# Sistemática de Cyclanthaceae

Eduardo da Silva Leal

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Tese apresentada ao Instituto de Biociências da Universidade de São Paulo, para obtenção do Título de Doutor em Ciências, na Área de Botânica.

Orientador: Prof. Dr. Renato de Mello-Silva

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Orientador

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# Index

# Resumo

Cyclanthaceae possui cerca de 230 espécies. São ervas terrestres, hemiepífitas, lianas ou epífitas distribuídas na região Neotropical, se estendendo do sul do México a Mata Atlântica do sul do Brasil. A família é dividida em duas subfamílias de acordo com a morfologia da inflorescência: Cyclanthoideae com flores estaminadas e pistiladas dispostas em ciclos alternos, incluindo apenas *Cyclanthus*; e Carludovicoideae com uma flor pistilada envolvida por quatro flores estaminadas e compreende o restante dos gêneros. Até o presente, estudos filogenéticos baseados somente em dados morfológicos, e com amostragem a nível genérico, não foram suficientes para clarificar suas relações. Além disso, um dos dois grandes grupos em Carludovicoideae emergiu como parafilético. Neste estudo, usamos dados morfológicos e de sete marcadores moleculares, cinco de cloroplastos e dois nucleares, com uma ampla amostragem à nível específico, para propor uma hipótese filogenética para Cyclanthaceae. Nosso resultado recuperou a família como monofilética e corroborou sua divisão em duas subfamílias. Os gêneros pertencentes a Carludovicoideae emergiram em três clados: (i) o gênero *Carludovica*; (ii) o clado Asplundia que contém *Asplundia*, *Dicranopygium* e *Schultesiophytum*; e (iii) o clado Evodianthus formado por *Chorigyne*, *Dianthoveus*, *Evodianthus*, *Ludovia*, *Sphaeradenia*, *Stelestylis* e *Thoracocarpus*. Todos os gêneros previamente circunscritos emergiram como monofiléticos. O grupo Sphaeradenia, composto por *Chorigyne*, *Ludovia*, *Sphaeradenia* e *Stelestylis* emerge como monofilético fortemente sustentado por caracteres morfológicos e moleculares. Para maximizar a informação filogenética, bem como facilitar a identificação, o gênero *Dianthoveus* é sinomizado em *Evodianthus*. No capítulo 2 uma chave de identificação para todas as espécies de Cyclanthaceae ocorrentes na Mata Atlântica é fornecida. As espécies endêmicas de *Asplundia* são revisadas, resultando em três táxons sinonimizados sob *A. brachypus*, e uma nova espécie, *A. orthostigma*, é descrita. No capítulo 3 é apresentado um índice taxonômico para todas as espécies já descritas de Cyclanthaceae. Nós indicamos 225 nomes aceitos e 60 sinônimos. Quatro lectótipos e dois neótipos são designados para quatro nomes. Para mais quatro nomes, a tipificação é completada, com a designação do segundo passo do lectótipo. Finalmente, doze nomes são considerados como novos sinônimos.

# Abstract.

Cyclanthaceae has ca. 230 species. They are terrestrial herbs, hemiephytic, climbing or epiphytic distributed in the Neotropics, ranging from the South Mexico to Southward Atlantic forest. The family is divided into two subfamilies based on the inflorescence morphology: Cyclanthoideae with staminate and pistillate flowers arranged in alternate whorls, includes only *Cyclanthus*; and Carludovicoideae which has a pistillate flower with four surrounding staminate flower, encompass the others genera. Nowadays, phylogenetic studies based on morphological data in generic level were insufficient to clarify its relationship. Furthermore, one of the groups of Carludovicoideae emerged as paraphyletic. In this study we combined morphological and seven molecular markers, five from plastid and two nuclear, in a broad sampling in species level to recover a consistent phylogenetic hypothesis to Cyclanthaceae. We reconstructed a monophyletic Cyclanthaceae with two subfamilies. Genera belonging to Carludovicoideae emerged in three clades: (i) the genus *Carludovica*, (ii) the Asplundia Clade which includes *Asplundia*, *Dicranopygium* and *Schultesiophytum*; and (iii) the Evodianthus Clade comprising *Chorigyne*, *Dianthoveus*, *Evodianthus*, *Ludovia*, *Sphaeradenia*, *Stelestylis* and *Thoracocarpus*. All previous known genera were recovered as monophyletic. The Sphaeradenia Group, which includes *Chorigyne*, *Ludovia*, *Sphaeradenia* and *Stelestylis*, emerged as monophyletic strongly supported by morphological and molecular characters. To maximize the phylogenetic outcome and make the identification easier *Dianthoveus* is synonymized under *Evodianthus*. In the Chapter 2 an identification key for all Cyclanthaceae species in Atlantic forest is provided. The endemic species of *Asplundia* are revisited resulting in three taxa synonymized under *A. brachypus*, and *A. orthostigma* newly described. In the Chapter 3 a taxonomic index for all Cyclanthaceae species is provided. We highlighted 225 accepted names and 60 synonyms heterotypics. Four lectotypes and two neotypes are designated. The typification is complemented to four taxa more with second-step lectotypification. Finally, twelve names are placed as synonyms.

# General Introduction

Cyclanthaceae are terrestrial herbs, hemiephytic, climbing or epiphytic plants distributed in the Neotropics, ranging from the South Mexico to Southward Atlantic forest (Harling & al., 1998). They are highly diversified in the biogeographic Choco lowland forest and cloudy forest from tropical Andes, reaching up to 3000 m elevation (Harling, 1958). Cyclanthaceae is recognized by its inflorescence with alternate cycles of staminate and pistillate flowers or a pistillate flower with four surrounding staminate flowers, and by the almost ubiquitous bifid leave. The inflorescence is sustained by an unbranched peduncle supporting bracts subtending the inflorescence in a cluster or loose arrangement. Flowers are arranged in a spiralled or ring continuum in Cyclanthoideae making impossible to recognize an isolated flower. Conversely, Carludovicoideae has actinomorphic or zigomorphic staminate flower with numerous stamens and absent perianth (Sajo & al., 2014) while the pistillate flower has tetramerous perianth arranged in one whorl. Four filiform and long staminoid are opposite to the tepals in this flower. Four stigma can be attached to the ovary summit or elevated by a style.

