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Authors: Galván-González, Luis G., Cerros-Tlatilpa, Rosa, Espejo-Serna, Adolfo, and Steinmann, Victor W.

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Phylogenetic Relationships of the Genera *Cladocolea* and *Struthanthus* (Loranthaceae) with Emphasis on the Mexican Species

Luis G. Galván-González,^{1,2,3} Rosa Cerros-Tlatilpa,^{2,5} Adolfo Espejo-Serna,³ and Victor W. Steinmann⁴

¹Doctorado en Ciencias Biológicas y de la Salud, Universidad Autónoma Metropolitana, Ciudad de México, México; luis.galvan@uaem.mx

²Laboratorio de Sistemática y Morfología, Facultad de Ciencias Biológicas, Universidad Autónoma del Estado de Morelos. Avenida Universidad 1001. 62209 Cuernavaca. Morelos, México; tlatilpa@uaem.mx

³Herbario Metropolitano, Departamento de Biología, División de Ciencias Biológicas, Universidad Autónoma Metropolitana. Avenida San Rafael Atlixco 186, 09340 Iztapalapa. CDMX, México; aes@xanum.uam.mx

⁴Instituto de Ecología, A.C., Centro Regional del Bajío. Avenida Lázaro Cárdenas 253, 61600 Pátzcuaro. Michoacán, México; victor.steinmann@inecol.mx or steinmav@gmail.com

⁵Author for correspondence (tlatilpa@uaem.mx)

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Abstract—*Cladocolea* (Loranthaceae) is a neotropical genus currently containing 24 species. Its taxonomic history has included changes in its circumscription and the transfers of some of its species to other genera in the family. Several phylogenetic studies of Loranthaceae have recognized a close relationship between *Cladocolea* and *Struthanthus*. However, both genera were poorly represented in these studies, so here we generate a phylogeny of Mexican species of *Cladocolea*, *Struthanthus*, and related genera of Psittacanthinae, using nuclear DNA sequences of the ITS region, as well as the chloroplast regions *matK* and *trnL-F*. The sample includes 112 new sequences and an additional 12 sequences obtained from GenBank. These represent 23 taxa of *Cladocolea*, 14 of *Struthanthus*, and 10 from nine other genera of Loranthaceae. In order to understand character evolution and estimate ancestral states, 13 morphological characters were mapped, both vegetative and reproductive. Bayesian inference and Maximum likelihood analyses were performed using independent matrices and a concatenated matrix of 2842 characters. Our results show that *Cladocolea* and *Struthanthus* are both polyphyletic genera. However, the Mexican species of *Cladocolea* and *Struthanthus* with convolute or sigmoid styles form a monophyletic group. Finally, the analysis of ancestral character states indicates a trend towards a reduction of inflorescences in the *Cladocolea-Struthanthus* complex. New combinations and synonymies are proposed.

Resumen—*Cladocolea* (Loranthaceae) es un género neotropical que actualmente comprende 24 especies. Su historia taxonómica incluye cambios en su circunscripción, así como la transferencia de algunas de sus especies a otros géneros de la familia. Varios estudios filogenéticos de Loranthaceae han reconocido una relación cercana entre *Cladocolea* y *Struthanthus*. Sin embargo, ambos géneros están escasamente representados en estos estudios, por lo que aquí generamos una filogenia de especies mexicanas de *Cladocolea*, *Struthanthus* y otros géneros de Psittacanthinae, usando secuencias de ADN nuclear de la región ITS, así como de las regiones de cloroplasto *matK* y *trnL-F*. Ciento doce individuos fueron muestreados y doce secuencias de GenBank fueron incluidas. Estos representan 23 taxa de *Cladocolea*, 14 de *Struthanthus* y 10 de otros nueve géneros de la familia Loranthaceae. Para estimar los estados ancestrales y evolución de caracteres, se mapearon 13 caracteres morfológicos vegetativos y reproductivos. Los análisis de Inferencia Bayesiana y Máxima verosimilitud fueron ejecutados usando matrices de datos independientes y una matriz concatenada de 2842 caracteres. Los resultados muestran que *Cladocolea* y *Struthanthus* son géneros polifiléticos. Sin embargo, las especies mexicanas de *Cladocolea* y *Struthanthus* con estilo convoluto o sigmoide forman un grupo monofilético. Finalmente, el análisis de estados ancestrales de carácter indica una tendencia a la reducción de las inflorescencias en el complejo *Cladocolea-Struthanthus*. Se proponen nuevas combinaciones y sinonimias.

Keywords—Mistletoes, parasitic plants, Santalales.

Cladocolea Tiegh. (Loranthaceae) is a neotropical genus of mistletoes with a complex taxonomic history that includes various changes in its circumscription. The genus was described by Van Tieghem (1895a) to accommodate four neotropical species with spike-like inflorescences, whose buds emerge from a cortical sac in the leaf axil. In the same year, van Tieghem described the genus *Loxania* Tiegh. (Van Tieghem 1895b), with two species, which is characterized by inflorescences in the form of pedunculate heads with six lateral bracteate flowers and one apical ebracteate flower. Subsequently, Kuijt (1975) recognized the genus *Cladocolea* and transferred into it the species of *Loxania*, as well as some species of *Loranthus* L., *Struthanthus* Mart., and *Phthirusa* Mart. According to Kuijt (1975), *Cladocolea* is defined by having simple, determinate inflorescences and flowers without bracteoles. However, some species currently placed in the genus do not have all these characteristics, for example, *C. cupulata*, *C. micrantha*, and *C. racemosa*.

Subsequent studies on *Cladocolea* and other neotropical genera of Loranthaceae have resulted in the description of new species and in the transfer of some *Cladocolea* species to

genera such as *Ixocactus* Rizzini (= *Phthirusa* Mart.), *Phthirusa* (sensu Eichler = *Passovia* H.Karst.), and *Peristethium* Tiegh., as well as the transfer of some species from *Phthirusa* (sensu Eichler) to *Cladocolea* (Kuijt 1987a, 1987b, 1991a, 1991b, 1992, 2003, 2009, 2011, 2012; Caires et al. 2021). Recently, Nickrent (2020) recognized 29 species in the genus, although in his study he did not include *C. spathiflora* (Galván-González et al. 2017). In addition, Carballo-Ortiz and Acevedo-Rodríguez (2019) established the name *C. biflora* as a synonym of *Schoepfia schreberi*. Subsequently, Caires et al. (2021) transferred and synonymized five South American taxa of *Cladocolea* to *Passovia*. Thus, *Cladocolea* currently comprises 24 species and is distributed from Mexico to northern South America.

The history of taxonomic and nomenclatural changes in *Cladocolea* reflects the complexity of establishing well-defined boundaries for the genus, as well as its affinity with other genera known as the small-flowered neotropical taxa (Kuijt 1981; Feuer and Kuijt 1985; Vidal-Russell and Nickrent 2008). In this regard, Kuijt (1975, 1981) emphasized a close relationship between some species of *Cladocolea* and some species of *Struthanthus*, particularly those distributed in Mexico. Both

genera share similarities in floral features and morphology, such as the presence of contortions or folds in the style and pollen (Feuer and Kuijt 1985). However, *Struthanthus* has indeterminate inflorescences that are raceme-like, spike-like, or head-like, with pedunculate or sessile paired triads (Kuijt 1981; Kuijt and Hansen 2015). The study of inflorescence morphology led Kuijt (1981) to hypothesize that evolution in floral and inflorescence structures occurred from a solitary or a group of sessile flowers in a leaf axil, passing to a more advanced stage, such as simple and determinate inflorescences, and finally developing complex structures, such as indeterminate and triadic inflorescences. Accordingly, Kuijt (1975, 1981, 2012) and Kuijt and Hansen (2015) suggested the possibility that *Struthanthus* was polyphyletic and derived from multiple ancestors with simple inflorescences similar to those of *Cladocolea*.

Previous phylogenetic studies of the family Lorantheaceae (Wilson and Calvin 2006; Vidal-Russell and Nickrent 2008; Su et al. 2015; Liu et al. 2018; Grimsson et al. 2018; Ortíz-Rodríguez et al. 2018; Nickrent et al. 2019) have confirmed the close relationship between *Cladocolea* and *Struthanthus* suggested by Kuijt (1975). Both genera, in addition to *Aetanthus* (Eichler) Engl., *Dendropemon* (Blume) Rchb., *Maracanthus* Kuijt, *Oryctanthus* (Griseb.) Eichler, *Oryctina* Tiegh., *Panamanthus* Kuijt, *Passovia*, *Phthirusa*, *Psittacanthus* Mart., and *Tripodanthus* (Eichler) Tiegh., constitute the subtribe Psithacanthinae, characterized by having a chromosome number of $n = 8$. Also, in some genera the anther connective is apiculate (Nickrent et al. 2010). However, in these studies, both *Cladocolea* and *Struthanthus* are not sufficiently represented to clarify the intergeneric and interspecific relationships. Consequently, the aim of the present study is to infer a phylogeny of *Cladocolea* and *Struthanthus*, with emphasis on the Mexican species and using nuclear and chloroplast DNA regions, test the monophyly of the genera, establish their relationships with other small-flowered neotropical Lorantheaceae, as well as understand character evolution and estimate ancestral states.

MATERIALS AND METHODS

Collection and Taxonomic Sampling—From August 2018 to June 2022, we collected specimens of small-flowered Lorantheaceae (*Cladocolea*, *Struthanthus*, *Phthirusa*, *Passovia*, and *Oryctanthus*, Fig. 1) in the Mexican states of Chiapas, Guerrero, Jalisco, Michoacán, Morelos, Oaxaca, Puebla, Tlaxcala, and Veracruz. Vouchers were deposited in the HUMO and UAMIZ herbaria (acronyms here and elsewhere following Thiers 2024); samples of healthy leaves were obtained and stored in bags with silica gel. Leaf samples were also obtained from specimens collected in Mexico and Central America, which are deposited in the HUMO, MEXU and UAMIZ herbaria. For the ingroup, material was obtained from 59 individuals representing 19 species and four undetermined taxa of *Cladocolea*, 34 individuals representing 13 species and one undetermined taxon of *Struthanthus*. We used 18 individuals representing 10 species of the genera *Oryctanthus*, *Passovia*, *Phthirusa*, *Psittacanthus* (Fig. 1), *Peristethium*, and *Tripodanthus* as the outgroup. Additionally, twelve sequences were obtained from GenBank of the genera *Aetanthus*, *Struthanthus*, and *Gaiadendron* G. Don. A complete list of species, specimens, and sequences obtained is shown in Appendix 1.

Obtaining Morphological Data—A matrix was elaborated in which 13 vegetative and reproductive characters were included; seven were binary and six were multistate. In addition, some species show polymorphisms, although alternate states occur less frequently. For inflorescence type, we follow the interpretation of Nickrent et al. (2019). We use the term cupular pedicel to refer a crateriform structure below the ovary resulting from the fusion of a recaulescent bract to the pedicel. This application ignores the description of Suaza-Gaviria et al. (2016) for genus *Passovia* and maybe

other small-flowered genera. When a flower lacked an obvious stalk, it was considered sessile. A description of the characters and their respective states is provided in Appendix 2.

DNA Extraction, Amplification, and Sequencing—Total DNA was extracted from dehydrated material collected in silica gel or from herbarium specimens using the Wizard® Genomic DNA Purification Kit (Promega, Madison, Wisconsin) and DNeasy Plant Pro Kit (QIAGEN, Valencia, California). For this study, the nuclear ribosomal ITS region (including exon 5.8s) was amplified with primers forward ITS-An5 and reverse ITS-An4 from Cheng et al. (2016). For the *trnL-F* region, primers forward B49317 and reverse A50272 from Taberlet et al. (1991) were used. Finally, for the chloroplast gene *matK*, the primers forward 78f and reverse 1420r were used from Vidal-Russell and Nickrent (2007).

