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

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Abstract*—Paradrymonia* Hanst. (Gesneriaceae) with 40 currently recognized species is a genus of facultative epiphytic herbs that inhabits 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) *psbA-trnH* intergenic spacer. Traditional *Paradrymonia* is resolved as polyphyletic 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, rosette habit, presence of leaf anisophylly, and lanceolate calyx lobe shape. Our results 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. Forty-three new combinations (11 in *Centrosolenia*, four in *Chrysothemis*, and 28 in *Trichodrymonia*) are made. The genus *Nautilocalyx* is moderately supported as lacking monophyly, but broader taxon sampling is necessary before new generic circumscriptions are provided.

Keywords*—Chrysothemis*, new combinations, plastid DNA, Columneinae, Gesnerieae, *Nautilocalyx*.

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; Weber et al. 2013). Pre-phylogenetic or traditional classifications had divided the family into three subfamilies (Gesnerioideae, Cyrtandroideae, and Coronantheroideae) (Wiehler 1983; Burtt and Wiehler 1995). Phylogenetic-based studies support the recognition of two subfamilies (Gesnerioideae and Cyrtandroideae) (Smith et al. 1997; Mayer et al. 2003; Weber 2004; Möller et al. 2009; Woo et al. 2011). More recently (Weber et al. 2013), a third subfamily (Sanangoideae) was added to accommodate the monotypic genus and subfamily that includes *Sanango racemosum* (Ruiz & Pav.) Barringer. 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 tribes: Beslerieae, Coronanthereae, Gesnerieae, Napeantheae, and Titanotricheae (Weber et al. 2013). Gesnerieae, the largest tribe in the family, includes what was previously classified in the following tribes: Gesnerieae, Gloxinieae, Episcieae, Sinningiae, and Sphaerorrhizeae (Weber et al. 2013). Coronanthereae (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 as 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 over 700 species (Clark et al. 2006, 2012; Clark, 2009). The Columneinae is distinguished from 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, in contrast to the conventional one-trace unilacunar nodal anatomy present in members of the other tribes of Gesnerioideae (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 *Nematanthus* Schrad.) (Wiehler 1978; Smith and Carroll 1997).

All genera in the Columneinae have been extensively evaluated (i.e. inclusion of generic type species and/or broad sampling) 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. For this study we conducted field expeditions to Central and South America to increase taxon sampling and include generic type species that were previously unavailable.

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.

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In contrast, *Paradrymonia, Nautilocalyx*, and *Chrysothemis* have traditionally been defined by a combination of symplesiomorphic characters. *Paradrymonia* has been historically recognized by its epiphytic rosette forming habit, anisophyllous leaves, campanulate corollas, and semi-fleshy bivalved dehiscent capsules; *Nautilocalyx* by an obligate terrestrial habit and isophyllous leaves; and *Chrysothemis* by an obligate terrestrial habit and connate calyx lobes.

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, which are abundant in mid-elevation montane forests (800–1,500 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 2,500 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 streambanks.

Paradrymonia is currently recognized with 40 species (Weber 2004; Skog and Boggan 2007). It is the fourth largest genus in Columneinae after *Columnea* (200 + species.), *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 yr later, Wiehler (1973) re-established *Paradrymonia* by transferring four species that were previously recognized in *Episcia* (section *Paradrymonia* (Hanst.) Leeuwenb.). Wiehler (1973) justified the re-circumscription and generic status by the presence of a rosette habit and oblong-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, 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, 2012) do not support the monophyly of *Paradrymonia*. The primary objectives of this study were 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 among *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* species.

Materials and Methods

Taxon Sampling—A total of 80 ingroup species belonging to 15 out of 22 genera of the subtribe Columneinae were sampled for the phylogenetic analyses (Appendix 1). *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 the 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).

The internal (ITS) and external transcribed spacers (ETS) of the nuclear ribosomal cistron, as well as the plastid *psbA-trnH* intergenic spacer, were sequenced for this study. 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 et al. 2003). Additionally, the combination of data from both regions has increased resolution and support (Markos and Baldwin 2001; Vander Stappen et al. 2003). The *psbA-trnH* 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 these loci: (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) *psbA-trnH* (Sang et al. 1997). Promega Taq DNA polymerase kits were used to amplify DNA in accordance with the manufacturer's instructions (Promega, Madison, Wisconsin).

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 *psbA-trnH* spacer were as follows: (1) initial denaturizing at 95°C; (2) 30 cycles of 1 min at 95°C, 30 s at 52°C, 30 s at 72°C; and (3) followed by a 7-min extension.

The PCR reactions were cleaned of 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 standard ethanol/sodium acetate 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 datasets for the phylogenetic analyses are available from TreeBASE (study number 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, *psbA-trnH*, required extensive manual editing.

Inversions for six species were detected for the *psbA-trnH* dataset. Each inverted region was replaced with its reverse complement, such that sequence homology was maximized across the alignment (Whitlock et al. 2010). Inversions are known to be frequent for the *psbA-trnH* region (Sang et al. 1997; Tate and Simpson 2003; Clark et al. 2006; Kårehed et al. 2008; 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; Štorchová 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). Additionally, inversions were scored as a presence/absence character. Three regions with a combined total of 146 characters were especially variable and difficult to align and were therefore excluded from the analyses.

Phylogenetic Analyses—Data were analyzed separately (ITS, ETS, *psbA-trnH*) for parsimony analyses, and in combination under maximum parsimony (MP), maximum likelihood (ML) (Felsenstein 1973), and Bayesian (Yang and Rannala 1997) methods.

No incongruence was detected from analyses of individual markers 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. Since there were no strongly supported nodes in conflict

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the three datasets were combined in a total evidence approach (Kluge 1989) as suggested by Seelanan et al. (1997) and Wiens (1998).

The MP analyses were performed using the heuristic search option in PAUP* (Swofford 2003) with the following settings: 100 random addition replications with tree bisection and reconnection (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 was conducted to assess support values for the MP analysis.

The best-fitting model of DNA substitution was determined using the Akaike information criterion (Akaike 1974) under ML settings as implemented by jModelTest (Posada, 2008). The best model of sequence evolution was the general time-reversible model (GTR+I+gamma) with some sites assumed invariant and with variable sites assumed to follow a gamma distribution. The following parameter estimates were obtained: (1) base frequencies of 0.2569 (A), 0.2172 (C), 0.2298 (G), 0.2960 (T); (2) 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); and (3) a gamma distribution shape parameter of 0.5030. A ML heuristic bootstrapping search was performed using the default parameters in RAxML 7.2.6 through the CIPRES portal (Stamatakis et al. 2008) for 100 replicates, repeated 10 times to generate 1,000 replicates, starting from random trees.

Bayesian posterior probabilities (PP) for the combined dataset were calculated using the Bayesian Markov Chain Monte Carlo algorithm (MCMC) of BEAST v1.8.0 (Drummond et al. 2012) to further investigate the impact of tree construction method on topology. The species tree prior was set to a Yule Process following author recommendations. We ran two independent runs of 50,000,000 generations and sampled every 5000 generations. Convergence was evaluated by comparing traces and posterior distributions of parameter estimates using Tracer (Rambaut and Drummond 2007), ensuring that the log-likelihood of the model had reached a plateau and the effective sampling size (ESS) of each parameter was at least 200 or greater. The two runs were then combined using LogCombiner after the first 25% of trees were discarded as part of the burn-in phase. The remaining trees were used to calculate posterior probabilities in a maximum credibility tree using TreeAnnotator (Drummond and Rambaut 2007) with a posterior probability threshold of 0.5 and median node. Trees were visualized in *FigTree* (Rambaut 2009).

Results

***Phylogenetic analyses*—**The total evidence analyses (MP, ML, and Bayesian inference) resulted in trees with similar topologies. The same strongly supported clades were recovered in all analyses, and differences in topology occurred only in clades with low support. Therefore, support values (Bootstrap/posterior probability values) were mapped onto the parsimony strict consensus tree (Fig. 1). The MP, ML, and Bayesian analyses of the combined regions consistently revealed three highly supported main clades in the subtribe Columneinae (Figs. 1, 2 Supplementary Fig. S1): (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).

Table 1 presents a summary of statistics for the MP analyses of the combined dataset and individual partitions. Among the individual partitions, the percentage of informative characters was highest in the ETS region (51%), while *psbA-trnH* had the lowest percentage of informative characters (14%, Table 1).

The strict consensus of the MP trees based on the plastid dataset (*psbA-trnH*) was mostly unresolved (Fig. S2), with only two pairs of species that were well-supported (BS MP > 90%) and congruent with the nrDNA datasets. Those species pairs are: *Rhoogeton cyclophyllus* + *R. viviparus* and *Nautilocalyx* sp. Mora 931 + *Nautilocalyx* sp. Mora 949 (Fig. S2). In contrast, the individual nuclear markers (e.g. ITS and ETS), as well as the combined analysis (Fig. 1), provided higher resolution and support than the plastid dataset.

The main difference between the topologies of the individual ITS and ETS consensus trees (not shown) 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 analyses result in a strongly supported sister-group relationship (BS = 100%) of the Guiana Shield clade and the Core Columneinae + *Paradrymonia* alliance clades (Fig. 1). In addition, a sister-group 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).

The traditionally recognized *Paradrymonia* is strongly supported as polyphyletic (i.e. *Paradrymonia* s. l. or Clade II in Fig. 1) based on the phylogenetic analyses of the combined datasets. 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; Figs. 1 & 2). The *Paradrymonia* alliance clade comprises seven strongly supported clades (herein referred to as clades I–VII in Figs. 1, 2). Among these clades, three contain species of *Paradrymonia* (clades I, II, and VII in Figs. 1, 2). Clade I (MP BS = 98%; ML BS = 98%; PP = 1) includes the type species (*P. glabra*), as well as *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 topology of the Bayesian maximum clade credibility (MCC) tree (Fig. 2) is more resolved than the topology of the MP tree (Fig. 1), but overall there were no strongly supported branches that are incongruent. Likewise, the ML tree (Fig. S1) is congruent with the MCC tree (Fig. 2). One main difference between the MCC (Fig. 2) tree in contrast to the MP tree (Fig. 1) is the placement of *Centrosolenia poryphyrotricha* (=*Nautilocalyx porphyrotrichus*). Its phylogenetic placement in the MCC tree is within *Centrosolenia* (Fig. 2) and it is unresolved near the base of the *Paradrymonia* alliance in the MP tree (Fig. 1). Relatively long branches (Fig. 2) were found in *Cremersia platula* (Guiana Shield clade) and *Codonanthopsis ulei* (Core Columneinae clade).

***Phylogenetic utility of ITS, ETS, and psbA-trnH*—**ITS and ETS were the most informative regions among the three markers. The nuclear regions provided four times as many parsimony-informative characters as the *psbA-trnH* cpDNA marker (Table 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). The sequence data from ETS and ITS provided more resolution and more parsimony-informative characters (Fig. S3) compared to *psbA-trnH.* Of the three markers, *psbA-trnH* resulted in the least number of variable and parsimony-informative