Cyclanthaceae encompass ca. 225 species distributed into 12 genera: *Asplundia* Harling (97 spp.), *Carludovica* Ruiz & Pav. (4 spp.), *Chorigyne* R. Erikss. (7 spp.), *Cyclanthus* Poit. ex A. Rich. (2 sp.), *Dianthoveus* Hammel & G.J. Wilder (1 sp.), *Dicranopygium* Harling (51 spp.), *Evodianthus* Oersted (1 sp.), *Ludovia* Brongn. (3 spp.), *Schultesiophytum* Harling (1 sp.), *Sphaeradenia* Harling (52 spp.), *Stelestylis* Drude (4 spp.) and *Thoracocarpus* Harling (1 sp.). Cyclanthaceae is represented by 29 species and nine genera in Brazil, specially occurring in Amazonic (21 spp.) and Atlantic (10 spp.) forest with seven endemic species at the latter (Leal, 2018). Amazonian-Atlantic forest disjunction was recorded only for *Evodianthus funifer* and *Thoracocarpus bissectus* whereas *Asplundia gardneri* occurs in the *brejos* and riparian forest in the Central Brazil.

The positioning of Cyclanthaceae in suprafamiliar categories has been subject of changes in successive classifications. Bentham & Hooker (1883) grouped it with Aroideae, Lemnaceae, Pandaneae and Typhaceae, in series Nudiflorae (category corresponding to order). Cronquist (1981, 1988) positioned it alone in order Cyclanthales, in subclass Arecidae, assuming the family's affinities with Araceae, Arecaceae, Lemnaceae and Pandanaceae. Dahlgren & al. (1985) also positioned

Cyclanthaceae alone in Cyclanthales, the sole order in superorder Cyclanthiforae. More recent classifications, based on molecular phylogenies, positioned Cyclanthaceae in order Pandanales, along with Pandanaceae, Stemonaceae, Triuridaceae and Velloziaceae (APG IV, 2016 and precedents). The order has been well supported in recent phylogenetic studies based on morphological (Rudall & Bateman, 2006) and molecular data (Chase & al. 2000, Caddick & al. 2002, Davis & al. 2004, Mennes & al. 2013). Cyclanthaceae is monophyletic and distinct from the remaining Pandanales by the following synapomorphies: leaves with open sheath and monoic inflorescences, one pistillate flower surrounded by four staminate flowers or alternating whorls of pistillate and staminate flowers.

The first infrafamiliar classification for Cyclanthaceae was proposed by Drude (1881), who recognized two tribes: Carludoviceae and Cyclantheae. He also proposed three sections in tribe Carludoviceae: Anomalae, Bifidae and Palmatae, according to leaf blade shape and division. Later, Harling (1954a, b) made profound taxonomic changes in genus *Carludovica*, splitting it into *Asplundia*, *Dicranopygium* and *Sphaeradenia*. Posteriorly, Harling, in his large monograph about the family (1958), elevated the tribes defined by Drude (1881) to subfamilies, taking into account mainly inflorescence structure. He characterized subfamily Cyclanthoideae, at the time containing only *Cyclanthus bipartitus* Poit. ex A.Rich., by the spadix containing alternating whorls of staminate and pistillate flowers, and subfamily Carludovicoideae with the remaining genera, characterized by groups of four staminate flowers surrounding one pistillate flower. Harling (1958) distributed the genera of Carludovicoideae in two groups not formally classified: a cohesive Sphaeradenia group, and Asplundia group, both inconsistent and presented as an attempt to position genera.

Eriksson (1994) performed a new morphological analysis of Cyclanthaceae, using sixty-three morphological and anatomical characters. Sphaeradenia group, comprehending *Chorigyne*, previously described by Eriksson (1989), *Ludovia*, *Sphaeradenia* and *Stelestylis*, emerged as monophyletic, supported by the synapomorphies plants predominantly epiphytes, distichous phyllotaxy, coriaceous leaf blade, apical or subapical placentation and endosperm with thickened cell walls. On the other hand, Asplundia group emerged as paraphyletic and affinities among genera remained uncertain, suggesting the need of analysis with more characters (Eriksson, 1994). Additionally, according to the hypothesis presented by Eriksson (1994)

*Asplundia*, the richest genus, is paraphyletic.

In this perspective, this thesis is the first to reconstruct the phylogeny of Cyclanthaceae with a broad sampling combining morphological and molecular data. Moreover, this thesis aims to contribute to the understanding to the species from Atlantic forest as well as provide a full taxonomic index of Cyclanthaceae. Thus, this study is presented in three chapters as follow:

Chapter 1. Phylogeny of Cyclanthaceae (the Panama-hat family) based on molecular and morphological data. This Chapter provide a phylogenetic reconstruction of the family based on seven molecular markers and 42 morphological and anatomical characters. All known genera were recovered as monophyletic according to Maximum Parsimony and Bayesian analysis.

Chapter 2. Revisiting the Atlantic forest cyclants with a key for the species and a revision of the endemic clade of *Asplundia*. Identification key for seven species from the Atlantic forest is provided. Three names are newly synonymized under *Asplundia brachypus*, and a new species is described.

Chapter 3. Nomenclator botanicus of the Cyclanthaceae. A total of 225 species are currently accepted. Four lectotypes and two neotypes are designated. Second-step lectotypification is given for four names. Twelve names are newly synonymized.