PCR reactions were carried out using the GoTaq Green MasterMix 2 × kit (Promega, Madison, Wisconsin), at a final volume of 25 μ l, with a standardized DNA concentration at 50 ng/ μ l. In the case of chloroplast sequence amplification, for each reaction we used 12.5 μ l of master mix, 1.25 μ l of each primer (forward and reverse) at 10 μ M, 1 μ l of bovine serum albumin (BSA) at 8%, 1 μ l of DNA, and 8 μ l of nuclease-free water. For ITS amplification, the reaction contained 12.5 μ l of master mix, 1.25 μ l of each primer (forward and reverse) at 10 μ M, 1 μ l BSA at 8%, 1 μ l of DNA, 1.25 μ l of dimethyl sulfoxide (DMSO), and 6.25 μ l of nuclease-free water.

For the ITS region, the thermal cycler was programmed with the following parameters: initial temperature 94°C for four minutes, then 34 cycles of 94°C for 30 sec, 55°C for 40 sec, and 72°C for one minute and, lastly a final extension at 72°C for ten minutes. For the *trnL-F* region, the program consisted of an initial temperature of 95°C for five minutes, then 40 cycles at 95°C for ten seconds, 55°C for one minute, and 72°C for 20 sec, and lastly a final extension at 72°C for seven minutes. Finally, for the *matK* region, an initial temperature of 95°C for five minutes was used, followed by five cycles at 94°C for one minute, 46°C for one minute, 72°C for one minute, then 35 cycles at 94°C for 30 sec, 50°C for 30 sec, and 72°C for one minute and, lastly a final extension at 72°C for ten minutes. The amplified products were sent to Macrogen (Seoul, Republic of Korea) for purification and sequencing.

Sequence Assembly and Alignment—Forward and reverse sequences were assembled and edited with the program GeneStudio™ Pro v2.2.0.0 (GeneStudio 1999–2011), where double peaks observed in the electropherograms were marked as ambiguities. The sequences were aligned with the program MUSCLE v3.8.31 (Edgar 2004) and subsequently edited manually with the program PhyDE v0.9971 (PhyDE 2010).

Evolutionary Model Selection and Phylogenetic Analysis—Maximum likelihood (ML) and Bayesian inference (BI) analyses were performed for the set of ITS sequences and a set of concatenated chloroplast sequences (*trnL-F* and *matK*), in addition to a set of the three concatenated regions. Multiple gene sequence alignments were concatenated with Mesquite v3.7 (Maddison and Maddison 2021). The software IQ-TREE v1.6.12 (Nguyen et al. 2015) was used to build phylogenetic trees from the ML analysis. The alignments of each nuclear and chloroplast regions were analyzed with ModelFinder (Kalyanamoorthy et al. 2017) integrated in IQ-TREE, and the best substitution models were chosen under Bayesian Informative Criteria (BIC), which in the case of ITS was SYM+I+G4, while for *trnL-F* and *matK* it was K3Pu+F+G4. Support values for the ML tree were estimated using the Ultra Fast Bootstrap Support Test (UFB; Minh et al. 2013), with 10,000 replicas. Minh et al. (2013) concluded that UFB support values are more unbiased and consider that a good support value should be equal to or greater than 95%. Phylogenetic and evolutionary model selection analyses were implemented on the IQ-TREE web server.

Evolutionary models for the BI analyses were selected with the software jModelTest v2.1.10 (Darriba et al. 2012), under three substitution schemes and with the BIONJ algorithm. The selected models were GTR+I+G for the ITS alignment and GTR+G for the *trnL-F* and *matK* sequence sets. BI analyses were performed using the program MrBayes v3.2.7 (Ronquist et al. 2012) and implemented on the CIPRES platform (Miller et al. 2010). Two independent runs were performed with four Markov chains, each with 20 million generations and resampling of trees every 1000 generations to avoid autocorrelation between themselves.

The consensus tree and posterior probability (PP) values were calculated by applying a burn-in value of 0.25. Phylogenetic trees from the ML and BI analyses were visualized with the software FigTree (v. 1.4.4). In both analyses, *Gaiadendron punctatum* (tribe Gaiadendreae) was used to root the trees as the functional outgroup. The topologies obtained for each nuclear and chloroplast region were compared to verify that no conflicting differences were observed between them, e.g. clades nested in another

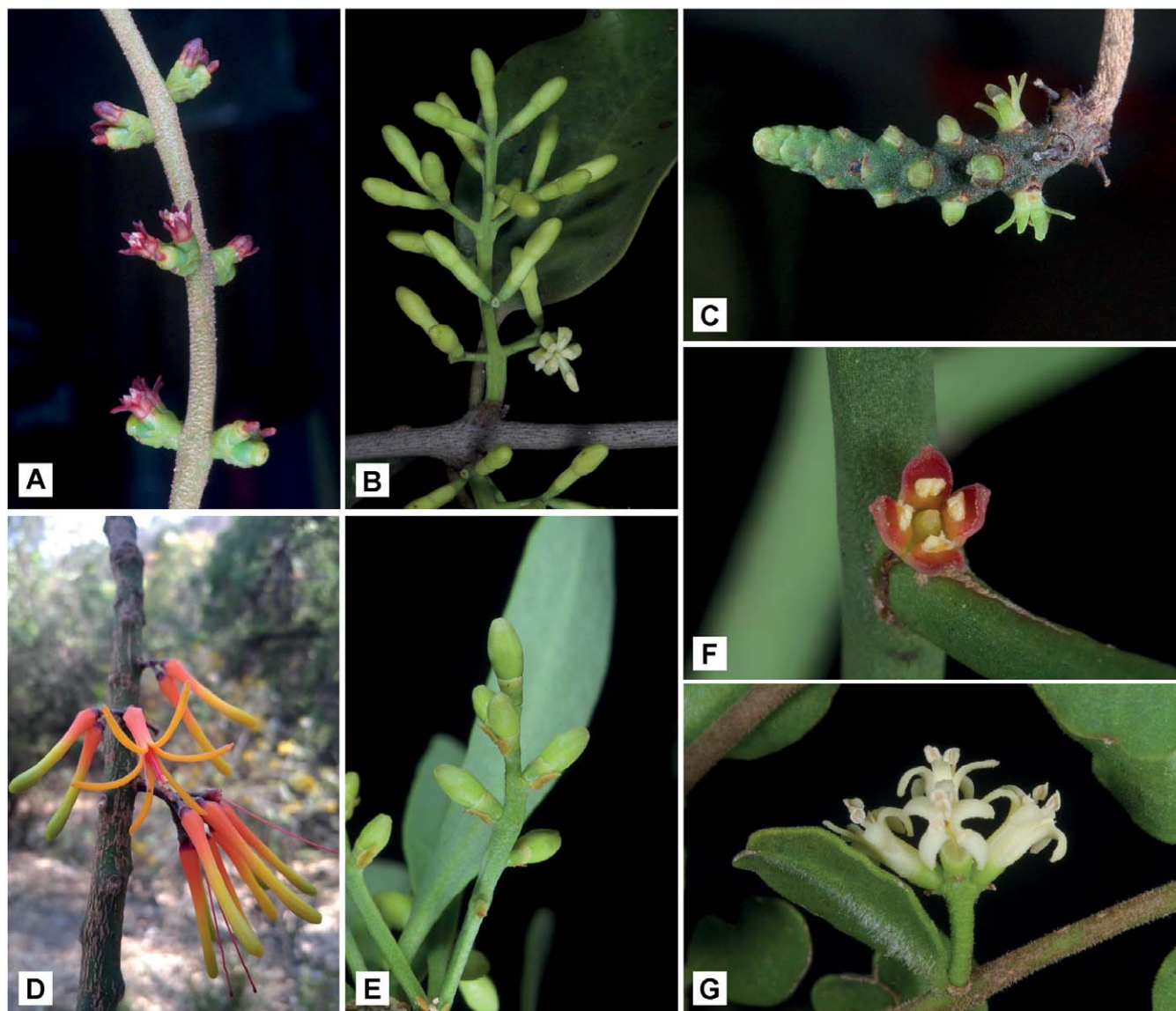


FIG. 1. Inflorescences of different genera of Psittacanthinae. A. Racemiform inflorescence of *Passovia pyrifolia* (Galván *et al.* 539). B. Racemiform inflorescence of *Struthanthus deppeanus* (Galván *et al.* 436). C. Spiciform inflorescence of *Oryctanthus cordifolius* (Galván *et al.* 537). D. Umbelliform inflorescence of *Psittacanthus ramiflorus* (Galván *et al.* 463). E. Spiciform inflorescence of *Cladocolea tehuacanensis* (Galván *et al.* 447). F. Uniflorous inflorescence of *Phthirusa inornata* (Galván *et al.* 364). G. Capitulum inflorescence of *C. kuijii* (Galván *et al.* 397). Photos by Rosa Cerros-Tlatilpa.

position or differences in species clustering, and that they had high support values.

Reconstruction of Ancestral Character States—A new concatenated data matrix was created in which each species was represented by only one individual. With this matrix, we ran a new ML analysis. Substitution models were chosen under the Bayesian Informative Criteria (BIC) using Model Finder. The evolutionary models selected for these new data sets were the SYM+I+G4 model for ITS, and the K3Pu+F+G4 model for each chloroplast region. Ancestral state mapping and reconstruction analysis were performed in Mesquite v3.7 (Maddison and Maddison 2021) using the “Trace character history” function and the likelihood reconstruction method, using the Markov k-state one parameter evolutionary model.

RESULTS

Alignment—The ITS alignment contained 115 sequences with 789 sites, of which 337 were parsimoniously informative and 379 were constant. The 116 sequences containing the concatenated *matK* and *trnL-F* regions formed a matrix of 2055 sites, of which 291 were parsimoniously informative

and 1537 were constant. A third matrix, which concatenated the three regions (ITS, *trnL-F* and *matK*), consisted of 115 individuals with 2842 sites with 617 parsimoniously informative sites and 1958 constant sites. In some samples, only one region could be sequenced. Furthermore, some species had only one sequence in GenBank. So, in the third matrix these individuals were excluded.

Phylogenetic Analysis of ITS and Chloroplast (*trnL-F*+*matK*)—Trees obtained by the maximum likelihood analysis for each data set (ITS and chloroplast) showed some differences, although most clades with few species were similar. However, some species or genera were nested in different positions. In contrast, the trees obtained by Bayesian inference showed several polytomies, with the ITS tree showing the most dichotomous branches. Despite the differences between the trees obtained for each data set, the discrepancies had low levels of support or corresponded to unresolved relationships, so it was considered that there were no conflicts

between them. Tree files for ML and BI trees with UFB and PP values for each data set are archived on Dryad (Galván-González et al. 2024).

Phylogenetic Analysis of Concatenated Data (ITS+trnL-F+matK)—The trees obtained by the ML and BI analysis were similar and grouped the same sets of species in minor clades, with *Psittacanthus* as the only genus that changed position between both trees. In the ML tree, support values vary from low to high (UFB \geq 95), while in the BI tree support values are mostly high (PP \geq 0.95). In both trees, *Tripodanthus acutifolius* is sister to the rest of the subtribe Psittacanthinae (clade A, Fig. 2A). In all analyses, each *Cladocolea* and *Struthanthus* were not recovered as monophyletic genera. Three *Cladocolea* species are nested within *Struthanthus* or occupy an uncertain position due to low support, whereas six *Struthanthus* species turned out to be closer to genera such as *Peristethium*, *Passovia*, and *Oryctanthus*. The tree presented in Fig. 2 was built using the three concatenated regions under a BI scenario; we decided to present this tree in the main text instead of the one produced by ML because its nodes were better supported. No conflicting topologies were found between the BI and ML trees (Fig. 2A–B; ML tree on Dryad, Galván-González et al. 2024).

We recognize 24 noteworthy clades in the Bayesian tree: A, B, I–IV, and a–r, most with high support values (PP \geq 0.95, UFB \geq 95). Several of these clades are resolved, but the relationships between some of them are unresolved. The following paragraphs will discuss the most relevant or best-supported clades.

Clade B. The Bayesian tree is composed of a polytomy of four clades (I, II, III and IV), while in ML analysis clade II is the first lineage to diverge from clade B with high support (UFB = 99).

