adjacent areas in eastern Colombia and northwestern Brazil, as well in the southern part of the Bolivar state of Venezuela in the lowlands south of the *tepuis* of the Guianan highlands. This species is also predicted to occur disjunctively in the eastern portion of the

Brazilian estate of Pará, near Belém. Likewise, the model predicted appropriate present-day conditions for *N. arenarius* on the western side of the Andes throughout the Pacific Coast and in the western slope of the Cordillera Occidental (western cordillera) in Colombia as well in the Rio Magdalena Valley in northern Colombia between the Cordillera Central and Cordillera Oriental (eastern cordillera). The paleodistribution model predicted a much more restricted and fragmented potential presence at the west of the Andes. Conversely, the model predicted a much broader and more continuous potential distribution at the LGM east of the Andes (Fig. 4.4). The LGM potential suitable habitat was predicted to be roughly 62% more than that estimated under contemporary environmental conditions (Table 4.1).

Eastern Amazonian/Guiana-centered species—Based on the point locality data and known species ranges three of the species analyzed here (i.e. *N. pictus, Centrosolenia densa*, and *Paradrymonia campostyla*) occur in the northeastern Amazonia-Guiana shield region. Maps comparing current potential distributions and during the LGM for *Paradrymonia campostyla*, are shown in Fig. 4.2. All of the species known to occur in the Guiana lowlands were predicted to occur not only in the contiguous Amazonian forests of Venezuela and Brazil but also in the more distant Amazonian forest of Colombia. A matrix of unsuitable habitat within the western and eastern Amazonian/Guiana regions was predicted for all the species under current environmental conditions. The ENM's for all species predicted presence of suitable habitat on the eastern flank of the Andes in Ecuador. Although there were areas of suitable habitat predicted on the west side of the Andes in northwestern Colombia and Central America, these areas consisted of scattered, small fragments. At the LGM *C. densa* and *P. campostyla* were reconstructed as having a 16–19 % larger area of suitability compared to current conditions (Table 4.1), especially toward the Atlantic Coast of the Guiana Shield. Conversely, the area of prediction for *Nautilocalyx pictus* during the LGM was reconstructed as 5% smaller than under current conditions. The predicted area of suitability was especially reduced towards the Central Amazon area.

Central America/Andean-centered species—*Chrysothemis friedrichsthaliana*, *Nautilocalyx colombianus* and *Trichodrymonia pedunculata* are known to have an exclusively trans-Andean distribution. Present-day potential distributions and LGM reconstructions for *Chrysothemis friedrichsthaliana* are shown in Fig. 4.2. Common areas of potential habitat suitability at the western side of the eastern Andes in Colombia included the northern portion of the central and western Andes, in the rainforest of the Choco and Antioquia departments, and in the middle Río Magdalena Valley (Fig. 4.1). *Chrysothemis friedrichsthaliana* and *T. pedunculata* which occur in both moist and wet forest, were also predicted to occur along the Chocó region on the Pacific slopes of Colombia. The former species was also predicted to occur throughout the Pacific Coast in northwestern Ecuador. *Nautilocalyx colombianus* under present-day climatic conditions was predicted to occur in the Darién and adjacent moist forest of the Urabá region in Colombia but absent in most of the Chocó region where wet and pluvial forests occur. In Central America all of the cis-Andean species assessed here were predicted to occur in the wet rainforest of Nicaragua, Costa Rica and Panama. These species were also predicted to occur at the eastern adjacent slopes of the Andes in Colombia (and Ecuador for *C. friedrichsthaliana*) as well as in the Amazon region and the Guiana Shield. During the LGM the suitable habitat for this species was considerably larger at the western side of the Andes (about 43-58%, Table 4.1) but the ranges at the eastern side of the Andes were predicted to be reduced and more fragmented in the Amazon region and in the Guiana Shield, except in some forests near the Atlantic coast in the Guianas.

Widespread species*—*Paradrymonia ciliosa is the only lowland species in the *Paradrymonia* alliance to occur on both sides of the Andes. This widespread species is distributed in northern South America and Central America (Fig. 4.2). Under current environmental conditions this species is predicted to occur throughout the entire upper Amazon region, on the eastern flank of the eastern Andes in Colombia, Ecuador and Peru as well as in the lowlands at the base of the *tepuis* of the Guianan highlands and lowlands of Guyana, Surinam and French Guiana. This species is also predicted to occur in the lowlands of the western side of the Andes at the northern end of the Central and Western Cordilleras of Colombia and in the humid Magdalena River valley as well as Central America. Conversely, *Paradrymonia ciliosa* was predicted absent from the forest of the Pacific lowlands of Colombia and Ecuador. Interestingly, this species was reconstructed as having 12 % larger potential distribution during LGM than at current conditions (Table 4.1), especially near the coast in Central America and in the Guianas.

DISCUSSION

One criticism of the Pleistocene refuge hypothesis is that hypothesized refugia correspond with the most intensively sampled sites rather than truly representing reservoirs of diversity (e.g., Endler, 1982; Knapp and Mallet, 2003). However, the bias in sampling is overcome when estimating potential distribution with the use of ENMs (Bonaccorso et al., 2006). Here I used ENM to estimate species distribution under current and past environmental conditions to assess the extent to which the Pleistocene LGM climate has influenced the distribution of some lowland Gesneriad species.

Although much interest has focused on forest refugia in the Amazon region, little attention has been given to the forest refugia at the west of the Andes with the exception of the Chocó refuge (e.g., Gentry,1982). I modeled species that occur either at the west of the Andes (*trans*-Andean) or at the east of the Andes (cis-Andean) or both (i.e. *Paradrymonia ciliosa*) to test how climate have influenced current distributions of forest species and if the areas of prediction at the LGM correspond with the postulated Pleistocene refugia by Haffter (1967, 1969) and Prance (1982).

PUTATIVE REFUGIA OF CIS-ANDEAN FOREST LOWLAND GESNERIADS

Western Amazonia**—**The paleodistribution model predicted a somewhat more fragmented and diminished range during the LGM at the eastern side on the Andes (cis-Andean) for *N. erytranthus*. The predicted distribution included much of the Ecuadorian Amazon and adjacent northernmost areas in Peru and in the northwestern portion of Brazil. This area of prediction corresponds spatially to the Napo refuge; the largest of the forest refugia postulated by Haffer (1969) which comprises the lowlands of Ecuador from the Andes to the Marañon River. This species is also predicted to occur in another refuge postulated by Prance (1982). Both refuges are concordant with high rainfall and low seasonality and an average annual precipitation of 3000 mm or higher (Kreft et al., 2004).

The paleodistribution for *Trichodrymonia aurea*, a facultative epiphytic species mainly from mid-elevation Andean forests, indicated that this species would have thrived in the western Amazonian lowlands where the postulated refugia are located, as well as in the surrounding lowlands of the Guiana shield *tepuis*. Our results are consistent with the view that climate change during the Pleistocene led to vegetation changes along Andean vegetation belts, allowing higher elevation taxa to colonize lower elevations during cooler conditions (e.g., van der Hammen, 1974, van der Hammen, and Hooghiemstra, 2000). Likewise, vegetation shifts might have occurred between the lowlands and higher elevation forests in the *tepuis* during the Pleistoscene (Huber, 1995; Rull 2004, 2005). Since western Amazonia was one of the least affected regions within Amazonia to drier and cooler Pleistocene climate the floristic composition in the area must have remained similar to today (Bush, 1996; Haffer and Prance, 2001; Kreif, 2004; Bush & Oliveira, 2006), but with invasion of Andean and *tepui* elements that dispersed into the Amazonia following their bioclimatic niche during the Pleistocene.

Higher diversity of trees (Gentry, 1988; Pitman et al., 2002; ter Stegee, 2010), lianas (Nabe-Nielsen, 2001), and epiphytes (Kreif et al., 2004) exist in western Amazonia than in other areas in the Amazon region. High rainfall and low seasonality is correlated with high tropical forest diversity. For instance, ter Steege et al. (2010) found that current climate explains 37% of the variation in tree-alpha diversity. Kreif (2004) suggest that recent and historic patterns of rainfall are the driving forces behind diversity. The fact that common areas of prediction in western Amazonia correspond with some refugia postulated originally by Haffer (1969), suggest that these areas are indeed reservoirs of diversity, and they are not an artifact of sampling as suggested by Endler (1982) and Knapp and Mallet (2003).

Eastern Amazonia/Guianas**—**The reconstructed potential distributions under present day and under LGM environmental conditions for the Eastern Amazonian/Guiana-centered species were generally spatially concordant across species. They were commonly reconstructed as being dissected in western and eastern portions, usually isolated by a large matrix of unsuitable habitat within each areas. The paleodistribution reconstruction at eastern Amazonia corresponds to a certain extent with the location of the Guiana refuge postulated by Haffer (1969); however the area in northwestern Amazonia predicted as suitable, does not match any proposed areas of Pleistocene refugia.

The fact that under current conditions there is a predicted matrix of unsuitable habitat separating humid upper (western) and lower (eastern) Amazonia, suggests that current regimes of precipitation and temperature greatly influence distributions for the lowland herbaceous gesneriads studied here. Although Central Amazonia is generally more seasonal and drier than Western Amazonia, the annual rainfall is higher on eastern coastal rainforests (up to 3000 mm year^{-1}) than in Central Amazonia (2000 mm year^{-1} or less) as indicated by different authors (e.g., Prance, 1973; Haffer, 1969; 2008).

Our paleodistribution habitat reconstructions indicate that overall distributional limits of species from the Guiana region were not dramatically different at LGM and present-day conditions. However, they showed retraction of the southwestern fringe towards the periphery of the Amazon basin, and expansion along the coastal lowlands of the Guianas (see *Paradrymonia campostyla*, Fig. 4.2). The increase in potential habitat during the Pleistocene in the coastal lowlands of the Guianas correlates with the expansion of seashore due to a drop of sea level in the order of 120 m during glaciations (Ray and Adams, 2001).

Central Amazonia—*Nautilocalyx arenarius,* a species from Western-Central Amazonia, occurs in low caatinga, a distinctive patchy and more open and scrubby vegetation distinct from the surrounding rainforest due to extremely poor white-sand soils (Franco and Dezzeo, 1994). The potential habitat expansion of about 62% during the LGM as compared with present-day conditions correlates with the expansion of non-rainforest vegetation in the Pleistocene in north-central Amazonia. Since low caatingas occur within a mosaic of rainforest and savannas, it is plausible that during cooler and drier climates this type of vegetation (savanna-forest mosaic) became more predominant while rainforest retracted. Several studies have suggested that during glacial periods, areas of rainforest, especially toward the marginal areas were replaced by seasonally dry forest, savannas and/or other intermediate drier vegetation types (Prado and Gibbs, 1993; Pennington et al. 2000; 2004; Prance, 1982; Haffer, 1969; 2008).

THE AMAZONIA PLEISTOCENE REFUGIA DEBATE

Today the Amazon appears to be a homogeneous dense block of continuous forest. This apparent homogeneous structure has been attributed to a “hyperdominance” of few species of trees with larger ranges than other taxa (ter Steege et al.2013). However, there is a general gradient in tree species richness and other plant life forms from west to east of the Amazon basin, following the trend in annual rainfall and seasonality (Clinebell et al., 1995; ter Steege et al. 2003; 2010). Local differences in precipitation and temperature combined with regional differences of soil types have produced a mosaic of different vegetation types (ter Steege et al.2013).