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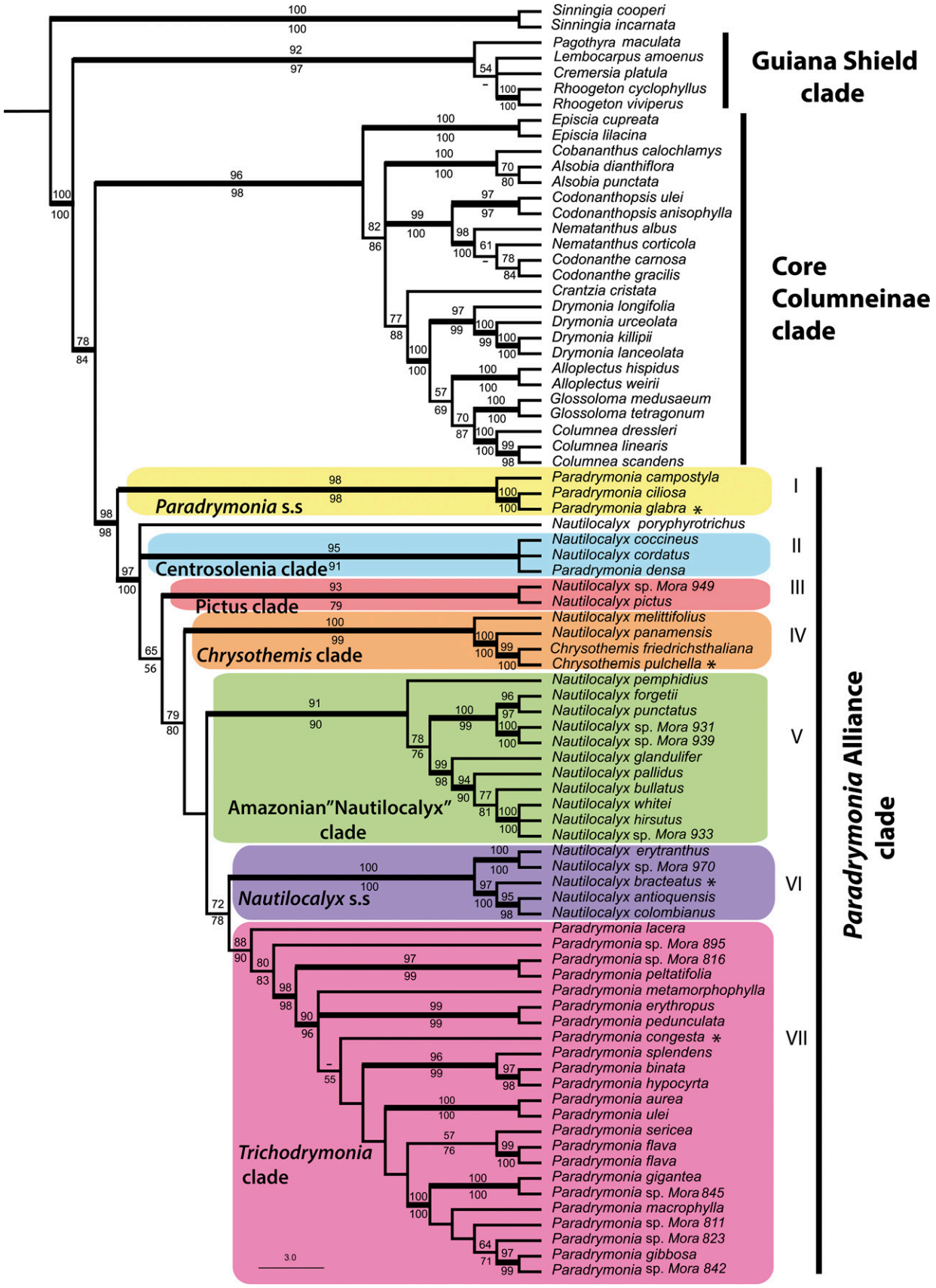


FIG. 1. Parsimony strict consensus tree from the total evidence analysis of three datasets (nrDNA ITS, nrDNA ETS, and cpDNA *trnH-psbA*) showing the three main clades within subtribe Columneinae and the principal monophyletic subclades within the *Paradrymonia* + *Nautilocalyx* + *Chrysothemis* clade (*Paradrymonia* alliance clade). MP 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.

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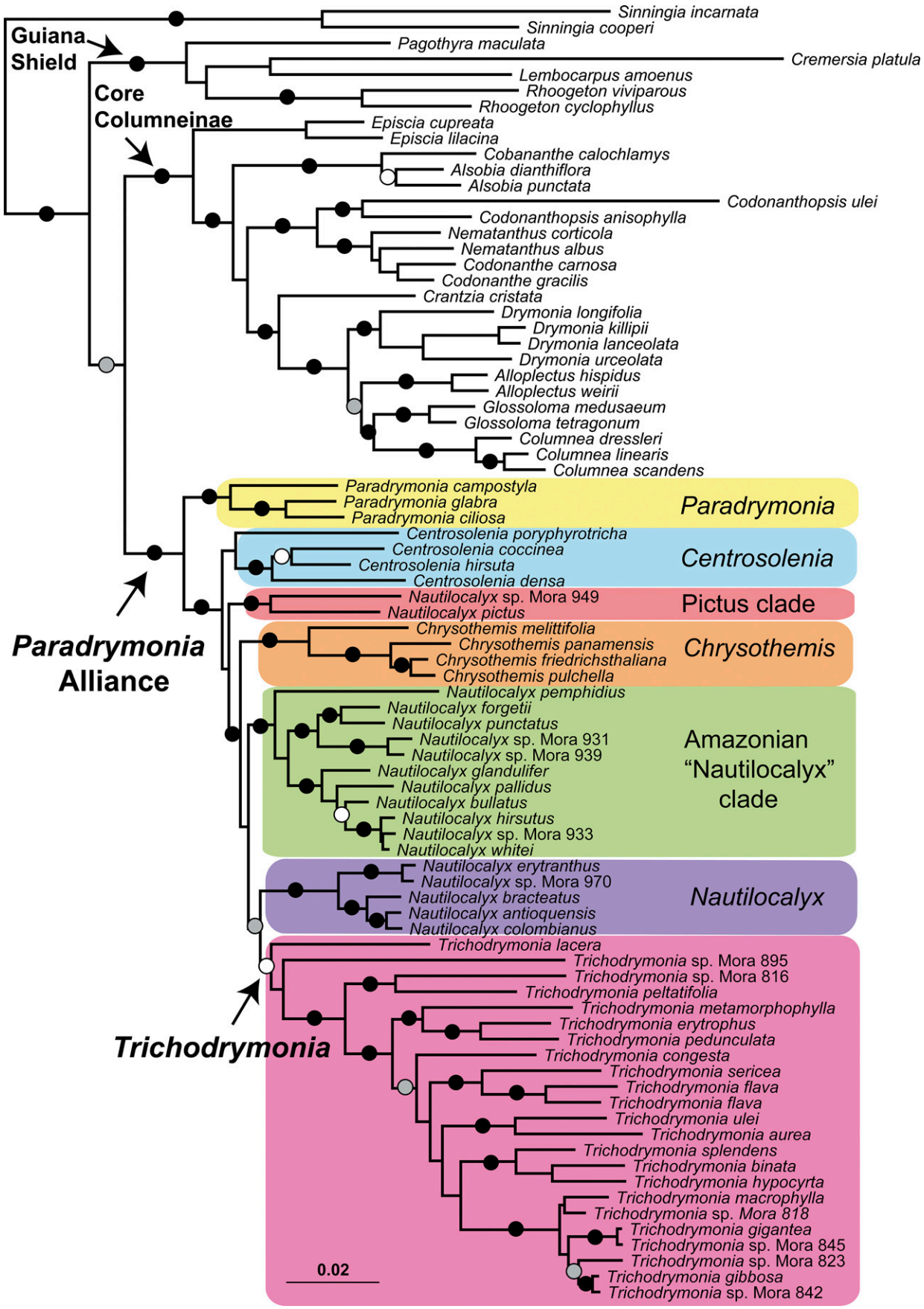


FIG. 2. Maximum clade credibility (MCC) tree of the combined dataset (ETS, ITS and *psbA-trnH*) for 82 taxa obtained from the BEAST analysis. Node support is given as Bayesian posterior probability (PP): black circles at nodes denote PP = 1.0, grey circles denote 0.95 ≤ PP ≤0.99, white circles denote 0.90 ≤ PP ≤ 0.94. Unlabelled nodes denote PP < 0.90.

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Table 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	73	82
Base pairs 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	470	1795
Number of MP trees	71	29	12	3	25
Tree length (steps)	1436	1193	2711	239	2977
Variable characters (%)	398 (52%)	373 (67%)	751 (57%)	153 (32%)	950 (53%)
Parsimony-informative characters (%)	283 (37%)	285 (51%)	576 (44%)	68 (14%)	638 (35%)
Consistency Index	0.407	0.503	0.443	0.574	0.463
Retention index	0.700	0.735	0.706	0.439	0.704

characters and provided little support for clades within the subtribe Columneinae (Fig. S2).

Discussion

***Comparison with other studies of Columneinae (=Episcieae) 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, 2012).

The placement of the Guiana Shield clade as the sister group to all the members of the subtribe Columneinae is moderately supported in our analyses (BS MP = 78%, BS ML = 84%, PP = 0.99; Figs. 1, 2). The sister-group relationship of the Guiana Shield clade with the Core Columneinae + *Paradrymonia* alliance clades is congruent with Clark et al. (2006), who used a total evidence analysis based on ITS, *psbA-trnH*, and morphological data to produce a comprehensive phylogeny of the subtribe Columneinae (155 species and 21 out of the 22 genera). However, the support for the placement of the Guiana Shield as sister clade to all of the remaining members of Columneinae 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 (ETS). The addition of ETS and increased taxon sampling resulted in more parsimony-informative characters and increased support at deep branches relative to previous studies (Table 1). The utility of ETS significantly increases support by adding 285 (51%) parsimony-informative characters compared to 283 (37%) for ITS and 165 (31%) for *psbA-trnH* (Table 1).

In contrast to Clark et al. (2006), the placement of the *Paradrymonia* alliance and Guiana Shield clades in the present study are not congruent with Clark et al. (2012). The different topology between these two studies could be attributed to the use of different loci. Clark et al. (2012) used four plastid and four nuclear loci for the analysis of the subtribe Columneinae with ITS as the only mutual marker in both studies. Interestingly, many of cpDNA markers in Clark et al. (2012) were limited in parsimony-informative characters. For example, Clark et al. (2012) generated 8,714 base pairs from 14 loci 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 + base pairs and resulted in 285 (51%) parsimony-informative characters (Table 1). An additional significant difference is taxon sampling where only 20 species are shared between the current study and Clark et al. (2012). It should be noted that the sister-group relationship of the Core Columneinae + Guiana Shield clades in Clark et al. (2012) is weakly supported in the MP and Bayesian analyses (MP BS = 61; PP = 0.77) and strongly supported in the ML analysis (ML BS = 100). In contrast, the sister-group relationship in the present study of the Core Columneinae and the *Paradrymonia* alliance clades is moderately supported in all the analyses (MP BS = 78; MP BS = 84; PP = 0.99). It is recommended that future studies of the Columneinae include ETS because it provides more parsimony-informative characters relative to previous studies that depended on large quantities of cpDNA markers that resulted in relatively few parsimony-informative characters.

Analyses by Perret et al. (2012) with a broader emphasis in the Gesnerioideae placed the *Paradrymonia* alliance clade as the sister group to all of the remaining Columneinae. One potential reason for this incongruence could be attributed to the use of plastid markers in Perret et al. (2012) in contrast to the use of nuclear markers here. A number of studies have shown that different genomes (e.g. nuclear vs. plastid markers) could produce incongruent phylogenetic trees due to different historic signals or processes such as hybridization, paralogy, incomplete lineage sorting, and scarcity of nucleotide homologies among others (e.g. Sang et al. 1997; Slovák et al. 2014; Zhang et al. 2015). Likewise, incongruence may also result from errors such as misspecification of models or problems during the sequencing and the alignment that are difficult to discard (Zhang et al. 2015).

Alternatively, discordance in tree topologies between the two studies might be due to differences in taxon sampling. The Perret et al. (2012) study lacked taxa from the Guiana Shield and included only four species from the *Paradrymonia* alliance clade (*Chrysothemis melittifolia*, *Chrysothemis pulchella*, *Trichodrymonia macrophylla*, and *Nautilocalyx aeneus*). As a result of limited taxon sampling, comparisons at the level of Columneinae phylogeny in the present study are of limited value with Perret et al. (2012).

Analyses presented support the sister-group relationship between the *Paradrymonia* alliance clade and the Columneinae core clade (Figs. 1, 2). 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*—**The alignment of the *psbA-trnH* region was particularly challenging due to the presence of numerous inversions and indels. Three regions with a total of 146 characters were especially variable and difficult to align and were

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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 *psbA-trnH* 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 *psbA-trnH* provides limited information relative to other markers and its use in future phylogenetic studies of the Gesneriaceae is not highly recommended.

Likewise, other phylogenetic studies of the Gesneriaceae have shown that the phylogenetic signal of *psbA-trnH* and other plastid markers are less informative than nuclear non-coding sequences. For example, in Clark et al. (2012), ITS yielded at least five times the percentage of phylogenetically informative characters as 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 from 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 support that when analyzed separately, 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. Therefore, the use of ETS for future analyses in the Gesneriaceae is encouraged.

Phylogenetic implications for the taxonomy of Columneinae and Paradrymonia s. l.—MP, ML, and Bayesian analyses for the combined ITS, ETS, and *psbA-trnH* datasets recovered similar phylogenies for subtribe Columneinae. Our results strongly support that *Paradrymonia* must be substantially re-circumscribed to reflect the phylogenetic results presented here (i.e. monophyletic genera). Formal nomenclatural changes regarding these findings are provided in the taxonomic section. Below we describe the clades presented in Figs. 1 and 2.