Clade I. This contains the large-flowered genera *Psittacanthus* and *Aetanthus* (the latter only shown in the independent ITS and chloroplast analyses, see Galván-González et al. 2024), although with an uncertain position in the Bayesian analysis.

Clade II. Includes clades a, and b. Clade a consists of two South American species of *Struthanthus* (three species in the ITS trees, see Galván-González et al. 2024) with lax inflorescences; long pedunculate triads, acute, recaulescent and persistent bracts; and sessile flowers with a straight style in the female flowers. Clade b contains the genera *Oryctanthus* and *Passovia*. In this study, the specimens of *Passovia micrantha* have reduced, simple, and determinate inflorescences. This relationship supports the proposal of Caires et al. (2021) to reject the transfer of *Passovia micrantha* made by Kuijt (1991a) to *Cladocolea* and accept the change proposed by Van Tieghem (1895a) from *Phthirusa micrantha* to the genus *Passovia*. In this clade, *Struthanthus martianus* is nested with *Passovia* (Galván-González et al. 2024).

Clade III. Clades c and d are grouped here. Clade c recovers the Mexican species of *Phthirusa* and its disjunct South American congener *P. rhynchophylla* as a monophyletic genus with high support value (UFB = 100 and PP = 1). The genus is characterized by axillary tetramerous, mostly bisexual sessile flowers with isomorphic stamens. Kuijt (1991b, 2011) described the presence of triads and monads in the leaf axils of *Ixocactus rhynchophyllus* (= *P. rhynchophylla*) and considered the possibility that in that species the flower clustering is in the process of evolving into an inflorescence. Clade d is composed of *Struthanthus hartwegii*, *S. orbicularis*, and

Peristethium leptostachyum. These *Struthanthus* species have triads with short peduncles and straight-styled female flowers, similar to those of the genus *Peristethium*. In the ML tree, clade I is sister to clade III, but with low support value (UFB = 69).

Clade IV. This clade includes four minor clades (e, f, g, h). The relationships among these clades are not resolved and form a polytomy. These clades include species of Mexican *Cladocolea* and *Struthanthus*, as well as some Central American species. Most of the included species have a gynoeceium with a sigmoid to convolute style.

Clade e. It comprises *Struthanthus condensatus*, *S. palmeri*, and *Cladocolea cupulata*. These species are distributed throughout western and northwestern Mexico. They develop compound inflorescences with pedunculate triads and sessile flowers, or simple inflorescence with pedicellate flowers in the case of *C. cupulata*. The pedicellate flowers are more evident in female specimens, in which there are also fewer floral nodes than in male inflorescences. In the *Struthanthus* species, the bracts and bracteoles persist after anthesis and expand at the base of the ovary to form a cupular structure.

Clade f. It includes *Struthanthus ibe-dzi*, *S. ramiro-cruzii*, and *Cladocolea racemosa* from southwestern Mexico. The triads have a sessile central flower and pedicellate lateral flowers. Clade f shows *Cladocolea racemosa* (simple and indeterminate inflorescence) as sister to *S. ramiro-cruzii*, with high support values (UFB = 100, PP = 1).

Clade g. This clade and several of its internal nodes have low support values. Taxa here included are distributed from central to southern Mexico; moreover, two Central American species (*S. oerstedii* and *S. woodsonii*) are nested in this clade.

Clade h is subdivided into clades i, j, k, and l. The relationship among these clades is not resolved. Most of the species are distributed from central to southern Mexico, mainly in the biogeographic provinces Transmexican Volcanic Belt, Balsas Basin, and Sierra Madre del Sur (names follows nomenclatural proposal of Morrone et al. 2022).

Clade i. This clade shows a relationship between *Struthanthus capitatus* and *Cladocolea spathiflora*, but has a low support value (UFB = 90, PP = 0.85). Despite appearing to have sessile flowers, *C. spathiflora* has flowers subtended by a cupular pedicel, while *S. capitatus* has pedunculate triads and sessile flowers. Both species have indeterminate inflorescences.

Clade j. This clade groups *Struthanthus interruptus* and *Struthanthus* sp. Both species have raceme-like inflorescences with sessile flowers on pedunculate triads. In ML analysis, this clade is sister to clade f.

Clade k. The included taxa have simple determinate inflorescences and are parasitic on species of *Quercus* (Fagaceae). Here, *Cladocolea pringlei* comes out as a sister to *C. diversifolia* and *C. pedicellata*. However, this relationship is poorly supported. The *C. diversifolia*-*C. pedicellata* group received a high support value (PP = 1, PB = 100), although relationships among individuals are not well resolved.

Clade l. This clade contains *Cladocolea* species grouped into subclades m, n, and o. These species develop simple, mostly determinate inflorescences. Flowers are all sessile. The clade is well resolved, and only a few nodes have low support.

Clades m and n are the first to diverge from clade l. All species have spiciform inflorescences. In clade m, individuals of *C. glauca* and *C. tehuacanensis* do not form distinct clades.

Clade o. In this group, taxa have a shrubby growth habit with stems branching from the base from a primary

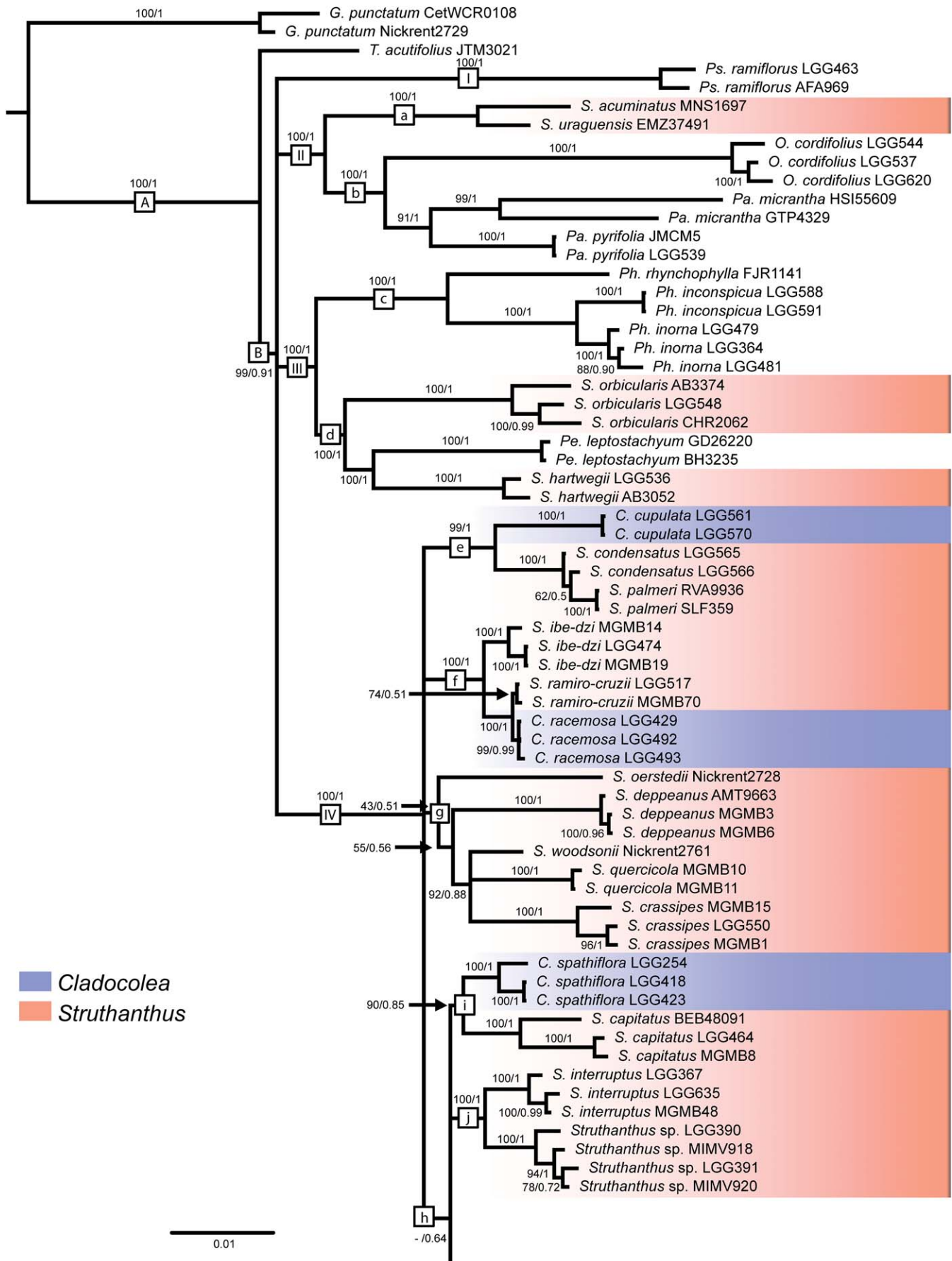


FIG. 2A–B. 50% majority consensus Bayesian phylogram of the *Cladocolea-Struthanthus* complex based on combined ITS, *trnL-F*, and *matK* data for 115 taxa. UFB and PP values are indicated above or below the branches, respectively, or indicated by an arrow and separated by a slash (/). An en dash (–) indicates that the node is not present in the ML tree.

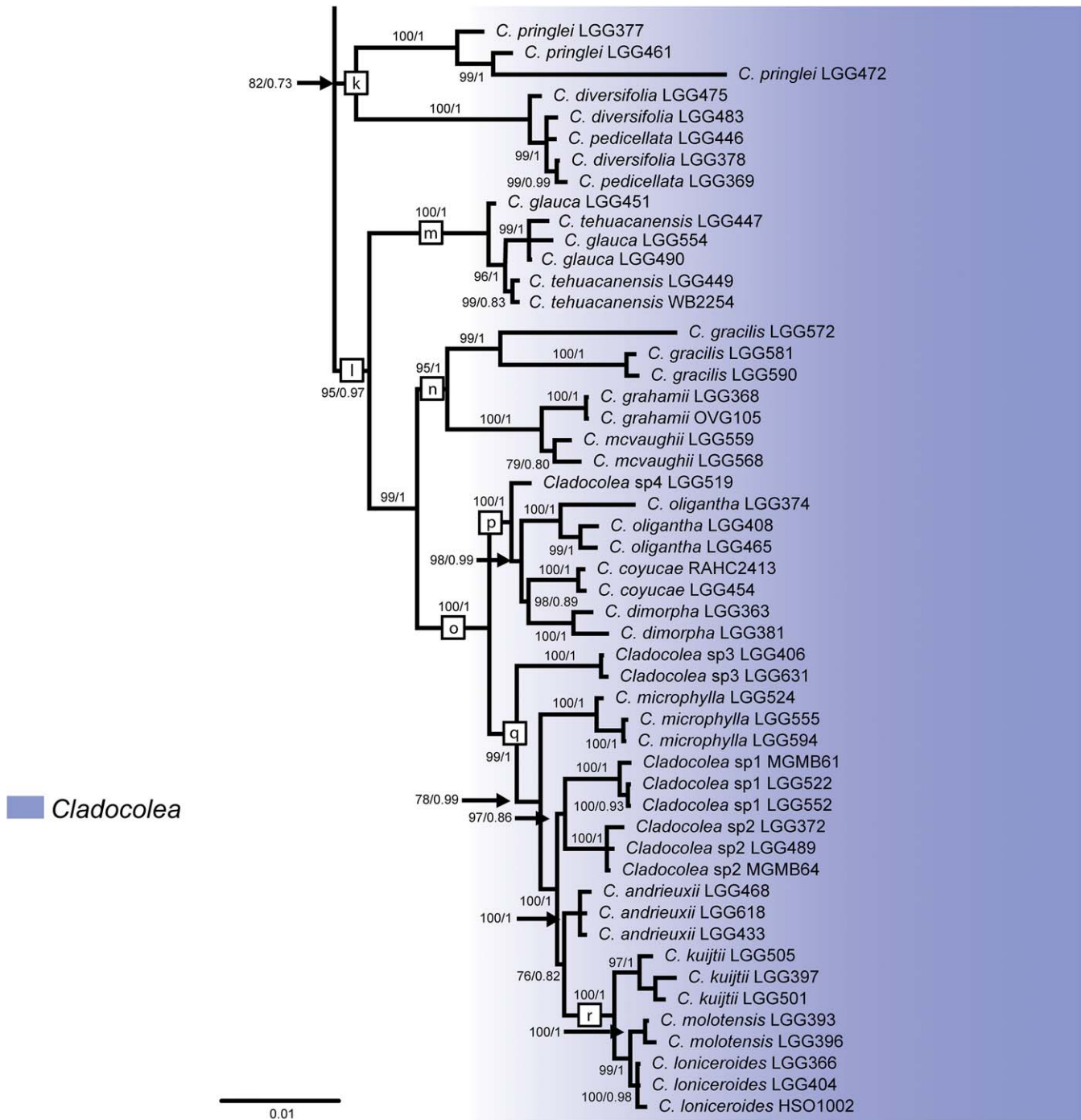


FIG. 2A–B. Continued.