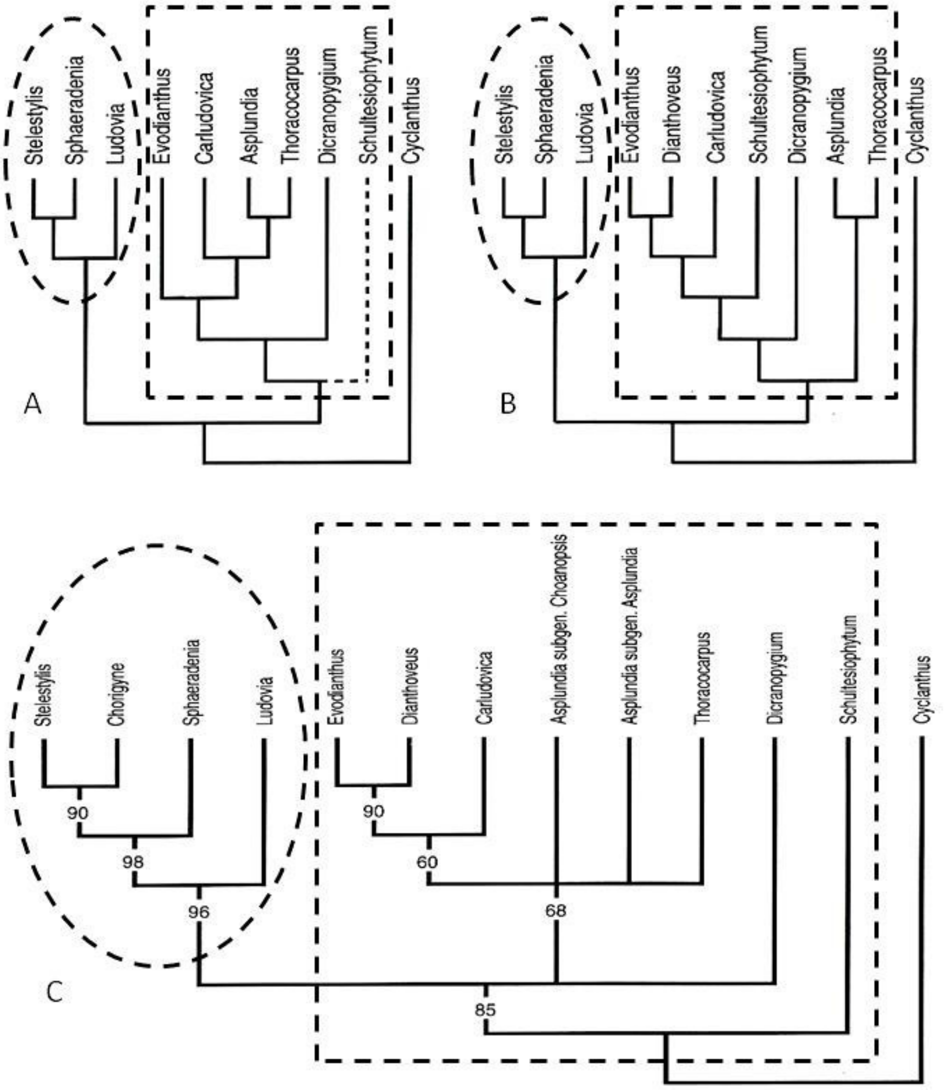

**Figura 1.** Cladograms showing the affinity between the genera of Cyclanthaceae. The Sphaeradenia group is evidenced by dashed ellipses and the Asplundia group by dashed rectangles. A-Harling (1958), the dashed line indicates the uncertainty of the position of Schultesiophytum. B-Hammel and Wilder (1989) indicating the two groups as monophyletic and C. Eriksson (1994) showing the non-monophyletic Asplundia group and monophyletic group Sphaeradenia, as well as two lineages for the genus *Asplundia*.

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# Chapter 1

# Phylogeny of Cyclanthaceae (the Panama-hat family) based on molecular and morphological data

**Abstract** The Cyclanthaceae, a Neotropical family, has never been the subject of species-level phylogenetic studies. In this work, we evaluate the generic relationships in Cyclanthaceae based on molecular data from the nuclear low-copy genes *phy*C and *rpb*2, the plastid spacers *atp*b-*rbc*L, *psb*A-*trn*H, *trn*L-*trn*F and *trn*Q-*rps*16, *mat*K and 42 morphological characters from 122 individuals representing 103 taxa from all genera of Cyclanthaceae, with 794 newly produced sequences, spanning the taxonomic and biogeographic diversity of the family. Phylogenetic relationships were inferred using maximum parsimony and Bayesian approaches. Our results of the combined molecular and total-evidence datasets support the monophyly of the Cyclanthaceae and establish the subfamily Cyclanthoideae, including only *Cyclanthus*, as sister to the rest of the family. Three major lineages are retrieved within the Carludovicoideae: (1) the Carludovica clade, including taxa assigned to genus *Carludovica*, (2) the Asplundia clade, comprising the genera *Asplundia, Dicranopygium*, and *Schultesiophytum*, and (3) the Evodianthus clade, including *Chorigyne*, *Dianthoveus*, *Evodianthus*, *Ludovia*, *Sphaeradenia*, *Stelestylis* and *Thoracocarpus*. We expanded the generic circumscription of the monotypic *Evodianthus* to encompass the also monotypic *Dianthoveus* and a new combination is provided. This propose is congruent with our phylogeny and maximizes both generic stability and ease of identification. This study provides the first phylogenetic backbone for Cyclanthaceae, being sufficiently robust to serve as starting point for future research into the evolutionary history of this neglected family.

**Keywords**: Asplundia clade, *Carludovica*, *Dianthoveus*, *Evodianthus*, Evodianthus clade.

## Introduction

Cyclanthaceae is a monocot family exclusively distributed in the Neotropical region, from Southern Mexico to the Atlantic Forest in Southern Brazil (Harling, 1958). It comprehends terrestrial herbs, epiphytes, hemiepiphytes or lianas, well-diversified in lowlands in the tropical rain forest and in the Andean region, in elevations of up to 3000 m, preferring humid habitats (Figure 1 and 2, Harling & al., 1998). In the current circumscription, Cyclanthaceae has 226 species distributed in 12 genera: *Asplundia* Harling (97 spp.), *Carludovica* Ruiz & Pav. (4 spp.), *Chorigyne* R.Erikss. (7 spp.), *Cyclanthus* Poit. ex A.Rich. (2 spp.), *Dianthoveus* Hammel & G.J.Wilder (1 sp.), *Dicranopygium* Harling (53 spp.), *Evodianthus* Oerst. (1 sp.), *Ludovia* Brongn. (3 spp.), *Schultesiophytum* Harling (1 sp.), *Sphaeradenia* Harling (52 spp.), *Stelestylis* Drude (4 spp.) and *Thoracocarpus* Harling (1 sp.).