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). The restricted distribution and endemism of the Columneinae in this clade could be the outcome of geology, topography, climatic factors (Kelloff and Funk 2004; Antonelli et al. 2009; Antonelli and Sanmartín 2011), geographic barriers to dispersal (Avise 2000), and low intrinsic dispersal ability (Croteau 2010), among others. Out of the eight genera endemic to this region, seven belong to the Columneinae: *Lembocarpus* Leeuwenb., *Rhoogeton* Leeuwenb., *Lampadaria* Feuillet & L. E. Skog, *Cremersia* Feuillet & 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—The Core Columneinae clade includes *Drymonia longifolia* Poepp., which had been recognized as a member of *Paradrymonia* (Wiehler 1973) but was originally described in *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 the early stage of anthesis and then developed into longitudinal slits as the flower matured (Clark, pers. obs.). The shift from 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, 2012) strongly support the placement of *Drymonia longifolia* as a member of *Drymonia*.

Paradrymonia alliance clade—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, 2012). Our results show that this clade comprises seven moderately to strongly supported lineages (clades I–VII in Fig. 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.

PARADRYMONIA S. S. (SUBCLADE I)—*Paradrymonia* s. s. is strongly supported as monophyletic (BS = 98, PP = 1) and includes the generic type species, *Paradrymonia glabra* (Figs. 3A, B), as well as *P. ciliosa* (Figs. 3C, 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. 3F). Characters that differentiate *Paradrymonia glabra* from *P. ciliosa* include the following: *P. glabra* has white, straight corollas covered with white trichomes (Fig. 3A), while *P. ciliosa* has cream-white, angulated corollas covered with red trichomes (Fig. 3C). Additionally, *P. glabra* is endemic to the Venezuelan Andes while *P. ciliosa* is a widespread taxon that is distributed from Nicaragua to northeastern Brazil.

As defined here, *Paradrymonia* s. s. includes species with anisophyllous leaves, succulent, large elliptic-oblanceolate leaf

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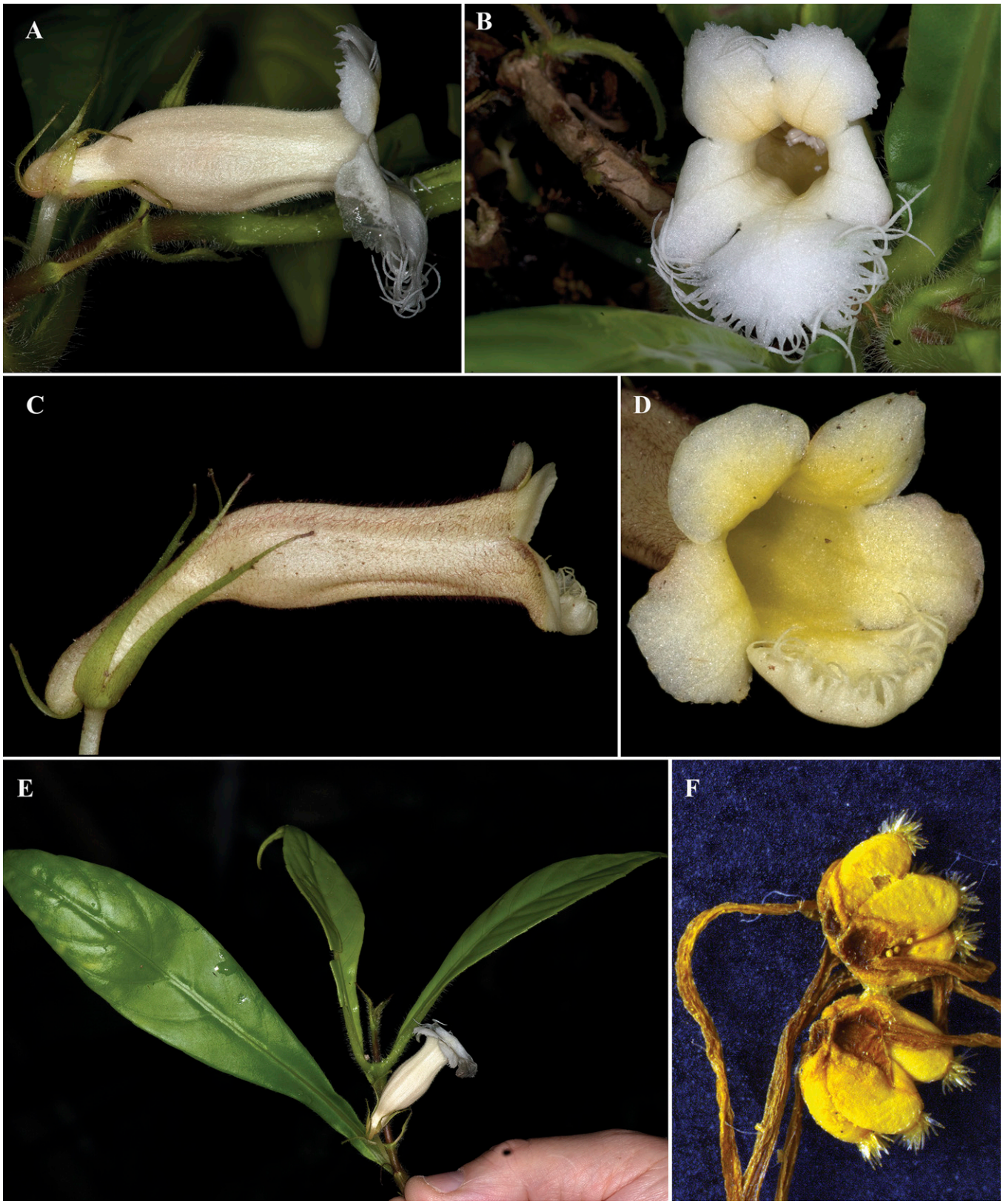


FIG. 3. *Paradrymonia* clade (*Paradrymonia* s. s. in *Paradrymonia* clade from Fig. 1). A. Lateral flower of *Paradrymonia glabra* showing straight (non-angulate corolla). B. Front view of *P. glabra* showing fimbriations on lower corolla lobe. C. Lateral flower of *P. ciliosa* showing angulate corolla. D. Flower of *P. ciliosa* showing fimbriations on lower corolla lobe. E. Leaves of *P. glabra*. F. Bearded anthers of *P. glabra*. Images from John L. Clark. A, B, and D from *J. L. Clark et al. 11331*. B and C from *J. L. Clark et al. 12490*.

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blades with decurrent bases (Fig. 3E), petioles longer than the inflorescence, flowers with calyx lobes linear to lanceolate (Fig. 3), corolla lobes crenate to fimbriate with elongate fimbriations on lower lobe (Figs. 3B, D), and anthers with an apical tuft of trichomes (i.e. "bearded anthers"; Fig. 3F). The presence of bearded anthers in *Paradrymonia* s. s. is a distinctive synapomorphy that has not been previously recognized at the generic level and 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 it is morphologically distinct from the core *Paradrymonia* clade based on the characters described above.

Centrosolenia (subclade II)—The *Centrosolenia* clade includes three species (Figs. 1, 2). *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. 4A) with asymmetrical bases and anastomosed tertiary venation; and (3) elongate narrow-tubular corollas (Fig. 4A). 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 subclade V (Amazonian "*Nautilocalyx*") and subclade VI (*Nautilocalyx* s. s.) is the presence of oblong-lanceolate to oblong-spathulate calyx lobes. The species of *Nautilocalyx* s. l. in subclades (V and VI) have calyx lobes that range from broadly ovate and leaf-like (Amazonian "*Nautilocalyx*", Fig. 4B) to linear-lanceolate (*Nautilocalyx* s. s., Figs. 4C, D). The ML and Bayesian analyses result in placing *Nautilocalyx porphyrotrichus* into *Centrosolenia*, but support is moderately low or weak (ML BS = 72; PP = 0.63; Figs. 2, S1). 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. For the reasons mentioned above, we propose to transfer *Nautilocalyx porpyrothrichus* to *Centrosolenia*. Interestingly, all of the species in the *Centrosolenia* clade represented in the phylogeny are from the Guiana Shield.

In addition to the species sampled here, it is predicted that other unsampled species 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. The genus *Centrosolenia* is re-established here with 12 new combinations (see taxonomic treatment below).

Pictus clade (subclade III)—This subclade includes *Nautilocalyx pictus* and a recently discovered, undescribed 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 melittifolius* (=*Chrysothemis melittifolia*), and *N. panamensis* (=*Chrysothemis panamensis*) (Figs. 1, 2). 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. 4E). These calyces have been described as "water calyces" because they often retain water and 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 floral herbivore.

The present phylogenetic analysis supports the expansion of *Chrysothemis* to include *N. panamensis*, and *N. melittifolius*. We also include new combinations for *N. adenosiphon* and *N. colonensis* in *Chrysothemis* based on the study of herbarium specimens. 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 V)—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. 4B). The calyx lobes are also leaf-like and cover the basal

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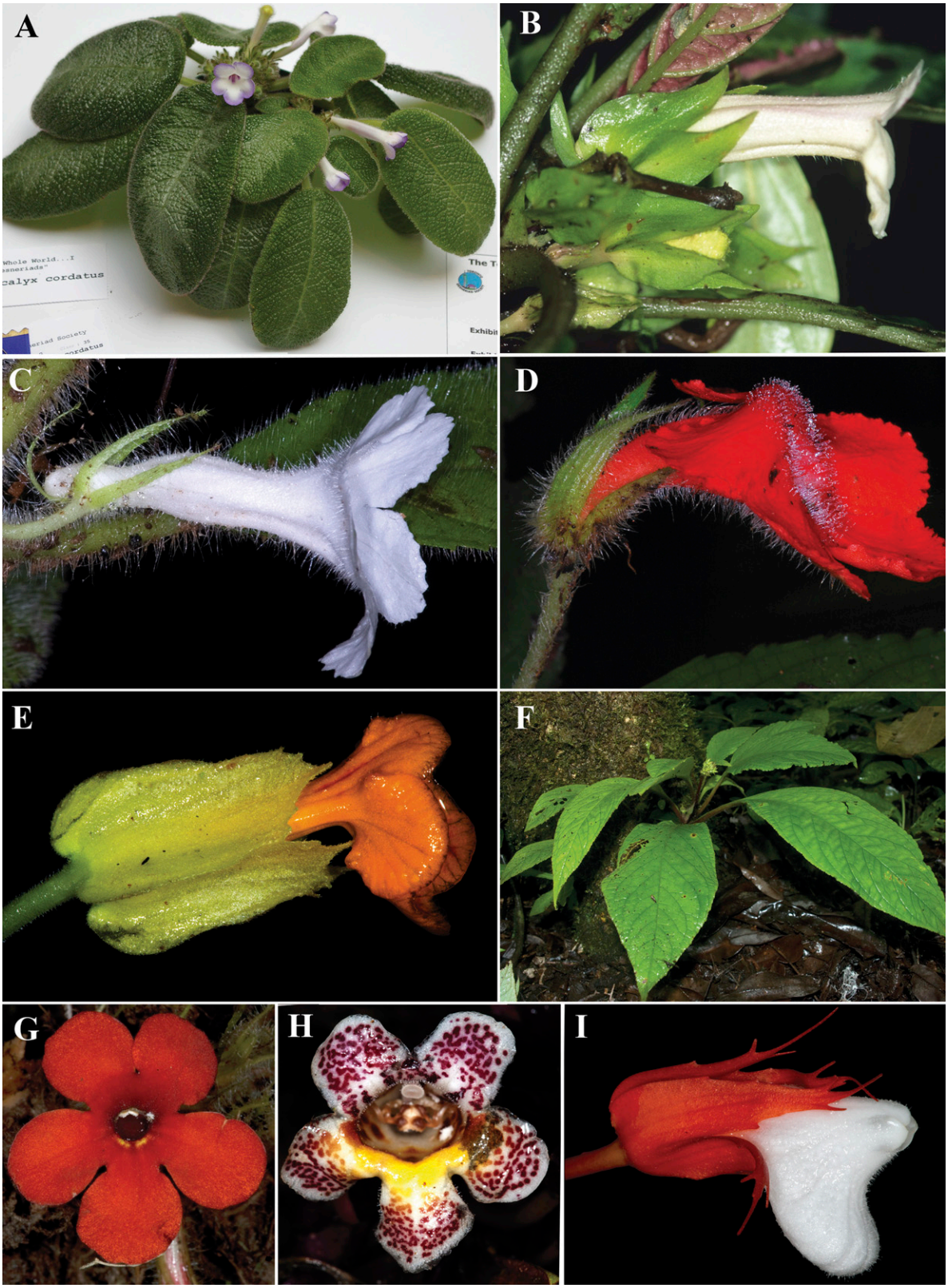


FIG. 4. Morphological characters in selected species from the *Paradrymonia* clade (from Fig. 1). A. *Centrosolenia hirsuta* (= *Nautilocalyx cordatus*, *Centrosolenia* clade) showing variegated leaves and elongate tubular corollas. B. Front view of *Nautilocalyx ecuadoranus* (Amazonian "Nautilocalyx" 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. *Trichodymonia pedunculata* (= *Paradrymonia pedunculata*; *Trichodrymonia* clade) showing rosette habit and elongated leaves with decurrent base. G–H. Flowers showing absence of fimbriations on 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 from R. Myrh (A) and J. L. Clark (B–I).