(embryonic) haustorium. Except for two species, they do not develop secondary haustoria derived from epicortical roots (as observed in *Cladocolea* sp. 1 and rarely in *C. loniceroides*). Most included species have epidermal emergences of papilla or trichomes on young stems, leaves and inflorescences, and these occasionally persist on mature stems. The inflorescences of this clade are always determinate.

Clade o is divided into clades p and q. The former contains species with younger stems tending to develop inflorescences reduced to three flowers, while capituliform inflorescences develop on mature stems with differentiated lenticels. The flowers are tetramerous with isomorphic stamens. On the

other hand, in clade q there are species with capituliform inflorescences or intermediate forms between the latter and spiciform inflorescences. The flowers vary from pentamerous to hexamerous, rarely tetramerous, but always with dimorphic stamens. Finally, clade q includes clade r, that comprises three species of *Cladocolea* with trichomes and persistent floral bracts.

Our results show that *C. racemosa*, *C. cupulata*, and *C. spathiflora* are nested with other *Struthanthus* species; however, the relationship between *C. spathiflora* and *S. capitatus* is not sufficiently supported. Thus, new combinations are proposed for the first two taxa. On the other hand, *C. pedicellata* and

C. glauca were inserted in two well-supported clades with *C. diversifolia* and *C. tehuacanensis*. Therefore, the former names should be synonymized. In addition to molecular data, we discuss morphological evidence for some of these proposals in the discussion section.

Reconstruction of Ancestral Character States—Thirteen characters were mapped on the ML tree constructed with only one individual per species (Fig. 3). In this tree, the subtribe Psittacanthinae is divided into two clades. The first contains clades I, II, and III, with *Tripodanthus* as a sister group, while the second consists of clade IV. The relationships between these clades and *Tripodanthus* were not well supported. However, this topology does not conflict with the previous one. The probability results for the reconstruction of ancestral character states will be discussed in the following paragraphs.

HABIT—For Psittacanthinae (clade A), the vine-like form is ancestral (probability = 0.79), whereas the shrubby habit arises independently in clades b, c, l, and o.

SECONDARY HAUSTORIA—Secondary haustoria are shown as an ancestral condition at node A (probability > 0.99). These haustoria are absent in two Mexican species of *Phthirusa* and at the node of clade o (probability = 0.91). In the latter, a regression occurs (*Cladocolea* sp. 2).

PHYLLOTAXY—The ancestral condition corresponds to opposite leaves at node A (probability = 0.97). Phyllotaxis in clades e, f, g, and j (clade IV) varies from opposite or subopposite to alternate in the same individual, with the first condition being the most frequent. At node l, phyllotaxis is alternate (probability = 0.87), with a reversion in *Cladocolea kuijtii*.

INDUMENTUM—The absence of trichomes and papillae is the ancestral condition at node A (probability = 0.97). Papilla and trichomes have been recorded in a few species of the genera *Psittacanthus* (Kuijt 2009), *Phthirusa* (Kuijt 2011), *Pusillanthus* (Caires et al. 2012), and *Struthanthus* (Kuijt 2003), and in these cases it is a convergent character. In clade o, epidermal projections have the same evolutionary origin.

INFLORESCENCE FORM—The racemiform inflorescence is considered ancestral at node A (probability = 0.99). Spiciform inflorescences could have been derived from the loss of the triad peduncle and have arisen from multiple independent events. On the other hand, simple capituliform inflorescences are observed as a constant character at node o (probability = 0.97) and were derived from simple spiciform inflorescences, probably due to inflorescence axis compactation.

INFLORESCENCE TYPE—Composite inflorescences constitute the plesiomorphic condition (probability > 0.70) of node A, being derived to simple inflorescences through several independent reduction events. In this regard, flower pedicels in simple inflorescences seems to be homologous to the triad peduncle.

TERMINAL FLOWERS—Indeterminate inflorescences are shown as ancestral in clade A (probability > 0.93), while the condition of terminal flowers appears to have arisen on more than one occasion by independent events.

BRACTEOLES—Ancestor at node A had bracteoles associated with lateral flowers (probability = 0.99). Bracteole loss appears to have occurred at least two times by independent events in *Cladocolea racemosa* and clade k. In *C. cupulata* and *C. spathiflora*, this condition is unknown, as the bracteoles could be fused with the cupular pedicels. For node III, it is not possible to establish a probability value, because it is

unknown whether the prophylls described in *Phthirusa* (Kuijt 1975, 1991b, 2011) are equivalent to the bracteoles of a sessile triad (Kuijt 2011) or whether they correspond to the prophylls observed at the base of the inflorescence, as in other genera of Psittacanthinae.

FLOWER SIZE—At node A, there is a high probability (≥ 0.99) that the ancestral condition was small flowers. This contrasts with the flower size of the genus *Psittacanthus* (clade I), sister to clade III. However, the relationships between these clades are not resolved, so it is not possible to determine the plesiomorphic state of the node that groups them.

NUMBER OF PETALS—For all small-flowered Psittacanthinae, the ancestral state is considered a hexamerous flower (probability ≥ 0.99). Subsequent independent events of reduction in the number of floral parts occurred in clades b, c, p, and r.

FLOWER SEX—There is a high probability that the ancestor of clades II and III had unisexual flowers (0.89), although it should be noted that the genera included are poorly represented and that the variation ranges from unisexual to bisexual species. For clade IV, there is a high probability (0.94) that the ancestral condition is that of unisexual flowers.

STAMEN DIMORPHISM—We consider it a high probability (0.96) that the ancestral condition for node A corresponded to dimorphic stamens. This condition changed at least twice, in *Phthirusa* (clade c) and in *Cladocolea* (clade p).

STYLE SHAPE—At node A, there is a probability of 0.68 that convolute style is plesiomorphic. However, for nodes II and III the straight style is considered the ancestral character (probability = 0.99). According to this analysis, sigmoid styles are derived from convolute styles. Convolute and sigmoid styles have also been reported in two species of *Peristethium* in clade III (Kuijt 2003, 2012).

DISCUSSION

As in previous Loranthaceae studies (Vidal-Russell and Nickrent 2008; Su et al. 2015; Liu et al. 2018; Nickrent et al. 2019), the genus *Tripodanthus* is sister to the rest of Psittacanthinae, while relationships among the rest of the genera are unresolved, and taxa are grouped into four clades that form a polytomy (Fig. 2A).

Results showed that both *Cladocolea* and *Struthanthus* are polyphyletic. Some *Cladocolea* species are nested in minor *Struthanthus* clades (clades e, f, k). These *Cladocolea* species share with *Struthanthus* the vine-like scandent habit, the presence of secondary haustorium through epicortical roots, and indeterminate inflorescences. *Struthanthus* species are divided into at least three clades, one of them close to *Oryctanthus* and *Passovia* (clade II) and the other nested with *Peristethium leptostachyum* (clade d). Finally, most species of Mexican *Cladocolea* and *Struthanthus* form a major monophyletic group (clade IV) with an unresolved relationship with the clades II and III. The polyphyletic origin of *Struthanthus* was suggested by Kuijt (Kuijt 1975, 1981, 2012; Kuijt and Hansen 2015).

The representatives of clade d are distributed from southern Mexico to northern South America. All three species have the straight style characteristic of most Central and South American *Struthanthus*. However, the basal chartaceous inflorescence bracts and terminal flowers have not been reported for *S. hartwegii* and *S. orbicularis*. Future analyses should include other *Peristethium* species to confirm whether these

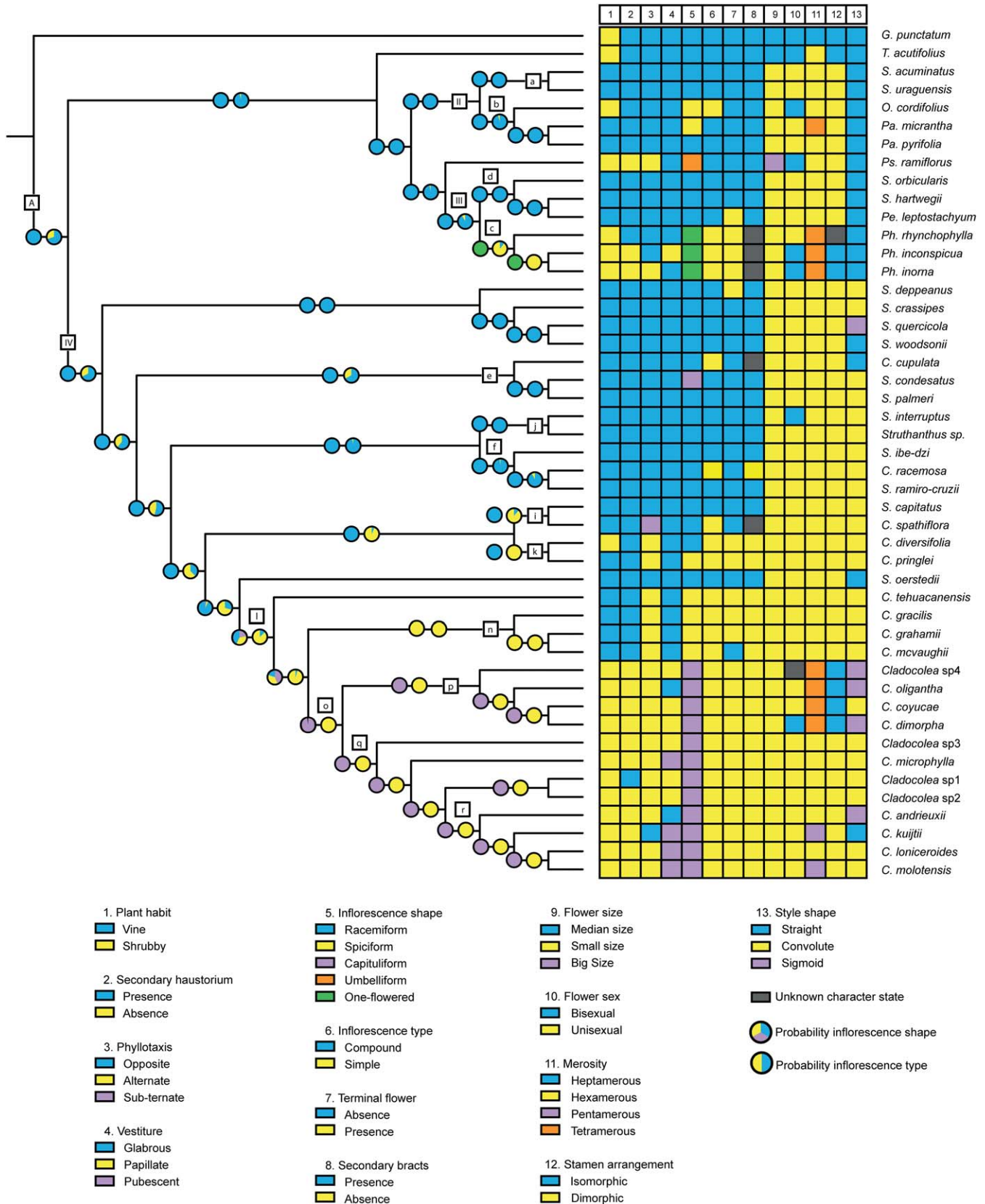


FIG. 3. Consensus ML cladogram of the *Cladocolea-Struthanthus* complex, based on combined ITS, *trnL-F*, and *matK* data for 47 species. Analyzed character states are shown in the grid preceding the species name. The left circle above each branch shows the estimated probability for the states of the character "inflorescence shape," while the right circle shows the probability for each state of the character "inflorescence type."