Some species are used as roofing material (Harling & al., 1998), for basket weaving (Baluarte-Vásquez, 2000; Balcázar-Vargas & van Andel, 2005), as fishing tools (Oliveira & al., 2006), as food (Chízmar-Fernández & al., 2009; Segura & al., 2018; G. Gonçalves pers. commun.), ornamentals (Medina & al., 2017) and in the manufacture of the traditional Panama hat, from the leaves of *Carludovica palmata* Ruiz & Pav. (Bennett & al., 1992; Fadiman, 2001).

The positioning of Cyclanthaceae in suprafamiliar categories has been subject of changes in successive classifications. Bentham & Hooker (1883) grouped it with Aroideae, Lemnaceae, Pandaneae and Typhaceae, in series Nudiflorae (category corresponding to order). Cronquist (1981, 1988) positioned it alone in order Cyclanthales, in subclass Arecidae, assuming the family's affinities with Araceae, Arecaceae, Lemnaceae and Pandanaceae. Dahlgren & al. (1985) also positioned Cyclanthaceae alone in Cyclanthales, the sole order in superorder Cyclanthiforae. More recent classifications, based on molecular phylogenies, positioned Cyclanthaceae in order Pandanales, along with Pandanaceae, Stemonaceae, Triuridaceae and Velloziaceae (APG IV, 2016 and precedents). The order has been well supported in recent phylogenetic studies based on morphological (Rudall & Bateman, 2006) and molecular data (Chase & al., 2000; Caddick & al., 2002; Davis & al., 2004; Mennes & al., 2013). Cyclanthaceae is monophyletic and distinct from the remaining Pandanales by leaves with open sheath and monoic inflorescences, one pistillate flower surrounded by four staminate flowers or alternating whorls of pistillate and staminate flowers (Eriksson, 2018).

The first infrafamiliar classification for Cyclanthaceae was proposed by Drude (1881), who recognized two tribes: Carludoviceae and Cyclantheae. He also proposed three sections in tribe Carludoviceae: Anomalae, Bifidae and Palmatae, according to leaf blade shape and division. Later, Harling (1954a, b) made profound taxonomic changes in genus *Carludovica*, splitting it into *Asplundia*, *Dicranopygium* and *Sphaeradenia*. Posteriorly, Harling, in his large monograph about the family (1958),