Our present-day and LGM habitat reconstructions indicated a split into western and eastern segments of species distributions isolated by a northwest/southeast belt of less suitable conditions. The patchy distribution of suitable habitats for most of the Amazonian/Guianan gesneriads studied here corresponds to centers of abundant rainfall (Anhuf et al., 2006), suggesting that these taxa are much more sensitive to certain temperature and precipitation combinations as compared with other Amazonia widespread species. Modeled distributional limits of species from western and eastern Amazonia were not dramatically different between LGM and present-day. This suggests that if the current distributions of Amazonian Gesneriad species are the result of separation into refugia, these refugia must have been formed in the

Pleistocene or before, and maintained today within a broader Amazonian vegetation. A recent reconstruction of vegetation patterns in the Amazon basin and surroundings during the LGM by Anhuf et al. (2006) suggests that LGM rainforests were embedded in a continuous area of semi-deciduous forest and to minor extent, transitional mosaics containing dry forests and savannas concordant with the paleodistribution predicted for *Nautilocalyx arenarius*. Despite this, evergreen rainforest areas were not markedly isolated considering that some semi-deciduous forests provide survival conditions for numerous rainforest taxa (e.g., Ledru et al., 2001; Pennington et al. 2004). Moreover, postulated refugia at the base of the Andes might have received species from higher altitudes during glaciation periods as is supported by current floristic compositions in Western Amazonian forests (Kreif et al., 2004). Although our study supports the presence of some postulated Amazonian refugia as reservoirs of diversity during the Pleistocene, it does not support refugia as pumps of rapid speciation.

PUTATIVE REFUGIA OF TRANS-ANDEAN FOREST LOWLAND GESNERIADS

Most of the Chocó region was predicted as highly suitable under LGM climatic conditions for all the trans-Andean species modelled. Surprisingly, the areas of suitable habitat were about 40-60% larger than under present-day conditions (Table 4.1). This indicates that rainforests of Central America and the Chocó region of Colombia and Ecuador remained substantially intact, likely due to heavy rainfall in these regions (Gentry, 1982). Additionally, coastal areas expanded during the Pleistocene as the sea level dropped, allowing habitat expansion in the coastal areas of the Pacific and/or Atlantic Ocean. The fact that the Choco forests and Central America appear more suitable for species known to occur in tropical moist forest such as *N. colombianus* suggests these areas were more mesic during the LGM than during current conditions allowing moist forest species to thrive.

All of the species that are known to occur in Costa Rica, Panama and northern Colombia were predicted to occur on the northern slope and the tip of the central and western Andes of Colombia. This area corresponds with the Nechí refuge postulated by Haffer (1967).

Based on the known species range and the phytogeographic pattern defined by Gentry (Andean vs. Amazonian taxa), all of the species' current potential distributions were over-predicted by the ENM. Species known to occur in Central America and/or on the west side of the Andes (trans-Andean) were also predicted to occur in the Amazon basin and/or in the Guiana shield. Concurrently, species predicted to occur only in the last region (cis-Andean) were predicted to be in Central America. Instead of a disadvantage, this "overprediction" from ENM actually permits assessment of ecological, evolutionary and biogeographical questions comparing potential and realized distributions (Peterson et al., 1999; Peterson and Vieglais, 2001; Anderson et al., 2002a, b, 2003). For example, if a species can potentially inhabit wet and humid lowland forest in both regions, the Central America-northern Andes and the Amazonian-Guiana shield region, what factors s other than the environmental ones limit the species's distribution?

Since the ENMs failed to explain the disjunctive distribution of the gesneriad species (trans-Andean vs. cis-Andean taxa) in present-day conditions, the most plausible explanation for this disjunctive pattern is the existence of a geographic barrier. The most conspicuous barrier that exists between the humid lowlands of Amazonia, and the wet forest on the western side of the Andes in Ecuador and Colombia, is the Andes Mountains. This implies that many lowland gesneriad species are not physiologically capable of surviving the severe mountainous climates to be able to reach the lowlands of the other side of the mountains. Many neotropical plant groups show the same pattern (Gentry 1982a; Antonelli et al., 2009; Antonelli and Sanmartin, 2011).

Besides the Andes, another barrier among cis-Andean and trans-Andean lowland forest taxa is the Colombian and Venezuelan Llanos savannah located at the northwestern Amazon basin. Under current climatic conditions, no forest corridor connects lowland forests at the northern tip of the Andes in Colombia. The lowland forest in the foothills of the eastern Andes is interrupted by the vast Llanos, stretches of the Caribbean Sea, and arid scrublands in the Caribbean lowlands north and east of the Andes (Eva et al., 2002; Miller et al., 2008). Haffer (1967) suggested that dispersal around the Andes through the north of Colombia lowlands was plausible during the humid periods of the Pleistocene and post-Pleistocene. However, none of the species modeled here showed a continuous distribution surrounding the Andes during LGM conditions or present-day conditions.

Of the species analyzed, only one species (i.e. *Paradrymonia ciliosa*) occurred at the Amazon basin and in northern Colombia and Central America. Climate during the LGM does not explain its current distribution. Dispersal through the northern Andes is not plausible under either current or LGM climate. A feasible explanation might be that this species colonized Central America before the end of the final uplift of the Andes, which according to Hoorn et al. (2010) occurred ~2.7 Mya ago. Phylogeographic reconstructions of *P. ciliosa* are necessary to clearly understand the role of the Andes in the dispersal of this species.

LGM distributions of cis-Andean lowland gesneriad taxa were largely congruent across species and commonly dissected into western and eastern sectors, usually with a large matrix of unsuitable habitat within each area. This pattern is consistent with shifts in species distribution influenced by Pleistocene climate. Similar results were obtained by Bonaccorso et al. (2006) using six forest birds and three forest woody plants, and by Peterson and Nyári (2007) using one forest bird species. The LGM reconstruction of these forest taxa supports Haffer's (1969) hypothesis of the location of refuges on the periphery of the Amazon basin. Reconstructed fragmentation of the suitable habitat during the LGM corroborates the Pleistocene refugia theory as a significant cause of distribution patterns in Amazonian and Guianan species.

Nearly all trans-Andean species were predicted to occur in the Chocó region at the LGM. This region is one of the richest and most distinctive centers of plant endemism in the neotropical lowlands (Prance 1982, Gentry 1982). This region was postulated as a refuge by Haffer (1967) and subsequently supported with phytogeographical evidence (e.g., Lellinger 1975; Gentry, 1982; Prance, 1982' Mora et al., 2006). The paleodistribution of trans-Andean gesneriad species analyzed here provides additional evidence for a Chocó refuge. Refugial areas of rich genetic diversity might be indicated by overlaps between modelled past and present distributions (Nogués-Bravo, 2009; Thomas et al. 2012). The correspondence between postulated refugia and hotspots of plant diversity and endemism stresses the importance of including these areas in conservation plans. An area deserving of special attention is the Chocó-Magdalena region which has been considered a biodiversity hotspot based on plant endemic richness and habitat loss (Myers et al., 2000).

The "overprediction" of ENMs on both side of the Andes, suggests a main role of the Andes as an ecological barrier in shaping lowland gesneriad disjunct distribution (Andes vs. Amazonia). Recent dated phylogenetic trees in combination with complex geological scenarios suggest a link between Andean orogeny and neotropical diversification (Antonelli et al., 2009). Andean orogeny have affected regional climate and has had a large impact on the landscape evolution in northern South America, including the Amazonia (Antonelli et al., 2009; Antonelli and Sanmartin, 2011; Hoorn et al., 2009). It is clear that these are not the only mechanisms involved in delineating the gesneriad species' ranges. Other historical, environmental and ecological factors and interactions among such factors need to be considered, especially because they might have interplayed since the Cenozoic, and not just during the LGM. Further studies combining molecular phylogeography and paleodistributions are necessary to understand more deeply the impact of the Andean uplift and the Pleistocene climate in the evolution and speciation of neotropical gesneriads.

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Table 4.1. Changes in predicted distributional area for modeled distributions of lowland species at present-day and Last Glacial Maximum (LGM). Shaded rows indicate species with a smaller potential habitat in the LGM than under current climatic conditions.

Species	**LGM area (±100) (km^2)**	**Present-day area ±100 (km^2)**	**percentage difference**
Central America/Andean-Centered			
Chrysothemis friedrichsthaliana	546,099	311,471	43%
Thrichodrymonia pedunculata	406,298	170,340	58%
Nautilocalyx colombianus	342,537	180,632	47%
Widespread species			
Paradrymonia ciliosa	1,962,567	1,733,014	12%
Amazon/Guiana Shield-centered			
Nautilocalyx erytranthus (Western Amazon)	860,250	925,780	7%
Trichodrymonia aurea (Western Amazon)	366,028	195,757	47%
Nautilocalyx arenarius (Central Amazon)	1,187,424	450,587	62%
Paradrymonia campostyla (Guiana shield)	991,715	801,441	19%
Nautilocalyx pictus (Guiana shield)	1,093,576	1,151,899	5%
Centrosolenia densa(Guiana shield)	621,657	525,014	16%

Fig. 4.1. Major geographical features of northern South America discussed in the text.

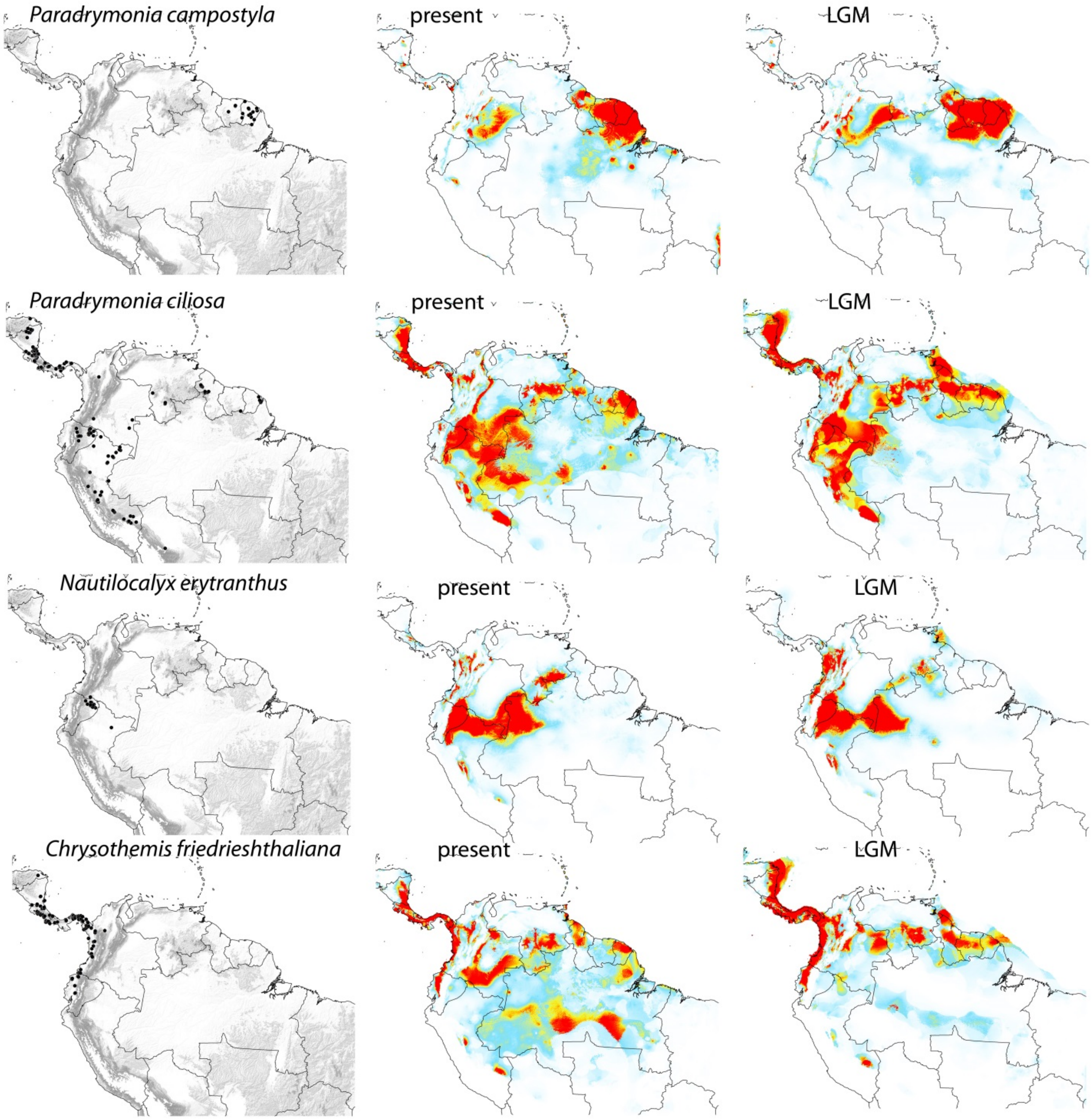

Fig. 4.2. Present-day and Last Glacial Maximum potential distributions for *Paradrymonia campostyla*. *P. ciliosa*, *Nautilocalyx erytranthus* and *Chrysothemis friedrichsthaliana*. Ecological niche models were based on occurrence points show on the maps at the left corner. Darker shading indicates greater model agreement in predicting potential presence.