Struthanthus species are nested within *Peristethium* or whether these species are grouped into sister clades. *Peristethium* currently consists of 15 species and was reestablished by Kuijt (2012) to include species previously classified in *Struthanthus* and *Cladocolea*.

According to our results, *Phthirusa* (clade c) came out sister to clade d with strong support. This result clarifies the position of *Phthirusa* concerning the results of Wilson and Calvin (2006) and Grimsson et al. (2018), in which *P. inorna* is sister to *Tripodanthus*, although with low support values. Floral and inflorescence morphology in both clades is contrasting. The inclusion of other tetramerous, vine-like taxa (e.g. *Pusillanthus*, *Cladocolea coriacea*, and *C. harlingii*) will provide clues to the evolutionary trend that led to the extreme reduction of inflorescences in *Phthirusa*.

Contrary to what Kuijt (1981, 2012) suggested, our results support that species with compound inflorescences did not derive from ancestors with simple inflorescences. On the other hand, ancestors of the small-flowered Psittacanthinae had inflorescences composed of pedunculate triads, whereas the appearance of monads occurred in isolated species in clades b, e, f, k, and l. In the latter clade, simple inflorescences are fixed and changed from indeterminate to determinate inflorescences.

It is not ruled out that morphological variation of small-flowered Psittacanthinae inflorescences can be explained by more than a single reduction pathway. In this regard, Suaza-Gaviria et al. (2017) considered that the reduction of dichasia (here referred to as triad) in Santalales could have occurred in at least five different ways.

It can be assumed that in Psittacanthinae, the loss of lateral flowers on triads occurred by several independent events and could include different processes. For example: 1) the loss of the triad peduncle, flowers, and bracteoles; 2) the fusion of bracts and pedicels, as well as bracts and bracteoles; 3) the development of apical flowers; and 4) the reduction of floral parts. Thus, several scenarios are possible in the development of simple and spiciform inflorescences arising from compound inflorescences with pedunculate triads (Fig. 4). These scenarios are provisional, considering that relationships among some genera are not well supported. In particular *Oryctanthus*, *Passovia*, and *Peristethium* are poorly represented, while other genera such as *Dendropemon*, *Maracanthus*, *Oryctina*, *Panamanthus*, and *Pusillanthus* were not included in our analysis.

The inflorescence reduction trends proposed in this study are similar to those suggested in other angiosperm families. For example, Savinov (2013) considered that within the spectrum of inflorescences in Celastrales, the reduction of thyrses (thyrsoid) to racemes (botryoid) is through the reduction of lateral dichasia to solitary flowers, while spikes could have originated from the loss of raceme pedicels. On the other hand, Pozner et al. (2012) and Zhang and Elomma (2024) mention that the capitulum of Asteraceae and the cephalium of Calyceraceae results from high suppression in the elongation of main axis internodes, cymose branches, and pedicels of a thyrsoid.

In addition to the trends observed in the phylogeny, individuals with polymorphic states that could be attributed to vestigial traits have been observed in at least four species of *Cladocolea*. They include, for example, triads present at the inflorescence base in *C. racemosa* (Fig. 5A–B) and *C. pedicellata* (Kuijt 1975, 1981; Fig. 5C–D), capituliform inflorescences with

opposite flowers along the peduncle, resembling a spiciform inflorescence in *C. microphylla* (Fig. 5E–F), and capituliform inflorescences in which the flowers appear to have a decussate arrangement (pers. obs.), as occurs in other spiciform inflorescences. Also, in proximal flowers of *C. spathiflora*, the cupular pedicel bears a pair of marginal decurrent projections (Fig. 5G); an inflorescence on the type specimen presents two concentric cupular pedicels that are clasped by a huge bract, resembling two lateral flowers of a triad (Fig. 5H). In the same specimen, a rare apical flower developed three bracts instead of one (Fig. 5I). On the other hand, monads and determinate inflorescences are rarely observed in *Struthanthus deppeanus* (Fig. 1B). However, these states are less common in populations and, according to Kuijt (1975, 1991b, 2011), could also have a teratogenic origin.

Taxonomic Implications—Our results indicate the polyphyly of *Struthanthus* and its fragmentation in three clades. Future studies should expand taxonomic sampling in this and other genera such as *Passovia* and *Peristethium*. In addition, it will be necessary to include in phylogenetic studies the type species of some genera, in particular *Struthanthus syringifolius*, which because of its morphological similarities and distribution, could be part of the South American clade a. Finally, the revision and possible reinstatement of disused names, such as *Eichlerina* Tiegh. and *Spirostylis* C.Presl, should not be ruled out, as well as the creation of new genera. Currently, the name *Spirostylis* is considered rejected in favor of retaining *Struthanthus* Mart., despite having been published one year before *Struthanthus* (Kuijt 1974).

Because the previously mentioned proposal requires a more extensive study, here we only propose to transfer *C. cupulata* and *C. racemosa* to *Struthanthus*. Although *C. spathiflora* is sister to *S. capitatus*, this relationship has low support and is therefore considered unresolved. With these changes, *Cladocolea* remains with more morphological homogeneity among most of its species. However, heterogeneity will be added to *Struthanthus*, which would now include species with simple inflorescences.

In consideration of the above, one of the challenges in the systematics of neotropical Loranthaceae consists of finding new taxonomic characters that help to establish well-defined boundaries between *Cladocolea* and *Struthanthus*, as well as with other small-flowered genera of Psittacanthinae. In this regard, studies of leaf architecture (Kuijt and Lye 2005; Caires 2012) and pollen grain morphology (Feuer and Kuijt 1985; Caires 2012) have been useful in delimiting the genera *Oryctanthus* and *Oryctina*. The variation of such characters in these genera is well documented. However, in other genera of neotropical Loranthaceae, only a few species have been studied.

TAXONOMIC TREATMENT

- CLADOCOLEA DIVERSIFOLIA (Benth.) Kuijt, Brittonia 32: 519. 1980. *Loranthus diversifolia* Benth., Pl. Hartw. 63. 1845. *Struthanthus diversifolius* (Benth.) Standl., Contr. U.S. Natl. Herb. 20: 212. 1919. TYPE: MEXICO, Michoacán, Tlalpujahua [Tlalpujahua], Graham 234 (Holotype: K-image!). *Cladocolea pedicellata* Kuijt, J. Arnold Arbor. 56(3): 319–322. 1975, syn. nov. TYPE: MEXICO, Estado de México, distrito de Temascaltepec, Nanchititla, G. B. Hinton 4091 (Holotype: K, Isotypes: CAS-image!, GH, MICH-image!, NY, P-image!, UC, US-image!).

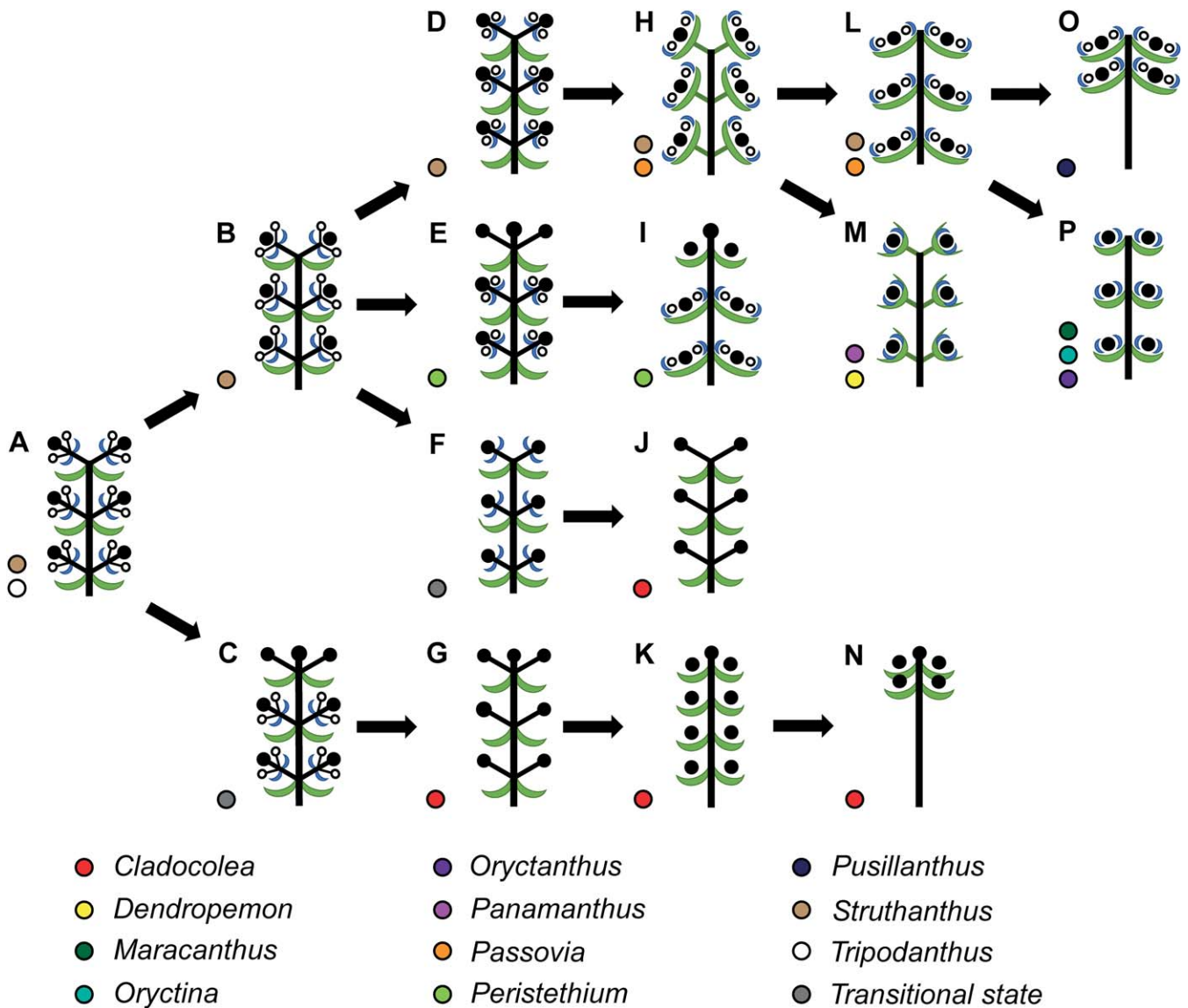


FIG. 4. Hypothetical evolution of inflorescences in the small-flowered Psittacanthinae. A. Racemiform inflorescences with pedunculate triads and pedicellate flowers. B. Loss of pedicel in the central flower of the triad. C. Appearance of apical flower and terminal monads. D. Loss of pedicels of lateral flowers of the triad. E. Gain of apical flower and monads from "B". F. Loss of lateral flowers of the triad. G. Loss of lateral flowers of the triad and bracteoles. H. Recaulcescence of primary bract on triad peduncle. I. Loss of basal triad peduncle and pedicels on monads. J. Loss of lateral flowers of the triad. K. Loss of monad pedicel. L. Loss of triad peduncle. M. Loss of lateral flowers and fusion of primary bract and bracteoles. N. Congestion of flower nodes. O. Congestion of triad nodes. P. Loss of lateral flowers of the triad.