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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 surfaces (Fig. 4B). The *Nautilocalyx* s. s. clade has calyx lobes that are nearly free, linear-lanceolate, and the corolla spur is exposed (Figs. 4C, D).

Nautilocalyx s. s. clade (subclade vi)—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 the circumscription of *Nautilocalyx*. The genus was established by Hanstein (1854) in an introduction on genera of Gesneriaceae in the New World, but 11 yr 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. 4C), and the recently described species of *Nautilocalyx erytranthus* (Fig. 4D). This clade is defined by a funnel- or trumpet-shaped corolla with spreading 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 Andes and inter-Andean valleys of Colombia. One exception is *N. erytranthus* (Fig. 4D), which occurs to the 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-yr 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 *Paradrymoni*a 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. 4F), 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. 4G–I) and presence in the latter (Figs. 4A–F). Additionally, bearded anthers are present in *Paradrymonia* (Fig. 3) and absent in *Trichodrymonia*. The following characters define *Trichodrymonia*: (1) facultative epiphytic herbs; (2) leaves clustered in an apical rosette (Fig. 4F); (3) maroon sulcate petioles; (4) corollas salverform (Fig. 4G) to trumpet-shaped (Fig. 4H), and occasionally hypocyrtoid (Fig. 4I); (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 traditionally recognized *Paradrymonia* provide the most resolved phylogeny available for the genus. *Paradrymonia* as previously defined is taxonomically evaluated and recircumscribed. New combinations are provided that are consistent with the recognition of monophyletic genera based on the present phylogeny and inferred morphological synapomorphies. *Paradrymonia* is reduced to eight species (See taxonomic treatment), while the remaining ex-*Paradrymonia* species are placed in other genera. *Chrysothemis* is monophyletic, but the results presented here strongly support a broader circumscription that includes some species previously recognized in *Nautilocalyx*. Our results also show that *Nautilocalyx* is clearly paraphyletic, but the recognition of additional new genera is not recommended until more comprehensive taxon sampling is included, as well as additional loci. The *Nautilocalyx* s. s. clade comprises species mostly 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-shaped 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. *Nautilocalyx* needs further taxon sampling before taxonomic changes are proposed.

Taxonomic Treatment

In the present treatment an identification key to major clades and genera in the *Paradrymonia* alliance is provided. *Trichodrymonia* and *Centrosolenia* are resurrected to accommodate species that were previously in *Paradrymonia*. Descriptions for *Chrysothemis*, *Paradrymonia* s. s. and for the resurrected genera *Trichodrymonia* and *Centrosolenia* are included. An index of names, including the new combinations, with the accepted names in bold, is provided to facilitate referencing currently recognized species circumscriptions with previous treatments (Appendix 2).

Key to the genera of the *Paradrymonia* alliance

1. Stem shorter than leaves or with leaves clustered at apex forming a rosette 2
   2. Leaves equal to subequal in a pair, usually variegated in young individuals, smaller leaf shaped like the larger one, not deciduous, leaf base cuneate, rounded or subcordate; margin crenate; calyx lobes oblong-spatulate to oblong-lanceolate, rounded or bluntly acute at the apex . . . . . *Centrosolenia*

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2. Leaves strongly unequal in a pair, never variegated, smaller leaf usually stipule-like or deciduous, leaf blade typically long decurrent on the petiole; margin serrate to serrulate, calyx lobes usually lanceolate to linear-lanceolate, acuminate at apex . . . 3
3. Ventral lobe of corolla entire, anthers glabrescent . . . *Trichodrymonia*
3. Ventral lobe of corolla fimbriate, anthers bearded with an apical tuft of elongate trichomes . . . *Paradrymonia*

1. Stem longer than leaves or with leaves evenly distributed along the stem . . . 4
4. Leaves strongly unequal in a pair, the smaller one usually stipule-like or deciduous . . . *Trichodrymonia*
4. Leaves equal to moderately unequal in a pair, if unequal, the smaller leaf shaped like the larger one . . . 5
5. Stem with adventitious roots along the nodes and internodes, ventral lobe of the corolla with margin long-fimbriate . . . *Paradrymonia barbata*
5. Stem with adventitious roots absent or present only at some nodes; ventral lobe of the corolla with margin entire to crenate, serrate or short-fimbriate . . . 6
6. Corolla narrow-tubular and elongate, tube about 5 × longer than broad . . . *Centrosolenia*
6. Corolla infundibuliform, trumpet shaped or salver-form, usually with tube less than 4 × longer than broad . . . 7
7. Leaf blade coriaceous with inconspicuous tertiary venation above . . . *Paradrymonia campostyla*
7. Leaf blade usually thin with conspicuous tertiary venation above . . . 8
8. Plants terrestrial, epiphytic, lithophytic or vining; stem decumbent, creeping or repent on the substrate; calyx lobes free or nearly free, usually narrow, linear-lanceolate, oblanceolate, never overlapping or conduplicate . . . 9
9. Stems usually more than 1 m long, flowers usually several per leaf axil; calyx lobes lanceolate to oblanceolate, corolla lobes less than 1 cm long (Amazon Basin and Guianas) . . . *Pictus* clade
9. Stems less than 1 m long, flowers usually 5 or fewer per leaf axil; infundibuliform to salverform calyx lobes linear-lanceolate to ovate-lanceolate; corolla lobes 1 cm or longer (Central America, Colombian inter-Andean valleys and Amazon Basin) . . . *Nautilocalyx* s. s.
8. Plants terrestrial; stem predominantly erect, free-standing; calyx lobes connate into a cup or if free, relatively wide, ovate-lanceolate, overlapping at the base or with margins folded in a conduplicate manner such that each lobe is appressed to an adjacent lobe and folded lengthwise with the margin curved upward . . . 10
10. Plants forming tubers, leaf blade usually ovoid-elliptic to elliptic, usually rounded or subcordate at base and ± oblique, sometimes decurrent into the petiole; leaf margin crenate to crenate-dentate; calyx lobes nearly free or usually connate into a tube, calyx lobes green, red or yellow; corolla yellow, orange, purplish or white, sometimes with the limb with red striations . . . *Chrysothemis*
10. Plants never forming tubers, leaf blade usually oblanceolate, and attenuate at base, decurrent into the petiole; leaf margin serrate; calyx lobes connate only at the very base, green or tinged with purple; corolla cream-white or light yellow, sometimes with the limb with spots wine-red to maroon-red . . . Amazonian "*Nautilocalyx*" clade

Centrosolenia Benth., emend. M.M. Mora & J.L. Clark

Centrosolenia Benth., London J. Bot. 5: 362. 1846.—TYPE: *Centrosolenia hirsuta* Benth.

Herbs, terrestrial or saxicolous; stems elongate, 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 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. Calyx lobes nearly free, spathulate-oblong to lanceolate, apex obtuse or rounded, shallowly 2–3 repand-dentate in upper one-third. Corolla oblique in calyx, narrowly tubular, gibbous basally on upper surface with slight ovate-oblong spur, villous throughout, white, violet, or deep red, corolla lobes orbicular, nearly equal with upper two lobes slightly reduced. Androecium with stamens adnate just above the base of the corolla tube, filaments coiling after anthesis, anthers suborbicular or reniform, coherent in pairs. Disc a single dorsal nectariferous gland. Gynoecium with narrowly ovoid ovary, pilose-sericeous, stigma stomatomorphic. Fruit a semi-succulent bivalved capsule.

Distribution and habitat—*Centrosolenia* currently includes 15 species that are endemic to the Guiana Shield. Most of the species are found growing on shady banks of rivers and streams, in crevices or on wet mossy rocks, or in the understory of the rainforests. In the Guiana region, they predominantly inhabit the slopes of the high tepuis (table mountains), the summit areas of low elevation tepuis, or the understory of the forested high plains between 300 and 1500 m.

1. **Centrosolenia bryogeton** (Leeuwenb.) M. M. Mora & J. L. Clark, comb. nov. *Episcia bryogeton* Leeuwenb., Acta Bot. Neerl. 7: 312, 400. 1958. *Nautilocalyx bryogeton* (Leeuwenb.) Wiehler, Selbyana 5: 30. 1978.—TYPE: GUYANA. Cuyuni-Mazaruni: Kurupung River, near Makreba Falls, *A.S. Pinkus 12* (holotype: NY!; isotype: US!).

2. **Centrosolenia chimantensis** (L. E. Skog & Steyerm.) M. M. Mora & J. L. Clark, comb. nov. *Nautilocalyx chimantensis* L. E. Skog & Steyerm., Novon 1: 217. 1991.—TYPE: VENEZUELA. Bolívar: Chimantá Massif, common along shaded wet bluffs and by waterfall along SW-facing sandstone bluffs and Chimantá-tepuí (Toronotepuí), near southern corner, 1700 m, 19–20 May 1953, *J.A. Steyermark 75473* (holotype: US!; isotypes: F!, VEN).

3. **Centrosolenia coccinea** (Feuillet & L. E. Skog) M. M. Mora & J. L. Clark, comb. nov. *Nautilocalyx coccineus* Feuillet & L. E. Skog, Brittonia 54: 352. 2003 ("2002").—TYPE: GUYANA. Potaro-Siparuni: 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!).

4. **Centrosolenia crenata** (Feuillet) M. M. Mora & J. L. Clark, comb. nov. *Nautilocalyx crenatus* Feuillet, J. Bot. Res. Inst. Texas 2: 825. 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,

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825 m, 4 May 1970 (fl), *J. A. Steyermark & G. Bunting 103068* (holotype: US!; isotypes: NY!, VEN!).

5. **Centrosolenia densa** (C. H. Wright) Sprague, Bull. Misc. Inform. Kew 1912: 87. 1912. *Episcia densa* C. H. Wright, Bull. Misc. Inform. Kew 1895: 17. 1895. *Paradrymonia densa* (C. H. Wright) Wiehler, Selbyana 5: 50. 1978.—TYPE: GUYANA. River Masouria, *G.S. Jenman 2414* (holotype: K!).

6. Centrosolenia hirsuta Benth., London J. Bot. 5: 362. 1846. *Episcia hirsuta* (Benth.) Hanst., Linnaea 34: 350. 1865 ("1865-1866"), non *Nautilocalyx hirsutus* (Sprague) Sprague (1912).—Type: Venezuela. Amazonas: banks of the Río Paramu ["Parama" in the protologue], *R.H. Schomburgk s.n.* (holotype: K!). The type label says "British Guiana" but this is an error based on expedition itineraries that were published by Rivière (2006) and van Dam (2002).

Episcia cordata Gleason, Bull. Torrey Bot. Club 58: 466. 1931. *Nautilocalyx cordatus* (Gleason) L.E. Skog in L. E. Skog & Steyerm., Novon 1: 217. 1991.—TYPE: VENEZUELA. Amazonas: Tate 878 (holotype: NY!, isotypes: K!, US!).

7. **Centrosolenia orinocensis** (Feuillet) M. M. Mora & J. L. Clark, comb. nov. *Nautilocalyx orinocensis* Feuillet, J. Bot. Res. Inst. Texas 2: 833. 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.C. Croizat 429* (holotype: NY!).

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

9. **Centrosolenia porphyrotricha** (Leeuwenb.) M. M. Mora & J. L. Clark, comb. nov. *Episcia porphyrotricha* Leeuwenb. Acta Bot. Neerl. 7: 311, Figure 26. 1958. *Nautilocalyx porphyrotrichus* (Leeuwenb.) Wiehler, Phytologia 27: 308. 1973.—TYPE: GUYANA. Cuyuni Mazaruni: Pakaraima Mountains, Wenamu River, Jul 1925 (fl), *Davenport 7* (holotype: K!).

10. **Centrosolenia pusilla** (Feuillet) M. M. Mora & J. L. Clark, comb. nov. *Nautilocalyx pusillus* Feuillet, J. Bot. Res. Inst. Texas 2: 827. 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!).

11. **Centrosolenia rosea** (Feuillet) M. M. Mora & J. L. Clark, comb. nov. *Nautilocalyx roseus* Feuillet, J. Bot. Res. Inst. Texas 2: 830. 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!).

12. **Centrosolenia rubra** (Feuillet) M. M. Mora & J. L. Clark, comb. nov. *Nautilocalyx ruber* Feuillet, J. Bot. Res. Inst. Texas 2: 830. 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!).

13. **Centrosolenia vestita** (Feuillet) M. M. Mora & J. L. Clark, comb. nov. *Nautilocalyx vestitus* Feuillet, J. Bot. Res. Inst. Texas 2: 833. 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!).