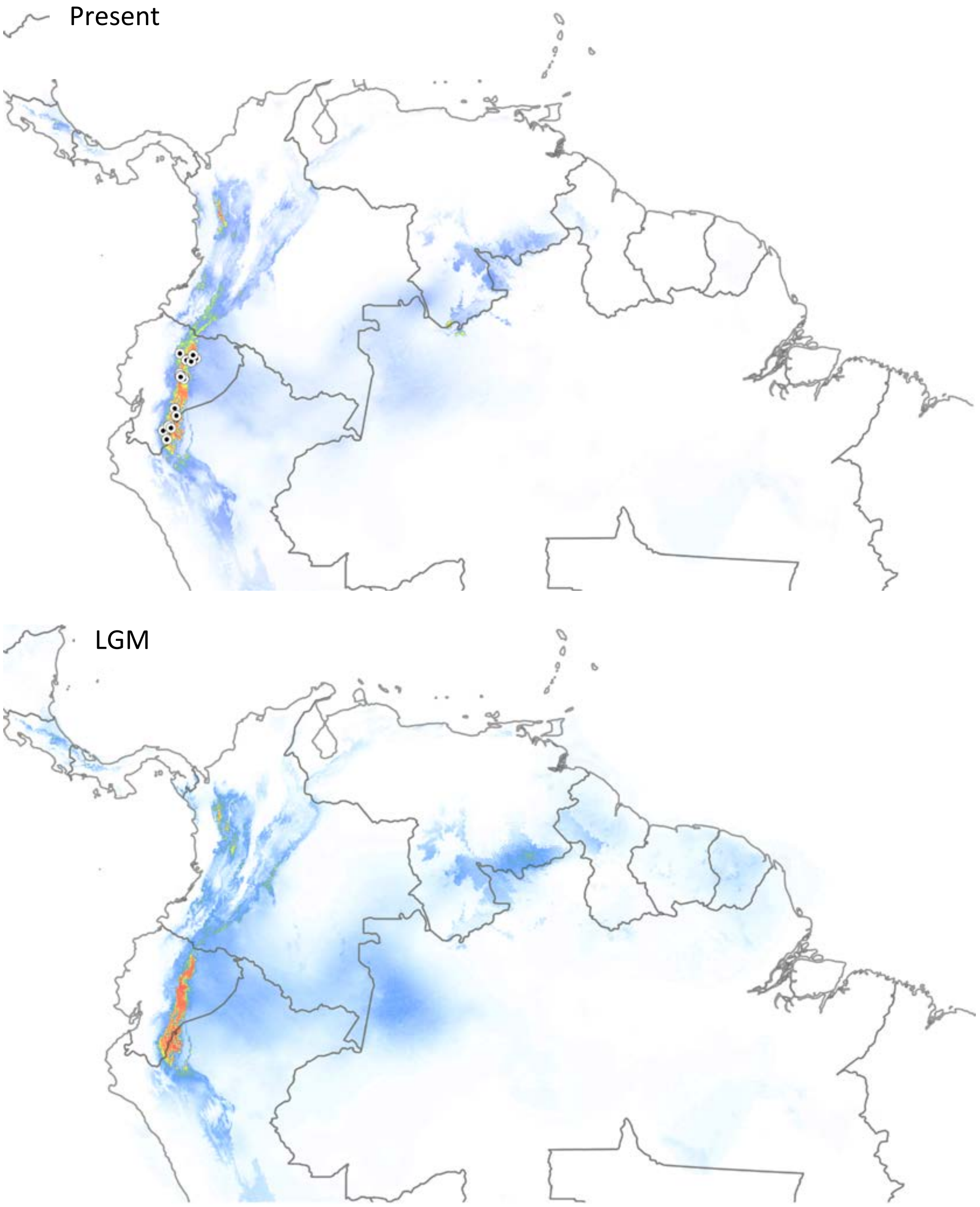

Fig. 4.3. Present-day and Last Glacial Maximum(LGM) potential distributions for *Trichodrymonia aurea*. Ecological niche models were based on occurrence points (dots) shown on the map on the top. Warmer colors indicate greater model agreement in predicting potential presence.

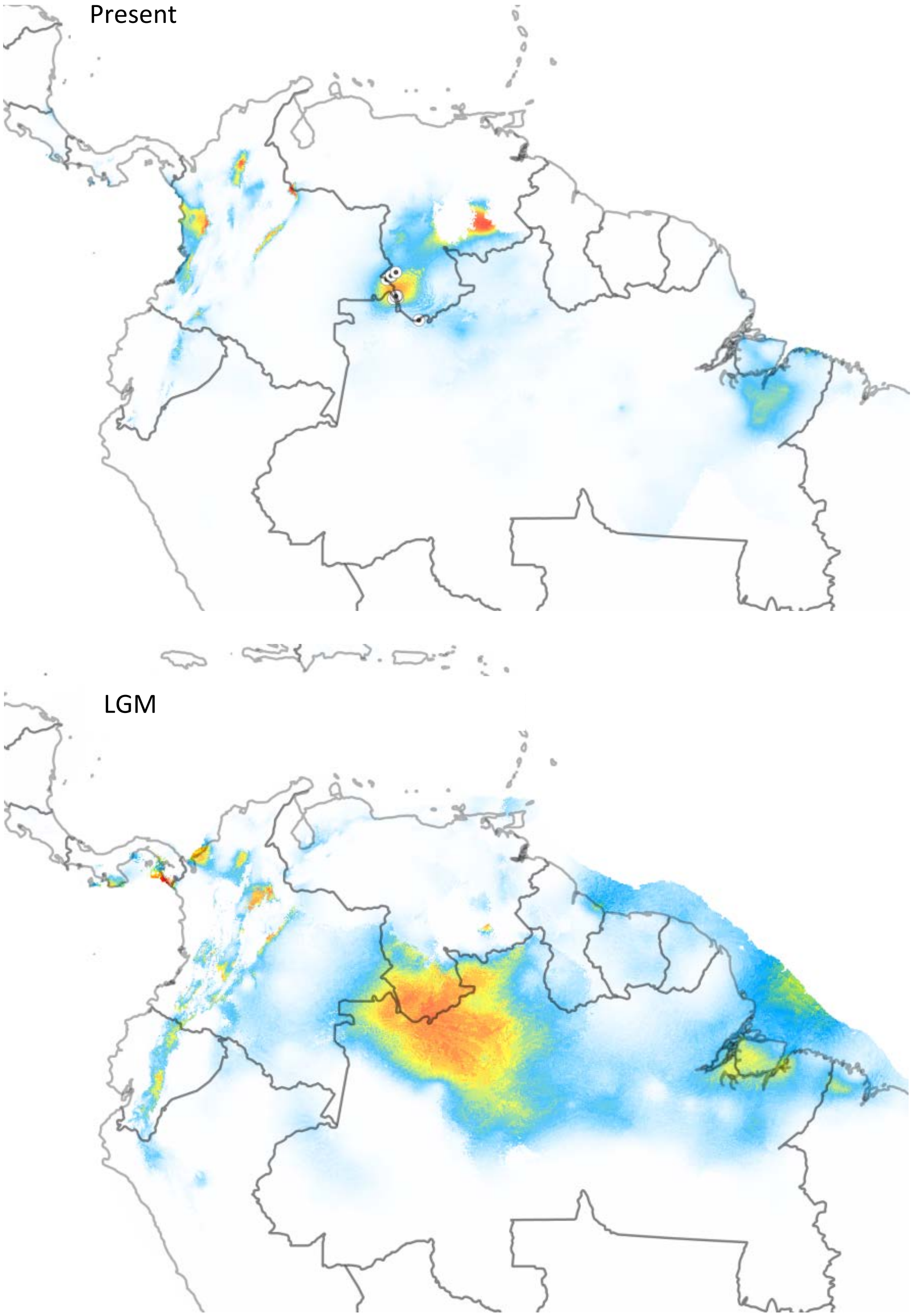

Fig. 4.4. Present-day and Last Glacial Maximum (LGM) potential distributions for *Nautilocalyx arenarius*. Ecological niche models were based on occurrence points (dots) showed on the map on the top. Warmer colors indicate greater model agreement in predicting potential presence.

Appendix 1. List of 19 environmental variables from the WorldClim database (Hijmans et al., 2005) used in ecological niche modeling.

BIO1 = Annual Mean Temperature

BIO2 = Mean Diurnal Range (Mean of monthly (max temp - min temp))

BIO3 = Isothermality (BIO2/BIO7) (* 100)

BIO4 = Temperature Seasonality (standard deviation *100)

BIO5 = Max Temperature of Warmest Month

BIO6 = Min Temperature of Coldest Month

BIO7 = Temperature Annual Range (BIO5-BIO6)

BIO8 = Mean Temperature of Wettest Quarter

BIO9 = Mean Temperature of Driest Quarter

BIO10 = Mean Temperature of Warmest Quarter

BIO11 = Mean Temperature of Coldest Quarter

BIO12 = Annual Precipitation

BIO13 = Precipitation of Wettest Month

BIO14 = Precipitation of Driest Month

BIO15 = Precipitation Seasonality (Coefficient of Variation)

BIO16 = Precipitation of Wettest Quarter

BIO17 = Precipitation of Driest Quarter

BIO18 = Precipitation of Warmest Quarter

BIO19 = Precipitation of Coldest Quarter

CHAPTER V

Paradrymonia apicaudata (Gesneriaceae), A New Species from Western Colombia[1]

ABSTRACT

A new species is described and illustrated from the Pacific slope of the Cordillera Occidental in the western Andes of Colombia. **Paradrymonia apicaudata** (Gesneriaceae; Episcieae) is distinguished from other species in the genus by the combination of spathulate leaf blades with a caudate apex, linear calyx lobes, and salverform white corollas.

RESUMEN

Se describe y se ilustra una nueva especie, **Paradrymonia apicaudata** (Gesneriaceae; Episcieae), de la vertiente del pacífico de la Cordillera Occidental en los Andes de Colombia. La nueva especie se distingue de otras especies en el género por sus láminas espatuladas con ápice caudado, por sus flores blancas hipocrateriformes y por sus lóbulos del cáliz lineares.