Remarks—Molecular evidence shows that *Cladocolea diversifolia* and *C. pedicellata* are the same taxon. Kuijt (1980) established the combination *C. diversifolia* to segregate this taxon from *C. pedicellata* and restricted the latter to the type specimen *Hinton 4091* (a female specimen), from Nanchititla, Estado de México. According to Kuijt (1980), *C. pedicellata* is distinguished from *C. diversifolia* by the partial fusion of the pedicel with the inflorescence axis, the straight flower bud, and the convolute style. However, these characters have been observed in female specimens from the states of State of México, Morelos, Puebla, and Querétaro, while male specimens from the same localities match the diagnostic characters of *C. diversifolia* (Fig. 6A–B). Therefore, in this case, it appears that two taxa were described as the result of sexual dimorphism in the same species. In specimens of both sexes, the presence of triads has been documented (Kuijt 1975; Fig. 5C–D).

CLADOCOLEA TEHUACANENSIS (Oliv.) Tiegh, Bull. Soc. Bot. France 42: 167. 1895. *Loranthus tehuacanensis* Oliv., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1864: 171. 1865. *Oryctanthus tehuacanensis* (Oliv.) Engl., Nat. Pflanzenfam. Nachtr. Zu III: 135. 1897. TYPE: MEXICO, Puebla, F.M. Liebmann 3129 (Holotype: C-image!, isotype: P).

Cladocolea glauca Kuijt, J. Arnold Arb. 56: 288–290. 1975, syn. nov. TYPE: MEXICO, Puebla, Huejotzingo, near Puebla, G. Arsène 1749 (Holotype: US-image!, isotypes: BM, GH-image!, MEXU!, MO-image!, NY, U-image!, US-image!).

Remarks—Descriptions of male specimens of *C. tehuacanensis* were not provided in the works of Oliver (1864), Van Tieghem (1895b), or Kuijt (1975), nor were male specimens noted as part of the examined material. According to our results, both names correspond to the same taxon with a

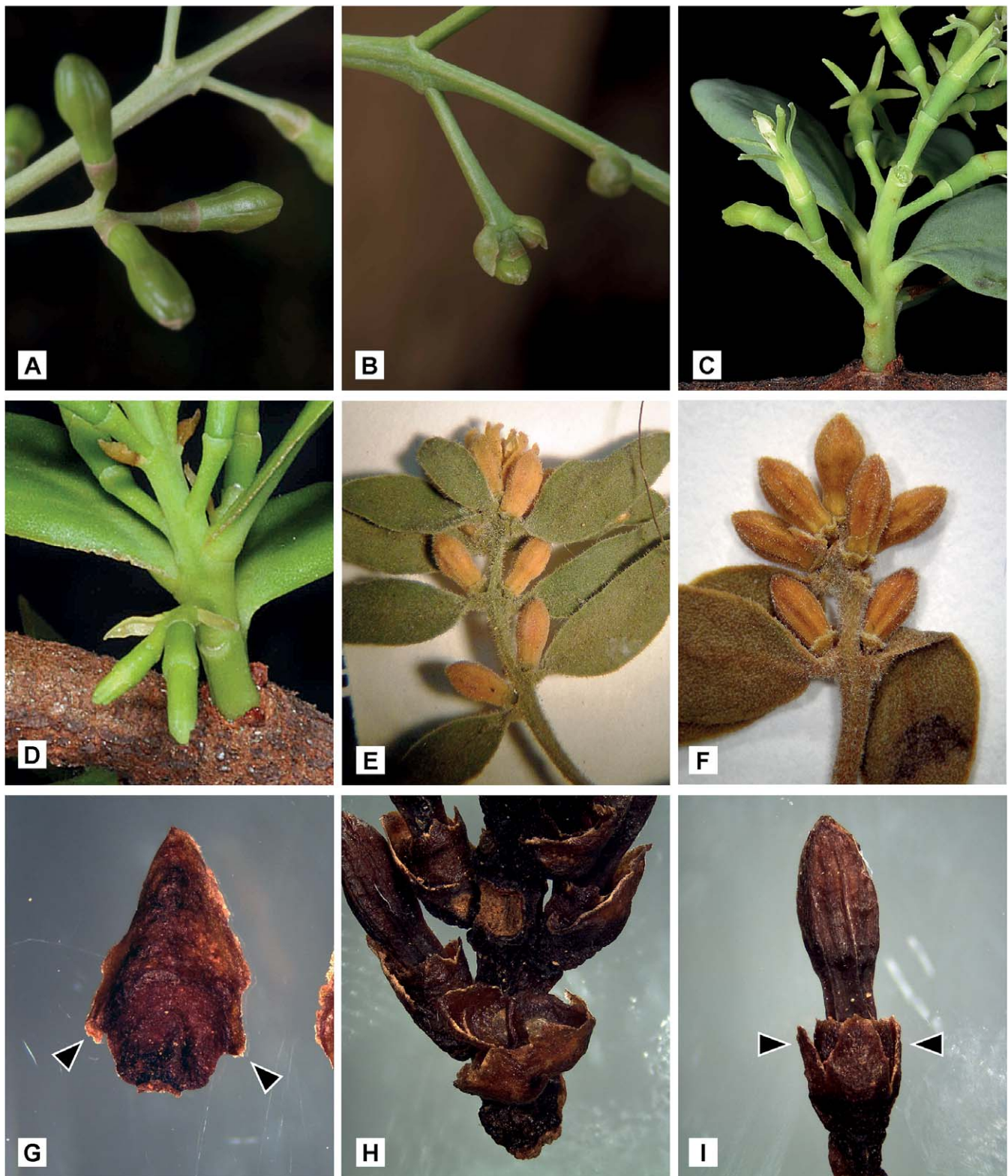


FIG. 5. Polymorphisms in some *Struthanthus* and *Cladoclea* inflorescences. A–B. Triads and monads in *S. racemosus* (Galván et al. 432, 493). C–D. Incomplete triads and monads in *C. diversifolia* (Galván et al. 225). E–F. Subopposite and opposite flowers on *C. microphylla* peduncles (J. Castañeda R. 1259, MEXU and J. Rzedowski 30390, ENCB). G. Spatheous pedicel and bract of *C. spathiflora* with decurrent projection (L.G. Galván et al. 254, HUMO). H. Concrescent cupular pedicels in *C. spathiflora*, same specimen. I. Rare apical flower with three bracts, same specimen. Photos A–D by Rosa Cerros-Tlatilpa, E–I by Luis G. Galván-González.

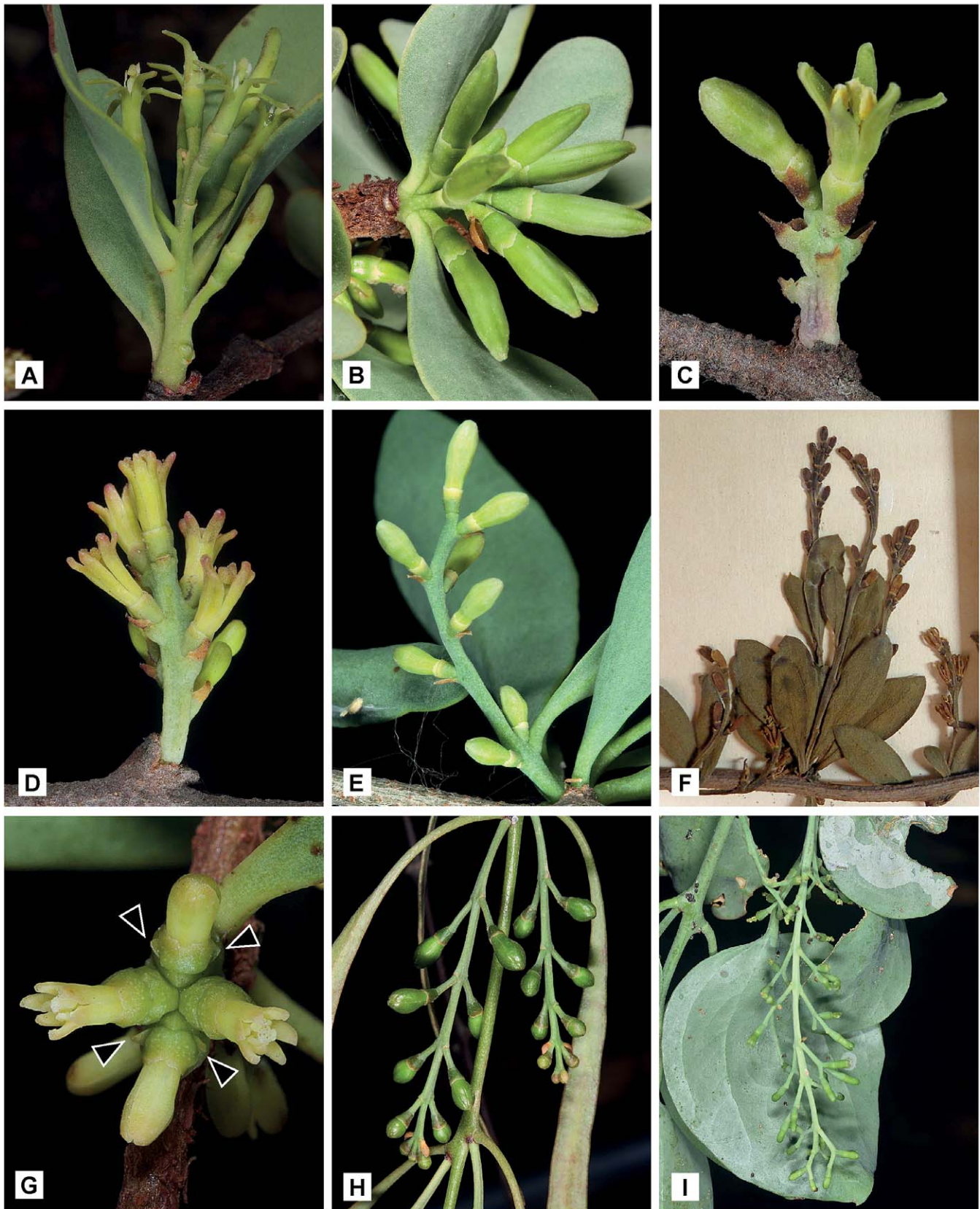


FIG. 6. Inflorescence morphology of some *Cladocolea* and *Struthanthus* species. A. Female inflorescence of *C. diversifolia* with long concaulescent pedicels in Olinalá, Guerrero (Galván *et al.* 484). B. Male inflorescence with short and free pedicels, same location (Galván *et al.* 485). C–D. Male and female inflorescences of *C. tehuacanensis* from Huejotzingo, Puebla (Galván *et al.* 441, 443). E–F. Male (Galván *et al.* 444) and female (W. Boege 2254, MEXU) inflorescences of *C. tehuacanensis* from Puebla, Puebla. G. Inflorescence of *C. cupulata* (Galván *et al.* 562); triangles point to marginal prominences. H. Simple male inflorescences and narrowly lanceolate leaf of *S. racemosus* (Galván *et al.* 432). I. Compound female inflorescence and wide ovate leaf of *S. ramiro-cruzii* (Maldonado *et al.* 65). Photos A–E and G–I by Rosa Cerros-Tlatilpa, F by Luis G. Galván-González.

wide range of variation in inflorescence length. Usually, specimens with inflorescences exceeding three centimeters in length and spaced floral internodes have been determined as *C. tehuacanensis*, while specimens with shorter inflorescences and short floral internodes have been identified as *C. glauca*. This inflorescence variation can be seen in Fig. 6C–F.

Struthanthus cupulatus (Kuijt) Galv.-González, comb. nov.
Cladocolea cupulata Kuijt, J. Arnold Arbor. 56: 285–286. 1975. TYPE: MEXICO, Jalisco, Atenguillo, pine forest on rolling mountain summits 6 mi NW of Cuautla, R. McVaugh 21127 (Holotype: MICH-image!).

Remarks—*Struthanthus cupulatus* is sister to *S. condensatus* and *S. palmeri*. Each flower is subtended by a cupular structure derived from the flower bract and a short pedicel. Besides its simple inflorescence, Kuijt (1981) noted that the cupular pedicel bears a pair of marginal prominences (Fig. 6G), which could be faint traces of bracteoles. However, such prominences are not evident in all flowers.