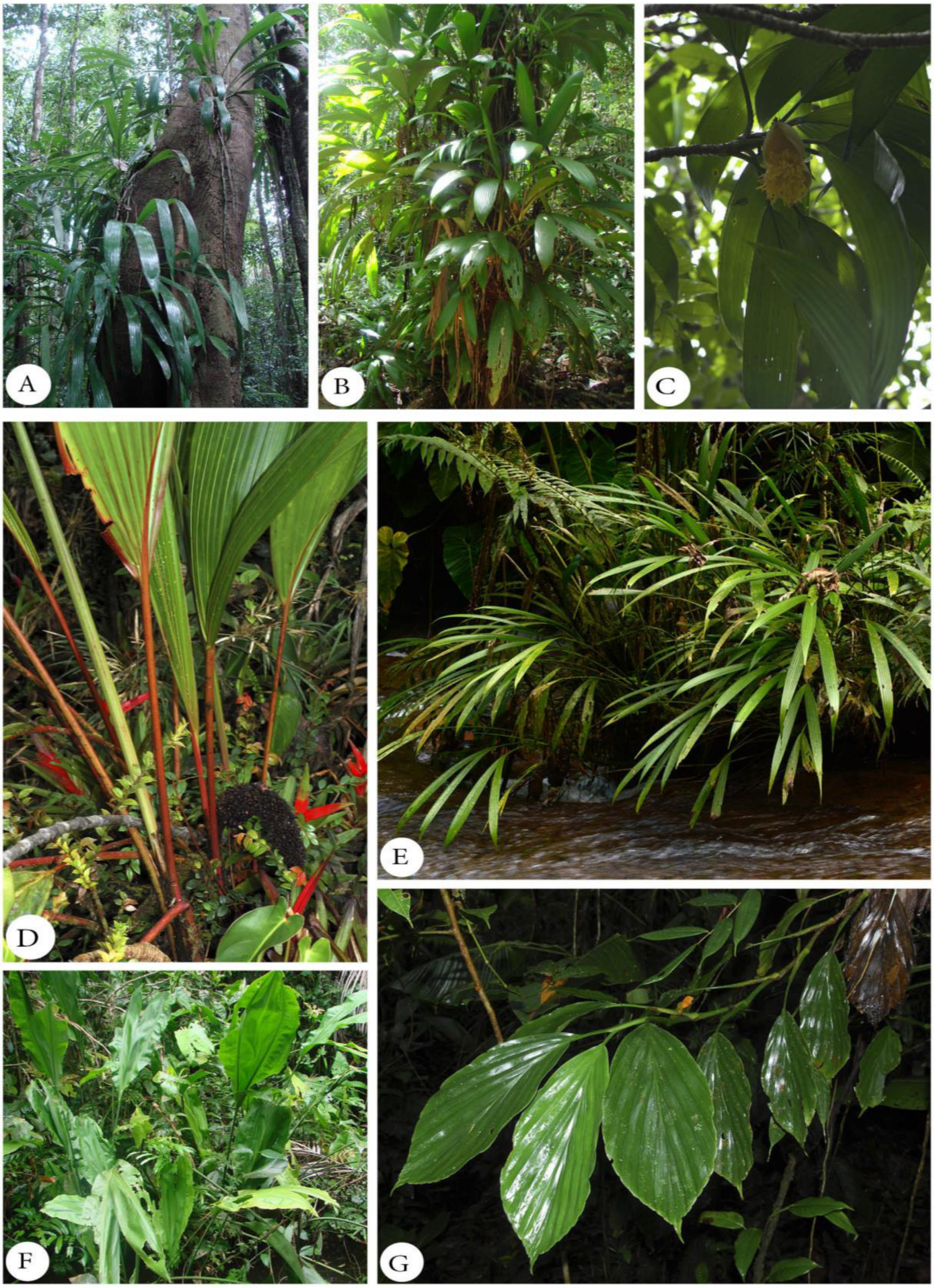

**Fig. 1.** Photos of the Cyclanthaceae taxa. **A.** *Evodianthus funifer*; **B.** *Asplundia guianensis*; **C.** *Thoracocarpus bissectus*; **D.** *Sphaeradenia* sp.; **E.** *Dicranopygium* sp.; **F.** *Cyclanthus bipartitus*; **G.** *Ludovia integrifolia*. — Image credits: Eduardo Leal (A, B, C and F); David Scherberich (D, E and G).

**Fig. 2.** Photos of the Cyclanthaceae taxa. **A.** Inflorescence of the *Asplundia gardneri*; **B.** Infructescence of the *A. callejasii*; **C.** Inflorescence of the *Dicranopygium* sp.; **D.** Infructescence of the *Dicranopygium* sp.; **E.** Inflorescence and infructescence of the *Evodianthus funifer*; **F.** Inflorescence of the *Ludovia lancifolia*; **G.** Inflorescence of the *Sphaeradenia duidae*; **H.** Infructescence of the *Stelestylis stylaris*; **I.** Infructescence and **J.** Inflorescence of the *Thoracocarpus bissectus*. — Image credits: Leonardo Leitão (A); Dino Tuberquia (B, D); David Scherberich (C, E); Leandro Freitas (F); Marcus Nadruz (G); Ricardo Azoury (H); Juliana El Ottra (I, J.).

elevated the tribes defined by Drude (1881) to subfamilies, taking into account mainly inflorescence structure. He characterized subfamily Cyclanthoideae, at the time containing only *Cyclanthus bipartitus* Poit. ex A.Rich., by the spadix containing alternating whorls of staminate and pistillate flowers, and subfamily Carludovicoideae with the remaining genera, characterized by groups of four staminate flowers surrounding one pistillate flower. Harling (1958) distributed the genera of Carludovicoideae in two groups not formally classified: a cohesive Sphaeradenia group, and Asplundia group, both inconsistent and presented as an attempt to position genera.

The morphological cladistics analysis of Hammel & Wilder (1989), including their new genus *Dianthoveus*, and 23 characters, corroborated the two informal groups presented by Harling (1958), and positioned *Dianthoveus* in the Asplundia group. Eriksson (1994) performed a new morphological analysis of Cyclanthaceae, using 63 morphological and anatomical characters. Sphaeradenia group emerged as monophyletic, comprehending *Chorigyne*, previously described by Eriksson (1989), *Ludovia*, *Sphaeradenia* and *Stelestylis*, emerged as monophyletic, supported by the synapomorphies of plants predominantly epiphytes, distichous phyllotaxy, coriaceous leaf blade, apical or subapical placentation and endosperm with thickened cell walls. On the other hand, Asplundia group emerged as paraphyletic and affinities among genera remained uncertain, suggesting a needful of analysis with more characters (Eriksson, 1994).

*Asplundia* is the largest genus in Cyclanthaceae, with approximately 100 species, distributed in two subgenera. Its geographical distribution coincides with that of the family. Hammel & Wilder (1989) did not take into account the genus subdivision, which emerged as sister of *Thoracocarpus*, forming a monophyletic group. On the other hand, Eriksson (1994) included the two subgenera as terminals in his analysis. As a result, *Asplundia* emerged as paraphyletic, in a polytomy of three distinct lineages: *Asplundia* subg. *Asplundia*, *A.* subg. *Choanopsis* and *Thoracocarpus*. *Asplundia* subg. *Asplundia* was supported by tricostate leaves, assymetrical flowers with flattened receptacle and usually terrestrial or hemiepiphytic habit. *Asplundia* subg. *Choanopsis* shares with *Thoracocarpus bissectus* (Vell.) Harling the unicostate leaves and symmetrical flowers with excavated receptacle. These two phylogenetic analyses of Cyclanthaceae, both based in relatively few morphological characters, did not satisfactorily clarify relationships among genera in subfamily Carludovicoideae and a less ambiguous evolutionary setting could not be delineated for the family.

The use of molecular characters in phylogenetic analysis of Cyclanthaceae is necessary in order to complement the studies already carried out, clarify the relationship among genera and provide support to its phylogeny reconstruction. Molecular data, allied with traditional morphological studies, and the comparison with existing classifications will allow questioning and reviewing genera delimitation in Cyclanthaceae, besides elaborating a new evolutionary hypothesis for these taxa.

The lack of a well-resolved phylogenetic hypothesis hinders the elaboration of a coherent classification, besides the investigation of biogeography and evolution of Cyclanthaceae, crucial to understanding the diversification of the group and of the Neotropical flora. This study presents a phylogeny for the Cyclanthaceae, based in seven molecular markers and forty-two morphological characters. The sampling in Cyclanthaceae includes all recognized genera and 123 terminals and, for the first time, presents molecular data for the genera *Dianthoveus*, *Schultesiophytum* and *Stelestylis*.