Key Words: Colombia, Gesneriaceae, *Paradrymonia*, Taxonomy.

INTRODUCTION

The plant family Gesneriaceae is mostly tropical or subtropical with over 3500 species distributed in 150–160 genera (Weber 2004; Weber & Skog 2007). The family is divided into four subfamilies with the subfamily Gesnerioideae found almost exclusively in the Neotropics

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[1] Published in: **Mora, M. M**., L. E. Skog & J. L. Clark. 2012. *Paradrymonia apicaudata* (Gesneriaceae), a new species from western Colombia. *J. Bot. Res. Inst. Texas* 6(1): 65 – 69.

(Burtt & Wiehler 1995; Smith & Carrol 1997). Although different tribal arrangements are recognized in the literature based on morphological data (e.g., Hanstein 1854; Fritsch 1893–1894; Wiehler 1983), more recent studies based on molecular evidence divide the subfamily Gesnerioideae into eight tribes (Weber 2004; Skog & Boggan 2007; Weber & Skog 2007). Of the eight tribes, Episcieae is the largest and most diverse with 22 genera and an estimated 784 species (Clark et al. 2006; Clark 2009).

Paradrymonia Hanst. with 38 currently recognized species is the fourth largest genus in tribe Episcieae after *Columnea* L. (200+ spp.), *Drymonia* Mart. (100+ spp.) and *Nautilocalyx* Linden ex Hanst. (ca. 60 spp.) (Clark 2009). The genus occurs throughout the Neotropics except southeast Brazil and the Caribbean, with centers of diversity in Colombia and Ecuador. Ongoing phylogenetic studies support that traditionally recognized *Paradrymonia, Nautilocalyx,* and *Chrysothemis* are not monophyletic. The new species described here shares the following morphological features with currently recognized members of an informal clade comprised of *Paradrymonia*: facultative epiphytic herbs; leaves clustered in a basal rosette; petioles U-shaped in cross section; corollas trumpet-shaped to salverform; anther dehiscence longitudinal; leaf pairs anisophyllous; and fruits a semi-fleshy bivalved dehiscent capsule. An ongoing taxonomic revision by the first author on *Paradrymonia* has revealed a new species endemic to Colombia that is described here.

Paradrymonia apicaudata M.M. Mora & J.L. Clark, sp. nov. (**Fig. 5.1**). Type: COLOMBIA. Valle: from Campoalegre into area controlled by Corporación Valle del Cauca, trail uphill behind last camp (El Chanco), 04°00'N 076°40'W, 400–610 m, 17 Feb 1989, *J.F. Smith, R. Bernal, X., Londoño and W. Devia 1357* (holotype: SEL; isotypes: F, MO, US, WIS).

Differs from other congeners by the combination of the following characters: epiphytic herbaceous habit; anisophyllous leaves; blades spathulate with decurrent base and caudate apex, sericeous surface, and denticulate margins; linear calyx lobes; and white salverform corollas.

Facultative epiphyte. Stems subwoody, subquadrate, elongate and creeping with erect shoots, internodes 3–6 cm long near base, becoming apically clustered, rhytidome glossy and tan, adventitious roots present. Leaves opposite, unequal in a pair, the larger leaf with petioles 1–2(–4) cm long, cross section U-shaped, wine-red, densely sericeous; the blade 8.5–24 × 3.5–6.5 cm wide, spathulate to oblanceolate with denticulate margins, base decurrent on petiole, apex abruptly acuminate to caudate, dark green above, light green below, sometimes tinged with purple, matte (non-glossy), sericeous on both surfaces, young leaves densely sericeous; the lateral pairs of veins 10–14(–16), departing the midrib at 40–50° angle. The smaller leaf strongly reduced, to 2 cm long, linear-lanceolate with denticulate margins. Inflorescence a reduced pair-flowered cyme, of 1–2 flowers in axillary clusters, the prophylls linear-lanceolate, denticulate, less than 2 cm long, reddish, sericeous; the pedicels 0.8–1.5 cm long, rose-colored, sericeous. Calyx lobes subequal 15–30 × 1–2 mm, linear, sericeous, pale green to yellowish green, with one or two subovoid teeth on the margin, the teeth sometimes in pairs. Corolla oblique relative to the calyx, ca. 3.5 cm long, salverform with a flattened limb and spreading lobes, spurred at base, pilose, proximal half a narrow tube, white, distal half gradually expanding with yellowish hues inside the tube, pilose outside, with short glandular hairs inside, the lobes 5, subequal, 0.5–0.6 cm, slightly broader than long. Androecium with 4 stamens, included, didynamous, 1.8–2.3 cm long, the filaments adnate for up to 3 mm from the base of the corolla tube, white, glabrous, each anther apically coherent in a pair, each thecae ca. 1 mm long, the thecae dehiscent by longitudinal slits. Gynoecium with the ovary ovoid, 7 mm long, densely sericeous, style up to 2.5

cm long, densely glandular-pilose, stigma capitate, nectary a bilobed dorsal gland, ca. 2 mm long, entire, glabrous. Fruit a bivalved semi-fleshy (not succulent) capsule, green, and sericeous. Seeds oblong-ovoid, tapered at both ends but more acutely at one end, 1.2–1.4 × 0.3–0.4 mm, light reddish brown marked with vertical striae.

Distribution and habitat.—*Paradrymonia apicaudata* is endemic to Colombia and is known from the western foothills of the Cordillera Occidental in the departments of Chocó and Valle. Its habitat ranges from Tropical wet forest (Twf) to Tropical rain forest (Trf) to Premontane (P) life zones (Holdridge et al. 1971). Collections range from sea level to 700 m in primary forest, fragmented tracts of primary forest with few large trees and many epiphytes, or growing on steep rocky roadside embankments.

Phenology.—*Paradrymonia apicaudata* has been collected in flower in October to May and in fruit in February to May.

Paradrymonia apicaudata is distinguished from other species in the genus by the combination of sericeous pubescence on the leaf blades, pedicels, and calyces; spathulate leaf blades with conspicuous caudate apices and denticulate margins; linear calyx lobes with subovoid teeth; and white salverform corollas. *Paradrymonia apicaudata* is similar to *P. ulei*, an endemic species from the northeastern Andes of Peru. Both species have salverform corollas with sericeous pedicels and calyces. However, *Paradrymonia apicaudata* differs from *P. ulei* by the presence of white corollas (vs. red-orange), linear calyces (vs. lanceolate) and conspicuously caudate leaf apices (vs. acuminate).

Etymology.—The specific epithet, apicaudata, is in reference to the apical portion of the leaf blade. The leaf apex is elongate and “tail-like” as in the order of Amphibians, Caudata (salamanders and newts), which is defined by the presence of tails as adults.

Conservation and IUCN Red list category.—Most of the specimens of *Paradrymonia apicaudata* are from the Bajo Calima region in the Department of Valle on the Pacific coast of Colombia near Buenaventura. From the 1950s until 1995, the Bajo Calima site was a timber concession to Cartón de Colombia. The site was logged on a 30-year rotational basis and during the late 1980s and 1990s the same timber company encouraged the scientific study of the site. Studies have indicated that the region is very rich in plant diversity (Faber-Langendoen and Gentry 1991). Bajo Calima is also known as one of the centers of diversity and endemism for the family Araceae (Bay 1996; Croat et al. 2008).

Paradrymonia apicaudata has been recorded from Bajo Calima as recently as 1988. Unfortunately, a 2009 expedition by the first author did not result in locating any extant populations because of the considerable deforestation occurring in the area. *Paradrymonia apicaudata* has not yet been found in any formally protected area in Colombia. Fieldwork in adjacent forests in the Departments of Chocó and Valle may result in the documentation of extant populations. According to the IUCN Red List criteria (IUCN 2001) the limited geographic range (B1a, severely fragmented or known to exist at no more than five locations) and limited population size estimation (C1), *Paradrymonia apicaudata* should be listed in the category EN (Endangered).

Paratypes. **COLOMBIA. Chocó:** Corcovada Region, upper Río San Juan; ridge along Yeracüí Valley, 24 Apr 1939, *E. Killip 35241* (COL, US); hills near highest point of Bagado-Certegui trail, 8 Dec 1983, *A. Juncosa 1551* (MO, US); hwy between Yutó and Lloró, 29 Dec 1982, *A. Juncosa 540* (MO, US). **Valle:** Santa Rosa, along Rio Caballete, 22 Sep 1922, *E. Killip 11542*

(US); trail leading from Campoalegre into area controlled by Corporación Valle del Cauca, trail from last camp (El Chanco) across stream via cable cart, uphill and to left to CVC altitude marker, 16 Feb 1989, *J. Smith*, *R. Bernal*, *X. Londoño* and *W. Devia 1317* (WIS); 18 Feb 1989, *J. Smith, R. Bernal*, *X. Londoño and W. Devia 1367* (US, WIS); Córdoba, 17 Feb 1939, *E. Killip* and *H. Garcia 33424* (US); Buenaventura, Bajo Calima, Concesión Pulpapel/Buenaventura, 22 Mar 1985, *M. Monsalve 819* (MO); 8 May 1985, *M. Monsalve 853* (MO); 1 Oct 1987, *M. Monsalve 1880* (MO); Buenaventura, Bajo Calima Region between Buenaventura and Río Calima, Carretera Hans at Km 22 on main road to Canalete, ca. 6 km N of main road, 21 Jul 1988, *T. Croat 69512* (MO).

ACKNOWLEDGMENTS

Support for this project was provided by the National Science Foundation (DEB-0841958 and DEB-0949169) to JLC, and The Gesneriad Society, Inc. to MM. We thank the Smithsonian Institution's National Museum of Natural History – Department of Botany (US), the Missouri Botanical Garden (MO), the Field Museum of Natural History (F), the Marie Selby Botanical Garden (SEL) and the University of Wisconsin (WIS) herbaria for access to their collections. We also thank Sue Blackshear for the illustration. Christian Feuillet and Jeremy Keene are acknowledged for providing helpful comments to an early version of the manuscript.