Struthanthus racemosus (Kuijt) Galv.-González, comb. nov.
Cladocolea racemosa Kuijt, Novon 2: 351. 1992. TYPE: MEXICO, Guerrero: 2.5 km al WNW de Tlaxco, camino de Totopec a San Miguel Amoltepec, bosque de pino, ladera de exposición; Lorea [Fonseca?] 1955 (Holotype: FCME [not found and presumed destroyed, lost or mislabeled], isotypes: LEA, WIS).

Remarks—*Struthanthus racemosus* and *S. ramiro-cruzii* are distributed in the Sierra Madre del Sur biogeographic province. Individuals of *S. racemosus* grow on *Pinus* L. sp. at Tlaxco, Guerrero (Mexico). The nearest known population of *S. ramiro-cruzii* is approximately 32 km away, where it grows on *Alnus* Mill. (Betulaceae), *Quercus* L. (Fagaceae), and *Crataegus* L. (Rosaceae). Both species have a vine-like habit and secondary haustoria through epicortical roots. The floral morphology of both species is similar. Some individuals of *S. racemosus* develop basal triads on the inflorescences (Fig. 5A–B) similar to those observed in *S. ramiro-cruzii*. The phylogenetic tree presented in Fig. 2 shows *S. racemosus* as sister to *S. ramiro-cruzii*. However, the support for *S. ramiro-cruzii* is weak, and there is little nucleotide variation. Considering the morphological differences in leaves shape, and simple versus compound inflorescences (Fig. 6H–I), as well as host usage, these entities are maintained as different species and an early speciation process is suggested.

Kuijt (1992) designated the male specimen F.G. Lorea 1955 (Tlaxco [Xalpatláhuac], Guerrero, “parasite on *Pinus*”) as the holotype of *Cladocolea racemosa*. The FCME herbarium staff mentioned that this specimen is not deposited in their collection and perhaps has been lost or destroyed. In addition, the male specimen R.M. Fonseca 1955 (Marquelia, Guerrero, “on *Spondias purpurea*”) was found in the collection. However, field expeditions by the authors to the locality of the latter specimen failed to locate it. Therefore, given that both specimens have the same collection number, it is conjectured that the specimen R.M. Fonseca 1955 is the one referred to by Kuijt in the protologue and was mislabeled. Samples used in this study for *C. racemosa* were collected at the type locality for the species.

In summary, this is the first detailed molecular phylogenetic study to broaden our knowledge on the phylogenetic relationships between *Cladocolea* and *Struthanthus*, as well as

other genera of the subtribe Psittacanthinae. Future analyses should expand the taxonomic sampling of *Cladocolea* and *Struthanthus*. Furthermore, the inclusion of *S. syringifolius* and other species could result in the restructuring of *Struthanthus* and the possible reinstatement of the genus *Spirostylis*. Therefore, we highlight the need for further study and understanding of the relationship between these genera.

Contrary to Kuijt’s (1981) hypothesis, inflorescence evolution shows a trend to reduction from compound inflorescences, and the emergence of determinate inflorescences is a derived condition. Our results indicate that this pattern is true, at least for most Mexican species of *Cladocolea* and *Struthanthus*. However, it is necessary to study this trend in the closely related genera *Passovia* and *Oryctanthus*. While species of *Oryctanthus* have simple inflorescences, those of *Passovia* develop both simple and compound inflorescences. It is also important to study *Peristethium*, in which both conditions are present.

We emphasize the need to explore new taxonomic characters that help to establish well-defined boundaries among the genera of small-flowered Loranthaceae, e.g. those obtained by the study of pollen, leaf and floral anatomy and architecture, which have been useful to delimit the genera *Oryctanthus* and *Oryctina* but have hardly been explored in other genera.

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AUTHOR CONTRIBUTIONS

LGGG participated in fieldwork, extracted DNA, conducted the phylogenetic analysis, elaborated the figures, and prepared the manuscript. RCT conceived the research plan, participated in fieldwork, developed the project, revised the manuscript, and provided photographs. AES participated in the development of the project and revision of the manuscript. VWS participated in fieldwork, the development of the project, and revision of the manuscript.

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APPENDIX 1. Voucher and Genbank numbers for taxa included in phylogenetic analyses. Listed as taxon, collector and number, herbarium acronym, country, region, and GenBank accession number (ITS, *trnL-F*, and *matK*). An asterisk (*) indicates data downloaded from the GenBank data repository. An em dash (—) indicates missing data.

Ingroup: *Cladocolea andrieuxii* Tiegh., L.G. Galván et al. 433, HUMO, UAMIZ, Mexico, Guerrero, OQ281552, OQ968143, OR047307; L.G. Galván et al. 468, HUMO, UAMIZ, Mexico, Oaxaca, OQ281555, OQ968144, OR047308; L.G. Galván et al. 618, HUMO, UAMIZ, Mexico,