## Material and Methods

**Taxon sampling.** — Relationships between the genera of Cyclanthaceae are still unclear (Eriksson, 1994). Because increased taxa sampling is an important determinant of phylogenetic resolution (Heath & al., 2008), an effort was made to maximize taxonomic representation in this study, thus allowing an improved phylogenetic framework for the family. Table 1 lists all terminals and voucher material for the molecular study. One hundred thirty-eight terminals were sampled, representing 118 species. Cyclanthaceae is represented by 103 taxons (43% of the family), from all genera, namely: 51 species (58 individuals) of *Asplundia*, 4 species (4 individuals) of *Carludovica*, 2 species (2 individuals) of *Chorigyne*, 1 species (4 individuals) of *Cyclanthus*, 1 species (1 individual) of *Dianthoveus*, 14 species (14 individuals) of *Dicranopygium*, 1 species (4 individuals) of *Evodianthus*, 3 species (7 individuals) of *Ludovia*, 1 species (1 individual) of *Schultesiophytum*, 22 species (22 individuals) of *Sphaeradenia*, 2 species (2 individuals) of *Stelestylis* and 1 species (3 individuals) of *Thoracocarpus*. The data represent ca. 48% of the species of *Asplundia*, 43% of *Chorigyne*, 50% of *Cyclanthus*, 24% of *Dicranopygium*, 40% of *Sphaeradenia*, 50% of *Stelestylis* and 100% of *Carludovica*, *Dianthoveus*, *Evodianthus*, *Ludovia*, *Schultesiophytum* and *Thoracocapus*. The outgroup comprehends 15 taxons belonging to the other families in order Pandanales and one species of Bromeliaceae to root the tree (sensu APG IV 2016, Table 1).

**DNA extraction, amplification and sequencing.** Most part of the DNA was extracted from leaf tissue dried in silica-gel. In few cases, herborized material was used. The extraction was carried out with the DNeasy plant mini kit (QIAGEN Inc., Valencia, California), with modifications proposed by Alexander & al. (2007). Herbarium samples were extracted with a longer incubation period and lower temperatures (24 h at 42˚C) and resuspended in smaller volumes of elution buffer (50 µL instead of 150 µL), which proved more effective for this kind of sample. To reconstruct the phylogeny within Cyclanthaceae, five regions of the plastid DNA were used, one being a coding region (*mat*K) and four being intergenic spacers (*atp*B-*rbc*L, *psb*A-*trn*H, *trn*L-*trn*F and *trn*Q-*rps*16) and also two low copy regions of nuclear DNA, the coding portion of phytochrome C gene (*phy*C) and the second larger subunit of the RNA polymerase II gene (*rpb*2). These molecular markers were previously used in phylogenetic and/or biogeographical studies of families closely related to Cyclanthaceae, such as Velloziaceae (Mello-Silva & al., 2011) and Pandanaceae (Buerki & al., 2012; Gallaher & al., 2014), showing good potential for phylogenetic resolution and not showing detectable paralogy problems. DNA amplification was performed through polymerase chain reaction (PCR), with a final volume of 15 µL, with the following ingredients: 0.5–0.7 µL DNA (c. 30 ng $\mu L^{-1}$), 7.5 µL 2x EconoTaq Plus Green (Lucigen Technologies), 2 µL of each primer (3µM), 0.75 µL spermidine (4 mM) and 2.5 µL of deionized water. PCR parameters and primers for amplification and sequencing were obtained from Manen & al. (1994) for *atp*B-*rbc*L, Ford & al. (2009) for *mat*K, Hertweck & al. (2015) for *phy*C, Shinozaki & al. (1986) for *psb*A-*trn*H, Denton & al. (1998), Roncal & al. (2005) and Saas & Specht (2010) for *rpb*2, Taberlet & al. (1991) for *trn*L-*trn*F and Shaw & al. (2007) for *trn*Q-*rps*16. All reactions were performed in Eppendorf® thermocycler. Amplification products were observed in electrophoresis in 1% agarose gel. If the presence of weak and/or multiple bands was detected, a second PCR reaction was conducted with the product of the first reaction diluted 10-fold, to amplify the region in two adjacent parts. The final reaction product was sequenced using the Sanger method. The sequences were obtained through the high yield sequencing service from Macrogen® (USA), with the same primers (forward and reverse) used for amplification. Voucher information and GenBank accession numbers are listed in Table 1. One hundred twelve new sequences of *atp*B-*rbc*L were obtained, 122 of *mat*K, 123 of *psb*A-*trn*H, 98 of *phy*C, 94 *rpb*2, 123 of *trn*L-*trn*F and 122 of *trn*Q-*rps*, totaling 794 sequences. The nuclear markers exhibited higher number of variable and informative base pairs. The marker *phy*C emerges as the most informative region from all individual markers. In contrast, chloroplast markers show lower percentages of variable and informative characters, with *psb*A-*trn*H being the most informative. The general statistics of the alignments for the individual and combined datasets are summarizes in Table 4.

**Table 1.** Studied taxa, voucher information, and GenBank accession number for the samples used in this work. Sequences newly generated for this study are labeled as "N". Letters after voucher number indicate that the specimen is in the phylogenetic trees. LCMO = Live collection from the Missouri Botanical Garden, RBGK = DNA bank from the Royal Botanic Gardens, Kew; B = Buerki & al. (2012); C = Callmander & al. (2003); Ch = Chen & al. (2010); G = Gallaher & al. (2014); Gi = Givnish & al. (2011); H = Hertweck & al. (2015); Hs = Hsua & al. (2013); L = Li & al. (2012); La = Lam & al. (2016); Li = Li & al. (2008); M = Maia & al. (2012); S = Silvestro & al. (2013); S&P = Sass & Specht (2010); V = Vongsak & al. (2008)