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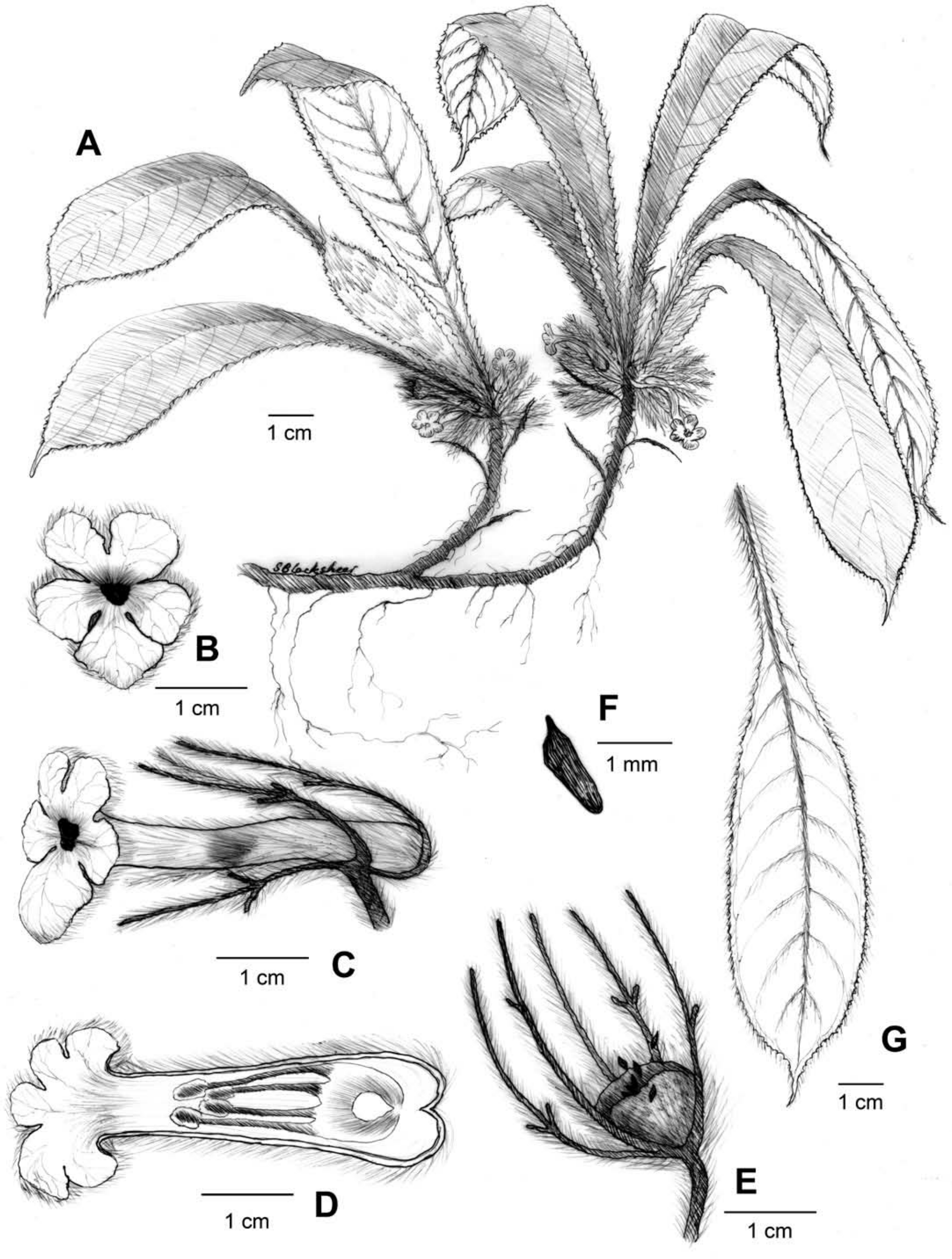

Fig. 5.1. Illustration of *Paradrymonia apicaudata*. A. Apical rosette habit. B. Front view of corolla. C. Lateral view of flower. D. Corolla open to show position of androecium. E. Persistent calyx and bivalved capsule with seeds. F. Seed. G. Leaf blade showing caudate apex. (A from *E.P. Killip & H. Garcia 33424* (US); B, C & D from *M. Monsalve 819* (MO); E from *A. Juncosa 1551* (MO); and F from the holotype, *J.F. Smith et al. 1317* (WIS)).

CHAPTER VI

Paradrymonia peltatifolia (Gesneriaceae), A Recently Discovered Species from Panama[1]

ABSTRACT

A recently discovered species is described from the Cobre mine site managed by Minera Panamá S.A. in Colón Province (Donoso District) in central Panama near the Caribbean coast. The new species, *Paradrymonia peltatifolia* J. L. Clark & M. Mora (Gesneriaceae, Episcieae), is easily distinguished from congeners by the presence of peltate leaf blades, which is a vegetative characteristic that is rare in the Gesneriaceae.

RESUMEN

Se describe una especie recientemente descubierta en la concesión Cobre Panamá manejada por la Minera Panamá S.A. en la provincia de Colón (distrito de Donoso) en el centro de Panamá cerca de la costa Caribe. La nueva especie, *Paradrymonia peltatifolia* J. L. Clark & M. Mora (Gesneriaceae, Episcieae), se distingue

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[1] Published in: Clark, J.L. & **M. M Mora.** 2014. *Paradrymonia peltatifolia* (Gesneriaceae), a recently discovered species from Panama. *Novon* 23: 18-20.

fácilmente de congéneres por la presencia de láminas peltadas, la cual es una característica vegetativa rara en las Gesneriáceas.

Key words: Gesneriaceae, IUCN Red List, Panama, *Paradrymonia*.

INTRODUCTION

Ongoing efforts to document and monitor plant biodiversity in the Colón Province of Panama have resulted in the discovery of numerous new species. These efforts have been promoted through collaborations between Minera Panamá S.A. (MPSA) and the Missouri Botanical Garden and are aimed at mitigating impacts of a large copper mining concession. Here we describe a species that was discovered as a result of this collaboration. The new species, *Paradrymonia peltatifolia* J. L. Clark & M. Mora, is a terrestrial herb in the flowering plant family Gesneriaceae. The current circumscription of *Paradrymonia* Hanst. includes 38 species (Mora et al., 2012) and is the main focus of a Ph.D. dissertation (M. Mora, in prep.).

Paradrymonia peltatifolia J. L. Clark & M. M. Mora, sp. nov. TYPE: Panama. Colón: Distr. Donoso, helipad ZP-P9, 8 º51’5’’9N, 80 º 40’19 W, 391 m, 20 July 2011 (fl.), J. L. *Clark & L. Martínez 12550* (holotype, US; isotypes, E, K, MO, NY, PMA, SCZ, SEL, UNA). Figure 6.1.

Differs from all congeners by the presence of peltate leaf blades.

Terrestrial herb with erect to creeping stems; stems subwoody, subquadrate, sulcate, elongate with shoots to 30 cm long, each shoot with leaves apically clustered, light tan to rose-colored, hirsute; internodes longer than broad, 3–6.5 cm long near base, more clustered at apex; adventitious roots present, pinkish. Leaves opposite, unequal in a pair, the larger leaf in a pair with petioles (5–)13– 40 cm, cross-section U-shaped, wine-red, densely hirsute; the blade (9–)16–21 3 7–16 cm, peltate with petiole attached 2–5 cm above margin of the leaf blade, ovate to orbiculate with dentate and ciliate margins, apex long-acuminate, base rounded, dark green and glabrescent to puberulous above, light green or purplish and hirsute along veins below; the lateral pairs of veins 5 or 6, departing midvein at a 50°–60° angle, tertiary veins distinct, reticulate; the smaller leaf strongly reduced, to 1 cm long, ovate to lanceolate, with serrate margins. Inflorescence a reduced pair-flowered cyme with 2 to 4 flowers that appear in axillary clusters, the prophylls oblong with ciliate margins, less than 10 × 1 mm, reddish green; the pedicels 1–4 cm long, rose-colored, hirsute. Flowers with calyx lobes subequal, 1.5–2 3 0.5–1.1 cm, ovate to lanceolate, hirsute, pale green to rose, serrate; corolla posture oblique relative to the calyx, ca. 3.5–4.5 cm long, trumpet-shaped, spurred at base for 5 mm, white to white suffused with pink, red streaks present in throat, sparsely sericeous, inside throat covered with glandular trichomes on upper surface, lobes 5, entire, subequal, ca. 10 3 10 mm, glabrous within; androecium with 4 stamens, included, didynamous, the filaments adnate for ca. 3 mm to the base of corolla tube, to 3 cm, white, glabrous, each anther apically coherent to its homologous pair, each anther 2 3 1 mm, the thecae dehiscent by longitudinal slits; gynoecium with the ovary ovoid, 4–4.5 mm, densely sericeous with long reddish trichomes, style ca. 2.1 cm, with sparsely distributed pubescence, stigma capitate, disc of a single bilobed gland on dorsal surface, ca. 2.3 mm long, entire, glabrous. Fruit a greenish yellow, bivalved, semi-fleshy (not succulent) capsule appearing laterally compressed; seed fusiform, striate, black, 5 × 3 mm, embedded in a fleshy funicle.

Distribution and habitat. *Paradrymonia peltatifolia* is endemic to Panama and is known only from the type locality in Colón Province. The lowland vegetation (i.e., below 500 m) of the

Caribbean slope where *P. peltatifolia* thrives is classified as Tropical Wet Forest (Holdridge, 1978).

IUCN Red List category. The only known populations of *Paradrymonia peltatifolia* are located inside a region that will be developed for a copper mine by MPSA. Population sizes of 10 to 15 individuals clustered along muddy streams were observed by the first author in two different localities. Six days of fieldwork during the summer of 2011 resulted in documenting one population near MPSA's Colina camp and a second population near helipad ZP-P9 (*J. L. Clark & L. Martinez 12578*). There are no known populations outside the copper mine concession, and therefore significant efforts are being implemented by MPSA to cultivate and transplant *P. peltatifolia*. These conservation efforts are ongoing for *P. peltatifolia* and other species as a way to mitigate the impacts to 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, *P. peltatifolia* should be listed in the category CR (Critically Endangered).

Phenology. *Paradrymonia peltatifolia* has been collected in flower in March and July and in fruit in July.

Etymology. The specific epithet is derived from the Latin pelta, meaning shield; it refers to the petiole attachment near the center of the blade (Fig. 6.1.C) instead of the more common attachment near the margin. A peltate leaf attachment is often associated with orbicular blades that appear shield-shaped.

Discussion. *Paradrymonia peltatifolia* is distinguished from its congeners by the presence of peltate leaves, in contrast to the more ubiquitous character state of blades that are attached at their basal margin to the petiole. *Paradrymonia peltatifolia* is the only known species of *Paradrymoni*a with peltate leaves. This unusual vegetative character is uncommon in the New World members of Gesneriaceae. It is also known to occur in *Drymonia peltata* (Oliv.) H. E. Moore, which is an endemic species of the very humid forests of the central Pacific slopes of Costa Rica. Another New World gesneriad, endemic to Colombia and with seemingly peltate leaves, is *Nautilocalyx peltatus* (C. V. Morton) Wiehler. Morton (1945) noted in the description that the petiole is attached 3–7 mm above the margin of the leaf blade.

However, the holotype and isotypes (*R. D. Metcalf & J. Cuatrecasas 30098*) of *N. peltatus* do not appear to have peltate leaves, despite the specific epithet and details provided in the description by Morton. Other species of Gesneriaceae with peltate leaves include *Sinningia tuberosa* (Mart.) H. E. Moore from Brazil, *Metapetrocosmea peltata* (Merr. & Chun) W. T. Wang from China, and *Cyrtandra peltata* Jack from Sumatra. Additional characters that differentiate *Paradrymonia peltatifolia* from its congeners are ovate to orbicular leaf blades (vs. elongate to broadly oblong) with dentate margins and white tubular corollas suffused with pink (vs. uniformly white, yellow, or red).

Paratypes. PANAMA. Colón: Distr. Donoso, Conseción de Minera Panamá S.A., Quebrada Colina, sendero to Sinaí, 300–400 m from camp. Colina, 8º50’9.4”N, 80º39’46.6”W, 200–220 m, 15 July 2011 (fl., fr.), *J. L. Clark & J. De Gracia 12450* (MO, PMA, SCZ, SEL, UNA, US); Distr. Donoso, Conces. Minera Panamá S.A., helipad ZP-P9, 8º 51’59”N, 80º40’19”W, 391 m, 20 July 2011 (fl.), *J. L. Clark & L. Martinez 12578* (MO, PMA, SEL, UNA, US); Teck Cominco Mining Concession, Camp Colina, forests along Quebrada Colina, 8º49’50”N, 80º39’30”W, 152 m, 2 Mar. 2008 (fl.), *M. Merello & J. I. Gonzalez* 3172 (MO).

ACKNOWLEDGMENTS.

This research was made possible through funding provided by the National Science Foundation to J. L. C. (DEB-0841958 and DEB-0949169). Blanca M. Araúz Servellón and José De Gracia from MPSA provided essential logistical support to the Cobre mine site in Colón Province during the summer of 2011. Additional logistical support was provided by Alvin Zapata, Laurencio Martinez, and Alex Guevara. This discovery was greatly facilitated by initial work by Mary Merello, Pete Lowry, Peter P. Phillipson, and Gordon McPherson from the Missouri Botanical Garden in collaboration with MPSA. We gratefully acknowledge helpful reviews from Alain Chautems, Christian Feuillet, and Laurence E. Skog.