Chrysothemis Decne., emend. M. M. Mora & J. L. Clark

Chrysothemis Decne., Rev. Hort. (Paris) ser. 3.3: 242. 1849.—TYPE: *Chrysothemis pulchella* Donn ex Sims

Herbs, terrestrial; tubers usually present; stems succulent, subquadrangular, erect, branched or not, mostly with spreading adventitious roots at the base. Leaves opposite, subequal in a pair; petiole flattened above, maroon or green, often winged along the margin; leaf blades elliptic or oblong-elliptic to oblong-lanceolate, apex acuminate, base cuneate and decurrent onto petiole or acute to rounded or subcordate at base and ± oblique, margins crenate or crenate-serrate, dark green above, paler green or purplish below, usually with margins red or purple; ends of primary veins arcuate, secondary veins reticulate. Inflorescence axillary, with or without peduncles, sometimes an umbellate or rarely compound umbellate, sometimes reduced to a single axillary flower, shorter than the subtended leaf; bracts, oblong, lanceolate or linear. Calyx lobes green, red or yellow, frequently fused for most of their length or sometimes connate only at the very base or free; usually fused in an elongate tube, when free the lobes are ovate. Corolla yellow, orange, purple or white, usually spotted or lined on the limb, trumpet-shaped nearly erect in the calyx or sometimes oblique in the calyx, base gibbous, rarely spurred, glabrous or pilose outside, inside with glandular hairs in the throat; tube cylindrical; limb spreading; lobes 5, subequal, suborbicular, entire. Androecium with 4 stamens, didynamous, included, connate at the base, inserted at the base of the corolla, anthers orbicular, dehiscent by a longitudinal slit. Gynoecium with superior ovary, pubescent, ovoid, style mostly glabrous, erect; stigma bilobed, pubescent with glandular hairs. Disc usually a single dorsal nectary gland, rarely four. Fruit a globose bivalved capsule. Seeds dark brown, obliquely striate, funiculi elongate, white, translucent.

***Distribution and habitat*—** A genus of nine species native to the West Indies, Mexico (Chiapas), Guatemala to Colombia, Venezuela, Guyana, Surinam, French Guiana and Brazil (Amazonas). Growing in shaded areas along roads and streams of wet forests.

1. **Chrysothemis adenosiphon** (Leeuwenb.) M. M. Mora and J. L. Clark, comb. nov. *Episcia adenosiphon* Leeuwenb. Acta Bot. Neerl. 18: 585. 1969. *Nautilocalyx adenosiphon* (Leeuwenb.) Wiehler, Selbyana 5: 29. 1978. TYPE: Venezuela. Bolívar, *Steyermark 88162* (holotype: WAG!; isotypes: VEN, WAG).

2. **Chrysothemis colonensis** (Wiehler) M. M. Mora and J. L. Clark, comb. nov. *Nautilocalyx colonensis* Wiehler, Selbyana 5: 89. 1978. TYPE: type collection made from

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greenhouse-grown plant (origin of material: Panama. Colón, Río Escandaloso, tributary of Rio Boquerón, near Mina #2, 20 May 1978, *R. Dressler 5817,* (PMA)), cultivated at the Marie Selby Botanical Gardens, MSBG live accession no. W-2573, 24 Aug 1978, *H. Wiehler 78137* (holotype: SEL!; isotypes: BH!, K!, MO!, NY!, PMA!, US!).

3. Chrysothemis dichroa Leeuwenb., Acta Bot. Neerl. 7: 331. 1958.—TYPE: COLOMBIA. Vichada, *R. Spruce 3612* (holotype: K!; isotypes: BM!, BR!, P!, W)

4. Chrysothemis friedrichsthaliana (Hanst.) H. E. Moore, Baileya 2: 87. 1954. *Tussacia friedrichsthaliana* Hanst., Linnaea 34: 337. 1865.—TYPE: GUATEMALA or PANAMA, *E. Friedrichsthal 3612* (holotype: W; isotypes: F, W).

5. Chrysothemis kuhlmannii Hoehne, Sellowia 9: 43. 1958.—TYPE: BRAZIL. Mato Grosso, J. *Kuhlmann 2300* (holotype: R).

6. **Chrysothemis melittifolia** (L.) M. M. Mora and J. L. Clark, comb. nov. *Besleria melittifolia* L. Sp. Pl. 2: 619. 1753. *Episcia melittifolia* (L.) Mart., Nov. Gen. Sp. Pl. 3: 42. 1829. *Skiophila melittifolia* (L.) Hanst., Linnaea 26: 207, 215, 1853. *Alloplectus melittifolius* (L.) Mart. ex Loud., ("mellitifolia") Encycl. Pl. (new ed.) : 1402. 1855. *Chrysothemis melittifolia* (L.) G. Don, ("melissaefolia"), Encycl. Pl. (new ed.) : 1402. 1855. *Episcia melittifolia* var. *typica* Urb., Symb. Antill. 2 : 354. 1901. *Episcia melittifolia* f. *typica* (Urb.) Stehlé, Bull. Soc. Bot. France 109: 31. 1962. *Episcia melittifolia* f. *guadalupensis* (DC.) Stehlé, Bull. Soc. Bot. France 109: 32. 1962. *Nautilocalyx melittifolius* (L.) Wiehler, Phytologia 27(5): 307. 1973. *Nautilocalyx melittifolius* var. *guadalupensis* (DC.) Fournet, comb. illeg., Fl. Ill. Phan. Guad. Mart. 1325. 1978.— Type: plate 48 in Burmann, Plant Amer. Car. Plumier. 1756 as "*Besleria pedunculis ramosis.*" (neotype, designated by Leeuwenberg, 1958: 308).

Besleria guadalupensis DC., Prodr. 7: 538. 1839. *Episcia guadalupensis* (DC.) Hanst. Linnaea 34 : 345. 1865.—TYPE: GUADELOUPE. *L'Herminier s.n.* (lectotype: G-DC).

Chrysothemis venosa Decne., Rev. Hort. [ser. 3, 3] 21 : 242. 1849.

7. **Chrysothemis panamensis** (Seem.) M. Mora and J. L. Clark, comb. nov. *Scheeria panamensis* Seem. Bot. Voy. Herald: 185. 1854. *Nautilocalyx panamensis* (Seem.) Seem., Bot. Voy. Herald, Suppl. 250. Figure 26. 1854. *Achimenes panamensis* (Seem.) Hemsl. in Godm. & Salv., Biol. Cent.-Amer., Bot. 2 : 475. 1882. *Episcia panamensis* (Seem.) C.V. Morton Acta Bot. Venez. 2(2): 71. 1966.— Type: Panama. *Seemann 235* (holotype: BM!; isotype: K!).

Drymonia villosa Kunth & Bouché, Index Seminum [Berlin] 1847: 12. 1847. *Episcia villosa* (Kunth & Bouché) Hanst., Linnaea 34: 348. 1865. *Nautilocalyx villosus* (Kunth & Bouché) Sprague, Bull. Misc. Inform. Kew 1912: 88. 1912.— Type: Venezuela, Caracas, Malcato. *Gollmer s.n.* (holotype: B†).

Episcia inclinata Brandegee, Univ. Calif. Publ. Bot. 6: 63. 1914.—TYPE: MEXICO: Chiapas: Finca Mexiquito, *Purpus 6851* (holotype: UC; isotypes: BM, F, MO!, NY!, US!, WAG(2)).

8. Chrysothemis pulchella (Donn ex Sims) Decne. *Besleria pulchella* Donn, nom. nud., *Besleria pulchella* Donn ex Sims, Bot. Mag. 28: pl. 1146. 1808. *Episcia pulchella* (Donn ex Sims) Mart. ex G. Don, Gen. Syst. 4: 656. 1838. *Tussacia pulchella* (Donn ex Sims) Riechenb. ex Walp., Repert Bot. Syst. 6: 740. 1847. *Skiophila pulchella* (Donn ex Sims) Hanst., Linnaea 26: 207. 1854.— Type: type collection made from cultivated material, "Cult. Hort. Kew," *J. Woodford s.n.* (holotype: BM).

Besleria melittifolia sensu Drapiez, non L., *Besleria umbellata* Herb. Banks ex Sims, nom. nud. pro syn.

Chrysothemis aurantiaca Decne., Rev. Hort. [ser. 3,4] 22: 381. 1855.— Type: type collection made from cultivated plant (origin of material: Colombia), cultivated at Culta H.R.P. [cultivé à Paris] Serre chaude, Aug 1850 (lectotype designated by Leeuwenberg, 1958: P!).

Cyrtandromoea minor Ridl., J. Straits Branch Roy. Asiat. Soc. 49: 20. 1908.—TYPE: MALAYSIA: Sarawak. HT: *Anon. s.n.* (SING).

Tussacia woodsonii C.V. Morton, Ann. Missouri Bot. Gard. 26: 308. 1939.—TYPE: PANAMA: Chiriquí: between Río Chiriquí and Remedios,15-50 m, 11 July 1938. *Woodson, Allen & Seibert 1195* (holotype: US!; isotypes: GH, MO!, NY!, US!).

Chrysothemis villosa (Benth.) Leeuwenb., Acta Bot. Neerl. 7: 338. 1958. *Tussacia villosa* Benth., London J. Bot. 5: 363. 1846.—TYPE: Guyana. Upper Takutu-Upper Essequibo, Kanuku Mts., *R. Schomburgk s.n.* (holotype: K!).

Chrysothemis semiclausa (Hanst.) Leeuwenb. Acta Bot. Neerl. 7: 338. 1958. *Tussacia semiclausa* Hanst., Illustr. Hortic. 17: 140, t. 28. 1870.— Type: Brazil. Rio Branco, *Wallis s.n. 1865* (holotype: B†?).

9. Chrysothemis rupestris (Benth.) Leeuwenb. Acta Bot. Neerl. 7: 336. 1958. *Tussacia rupestris* Benth., London J. Bot.5: 363.— Type: Guyana: Kanuku Mts., *R. Schomburgk s.n.* (holotype: K!; photos: U, WAG).

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.

Epiphytes, facultative; stems subwoody, elongate, creeping or ascending with many adventitious roots. Leaves usually clustered on a short stem, opposite, rarely equal, usually strongly unequal in a pair, when strongly anisophyllous, the smaller leaf usually sessile, reduced, subulate and early deciduous; larger leaf semi-erect and extending beyond the shoot apex; often rather long–petiolate, petiole winged adaxially (U-shaped in cross section), stout and succulent; blade of the larger leaf obovate to widely oblanceolate, acuminate at the apex, cuneate at the base or long decurrent on the petiole, coriaceous to succulent, margin serrulate sometimes with glandular teeth. Leaves of isophyllous species (i.e. *P. campostyla* and *P. barbata*) rather short–petiolate; leaf blade lanceolate to rarely oblanceolate, rounded to subcordate at base, coriaceous, hirsute, the margin crenate and ciliose. Inflorescences axillary, reduced pair-flowered cyme and appearing in fascicles; bracts linear, pedicel hirsute. Calyx lobes nearly free, hirsute; 4 subequal, linear to lanceolate, apex acuminate; fifth (ventral) lobe smaller and narrower.

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Corolla oblique in the calyx, tubular with a broad limb, base with well-developed spur, corolla lobes subequal, ventral lobe slightly larger, margins range from entire to crenate, or with fimbriations (on ventral lobe). Androecium with stamens adnate just above the base of the corolla tube, filaments coiling after anthesis, anthers oblong, elongate trichomes clustered at base (barbate), longitudinally dehiscent, coherent in pairs. Nectary reduced to a large double-connate dorsal gland, white, glabrous. Gynoecium with ovary villous or sericeous. Fruit a semi-fleshy, bivalved, dehiscent capsule.

Distribution and habitat—A genus with approximately 10 species distributed in the understory of rainforests of Central America, the Amazon basin, and the Guianas. Most species grow on moist rocks or logs in primary and secondary rainforests.

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), *T. McDowell & A. Stobey 3810* (holotype: BRG; isotypes; K! US!).

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!).

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!).

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]).— Type: 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. Limón: Finca Montecristo, on Río Reventazón, below El Cairo, 25 m, 18–19 Feb 1926. *P.C. Standley & J. 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, 23 Apr 1986, *H. Wiehler & GRF Expedition 86184* (holotype: SEL!: isotype: QCA!).

Paradrymonia glandulosa Feuillet, J. Bot. Res. Inst. Texas 3: 583. 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), *J. Steyermark & B. Holst 130443* (holotype: US!; isotypes: MO!, VEN!).