| Species | *atpB-rbcL* | *matK* | *phyC* | *psbA-trnH* | *rpb2* | *trnL-trnF* | *trnQ-rps16* | Voucher and herbarium |
|---|---|---|---|---|---|---|---|---|
| **Outgroup** | | | | | | | | |
| *Aechmea bromeliifolia* (Rudge) Baker ex Benth. & Hook.f. | JF280678 - Gi | JN202208 - M | JX649386 - S | - | FJ942788 - S&P | HQ882707 - Gi | - | - |
| *Benstonea affinis* (Kurz) Callm. & Buerki | - | JX286801 - B | KJ681806 - G | - | - | JX286957 - B | JX287150 - B | |
| *Freycinetia arborea* Gaudich. | - | JX286815 - B | KJ681799 - G | | - | KJ681511 - G | JX287164 - B | - |
| *Martellidendron gallinarum* (Callm.) Callm. | AY337625 - C | JX286738 - B | - | - | - | AY337669 - C | JX287087 - B | - |
| *Pandanus tectorius* Parkinson | - | JX286775 - B | KJ681789 - G | JN407018 - L | - | JX286937 - B | JX287123 - B | - |
| *Sararanga sinuosa* Hemsl. | AY337638 - C | JX286874 - B | KJ681807 - G | - | - | AY337682 - C | JX287223 - B | - |
| *Croomia pauciflora* Torr. ex Torr. & A.Gray | EU075377 - Li | KP083061 - H | - | - | - | DQ831506 - Li | JX287063 - B | - |
| *Pentastemona sumatrana* Steenis | - | KU127303 - La | - | - | - | - | - | - |
| *Stemona tuberosa* Lour. | JQ733661 - Hs | GQ434036 - Ch | | GQ434873 - Ch | - | FJ194463 - Li | - | - |
| *Stichoneuron caudatum* Ridl. | - | JX286712 - B | - | AB373200 - V | - | - | JX287061 - B | - |