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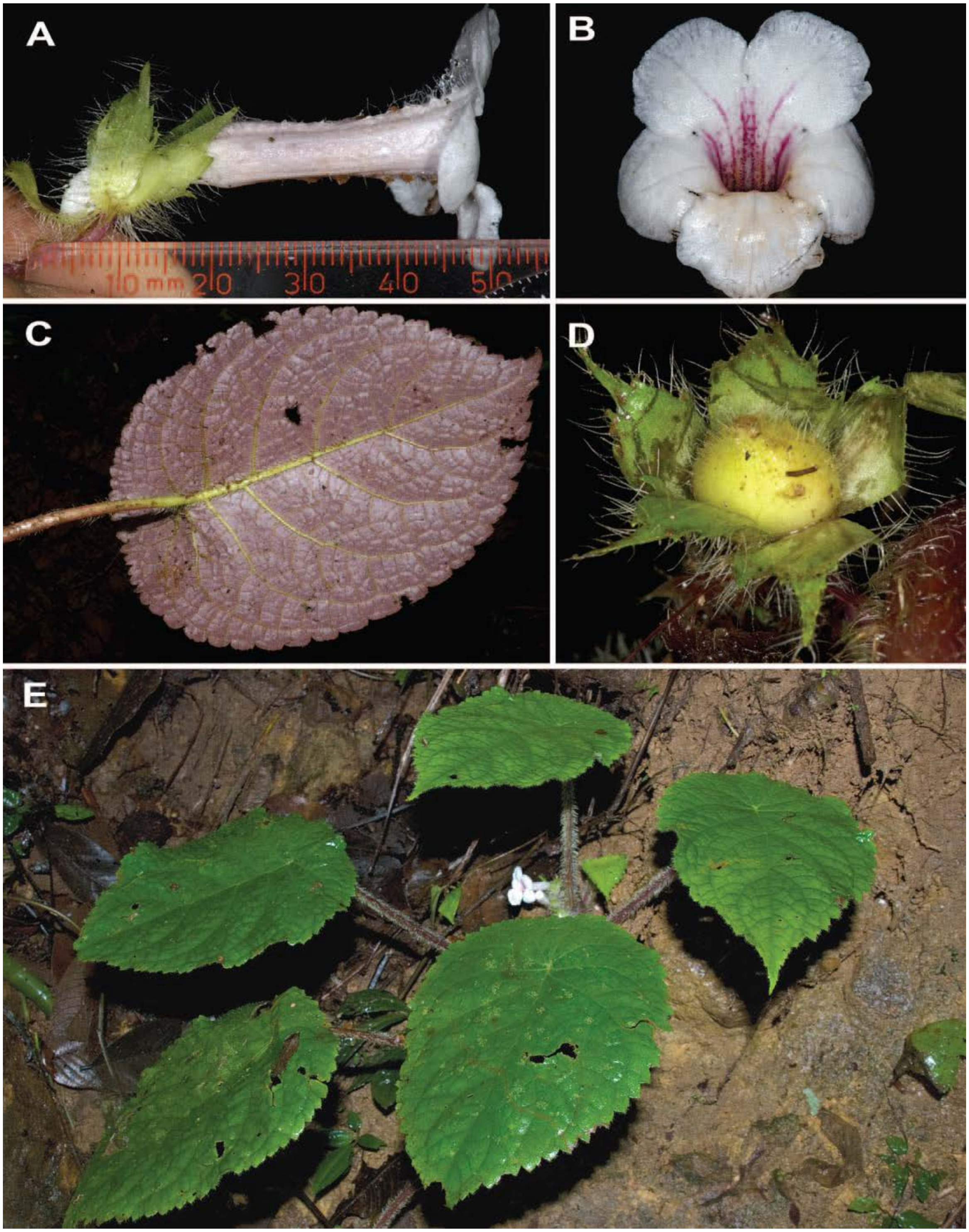

Figure 6.1. *Paradrymonia peltatifolia* J. L. Clark & M. M. Mora. —A. Lateral view of flower. —B. Front view of corolla. —C. Abaxial leaf surface showing peltate blade. —D. Immature fruit. —E. Habit showing clusters of leaves with peltate blades. Images of field collections in A, B, and E are from *J. L. Clark & L. Martinez 12550* (holotype, US), C from *J. L. Clark & L. Martinez 12578* (US), and D from *J. L. Clark & J. De Gracia 12450* (US).

CHAPTER VII

Nautilocalyx erytranthus (Gesneriaceae), A New Species from Northwestern Amazonia[1]

ABSTRACT

A new species from western Amazonia is described and illustrated. *Nautilocalyx erytranthus* (Gesneriaceae) is characterized by an obligate terrestrial habit; leaf blades that are cuneate to attenuate at the base; corolla red, funnelform with an oblique limb and reflexed petal lobes with glandular trichomes clustered on the lateral and lower inner surfaces of the throat.

RESUMEN

Se describe y se ilustra una nueva especie del occidente Amazónico. *Nautilocalyx erytranthus* (Gesneriaceae) se caracteriza por su hábito estrictamente terrestre; por sus láminas foliares cuneadas o atenuadas en la base; y por sus flores de corola roja, infundibuliforme con un limbo oblicuo y los lóbulos de los pétalos reflexos con tricomas glandulares capitados agrupados en la superficie lateral e inferior de la garganta de la corola.

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[1] Published in: Mora, M. & Clark J.L. 2014. *Nautilocalyx erytranthus* (gesneriaceae), a new species from northwestern Amazonia. *Phytotaxa* 164: 183–189.

INTRODUCTION

The neotropical genus *Nautilocalyx* Linden *ex* Hanstein (1854: 207) is a member of the tribe Gesnerieae and subtribe Columneinae, which is the largest subtribe with 24 genera and 21% of the total species diversity in the family (Weber et al. 2013). The most recent treatment of the genus is more than one hundred years old (Sprague 1912). During the last 35 years new species of *Nautilocalyx* have been published (e.g., Skog 1974, 1989; Wiehler 1975, 1977, 1978; Skog & Steyermark 1991; Feuillet & Skog 2003; Kriebel 2004; Feuillet 2008), but there are still many undetermined specimens in museum collections. Preliminary molecular phylogenetic analyses support that *Nautilocalyx* as currently circumscribed is paraphyletic (Clark et al. 2006, 2012). An updated classification based on molecular sequence data and extensive taxon sampling will include revised circumscriptions of *Paradrymonia, Nautilocalyx,* and *Chrysothemis* (Mora and Clark in review).

Nautilocalyx erytranthus was collected by the second author during expeditions in 2006, 2007 and 2009 to the Tipituni Biological Research Station on the outskirts of the Yasuní National Park in the western Amazon basin of Ecuador. Additional research in herbaria resulted in the documentation of populations from other regions of the Amazon basin (Colombia and Peru) that indicates a relatively wide distribution.

Nautilocalyx erytranthus is commonly grown by horticulturalists and especially by members of The Gesneriad Society, Inc. It is likely that the material currently in cultivation originated from a single introduction by Richard W. Dunn that resulted from a 1995 expedition to the Aguas Negras region located in Ecuador's Cuyabeno Reserve (Dunn 1996).

TAXONOMY

Nautilocalyx erytranthus J.L. Clark & M.M. Mora, *sp. nov*. (Figs. 7.1–7.2)

Differs from congeners by the combination of the following characters: obligate terrestrial habit; elliptic to obovate leaf blades with cuneate to attenuate base; red, funnelform corolla shape; reflexed petal lobes; and clusters of glandular trichomes on the lower inner surface of throat.

Type:—ECUADOR. Orellana: Aguarico, Yasuní Biosphere Reserve, Tiputini Biodiversity Station, tierra firme rainforest, 00°38'11’’S, 76°08' 57’’W, 200 m, 24 June 2006, *J. L. Clark et al. 9484* (holotype US!; isotypes AAU!, CAS!, E!, F!, MO!, NY!, QCNE!, SEL!, UNA!).

Terrestrial herb. Stems decumbent with branching erect shoots 15–60 cm tall, subquadrate, succulent; internodes 3–7 (–10.5) cm long, glabrescent to moderately hirsute at the apical nodes, glabrescent at the basal nodes. **Leaves** opposite, subequal to slightly unequal in a pair; **petioles** 1.0–2.5 cm long, green, tinged wine-red below, usually glabrescent, sometimes hirsute in new leaves; **lamina** 7.5–17.0 × (1.5–) 3–8 cm wide, elliptic to obovate-elliptic, sometimes narrowly lanceolate with crenate-serrate margins, base cuneate to attenuate, apex acute, adaxial surface dark green, abaxial surface light green, sometimes tinged with purple, glabrescent on both surfaces; the lateral pairs of veins 6–10 (–12), departing the midrib at 45–55° angle, tertiary venation anastomosing, forming series of areoles between adjacent secondary veins reaching almost to the margin. **Inflorescence** a reduced pair-flowered cyme, of 1–2 flowers in axillary clusters, the prophylls lanceolate, entire or with glandular teeth, up to 2 cm long, green suffused with reddish purple at the margins and the apex, tomentose; the pedicels 2.5–6 cm long, green to reddish purple, pubescent. **Calyx lobes** subequal 12–25 (–30) × 5–6 (–8) mm, ovate-lanceolate, glabrescent to hirsute, light green, with 2–5 glandular teeth on the margin. **Corolla** oblique relative to the calyx, 3.3–4.5 cm long, funnelform, spurred at base; limb flattened with reflexing lobes; corolla tube pubescent with translucent hairs, distal half a narrow tube, proximal half gradually expanding; corolla lobes subequal, 1.3–2.0 cm, slightly longer than broad; throat with glandular trichomes clustered on the lateral and lower surfaces. **Androecium** of 4 stamens, included, didynamous, 2.5–3.0 cm long, the filaments adnate to the base of the corolla tube up to 5.0 mm, white, glabrous, anthers apically coherent into a square, each pair of thecae ca. 2 mm long, oblong, dehiscent by longitudinal slits. **Nectary** a bilobed dorsal gland, entire and glabrous. **Gynoecium** with an ovoid ovary, 0.7 × 0.35 mm, densely sericeous, style up to 2.0 cm long, glabrous, stigma bilobed with glandular capitate hairs. **Fruit** a bivalved capsule, seeds not seen.

Distribution and habitat:—*Nautilocalyx erytranthus* occurs in the western Amazon basin of Colombia, Ecuador and Peru (100–700 m). It grows in abundant populations (10-15 individuals) in shady areas of mature forest. The vegetation zone (Holdridge 1967) where *N. erytranthus* occurs is classified as Tropical wet forest (Twf) to Tropical rain forest (Trf).

Phenology:—*Nautilocalyx erytranthus* has been collected in flower during the months of January, March, May, June and August to November.

Etymology:—The specific epithet, *erytranthus* refers to the red flowers.