- Oaxaca, OQ281554, OQ968145, OR047309; *C. coyuca* Kuijt, L.G. Galván et al. 454, HUMO, UAMIZ, Mexico, Puebla, OQ281556, OQ968146, OR047310; R.A. Hernández 2413, HUMO, UAMIZ, Mexico, OQ281553, OQ968147, OR047311; *C. cupulata* Kuijt, L.G. Galván et al. 561, HUMO, UAMIZ, Mexico, Jalisco, OQ270636, OQ968148, OR047312; L.G. Galván et al. 570, HUMO, UAMIZ, Mexico, Jalisco, OQ270756, OQ968149, OR047313; *C. dimorpha* Kuijt, L.G. Galván et al. 363, HUMO, UAMIZ, Mexico, Morelos, OQ300376, OQ968150, OR047314; L.G. Galván et al. 381, HUMO, UAMIZ, Mexico, Guerrero, OQ300387, OQ968151, OR047315; *C. diversifolia* (Benth.) Kuijt, L.G. Galván et al. 378, HUMO, UAMIZ, Mexico, Guerrero, OQ300378, OQ968152, OR047316; L.G. Galván et al. 475, HUMO, UAMIZ, Mexico, Oaxaca, OQ300375, OQ968153, OR047317; L.G. Galván et al. 483, HUMO, UAMIZ, Mexico, Guerrero, OQ300384, OQ968154, OR047318; *C. glauca* Kuijt, L.G. Galván et al. 451, HUMO, UAMIZ, Mexico, Puebla, OQ300377, OQ968155, OR047319; L.G. Galván et al. 490, HUMO, UAMIZ, Mexico, Guerrero, OQ300380, OQ968156, OR047320; L.G. Galván et al. 554, HUMO, UAMIZ, Mexico, Puebla, OQ300381, OQ968157, OR047321; *C. gracilis* Kuijt, L.G. Galván et al. 572, HUMO, UAMIZ, Mexico, Jalisco, OQ282840, OQ968158, OR047322; L.G. Galván et al. 581, HUMO, UAMIZ, Mexico, Michoacán, OQ282837, OQ968159, OR047323; L.G. Galván et al. 590, HUMO, UAMIZ, Mexico, Michoacán, OQ282849, OQ968160, OR047324; *C. grahhamii* (Benth.) Tiegh., L.G. Galván et al. 368, HUMO, UAMIZ, Mexico, Morelos, OQ304538, OQ968161, OR047325; O. Villafranco 105, HUMO, UAMIZ, Mexico, Morelos, OQ304539, OQ968162, OR047326; *C. kuitjii* Martínez-Ambr. & Cruz Durán, L.G. Galván et al. 397, HUMO, UAMIZ, Mexico, Guerrero, OQ300379, OQ968163, OR047327; L.G. Galván et al. 501, HUMO, UAMIZ, Mexico, Guerrero, OQ300385, OQ968164, —; L.G. Galván et al. 505, HUMO, UAMIZ, Mexico, Guerrero, OQ300383, OQ968165, OR047328; *C. loniceroides* (Thieg.) Kuijt, L.G. Galván et al. 366, HUMO, UAMIZ, Mexico, Morelos, OQ304533, OQ968166, OR047329; L.G. Galván et al. 404, HUMO, UAMIZ, Mexico, Guerrero, OQ304534, OQ968167, OR047330; M.H. Sandoval 1002, HUMO, HUAA, Mexico, Aguascalientes, OQ304535, OQ968168, —; *C. mcraughii* Kuijt, L.G. Galván et al. 559, HUMO, UAMIZ, Mexico, Jalisco, OQ304541, OQ968169, OR047331; L.G. Galván et al. 568, HUMO, UAMIZ, Mexico, Michoacán, OQ304540, OQ968170, OR047332; *C. microphylla* (Kunth) Kuijt, L.G. Galván et al. 524, HUMO, UAMIZ, Mexico, Morelos, OQ304542, OQ968171, OR047333; L.G. Galván et al. 555, HUMO, UAMIZ, Mexico, Michoacán, OQ304543, OQ968172, OR047334; L.G. Galván et al. 594, HUMO, UAMIZ, Mexico, Michoacán, OQ304544, OQ968173, OR047335; *C. molotensis* Martínez-Ambr. & Lozada-Pérez, L.G. Galván et al. 393, HUMO, UAMIZ, Mexico, Guerrero, OQ304536, OQ968174, OR047336; L.G. Galván et al. 396, HUMO, UAMIZ, Mexico, Guerrero, OQ304537, OQ968175, OR047337; *C. oligantha* (Standl. & Steyerl.) Kuijt, L.G. Galván et al. 374, HUMO, UAMIZ, Mexico, Guerrero, OQ304545, OQ968176, OR047338; L.G. Galván et al. 408, HUMO, UAMIZ, Mexico, Guerrero, OQ304546, OQ968177, OR047339; L.G. Galván et al. 465, HUMO, UAMIZ, Mexico, Oaxaca, OQ304547, OQ968178, OR047340; *C. pedicellata* Kuijt, L.G. Galván et al. 369, HUMO, UAMIZ, Mexico, Morelos, OQ300388, OQ968179, OR047341; L.G. Galván et al. 446, HUMO, UAMIZ, Mexico, Puebla, OQ300389, OQ968180, —; *C. pringlei* Kuijt, L.G. Galván 377, HUMO, UAMIZ, Mexico, Guerrero, OQ304548, OQ968181, —; L.G. Galván et al. 461, HUMO, UAMIZ, Mexico, Puebla, OQ304549, OQ968182, OR047342; L.G. Galván et al. 472, HUMO, UAMIZ, Mexico, Puebla, OQ304550, OQ968183, OR060882; *C. racemosa* Kuijt, L.G. Galván et al. 429, HUMO, UAMIZ, Mexico, Guerrero, OQ304551, OQ968184, OR047343; L.G. Galván et al. 492, HUMO, UAMIZ, Mexico, Guerrero, OQ304552, OQ968185, OR047344; L.G. Galván et al. 493, HUMO, UAMIZ, Mexico, Guerrero, OQ304553, OQ968186, OR047345; *C. spathiflora* Galv.-González, Cerros, Espejo & López-Ferr., L.G. Galván et al. 254, HUMO, UAMIZ, Mexico, Guerrero, OQ304554, OQ968196, —; L.G. Galván et al. 418, HUMO, UAMIZ, Mexico, Guerrero, OQ304556, OQ968197, OR047353; L.G. Galván et al. 423, HUMO, UAMIZ, Mexico, Guerrero, OQ304555, OQ968198, OR047354; *C. tehucanensis* (Oliv.) Tiegh., L.G. Galván et al. 447, HUMO, UAMIZ, Mexico, Puebla, OQ300382, OQ968199, OR047355; L.G. Galván et al. 449, HUMO, UAMIZ, Mexico, Puebla, OQ300386, OQ968200, OR047356; W. Boege 2254, MEXU, Mexico, Puebla, OQ709137, OQ968201, OR047357; *Cladocolea* sp1, L.G. Galván et al. 522, HUMO, UAMIZ, Mexico, Morelos, OQ304557, OQ968187, OR047346; L.G. Galván et al. 552, HUMO, UAMIZ, Mexico, Morelos, OQ304558, OQ968188, OR047347; M.G. Maldonado 61, HUMO, UAMIZ, Mexico, Guerrero, OQ304559, OQ968189, OR047348; *Cladocolea* sp2, L.G. Galván et al. 372, HUMO, UAMIZ, Mexico, Guerrero, OQ304560, OQ968190, OR060881; L.G. Galván et al. 489, HUMO, UAMIZ, Mexico, Guerrero, OQ304561, OQ968191, OR047349; M.G. Maldonado 64, HUMO, UAMIZ, Mexico, Guerrero, OQ304562, OQ968192, OR047350; *Cladocolea* sp3, L.G. Galván et al. 406, HUMO, UAMIZ, Mexico, Guerrero, OQ304563, OQ968193, OR047351; L.G. Galván et al. 631, HUMO, UAMIZ, Mexico, Guerrero, OQ304564, OQ968194, OR047352; *Cladocolea* sp4, L.G. Galván et al. 519, HUMO, UAMIZ, Mexico, Morelos, OQ304565, OQ968195, OR060880; *Struthanthus acuminatus* (Ruiz & Pav.) Kuijt, M. Nee 51697, MEXU, Bolivia, Obispo Santistevan, OQ709138, OQ968216, OR047370; *S. capitatus* Lundell, D.E. Breedlove 48091, MEXU, Mexico, Chiapas, OQ709139, OQ968219, —; L.G. Galván et al. 464, MEXU, Mexico, Oaxaca, OQ304566, OQ968217, OR047371; M.G. Maldonado 8, HUMO, UAMIZ, Mexico, Oaxaca, OQ304567, OQ968218, OR047372; *S. condensatus* Kuijt, L.G. Galván et al. 565, HUMO, UAMIZ, Mexico, Jalisco, OQ304568, OQ968220, OR047373; L.G. Galván et al. 566, HUMO, UAMIZ, Mexico, Jalisco, OQ304569, OQ968221, —; *S. crassipes* (Oliv.) Eichler, L.G. Galván et al. 550, HUMO, UAMIZ, Mexico, Veracruz, OQ304570, OQ968222, OR047374; M.G. Maldonado 1, HUMO, UAMIZ, Mexico, Veracruz, OQ304571, OQ968223, OR047375; M.G. Maldonado 15, HUMO, UAMIZ, Mexico, Oaxaca, OQ304572, OQ968224, OR047376; *S. deppeanus* (Schltdl. & Cham.) G.Don, A. Méndez 9663, MEXU, Mexico, Chiapas, OQ709140, OQ968227, —; M.G. Maldonado 3, HUMO, UAMIZ, Mexico, Oaxaca, OQ304573, OQ968225, OR047377; M.G. Maldonado 6, HUMO, UAMIZ, Mexico, Oaxaca, OQ304573, OQ968226, —; *S. hartwegii* (Benth.) Standl., A. Burgos 3052, HUMO, UAMIZ, Mexico, Chiapas, OQ304597, OQ968229, OR047379; L.G. Galván et al. 536, HUMO, UAMIZ, Mexico, Chiapas, OQ304596, OQ968228, OR047378; *S. ibe-dzi* Mald.-Borja & Cerros, L.G. Galván et al. 474, HUMO, UAMIZ, Mexico, Oaxaca, OQ304582, OQ968243, OR047389; M.G. Maldonado 14, HUMO, UAMIZ, Mexico, Oaxaca, OQ304583, OQ968244, OR047390; M.G. Maldonado 19, HUMO, UAMIZ, Mexico, Oaxaca, OQ304584, OQ968245, OR047391; *S. interruptus* (Kunth) G.Don, L.G. Galván et al. 367, HUMO, UAMIZ, Mexico, Morelos, OQ304575, OQ968230, OR047380; L.G. Galván et al. 635, HUMO, UAMIZ, Mexico, Morelos; OQ304576, OQ968231, OR047381; M.G. Maldonado 48, HUMO, UAMIZ, Mexico, Guerrero, OQ304577, OQ968232, OR047382; *S. martianus* Dekkete & Waechter, Bolson 489, KT709682*, —, —; *S. oerstedii* (Oliv.) Standl., S. Sargent sn, Costa Rica, —, EU544509*, EU544457*; *S. orbicularis* (Kunth) Blume, A. Burgos 3374, HUMO, UAMIZ, Mexico, Chiapas, OQ304595, OQ968234, —; C.H. Ramos 2062, MEXU, Mexico, Campeche, OQ709141, OQ968235, —; L.G. Galván et al. 548, HUMO, UAMIZ, Mexico, Chiapas, OQ304594, OQ968233, OR047383; *S. palmeri* Kuijt, R. Vega 9936, UAS, Mexico, Sinaloa, OQ709142, OQ968236, OR047384; S.L. Friedman 359, MEXU, Mexico, Sonora, OQ709143, OQ968237, OR047385; S. cf. *polyrhizos*, Bolson & Imig 490, Brazil, KT709681*, —, —; *S. quercicola* (Schltdl. & Cham.) Blume, M.G. Maldonado 10, HUMO, UAMIZ, Mexico, Oaxaca, OQ304578, OQ968238, —; M.G. Maldonado 11, HUMO, UAMIZ, Mexico, Oaxaca, OQ304579, OQ968239, OR047386; *S. ramiro-cruzi* Martínez-Ambr. & Sorian-Benítez, L.G. Galván et al. 517, HUMO, UAMIZ, Mexico, Guerrero, OQ304580, OQ968240, OR047387; M.G. Maldonado 70, HUMO, UAMIZ, Mexico, Guerrero, OQ304581, OQ968241, OR047388; *S. uraguensis* G.Don., E.M. Zardini 37491, MEXU, Paraguay, Boquerón, OQ709144, OQ968242, —; *S. woodsonii* Cufod., D.L. Nickrent 2761, Costa Rica, —, EU544510*, EU544458*; *Struthanthus* sp., L.G. Galván et al. 390, HUMO, UAMIZ, Mexico, Guerrero, OQ304585, OQ968246, OR047392; L.G. Galván et al. 391, HUMO, UAMIZ, Mexico, Guerrero, OQ304586, OQ968247, OR047393; M.I. Miguel 918, HUMO, UAMIZ, Mexico, Guerrero, OQ304587, OQ968248, OR047394; M.I. Miguel 920, HUMO, UAMIZ, Mexico, Guerrero, OQ304588, OQ968249, OR047395.
- Outgroups:** *Actanthus dichotomus* (Ruiz & Pav.) Kuijt, ED737, LT599655*, —, —; *A. nodosus* (Desrl.) Engl., D.L. Nickrent 4561, Ecuador, —, —, EU544409*; *Gaidendron punctatum* (Ruiz & Pav.) G.Don, Calvin & Wilson CR01-08, Costa Rica, DQ333866*, DQ340617*, —; D.L. Nickrent 2729, Costa Rica, —, DQ788715*, DQ787445*; *Oryctanthus cordifolius* (C. Presl) Urb., L.G. Galván et al. 537, HUMO, UAMIZ, Mexico, Chiapas, OQ304598, OQ968202, OR047358; L.G. Galván et al. 544, HUMO, UAMIZ, Mexico, Chiapas, OQ304599, OQ968203, OR047359; L.G. Galván et al. 620, HUMO, UAMIZ, Mexico, Guerrero, OQ304600, OQ968204, OR047360; *Passovia micrantha* (Eichler) Tiegh., G.T. Prance 4329, MEXU, Brazil, Boca da Mata, OQ709145, OQ968205, —; H.S. Irwin 55609, MEXU, Surinam, Lucie River, OQ709146, OQ968206, —; *P. pyrifolia* (Kunth) Tiegh., J.M. Caspeta 5, HUMO, UAMIZ, Mexico, Chiapas, OQ304602, OQ968208, OR047368; L.G. Galván et al. 539, HUMO, UAMIZ, Mexico, Chiapas, OQ304601, OQ968207, OR047367;

Peristethium leptostachyum (Kunth) Tiegh., *G. Davidse* 26220, MEXU, Costa Rica, Puntarena, OQ709147, OQ968250, OR047366; *B. Hammel* 3235, MEXU, Panama, Colón, OQ709148, OQ968251, —; *Phthirusa inconspicua* (Benth.) Eichler, L.G. Galván et al. 588, HUMO, UAMIZ, Mexico, Michoacán, OQ304590, OQ968209, OR047361; L.G. Galván et al. 591, HUMO, UAMIZ, Mexico, Michoacán, OQ304589, OQ968210, OR047362; *P. inorna* (B.L. Rob. & Greenm.) Kuijt, L.G. Galván et al. 364, HUMO, UAMIZ, Mexico, Morelos, OQ304593, OQ968211, OR047363; L.G. Galván et al. 479, HUMO, UAMIZ, Mexico, Puebla, OQ304592, OQ968212, OR047364; L.G. Galván et al. 481, HUMO, UAMIZ, Mexico,

Puebla, OQ304591, OQ968213, OR047365; *P. rhynchophylla* (Kuijt) Kuijt, F.J. Roldán 1141, MEXU, Colombia, Antioquia, OQ709149, OQ968252, —; *Psittacanthus ramiflorus* (DC.) G. Don, A. Flores 969, HUMO, UAMIZ, Mexico, Jalisco, OQ304603, OQ968214, —; L.G. Galván et al. 463, HUMO, UAMIZ, Mexico, Oaxaca, OQ304604, OQ968215, OR047369; *Tripodanthus acutifolius* (Ruiz & Pav.) Tiegh., T.T. Motta 3021, MEXU, Brazil, Paraná, OQ709150, OQ968253, OR047396.

APPENDIX 2. Coding and description of the character states used in this study.

Character	Description	Code
Habit		
Vine	Plants not branched from the base. Long, pendulous and flexuous branches. Standing stems with multiple footholds on host branch.	0
Shrub	Plants branched from the base. Upright branches. Standing stems without multiple footholds on host branch.	1
Secondary haustorium		
Absent	Plants with only one haustorium derived from the embryo.	0
Present	Plants with multiple haustoria connections, derived from the stems or stem roots.	1
Phyllotaxis		
Alternate	One leaf per node.	0
Opposite	Two leaves per node.	1
Subternate	Three leaves per node	2
Vestiture		
Glabrous	Without epidermal projections.	0
Papillate	Epidermal projection 1–2 times longer than wide, with obtuse to round apex.	1
Pubescent	Epidermal projection at least three times longer than wide, with acute apex.	2
Inflorescence form		
One-flowered	Sessile flower in the leaf axil, single or clustered, as in <i>Phthirusa</i>	0
Racemiform	Inflorescences axis with secondary branches, supporting triads, dyads, or monads.	1
Spiciform	Inflorescence with sessile triads or monads along the axis.	2
Capituliform	Inflorescence with sessile triads or monads concentrated at the distal end of the inflorescence axis.	3
Umbelliform	With pedicellate monads or pedunculate triads grouped at the distal end of the inflorescence axis.	4
Inflorescence type		
Simple	Inflorescences in which the flower is the basic unit (monad).	0
Compound	Inflorescences in which a group of 2–3 flowers form the basic unit of the inflorescence (dyad or triad).	1
Terminal flower		
Absent	The inflorescence is indeterminate.	0
Present	The inflorescence is determinate.	1
Secondary bracts		
Absence	Monad or central flower of the triad only with basal bract.	0
Presence	Monad or central flower of the triad with a pair of secondary bracts (bracteoles), in lateral position in relation to the primary basal bract.	1
Flower size		
Small	Flowers from 0.3 to 1.2 cm long.	0
Median	Flowers from 1.3 to 2 cm long.	1
Large	Flowers more than 2 cm long.	2
Flower sex		
Unisexual	Flowers with only one functional reproductive whorl.	0
Bisexual	Flowers with two functional reproductive whorls.	1
Merosity		
Tetramerous	Flower with four petals.	0
Pentamerous	Flower with five petals.	1
Hexamerous	Flower with six petals.	2
Heptamerous	Flower with seven petals.	3
Stamen form		
Isomorphic	All stamens with same length.	0
Dimorphic	Stamens groups in two sets with different length.	1
Style shape		
Straight	Style without folds or with a very open bend of more than 160° along the entire length of the style.	0
Sigmoid	Style with a fold or bend along style.	1
Convolute	Style with two or more vertical or transversal folds along style.	2