Paradrymonia hamata Feuillet, J. Bot. Res. Inst. Texas 3: 585. 2009.— Type: Venezuela. Amazonas. Depto. Río Negro, Cerro de la Neblina, Río Yatúa, 140–1700 m, 31 Dec 1957 (fl), *B. Maguire, J.J. Wurdack & C.K. Maguire 42563* (holotype: NY!).

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.—TYPE: type collection made from greenhouse-grown plant (origin of material: Venezuela, La Guayra), cultivated at the Royal Botanic Gardens, Kew, *H. Wagener s.n.* (holotype: K!; isotype: K!).

6. Paradrymonia lutea Feuillet, J. Bot. Res. Inst. Texas 3: 585. 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), *G. Davidse & J.S. Miller 27212* (holotype: US!; isotypes: MO!, NY! VEN).

7. Paradrymonia tepui Feuillet, J. Bot. Res. Inst. Texas 3: 588. 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), *R.L. Liesner & G. Carnevali 22679* (holotype: US!; isotype: MO!).

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

Trichodrymonia Oerst. emend. M. M. Mora & J. L. Clark

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

Epiphytes, facultative; stems subwoody, usually reduced to basal rosette, with numerous adventitious roots. Leaves opposite, equal to strongly unequal in a pair, usually clustered during anthesis or widely spread on an elongate shoot when young; petioles short or elongate, but always shorter than the leaf-blade, larger leaf of anisophyllous plants semi-erect and extending beyond the shoot apex; smaller leaf sessile, reduced, subulate and early deciduous; the petiole of the larger leaf of a pair well-developed, winged adaxially (U-shaped in cross section), stout and succulent, usually maroon; leaf blades obovate to widely oblanceolate, sometimes ovate, apex acuminate; base usually cuneate or long decurrent along petiole, rarely subcordate; thin to coriaceous; margin dentate to serrulate. Inflorescences many-flowered, in sessile or short-pedunculate pair-flowerd cymes; bracts linear to ovate; pedicels glabrous or hirsute. Calyx lobes nearly free, linear to lanceolate, apex acuminate, glabrous to hirsute. Corolla oblique in the calyx, infundibuliform, trumpet-shaped or salverform, rarely hypocyrtoid, spurred at the base. Androecium with stamens adnate just above the base of the corolla tube, filaments coiling after anthesis, anthers oblong, glabrous, longitudinally dehiscent, coherent in pairs. Nectary

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reduced to a large double-connate dorsal gland, white, glabrous. Gynoecium with ovary glabrous to sericeous. Fruit a semi-fleshy, bivalved, dehiscent capsule, rarely a berry.

***Distribution and habitat*—**A genus of 40 currently recognized species and 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.

1. **Trichodrymonia alata** (Kriebel) M. M. Mora & J. L. Clark, comb. nov. *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, 10°00′10″N, 83°25′30″W, 100 m, 5 Nov 1988, *G. Herrera 2287* (holotype: INB; isotype: MO!).

2. **Trichodrymonia alba** (Wiehler) M. M. Mora & J. L. Clark, comb. nov. *Paradrymonia alba* Wiehler, Selbyana 5: 46, pl. 12A. 1978.— Type: Panama. Bocas del Toro: Filo de Almirante, valley beyond ridge when approaching from Almirante, 22 May 1972, *H. Wiehler & R. Dressler 72303* (holotype: SEL!).

3. **Trichodrymonia 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: 66. 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, *J. F. Smith, R. Bernal, X. Londoño & W. Devia 1357* (holotype: SEL!; isotypes: F!, MO!, US!, WIS!).

4. **Trichodrymonia aurea** (Wiehler) M. M. Mora & J. L. Clark, comb. nov. *Paradrymonia aurea* Wiehler, Selbyana 5: 46, pl 12B. 1978.— Type: Ecuador. Pastaza: road Puyo to Canelos, 8 km E of Puyo, 21 Apr 1986, *H. Wiehler & GRF Expedition 86129* (neotype, designated by Clark et al. 2003: SEL!; isoneotype: US!).

Paradrymonia fuquaiana Wiehler, Phytologia 73: 232. 1992.— Type: Ecuador. Napo: N of Tena, road Hollin-Loreto, 21 Apr 1986, *H. Wiehler & GRF Expedition 95116* (neotype, designated by Clark et al. 2003: SEL!).

5. **Trichodrymonia binata** (Wiehler) M. M. Mora & J. L. Clark, comb. nov. *Paradrymonia binata* Wiehler, Phytologia 73: 231. 1992.— Type: Ecuador. Esmeraldas: km 5–18 on road Lita to Alto Tambo, 18 Jan 1987, *C. H. Dodson, A. Hitrz, D. Benzing, C. Luer & J. Luer 16833* (neotype, designated by Clark et al. 2003: SEL!; isoneotype: MO).

6. **Trichodrymonia conferta** (C. V. Morton) M. M. Mora & J. L. Clark, comb. nov. *Centrosolenia conferta* C. V. Morton, J. Wash. Acad. Sci. 35(4): 126. 1945. *Episcia conferta* (C. V. Morton) Leeuwenb., Acta Bot. Neerl. 8: 52. 1959. *Paradrymonia conferta* (C. V. Morton) Wiehler, Selbyana 5(1): 50. 197.— Type: Colombia. Antioquia: north of Dabeiba, on road to Turbo, 300–350 m, 25 Feb – 1 Mar 1942, *R. D. Metcalf & J. Cuatrecasas 30200* (holotype: US!; isotype: US!).

7. **Trichodrymonia congesta** Oerst., Centralamer. Gesner. 38–39. 1858. *Episcia congesta* (Oerst.) Hanst. Linnaea 34: 347. 1865. *Centrosolenia congesta* (Oerst.) C. V. Morton, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1159. 1938. *Paradrymonia congesta* (Oerst.) Wiehler, Selbyana 5: 50. 1978.— Type: Mexico. Oaxaca: Chinantla, Oct 1842, *F. M. Liebmann 9214* (holotype: C!; isotypes: C!, F!, K!, M, US!).

8. **Trichodrymonia darienensis** (Seem.) M. M. Mora & J. L. Clark, comb. nov. *Alloplectus darienensis* Seem., Bot. Voy. Herald: 187. 1854. *Episcia dariensis* (Seem.) Leeuwenb., Acta. Bot. Neerl. 8: 52. 1959. *Paradrymonia darienensis* (Seem.) Wiehler, ("dariensis"), Selbyana 5: 50. 1978.— Type: Panama. Darién: Cape Corrientes, dark woods, *B. T. Seemann 1058*; (holotype: K!; isotypes: BM!, MO!).

9. **Trichodrymonia erythropus** (Hook. f.) M. M. Mora & J. L. Clark, comb. nov. *Episcia erythropus* Hook. f., Bot. Mag. 102: t. 6219. 1876. *Paradrymonia erythropus* (Hook. f.) Wiehler, Selbyana 5: 50. 1978.—TYPE: type collection from cultivated material (origin of material: Colombia), cultivated at Royal Botanic Gardens, Kew, *Veitch s.n.* (holotype: K!).

10. **Trichodrymonia flava** (Wiehler) M. M. Mora & J. L. Clark, comb. nov. *Paradrymonia flava* Wiehler, Selbyana 5: 51, pl. 12C. 1978.— Type: Panama: Colón: Río Guanche, near Portobelo, 10 Aug 1971. *H. Wiehler & R. Dressler 71158.* (holotype: SEL; isotypes: MO!, PMA).

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

12. **Trichodrymonia gigantea** (Wiehler) M. M. Mora & J. L. Clark, comb. nov. *Paradrymonia gigantea* Wiehler, Selbyana 5: 53, pl. 12A. 1978.—TYPE: type collection made from greenhouse-grown plant (origin of material: Colombia. Valle: old road from Cali to Buenaventura, near La Elsa, 30 Apr 1972, *H. Wiehler et al. 7236* (SEL)), cultivated at Marie Selby Botanical Gardens, live accession no W-1687, 3 Nov 1976, *H. Wiehler et al. 76247* (holotype: SEL!; isotype: US!).

13. **Trichodrymonia hirta** (L. E. Skog) M. M. Mora & J. L. Clark, comb. nov. *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, cloud forest and mossy forest. *Kirkbride & Duke 1293* (holotype: MO!)

14. **Trichodrymonia hypocyrta** (Wiehler) M. M. Mora & 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, 30 May 1976, *C. H. Dodson 6092* (holotype: SEL!).

15. **Trichodrymonia lacera** (Wiehler) M. M. Mora & 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, *C. H. Dodson & A. H. Gentry 10194* (holotype: SEL!; isotypes: QCA!, QCNE!).

16. **Trichodrymonia lineata** (C. V. Morton) M. M. Mora & J. L. Clark, comb. nov. *Centrosolenia lineata* C. V. Morton,

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Ann. Missouri Bot. Gard. 29: 41. 1942. *Episcia lineata* (C. V. Morton) Leeuwenb., Acta Bot. Neerl. 8: 53. 1959. *Paradrymonia lineata* (C. V. Morton) Wiehler, Phytologia 27: 308. 1973.— Type: Panama. Coclé: hills on trail to La Mesa, north of El Valle de Anton, 1000 m, 31 Aug 1941, *P.H. Allen 2717* (holotype:US!; isotypes: MO!).

Paradrymonia lurida (C. V. Morton & Raymond) Wiehler, Phytologia 27: 308. 1973. *Episcia lurida* C. V. Morton & Raymond, Baileya 18: 9. 1971.—Type: type collection made from greenhouse-grown plant (origin of material: Costa Rica. Alajuela, Cariblanco, Sarapiqui Valley, cuttings then received by the Bailey Hortorium, Ithaca, NY through H. E. Moore) cultivated at the Jardin Botanique de Montreal, live accession no. 2209–60, Aug 1966, *C. Horich s.n.* (holotype: US!; isotype: MTJB).

17. **Trichodrymonia longipetiolata** (Donn. Sm.) M. M. Mora & J. L. Clark, comb. nov. *Episcia longipetiolata* Donn. Sm. Bot. Gaz. 25: 152–153. 1898. *Centrosolenia longipetiolata* (Donn. Sm.) C.V. Morton, Publ. Field Mus. Nat. Hist., Bot. Ser. 18 : 1159. 1938. *Paradrymonia longipetiolata* (Donn. Sm.) Wiehler, ("longipedunculata") Selbyana 5: 54. 1978.— Type: Costa Rica. Guanacaste: borders of the road to Carrillo, 300 m, Jun 1890, *A. Tonduz 2493* (holotype: US!; isotypes: BR!, CR, WAG!).

18. **Trichodrymonia macrophylla** (Wiehler) M. M. Mora & J. L. Clark, comb. nov. *Paradrymonia macrophylla* Wiehler, Selbyana 5: 56, pl. 13B. 1978.— Type: Panama. Coclé: hills N of El Valle de Anton, 15 Aug 1971, *H. Wiehler & R. Dressler 71286* (holotype: SEL!).

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

20. **Trichodrymonia metamorphophylla** (Donn. Sm.) M. M. Mora & J. L. Clark, comb. nov. *Alloplectus metamorphophyllus* Donn. Sm. Bot. Gaz. 52: 52. 1911. *Paradrymonia metamorphophylla* (Donn. Sm.) Wiehler, Phytologia 27: 327. 1973.— Type: Panama. Coclé: hills N of El Valle de Anton, 15 Aug 1971, *H. Wiehler & R. Dressler 71286* (holotype: SEL!; isotype: F!, K!, MO!, NY!, PMA, US!).

21. **Trichodrymonia ommata** (L. E. Skog) M. M. Mora & J. L. Clark, comb. nov. *Paradrymonia ommata* L.E. Skog, Brittonia 30: 324. 1978.— Type: Panama. Bocas Del Toro: Quebrada Huron, 90–120 m, 11 Apr 1968, *J. Kirkbride & J. Duke 437* (holotype: MO!; isotypes: REED, SCZ).

22. **Trichodrymonia pedunculata** (L. E. Skog) M. M. Mora & J. L. Clark, comb. nov. *Paradrymonia pedunculata* L. E. Skog, Brittonia 30: 325. 1978.— Type: Panama. Darién: Puerto St. Dorothea, 21 Jul 1962, *J. Dwyer 2268* (holotype: MO!; isotype: US!).

Rhoogeton panamensis Wiehler, Phytologia 73: 239. 1992.— Type: type collection made from greenhouse-grown plant (origin of material: Panama. Coclé: El Valle de Anton, La Mesa, 19 Jun 1978, *Dressler s. n.*), cultivated at the Gesneriad Research Foundation (GRF), live accession no. G-2633, 8 Jul 1985, *H. Wiehler 8356* (holotype: GES, not found).— Costa Rica. "Terres, rochers humides des plaines de Surubres," Jul 1890, *H Pittier & H.T. Durand 2654* [*Biolley 343*] (neotype, designated by Clark et al. 2003: US!; isotype: BR).