Conservation Status:—Most collections of *Nautilocalyx erytranthus* are from the protected area of the Yasuní Biosphere Reserve in Amazonian Ecuador. The distribution of *N. erytranthus* includes three countries and at least two protected areas in Ecuador (Yasuní National Park and Cuyabeno Reserve). The Yasuní Biosphere Reserve (an area that includes the Yasuní National Park) is one of the most biologically diverse forests on Earth. It encompasses an area of approximately 10,000 km2 between the Napo and Curaray rivers in the provinces of Napo and Pastaza. The Yasuní National Park was designated as a UNESCO Biosphere Reserve in 1989 and received formal protection by the Ecuadorian government's Ministerio del Ambiente. Ecuador's Congress under the presidency of Rafael Correa created an initiative to protect Yasuní National Park's natural resources by raising funds from the international community to prevent oil drilling. This initiative was abandoned in 2013 because of insufficient support and President Correa is in the process of formally opening the park for drilling. According to the IUCN Red List criteria for estimated range, area of occupancy and population size (IUCN 2001), and considering the uncertain future of habitat conservation in the Yasuní Biosphere Reserve, *Nautilocalyx erytranthus* should be listed in the category NT (Near Threatened).

Nautilocalyx erytranthus is characterized by an obligate terrestrial habit and red corollas with reflexed lobes. The presence of red flowers in *Nautilocalyx* is relatively uncommon. The leaves of *N. erytranthus*are variable in color and texture. The abaxial leaf surface is either uniformly dark red to purple or uniformly light green. Variation of leaf color was observed in populations from the Yasuní Biosphere Reserve where it is locally abundant. It was observed to be a common terrestrial herb in the Tiputini Biodiversity Station. A commonly cultivated form of *Nautilocalyx erytranthus* has bullate leaves and future studies may recognize this taxon as a heterospecific from the holotype of *N. erytranthus,* which has non-bullate leaves. The locality of the cultivated material with bullate leaves is from the Cuyabeno Reserve (Reserva de Producción

Faunística Cuyabeno) in the Sucumbios Province of Ecuador where it was collected and brought into cultivation during an expedition by Richard W. Dunn (Dunn 1996).

Nautilocalyx erytranthus is similar to *N. urticifolius* (Leeuwenberg 1958: 314) Wiehler (1978: 43), which is endemic to Colombia and also has red corollas. These species are differentiated by the presence of erect corolla lobes (i.e., non-reflexed) and leaf blades less than 8 cm long in *N. urticifolius.* The corolla lobes in *N. erytranthus* are reflexed and the leaves are longer (7.0 to 17 cm long). Many museum collections of *N. erytranthus* were annotated as *N. lucianii* (Linden & Fournier 1876: 43) Wiehler (1978: 36). The presence of variegated foliage with reticulate bullae differentiates *N. lucianii* from the non-variegated leaves and non-reticulate bullae in *N. erytranthus*. These two species are geographically isolated with *N. lucianii* endemic to Colombia (Antioquia and Caldas) and *N. erytranthus* mostly in Ecuador and Peru with a single collection from Putumayo (Fig. 7.a3).

Additional specimens examined:—Colombia. PUTUMAYO. Eastern slopes of the Cordillera Oriental, near San Diego de Colorado, tributary of Río Putumayo, between Umbria and Puerto Asis, 16 January 1945, *Ewan 16783* (US, SEL). Ecuador. ORELLANA. Cantón Aguarico, Yasuní Forest Reserve, E of Pontificia, 15 June 1995, 0°40.9'S 76°23.7'W, *Acevedo & Cedeño 7307* (US); Parque Nacional Yasuní, Pozo Amo 2, Trochas de Amosur,

0°52'S 76°0.5'W, 9-13 January 1988, *Cerón et al. 3185* (MO); Parque Nacional Yasuní, Pozo petrolero Daimi 2, 1°1'S 75°47'W, 200 m, May-June 1988, *Cerón & Hurtado 4070* (US); Cantón Aguarico, Parque Nacional Yasuní, Lagunas de Garza Cocha, 0°55'S 76°11'W, 200 m, 22 September 1988, *Cerón & Gallo 5042* (MO); Cantón Orellana, Yasuní Biosphere Reserve, Tiputini Biodiversity Station (Universidad San Francisco, Quito), sendero Guacamayo, 10°38’11”S 76°8’58”W, 200 m, May 5, 2007, *Clark et al. 9550* (NY, QCNE, SEL, UNA, US); Cantón Orellana, Yasuní Biosphere Reserve, Tiputini Biodiversity Station (Universidad San Francisco, Quito), sendero Harbia, 10°38’11”S 76°8’58”W, 200-250 m, May 20, 2008, *Clark et al. 10181* (QCNE, UNA, US); Parque Nacional Yasuní, carretera y oleoducto de Maxus en construcción, km 46 al Pozo Capiron, 0°41’S 76°29’W, 244 m, 6-12 September 1993, *Dik 357* (SEL, US); 9-11 km S of Coca on road to Auca oil field, 0°30’5”S 76°55’22”W, 5 November 1974, *Gentry 12502* (MO, US); Road from Coca (Puerto Francisco de Orellana) to oil wells of the Auca district, ca. 30 km south of Coca, 1 Oct 1973, *Lugo 2572* (SEL); 14 January 1973, *Lugo 2733* (GB, SEL); 18 November 1973, *Lugo 3442* (SEL, US); Cantón Aguarico, Samona Yuturi, Quichua community on south bank of Río Napo, 0°32’S 76°0’W, 200 m, 11 November 1991, *Neill & Rojas 9946* (MO, UNA); Cantón Orellana, Yasuní National Park, Maxus road and pipeline under construction, km 3 of NPF-Puerto Maxus branch, 0°36’S 76°29’W, 250 m, 8 June 1994, *Pitman & Aulestia 210* (US); Cantón Aguarico, Estación Científica Yasuní; alrededores de la Estación, Sendero Botánico, 0°38’S 76°30’W, 200-300 m, 12 June 1995, *Romoleroux & Foster 1696* (US); Cantón Aguarico, Estación Científica Yasuní, Río Tiputini, al noroeste de la confluencia con el Río Tivacuno, 6 km este de la carretera Maxus, km 44, desvio hacia el pozo Tivacuno, Parcela de 50 hectarias, 0°38’S 76°30’W, 200-300 m, 12 October 1996, *Romoleroux et al. 2587* (US). SUCUMBÍOS. Lago Agrio, 250 m, 31 March 1980, *Brandbyge & Asanza 30384* (US-2 sheets); San Pablo de los Secoyas, Río Wai Si Aya, small northern tributary to Río Aguarico, path going S-SE, 0°14-15’S 76°21-27’W, 300 m, 7 August 1980, *Brandbyge et al. 32573* (AAU, US-2 sheets); Cuyabeno, Aguas Negras, Indian village, 0°05’23”S 76°08’29”W, 81-191 m, April 1996, *Dunn & Smith 9604023* (live material only); Cantón Cascales, Parroquia El Dorado, cooperativa Los Angeles, Bloque 11 Compañía Santa Fe, 3 km entre La Troncal y

Los Angeles, 0°0’S 77°12’W, 250 m, 3 May 1997, *Freire et al. 2169* (US); Cantón Gonzalo Pizarro, Parroquia El Dorado, Sector Los Angeles, Pozo Rubi, petrolera Santa Fe, via desde La Troncal hacia pozo Rubi 2, km 5, 0°2’S 77°11’W, 250 m, 12 March 1998, *Freire & Vergara 3077* (US); Along Río Cuyabeno, near Puente Cuyabeno where road from Lago Agrio crosses river, 0°05’S 76°20W, 400 m, 3 April 1996, *Smith & Dunn 3397* (AAU, QCNE, SRP, US). Peru. LORETO. Provincia Maynas, Caserío Mishana, Río Nanay, Campamento no. 1, 3°50’S 73°30’W, 140 m, 19 November 1981, *Ruíz & Murphy 232* (US).

ACKNOWLEDGMENTS

Support for this project was provided by the National Science Foundation (DEB-0841958 and DEB-0949169 to JLC) and The Gesneriad Society, Inc. We thank the following herbaria for access to their collections: Smithsonian Institution’s National Museum of Natural History – Department of Botany (US), Missouri Botanical Garden (MO), Field Museum of Natural History (F), Marie Selby Botanical Gardens (SEL) and University of Wisconsin (WIS). We thank Henry Arellano for the illustration. We are especially grateful to David and Consuelo Romo from the Universidad San Francisco de Quito for arranging logistical support to visit the Estación de Biodiversidad Tiputini in 2006, 2007 and 2009. Richard W. Dunn is acknowledged for his help in documenting *Nautilocalyx erytranthus* through collections and photographs. Michael Wenzel, Laurence E. Skog and an anonymous reviewer provided helpful comments on an early version of the manuscript.

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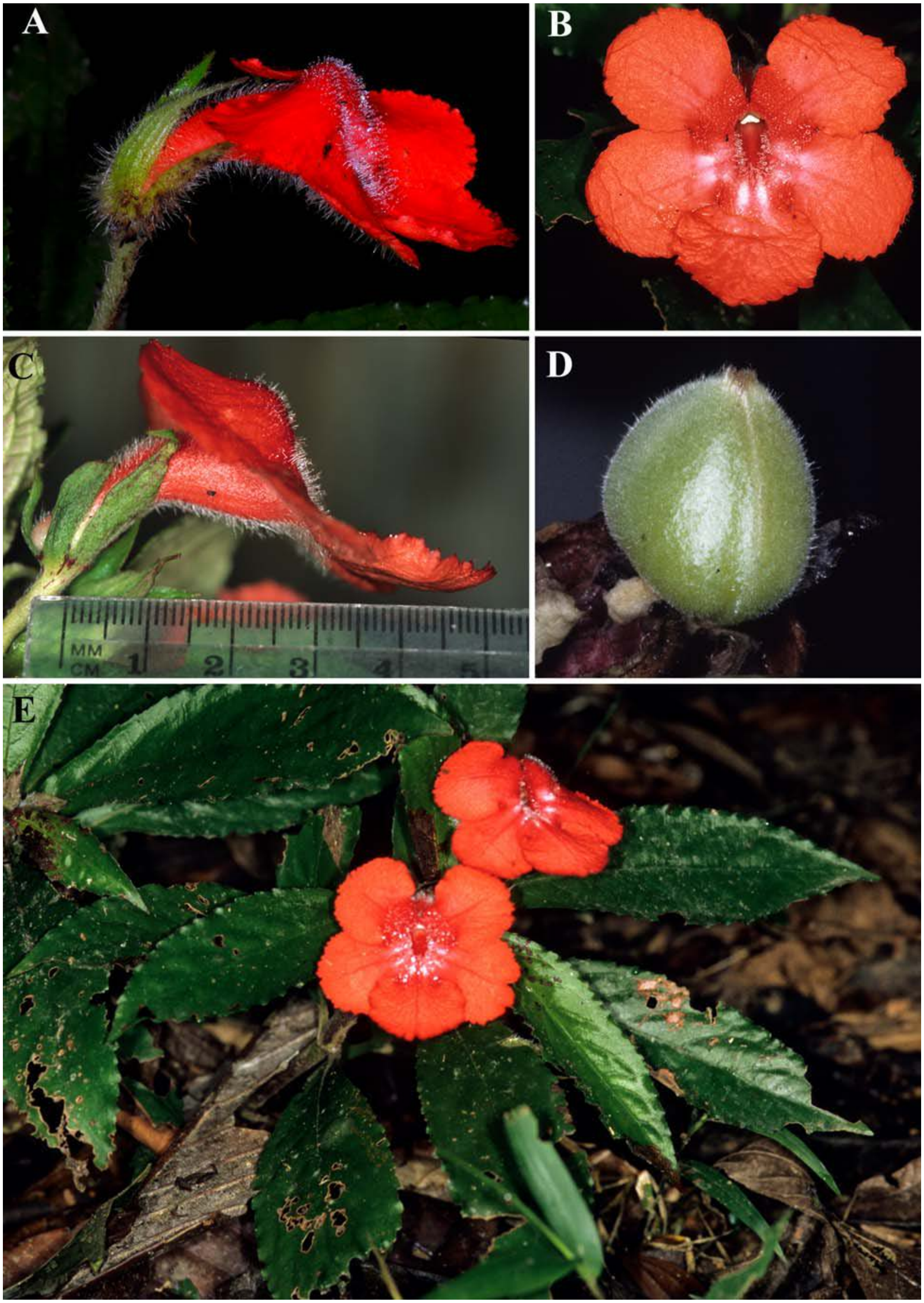

FIGURE 7.1. *Nautilocalyx erytranthus*. A. Lateral view of flower (*J.L. Clark 10181*), B. Front view of flower (*J.L. Clark 9484*), C. Lateral view of flower with ruler (*J.L. Clark 8268*), D. Immature fruit (*R.W. Dunn & J.F. Smith 9604023*), E. Terrestrial habit (*J.L. Clark 9484*).

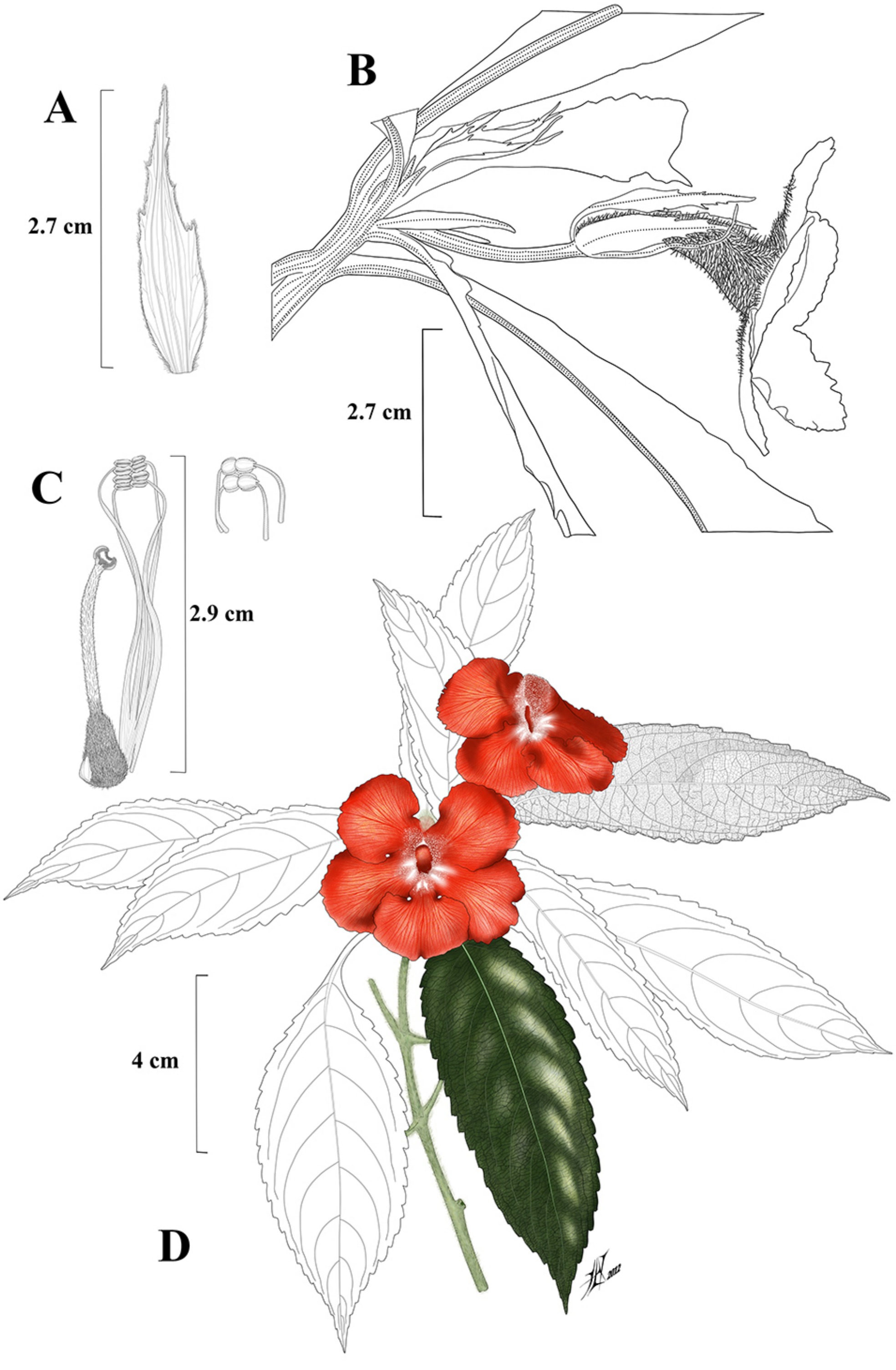

FIGURE 7.2. *Nautilocalyx erytranthus*. A. Calyx lobe. B. Lateral view of flower and foliage. C. Androecium and gynoecium. D. Habit (A–D from *J.L. Clark et al. 9550*).

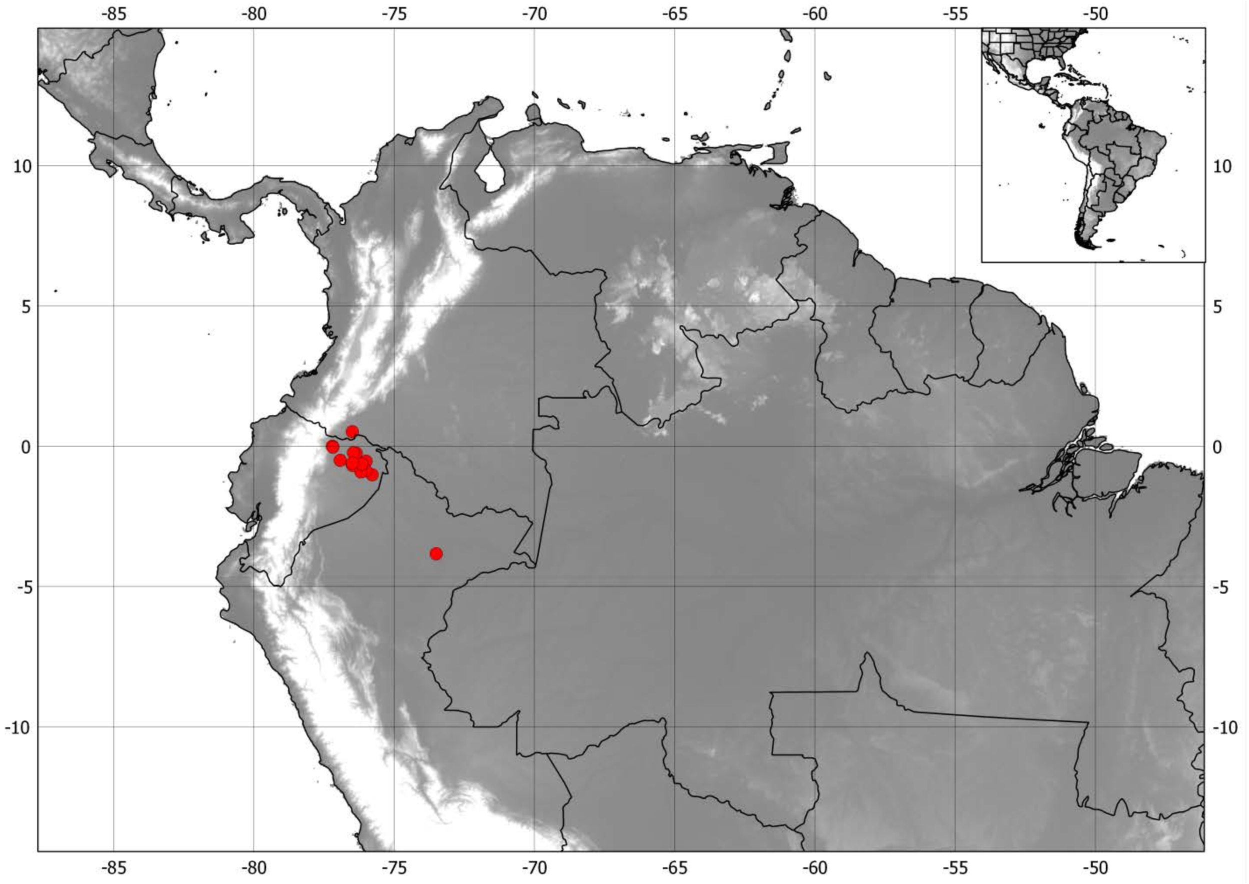

FIGURE 7.3. Distribution of *Nautilocalyx erytranthus* indicated by circles.

OVERALL CONCLUSIONS

Monophyly of *Paradrymonia* and species relationships within the genus and closely related genera in the subtribe Columneinae were evaluated based on molecular sequence data. Traditional *Paradrymonia* was found to be paraphyletic and included taxa in three clades. The clade that contained the type species, *P. glabra*, was recognized as *Paradrymonia* sensu stricto (*s.s*). The *Paradrymonia* s.s. is nested in a diverse clade referred to here as the *Paradrymonia* alliance that includes *Nautilocalyx*, *Chrysothemis* and most of the species traditionally recognized as *Paradrymonia*. The following seven well-supported clades in the *Paradrymonia* alliance are described: 1). *Paradrymonia*; 2) *Centrosolenia*; 3) Pictus clade; 4) *Chrysothemis*; 5) Amazonian "*Nautilocalyx*" Clade; 6) *Nautilocalyx* s.s. clade; and 7) *Trichodrymonia*.

Characters useful for circumscribing generic boundaries included bearded anthers, habit, presence of leaf anisophylly, and calyx lobe shape. Phylogenetic results support the resurrection of two previously recognized genera, in order to accommodate the remaining ex-*Paradrymonia* species. *Paradrymonia* was reduced to eight species, *Paradrymonia densa* was transferred to *Centrosolenia* and the remaining ex-*Paradrymonia* species were transferred to *Trichodrymonia*. New combinations, synonymies and further nomenclatural recommendations consistent with the recognition of monophyletic genera are suggested. Ancestral reconstructions suggested that the most recent common ancestor of the *Paradrymonia* alliance originated in the Guiana Shield roughly 10 Mya, diversified there, and new taxa subsequently spread radially throughout the Amazon Basin and northern Venezuela and Colombia. Multiple unidirectional shifts from entomophily to ornitophily have evolved in the *Paradrymonia* alliance. A single origin of hypocytoid corolla is strongly supported. Most of the evaluated characters for genera/clades within the *Paradrymonia* alliance were homoplastic, suggesting convergent evolution as adaptation to shady understory environments, nutrient-poor habitats, and similar pollinators among others.

The Pleistoscene Forest Refugia hypothesis was tested using paleodistribution modeling of lowland gesneriad species. Although the results supported the presence of refugia, they were not as fragmented and/or isolated as stipulated by the hypothesis. On the other hand, results presented here support the hypothesis that the Andean Mountains together with the presence of the llanos savannas of Colombia and Venezuela have created a vicariant barrier between trans-Andean (west of the Andes) and cis-Andean (east of the Andes) lowland forest taxa.

The results of this study lead to a better understanding of the taxonomy, biogeography and evolution of *Paradrymonia*, a historically taxonomic confusing and understudied genus. Future studies should target other clades within the *Paradrymonia* alliance. The paraphyletic genus *Nautilocalyx* is especially in need of revision. Additionally, the inclusion of dated phylogenies and to gain a better insight into the complex role of climate oscillations, pollination and vicariant barriers, among others mechanisms, in the evolution and diversification of gesneriads in the *Paradrymonia* alliance clade.