23. **Trichodrymonia peltata** (C. V. Morton) M. M. Mora & J. L. Clark, comb. nov. *Episcia peltata* C. V. Morton, J. Wash. Acad. Sci. 35: 131. 1945. *Nautilocalyx peltatus* (C. V. Morton) Wiehler, Selbyana 5(1): 39. 1978.— Type: Colombia. Antioquia: Collected on banks of Río Cauca at Puerto Valdivia, 240–260 m, 17–20 Feb 1942. *R.D. Metcalf & J. Cuatrecasas 30098* (holotype: US!; isotypes: F!, GH, UC).

24. **Trichodrymonia peltatifolia** (J. L. Clark & M. M. Mora) M. M. Mora & J. L. Clark, comb. nov. *Paradrymonia peltatifolia* J. L. Clark & M. M. Mora, Novon 23: 18. 2014.— Type: Panama. Colón: Distr. Donoso, helipad ZP-P9, 391 m, 08°51′5″N, 080°40′19″ W, 20 Jul. 2011 (fl.), *J. L. Clark & L. Martinez 12550* (holotype: US!; isotypes: E!, K!, MO!, NY!, PMA!, SCZ!, SEL!, UNA!).

25. **Trichodrymonia sastrei** (Wiehler) M. M. Mora & J. L. Clark, comb. nov. *Paradrymonia sastrei* Wiehler, Gesneriana 1: 71, Figure 21. 1995.— Type: Colombia. Amazonas: Río Igara-Parana (tributary of Río Putumayo), corregimiento La Chorrera, San Antonio, loma Obiraehidi, 9 Jul 1974, *C. Sastre 3608* (holotype: P!).

26. **Trichodrymonia sericea** (Wiehler) M. M. Mora & J. L. Clark, comb. nov. *Paradrymonia sericea* Wiehler, Selbyana 5: 57, pl 13C. 1978.— Type: type collection made from greenhouse-grown plant (origin of material: Colombia. Valle: old road from Cali to Buenaventura, below La Elsa, on clay cliff near waterfall, 30 Apr 1972, *H. Wiehler et al. 7261*, sterile collection at SEL), cultivated at the Marie Selby Botanical Gardens, MSBG live accession no. W-1644, 13 May 1975, *H. Wiehler 75270* (holotype: SEL!).

27. **Trichodrymonia splendens** (Freiberg) M. M. Mora & J. L. Clark, comb. nov. *Paradrymonia splendens* Freiberg, Phyton (Horn, Austria) 37: 136.1997.— Type: Ecuador. Imbabura: Los Cedros Biological Station, 17 Mar 1996, *M. Freiberg 96008* (holotype: QCA; isotype: ULM!).

28. **Trichodrymonia tylocalyx** (Wiehler) M. M. Mora & J. L. Clark, comb. nov. *Paradrymonia tylocalyx* Wiehler, Selbyana 5: 58, pl. 13D. 1978.— Type: type collection from cultivated material (origin of material: Colombia. Valle: old road from Cali to Buenaventura, below La Elsa, 30 Apr 1972, *H. Wiehler et al. 7253* (SEL)), cultivated at the Marie Selby Botanical Gardens, MSBG live accession no. W-1691, 13 May 1975, *H. Wiehler 75271* (holotype: SEL!).

29. **Trichodrymonia ulei** (Wiehler) M. M. Mora & J. L. Clark, comb. nov. *Paradrymonia ulei* Wiehler, Gesneriana 1: 71, Figure 22. 1995.— Type: Peru. Loreto: Pongo de Cainarachi, below Yurimaguas, Sep 1902, *E. Ule 6328* (holotype: HBG!).

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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 grown 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 (2015).

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

Ingroup—Alloplectus hispidus (Kunth) Mart., *J.L. Clark 7720* (US), Ecuador, DQ211111, KF040256, DQ211219; ***Alloplectus weirii*** (Kuntze) Wiehler, *J.L. Clark 5788* (US), Ecuador, AF543233, KF040257, DQ211192; ***Alsobia dianthiflora*** (H. E. Moore & R. G. Wilson) Wiehler, *J. Hall s. n.* (SEL), Cultivated (Costa Rica), DQ211160, KF040258, DQ211303; ***Alsobia punctata*** (Lindl.) Hanst. *, *J.L. Clark 8851* (US), Cultivated (Mexico), DQ211159, KF040259, DQ211302; ***Chrysothemis friedrichstaliana*** (Hanst.) H. E. Moore, *J.L. Clark* 10018 (US), Colombia, KF040179, KF040261, KF040106; ***Chrysothemis pulchella*** (Donn. Sm. ex Sims) Decne. *, *J.L. Clark 8864* (US), Cultivated (unknown), KF040180, KF040262, DQ211344; ***Cobananthus calochlamys*** (Donn. Sm.) Wiehler *, *J.L. Clark 5613* (US), Cultivated (Guatemala), AF543273, KF040263, DQ211304; ***Codonanthe***

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carnosa (Gardner) Hanst., *J.L. Clark 6268* (US), Cultivated (Brazil), AF543271, KF040264, DQ211296; ***Codonanthe gracilis*** (Mart.) Hanst., *J.F. Smith 3721* (US), Cultivated (Brazil), KF040183, KF040265, KF040110; ***Codonanthopsis anisophylla*** (Feuillet & L.E. Skog) Chautems & Mat. Perret, *H.D. Clarke 10413* (US), Guyana, DQ211181, KF040305, DQ211334; ***Codonanthopsis ulei*** Mansf., *J.L. Clark 8868* (US), Cultivated (Brazil), DQ211167, KF040260, DQ211314; ***Columnea dressleri*** Wiehler, *J.L. Clark 8559* (US), Panama, DQ211117, KF040266, DQ211230; ***Columnea linearis*** Oerst., *J.L. Clark 6274* (US), Cultivated (Costa Rica), AF543240, KF040267, DQ211243; ***Columnea scandens*** L., *J.L. Clark 8879* (US), Cultivated (unknown), KF040186, KF040268, KF040113; ***Crantzia cristata*** (L.) Scop., *J.L. Clark 6546* (US), Martinique, DQ211154, KF040269, DQ211294; ***Cremersia platula*** Feuillet & L.E. Skog *, *J.J. de Granville 14868* (CAY), French Guiana, DQ211152,—,—; ***Drymonia killipii*** Wiehler, *J.L. Clark 7521* (US), Ecuador, DQ211136, KF040270, DQ211271; ***Drymonia lanceolata*** (Hanst.) C.V.Morton, *J.L. Clark 8553* (US), Panama, DQ211139, KM079401, DQ211276; ***Drymonia longifolia*** Poepp., *J.L. Clark 6262* (US), Ecuador, AF543264, KM079371, DQ211340; ***Drymonia urceolata*** Wiehler, *J.L. Clark 5225* (US), Ecuador, AF543265, KF040273, DQ211289; ***Episcia cupreata*** (Hook.) Hanst., *J.L. Clark 8844* (US), Cultivated (Colombia), DQ211165, KF040274, DQ211312; ***Episcia lilacina*** Hanst., *J.L. Clark 8881* (US), Costa Rica, KF040194, KF040275, DQ211309; ***Glossoloma medusaeum*** (L.E. Skog) J.L.Clark, *J.L. Clark 4973* (US), Ecuador, AF543223, KF040276, DQ211200; ***Glossoloma tetragonum*** Hanst., *J.L. Clark 8547* (US), Panama, DQ211104, KF040277, DQ211207; ***Lembocarpus amoenus*** Leeuwenb. *, *J.L. Clark 8841* (US), Cultivated (French Guiana), DQ211172,—, DQ211323; ***Nautilocalyx antioquensis*** Wiehler, *M.M. Mora 806* (US), Colombia, KF040205, KF040285, KF040130; ***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, *H.D. Clarke 10295* (US), Guyana, DQ211185, KF040288, DQ211338; ***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 erytranthus*** J.L. Clark & M.M. Mora, J.L. *Clark 8268* (US), Ecuador, KF040199, KF040279, KF040125; ***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,—; ***Nautilocalyx melittifolius*** (L.) Wiehler, *J.L. Clark 6540* (US), Martinique, GQ344532, KF040293, DQ211326; ***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,—; ***Nautilocalyx pemphidius*** L.E. Skog, *D. Bell 324* (US), Venezuela, DQ211176, KF040296, DQ211328; ***Nautilocalyx pictus*** (W. Hook.) Sprague, *H.D. Clarke 9974* (US), Guyana, DQ211188,—, DQ211342; ***Nautilocalyx porphyrotrichus*** (Leeuwenb.) Wiehler, *J.L. Clark 10449* (UNA), Cultivated (unknown), KF040218, KF040297,—; ***Nautilocalyx punctatus*** Wiehler, *K. Redden 3407* (US), Venezuela, KF040219, KF040298, KF040142; ***Nautilocalyx whitei*** Rusby, *J.L. Clark 6793* (US), Bolivia, DQ211189, KF040299, DQ211343; ***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), AF543270, KF040300, DQ211318; ***Nematanthus corticola*** Schrad. *, *J.L. Clark 6271* (US), Cultivated (Brazil), AF543268, KF040301, DQ211316; ***Pagothyra maculata*** (Hook. f.) J.F. Sm. & J.L. Clark *, *K. Redden 2231* (US), French Guiana, KF040245, KF040321,—; ***Paradrymonia aurea*** Wiehler, *J.L. Clark 5409* (US), Ecuador, KF040228, KF040306, KF040150; ***Paradrymonia binata*** Wiehler, *J.L. Clark 8848* (US), Ecuador, KF040229,—, DQ211307; ***Paradrymonia campostyla*** (Leeuwenb.) Wiehler, *J.L. Clark 8855* (US), Cultivated (French Guiana), DQ211180, KF040307, DQ211333; ***Paradrymonia ciliosa*** (Mansf.) Wiehler, *H.D. Clarke 10239* (US), Guyana, DQ211182, KF040308, DQ211335; ***Paradrymonia congesta*** (Oerst.) Wiehler, *M.M. Mora 969* (US), Mexico, KF040232, KF040309, KF040154; ***Paradrymonia densa*** (C.H. Wright) Wiehler, *K. Redden 1060* (US), Guyana, DQ211184, 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 832* (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, DQ211174, KF040319, DQ211325; ***Paradrymonia macrophylla*** Wiehler, *M.M. Mora 811* (US), Ecuador, KF040244, KF040320, KF040164; ***Paradrymonia metamorphophylla*** (Donn. Sm.) Wiehler, *J.L. Clark 6028* (US), Ecuador, DQ211178, KF040322, DQ211330; ***Paradrymonia pedunculata*** L.E. Skog, *USBRG 1994-184* (US), Cultivated (Costa Rica & Panama), DQ211179, KF040323, DQ211332; ***Paradrymonia peltatifolia*** J.L. Clark & M.M. Mora, *J.L. Clark 12550* (US), Panama, KF040248, KF040324, KF040167; ***Paradrymonia sericea*** Wiehler, *M.M. Mora 838* (US), Colombia, KF040249, KF040325, KF040168; ***Paradrymonia splendens*** M.Freiberg, *J.L. Clark 7351* (US), Ecuador, DQ211173,—,—; ***Paradrymonia ulei*** Wiehler, *M.M. Mora 866* (US), Peru, KF040251, KF040326, KF040169; ***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 845**, *M.M. Mora 845* (US), Colombia, KF040239, KF040315,—; ***Paradrymonia* sp. Mora 842**, *M.M. Mora 842* (US), Colombia, KF040225, KF040303, KF040148; ***Paradrymonia* sp. Mora 895**, *M.M. Mora 895* (US), Colombia, KF040226, KF040304,—; ***Rhoogeton cyclophyllus*** Leeuwenb. *, *H.D. Clarke 10350* (US), Guyana, DQ211163, KF040327, DQ211310; ***Rhoogeton viviparus*** Leeuwenb., *H.D. Clarke 9255* (US), Guyana, DQ211164, KF040328, DQ211311.

Outgroup—Sinningia cooperi (Paxt.) Wiehler, *J.L. Clark 8857* (US), Cultivated (Brazil), DQ211097, KF040329, DQ211299; ***Sinningia incarnata*** (Aubl.) D.L. Denham, *J.L. Clark 8849* (US), Cultivated (Colombia), JQ953785, KF040330, DQ211300.

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Appendix 2. Index of names for *Centrosolenia*, *Chrysothemis*, *Paradrymonia* and *Trichodrymonia* (Accepted names in bold).

Alloplectus darienensis Seem.	***Trichodrymonia darienensis***
Alloplectus metamorphophyllus Donn. Sm.	***Trichodrymonia metamorphophylla***
Besleria melittifolia L.	***Chrysothemis melitifolia***
Besleria pulchella Donn ex Sims	***Chrysothemis pulchella***
Besleria pulchella Donn, nom. nud.	***Chrysothemis pulchella***
Centrosolenia bryogeton (Leeuwenb.) M. M. Mora & J. L. Clark	
Centrosolenia chimantensis (L. E. Skog & Steyermark) M. M. Mora & J. L. Clark	
Centrosolenia coccinea (Feuillet & L. E. Skog) M. M. Mora & J. L. Clark	
Centrosolenia conferta C. V. Morton	***Trichodrymonia conferta***
Centrosolenia congesta (Oerst.) C. V. Morton	***Trichodrymonia congesta***
Centrosolenia crenata (Feuillet) M. M. Mora & J. L. Clark	
Centrosolenia decurrens C. V. Morton	***Paradrymonia ciliosa***
Centrosolenia densa (C. H. Wright) Sprague	
Centrosolenia glabra Benth.	***Paradrymonia glabra***
Centrosolenia hirsuta Benth	
Centrosolenia lineata C.V. Morton	***Trichodrymonia lineata***
Centrosolenia orinocensis (Feuillet) M. M. Mora & J. L. Clark	
Centrosolenia paujiensis (Feuillet) M. M. Mora & J. L. Clark	
Centrosolenia porphyrotricha (Leeuwenb.) M. M. Mora & J. L. Clark	
Centrosolenia pusilla (Feuillet) M. M. Mora & J. L. Clark	
Centrosolenia rosea (Feuillet) M. M. Mora & J. L. Clark	
Centrosolenia rubra (Feuillet) M. M. Mora & J. L. Clark	
Centrosolenia vestita (Feuillet) M. M. Mora & J. L. Clark	
Chrysothemis adenosiphon (Leeuwenb.) M. M. Mora and J. L. Clark	
Chrysothemis colonensis (Wiehler) M. M. Mora and J. L. Clark	
Chrysothemis dichroa Leeuwenb.	
Chrysothemis friedrichsthaliana (Hanst.) H. E. Moore	
Chrysothemis kuhlmannii Hoehne	
Chrysothemis melitifolia (L.) M. M. Mora and J. L. Clark	
Chrysothemis panamensis (Seem.) M. M. Mora and J. L. Clark	
Chrysothemis pulchella (Donn ex Sims) Decne.	
Chrysothemis rupestris (Benth.) Leeuwenb.	
Chrysothemis semiclausa (Hanst.) Leeuwenb.	
Columnea ciliosa (Mart.) Kuntze	***Paradrymonia ciliosa***
Drymonia campostyla Leeuwenb.	***Paradrymonia campostyla***
Episcia adenosiphon Leeuwenb.	***Chrysothemis adenosiphon***
Episcia bryogeton Leeuwenb.	***Centrosolenia bryogeton***
Episcia buchtienii Mansf.	***Paradrymonia buchtienii***
Episcia ciliosa (Mart.) Hanst.	***Paradrymonia ciliosa***
Episcia conferta (C.V. Morton) Leeuwenb.	***Trichodrymonia conferta***
Episcia congesta (Oerst.) Hanst.	***Trichodrymonia congesta***
Episcia cordata Gleason	***Centrosolenia hirsuta***
Episcia dariensis (Seem.) Leeuwenb.	***Trichodrymonia darienensis***
Episcia decurrens (C. V. Morton) Leeuwenb.	***Paradrymonia ciliosa***
Episcia densa C. H. Wright	***Centrosolenia densa***
Episcia erythropus Hook. f.	***Trichodrymonia erythropus***
Episcia glabra (Benth.) Hanst.	***Paradrymonia glabra***
Episcia hansteiniana Mansf.	***Paradrymonia ciliosa***
Episcia hirsuta (Benth.) Hanst.	***Centrosolenia hirsuta***
Episcia lineata (C. V. Morton) Leeuwenb.	***Trichodrymonia lineata***
Episcia longipetiolata Donn. Sm.	***Trichodrymonia longipetiolata***
Episcia lurida C. V. Morton & Raymond	***Trichodrymonia lineata***
Episcia peltata C. V. Morton	***Trichodrymonia peltata***
Episcia porphyrotricha Leeuwenb.	***Centrosolenia porphyrotricha***
Episcia pulchella (Donn ex Sims) Mart. ex G. Don	***Chrysothemis pulchella***
Hypocyrta ciliosa Mart.	***Paradrymonia ciliosa***
Nautilocalyx bryogeton (Leeuwenb.) Wiehler	***Centrosolenia bryogeton***
Nautilocalyx chimantensis L. E. Skog & Steyermark	***Centrosolenia chimantensis***
Nautilocalyx coccineus Feuillet & L. E. Skog	***Centrosolenia coccinea***
Nautilocalyx colonensis Wiehler	***Chrysothemis colonensis***
Nautilocalyx cordatus (Gleason) L. E. Skog	***Centrosolenia hirsuta***
Nautilocalyx crenatus Feuillet	***Centrosolenia crenata***
Nautilocalyx orinocensis Feuillet	***Centrosolenia orinocensis***
Nautilocalyx panamensis (Seem.) Seem.	***Chrysothemis panamensis***
Nautilocalyx paujiensis Feuillet	***Centrosolenia paujiensis***
Nautilocalyx porphyrotrichus (Leeuwenb.) Wiehler	***Centrosolenia porphyrotricha***
Nautilocalyx pusillus Feuillet	***Centrosolenia pusilla***
Nautilocalyx roseus Feuillet	***Centrosolenia rosea***
Nautilocalyx ruber Feuillet	***Centrosolenia rubra***
Nautilocalyx vestitus Feuillet	***Centrosolenia vestita***
Nautilocalyx villosus (Kunth & Bouché) Sprague	***Chrysothemis panamensis***
Paradrymonia alata Kriebel	***Trichodrymonia alata***

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Appendix 2. (Continued).

Paradrymonia alba Wiehler	***Trichodrymonia alba***
Paradrymonia apicaudata M. M. Mora & J. L. Clark	***Trichodrymonia apicaudata***
Paradrymonia aurea Wiehler	***Trichodrymonia aurea***
Paradrymonia barbata Feuillet & L. E. Skog	
Paradrymonia binata Wiehler	***Trichodrymonia binata***
Paradrymonia buchtienii (Mansf.) Wiehler	
Paradrymonia campostyla (Leeuwenb.) Wiehler	
Paradrymonia ciliosa (Mart.) Wiehler	
Paradrymonia conferta (C.V. Morton) Wiehler	***Trichodrymonia conferta***
Paradrymonia congesta (Oerst.) Wiehler	***Trichodrymonia congesta***
Paradrymonia darienensis (Seem.) Wiehler	***Trichodrymonia darienensis***
Paradrymonia decurrens (C. V. Morton) Wiehler	***Paradrymonia ciliosa***
Paradrymonia densa (C.H. Wright) Wiehler	***Centrosolenia densa***
Paradrymonia erythropus (Hook. f.) Wiehler	***Trichodrymonia erythropus***
Paradrymonia flava Wiehler	***Trichodrymonia flava***
Paradrymonia fuquaiana Wiehler	***Trichodrymonia aurea***
Paradrymonia gibbosa Wiehler	***Trichodrymonia gibbosa***
Paradrymonia gigantea Wiehler	***Trichodrymonia gigantea***
Paradrymonia glabra (Benth.) Hanst.	
Paradrymonia glandulosa Feuillet	***Paradrymonia ciliosa***
Paradrymonia hamata Feuillet	***Paradrymonia ciliosa***
Paradrymonia hansteiniana (Mansf.) Wiehler	***Paradrymonia ciliosa***
Paradrymonia hirta L.E. Skog	***Trichodrymonia hirta***
Paradrymonia hypocyrta Wiehler	***Trichodrymonia hypocyrta***
Paradrymonia lacera Wiehler	***Trichodrymonia lacera***
Paradrymonia lineata (C. V. Morton) Wiehler	***Trichodrymonia lineata***
Paradrymonia longipetiolata (Donn. Sm.) Wiehler	***Trichodrymonia longipetiolata***
Paradrymonia lurida (C. V. Morton & Raymond) Wiehler	***Trichodrymonia lineata***
Paradrymonia lutea Feuillet	
Paradrymonia macrophylla Wiehler	***Trichodrymonia macrophylla***
Paradrymonia maguirei Feuillet	***Trichodrymonia maguirei***
Paradrymonia metamorphophylla (Donn. Sm.) Wiehler	***Trichodrymonia metamorphophylla***
Paradrymonia ommata L. E. Skog	***Trichodrymonia ommata***
Paradrymonia pedunculata L. E. Skog	***Trichodrymonia pedunculata***
Paradrymonia peltatifolia J. L. Clark & M. M. Mora	***Trichodrymonia peltatifolia***
Paradrymonia prististoma Wiehler	***Paradrymonia ciliosa***
Paradrymonia sastrei Wiehler	***Trichodrymonia sastrei***
Paradrymonia sericea Wiehler	***Trichodrymonia sericea***
Paradrymonia splendens Freiberg	***Trichodrymonia splendens***
Paradrymonia tepui Feuillet	
Paradrymonia tylocalyx Wiehler	***Trichodrymonia tylocalyx***
Paradrymonia ulei Wiehler	***Trichodrymonia ulei***
Paradrymonia yatua Feuillet	
Rhoogeton panamensis Wiehler	***Trichodrymonia pedunculata***
Scheeria panamensis Seem.	***Chrysothemis panamensis***
Skiophila melittifolia (L.) Hanst.	***Chrysothemis melittifolia***
Skiophila pulchella (Donn ex Sims) Hanst.	***Chrysothemis pulchella***
Trichodrymonia alata (Kriebel) M.M. Mora & J.L. Clark	
Trichodrymonia alba (Wiehler) M.M. Mora & J.L. Clark	
Trichodrymonia apicaudata (M. M. Mora & J. L. Clark) M. M. Mora & J. L. Clark	
Trichodrymonia aurea (Wiehler) M. M. Mora & J. L. Clark	
Trichodrymonia binata (Wiehler) M. M. Mora & J. L. Clark	
Trichodrymonia conferta (C.V. Morton) M. M. Mora & J. L. Clark	
Trichodrymonia congesta Oerst.	
Trichodrymonia darienensis (Seem.) M. M. Mora & J. L. Clark	
Trichodrymonia erythropus (Hook. f.) M. M. Mora & J. L. Clark	
Trichodrymonia flava (Wiehler) M. M. Mora & J. L. Clark	
Trichodrymonia gibbosa (Wiehler) M. M. Mora & J. L. Clark	
Trichodrymonia gigantea (Wiehler) M. M. Mora & J. L. Clark	
Trichodrymonia hirta (L. E. Skog) M. M. Mora & J. L. Clark	
Trichodrymonia hypocyrta (Wiehler) M. M. Mora & J. L. Clark	
Trichodrymonia lacera (Wiehler) M. M. Mora & J. L. Clark	
Trichodrymonia lineata (C. V. Morton) M. M. Mora & J. L. Clark	
Trichodrymonia longipetiolata (Donn. Sm.) M. M. Mora & J. L. Clark	
Trichodrymonia macrophylla (Wiehler) M. M. Mora & J. L. Clark	
Trichodrymonia maguirei (Feuillet) M. M. Mora & J. L. Clark	
Trichodrymonia metamorphophylla (Donn. Sm.) M. M. Mora & J. L. Clark	
Trichodrymonia ommata (L. E. Skog) M. M. Mora & J. L. Clark	
Trichodrymonia pedunculata (L. E. Skog) M. M. Mora & J. L. Clark	
Trichodrymonia peltata (C. V. Morton) M. M. Mora & J. L. Clark	
Trichodrymonia peltatifolia (J. L. Clark & M. M. Mora) M. M. Mora & J. L. Clark	
Trichodrymonia sastrei (Wiehler) M. M. Mora & J. L. Clark	

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Appendix 2. (Continued).

Trichodrymonia sericea (Wiehler) M. M. Mora & J. L. Clark	
Trichodrymonia splendens (Freiberg) M. M. Mora & J. L. Clark	
Trichodrymonia tylocalyx (Wiehler) M. M. Mora & J. L. Clark	
Trichodrymonia ulei (Wiehler) M. M. Mora & J. L. Clark	
Tussacia friedrichsthaliana Hanst.	***Chrysothemis friedrichsthaliana***
Tussacia pulchella (Donn ex Sims) Riechenb. ex Walp.	***Chrysothemis pulchella***
Tussacia rupestris Benth.	***Chrysothemis rupestris***
Tussacia semiclausa Hanst.	***Chrysothemis semiclausa***
Tussacia woodsonii C.V. Morton	***Chrysothemis pulchella***

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