|  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|
| *Sciaphila densiflora* Schltr. |  | KU127272 - La | - | - | - |  |  | - |
| *Acanthochlamys bracteata* P.C.Kao | JN016989 | KP083039 - H | - | JN017041 | - | JN016885 | - | *Chase 842* (K) |
| *Barbaceniopsis boliviensis* (Baker) L.B.Sm. | JN016996 | - | - | JN017048 | - | JN016892 | - | *Mello-Silva 2107* (SPF) |
| *Vellozia candida* J.C.Mikan | JN017017 | - | - | JN017069 | - | JN016913 | - | *Mello-Silva 2877* (SPF) |
| *Xerophyta elegans* Baker | JN017009 | AY491664 - Hi | - | JN017061 | - | JN016905 | JX287059 - B | *Chase 253* (K) |
| *Xerophyta retinervis* Baker | JN017040 | KU127267 - La | - | JN017092 | - | JN016936 | JX287264 - B | *Uconn 199700041* |
| **Ingroup** |  |  |  |  |  |  |  |  |
| *Asplundia alata* Harling | N | N | N | N | N | N | N | *Canal 427* (JBB) [a] |
| *Asplundia alata* Harling | N | N | N | N | N | N | N | *Canal 457* (JBB) [b] |
| *Asplundia* aff. *albicarpa* Hammel | N | N | N | N | - | N | N | *Canal 535* (JBB)[a] |
| *Asplundia* aff. *albicarpa* Hammel | N | N | N | N | - | N | N | *Canal 663* (JBB)[b] |
| *Asplundia allenii* Hammel | N | N | - | N | N | N | N | *Canal 481* (JBB) |
| *Asplundia antioquiae* Harling | N | N | N | N | N | N | N | *Canal 605* (JBB) |
| *Asplundia* cf. *aurantiaca* Harling | N | N | N | N | - | N | N | *Canal 635* (JBB) |
| *Asplundia brachyphylla* Harling | - | N | N | N | N | N | N | *Leal 432* (SPF) |
| *Asplundia brachypus* (Drude) Harling | N | N | N | N | N | N | N | *Leal 462* (SPF) [a] |
| *Asplundia brachypus* (Drude) Harling | N | N | - | N | - | N | N | *Sarnaglia 658* (RB) [b] |
| *Asplundia brunneistigma* Hammel | N | N | N | N | - | N | N | *Canal 594* (JBB) |
| *Asplundia callejasii* Tuberq. & E.S.Leal | N | N | N | N | N | N | N | *Tuberquia 3412* (HUA) |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Asplundia cymbispatha* Harling | N | N | N | N | N | N | N | *Canal 716* (JBB) |
| *Asplundia fanshawei* (Maguire) Harling | N | N | N | N | N | N | N | *Leal 459* (SPF) |
| *Asplundia* aff. *ferruginea* Hammel | N | N | N | N | | N | N | *Canal 592* (JBB) |
| *Asplundia flavovaginata* Harling | - | N | N | N | N | N | N | *Tuberquia 3413* (HUA) |
| *Asplundia gamotepala* Harling | N | N | N | N | N | N | N | *Canal 543* (JBB) |
| *Asplundia gardneri* (Hook.) Harling | N | N | N | N | N | - | N | *Forzza 6433* (RB) [a] |
| *Asplundia gardneri* (Hook.) Harling | N | N | N | N | N | N | N | *Simon 2959* (CEN) [b] |
| *Asplundia glandulosa* (Gleason) Harling | - | N | - | N | - | N | N | *Leal 431* (SPF) |
| *Asplundia* aff. *helicotricha* (Harling) Harling | N | N | N | N | N | N | N | *LCMO 1993-1666* |
| *Asplundia heteranthera* Harling | - | N | N | N | N | N | N | *Leal 435* (SPF) |
| *Asplundia insignis* (Duchass. ex Griseb.) Harling | - | JX286834 | - | N | N | N | JX287183 | *RBGK37929* |
| *Asplundia longitepala* Harling | N | N | N | N | N | N | N | *Canal 644* (JBB) |
| *Asplundia maguirei* Harling | N | N | - | N | - | N | N | *Tillett 44979* (NY) |
| *Asplundia peruviana* Harling | N | N | N | N | N | N | N | *Canal 718* (JBB) |
| *Asplundia pittieri* (Woodson) Harling | N | N | N | N | N | N | N | *Canal 454* (JBB) |
| *Asplundia platyphylla* Harling | N | N | N | N | N | N | N | *Canal 501* (JBB) [a] |
| *Asplundia platyphylla* Harling | N | N | N | N | N | N | N | *Canal 641* (JBB) [b] |
| *Asplundia pycnantha* Harling | N | N | N | N | N | N | N | *Canal 455* (JBB) [a] |
| *Asplundia pycnantha* Harling | N | N | N | N | | N | N | *Canal 545* (JBB) [b] |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| *Asplundia rigida* (Aubl.) Harling | - | N | - | N | - | N | N | *Hill 21349* (NY) |
| *Asplundia rivularis* (Lindm.) Harling | N | N | N | N | N | N | N | *Leal 463* (SPF) [a] |
| *Asplundia rivularis* (Lindm.) Harling | N | N | N | N | N | N | N | *Leal 465* (SPF) [b] |
| *Asplundia sanctae-ritae* Galeano & R.Bernal | N | N | N | N | N | N | N | *Canal 628* (JBB) |
| *Asplundia* aff. *sanctae-ritae* Galeano & R.Bernal | N | N | N | N | N | N | N | *Canal 638* (JBB) |
| *Asplundia stenophylla* (Standl.) Harling | N | N | N | N | - | N | N | *Canal 665* (JBB) |
| *Asplundia utilis* (Oerst.) Harling | N | N | N | N | N | N | N | *Canal 458* (JBB) [a] |
| *Asplundia utilis* (Oerst.) Harling | N | N | N | N | N | N | N | *Canal 532* (JBB) [b] |
| *Asplundia vagans* Harling | N | N | N | N | N | N | N | *Canal 456* (JBB) [a] |
| *Asplundia vagans* Harling | - | N | N | N | N | N | N | *Canal 533* (JBB) [b] |
| *Asplundia vaupesiana* Harling | N | N | N | N | - | N | N | *Giaretta 1510* (SPF) |
| *Asplundia xiphophylla* Harling | - | N | - | N | - | N | N | *Giaretta 1511* (SPF) [a] |
| *Asplundia xiphophylla* Harling | N | N | N | N | N | N | N | *Giaretta 1513* (SPF) [b] |
| *Asplundia* sp. nov. 1 | N | N | N | N | N | N | N | *Leal 460* (SPF) |
| *Asplundia* sp. nov. 2 | N | N | N | N | N | N | N | *Canal 480* (JBB) [a] |
| *Asplundia* sp. nov. 2 | N | N | N | N | N | N | N | *Canal 627* (JBB) [b] |
| *Asplundia* indet. 1 | N | N | N | N | N | N | N | *LCMO 1993-0615* |
| *Asplundia* indet. 2 | N | N | N | N | N | N | N | *Canal 428* (JBB) |
| *Asplundia* indet. 3 | N | N | N | N | N | N | N | *Canal 500* (JBB) |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Asplundia* indet. 4 | N | N | N | N | N | - | N | *Canal 504* (JBB) |
| *Asplundia* indet. 5 | N | N | N | N | N | N | N | *Canal 537* (JBB) |
| *Asplundia* indet. 6 | N | N | - | N | - | N | N | *Canal 539* (JBB) |
| *Asplundia* indet. 7 | N | N | N | N | N | N | N | *Canal 541* (JBB) |
| *Asplundia* indet. 8 | N | N | N | N | - | N | N | *Canal 544* (JBB) |
| *Asplundia* indet. 9 | N | N | N | N | N | N | N | *Canal 606* (JBB) |
| *Asplundia* indet. 10 | N | N | N | N | - | N | N | *Canal 607* (JBB) |
| *Asplundia* indet. 11 | N | N | N | N | - | N | N | *Canal 625* (JBB) |
| *Carludovica drudei* Mast. | N | N | N | N | N | N | N | *LCMO 1989-1189* |
| *Carludovica palmata* Ruiz & Pav. | N | N | N | N | N | N | N | *LCMO 1990-3372* |
| *Carludovica rotundifolia* Schaedtler | N | N | N | N | N | N | N | *LCMO 1989-1191* |
| *Carludovica sulcata* Hammel | N | N | N | N | N | N | N | *LCMO 1995-1914* |
| *Chorigyne cylindrica* R.Erikss. | N | N | - | N | - | N | N | *LCMO 1989-1186* |
| *Chorigyne pendula* (Hammel) R.Erikss. | - | N | KP083119 | N | - | N | N | *LCMO 1995-1915* |
| *Cyclanthus bipartitus* Poit. ex A.Rich. | N | N | N | N | N | N | N | *Canal 590* (JBB) [a] |
| *Cyclanthus bipartitus* Poit. ex A.Rich. | N | N | - | N | N | N | N | *Canal 667* (JBB) [b] |
| *Cyclanthus bipartitus* Poit. ex A.Rich. | N | N | N | N | N | N | N | *LCMO 1989-1176* [c] |
| *Cyclanthus bipartitus* Poit. ex A.Rich. | N | N | N | N | N | N | N | *Leal 437* (SPF) [d] |
| *Dianthoveus cremnophilus* Hammel & G.J.Wilder | N | N | N | N | N | N | N | *LCMO 1990-1888* |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| *Dicranopygium goudotii* Harling | N | N | - | N | N | N | N | *Canal 637* (JBB) |
| *Dicranopygium lugonis* Harlling | N | N | - | N | - | N | N | *Luteyn 9091* (NY) |
| *Dicranopygium pygmaeum* (Gleason) Harling | N | N | N | N | N | N | N | *Gonzalez 4102* (SPF) |
| *Dicranopygium stenophyllum* Harling | N | N | - | N | - | N | N | *Palacios 10171* (NY) |
| *Dicranopygium* aff. *umbrophillum* Hammel | N | N | N | N | N | N | N | *Canal 643* (JBB) |
| *Dicranopygium wallisii* (Regel) Harling | N | N | N | N | N | N | N | *LCMO 1991-0006* |
| *Dicranopygium* indet. 1 | N | N | N | N | N | N | N | *LCMO 2002-0938* |
| *Dicranopygium* indet. 2 | - | N | N | N | - | N | N | *LCMO 2002-0926* |
| *Dicranopygium* indet. 3 | N | N | N | N | N | N | N | *Canal 502* (JBB) |
| *Dicranopygium* indet. 4 | N | N | N | N | - | N | N | *Canal 505* (JBB) |
| *Dicranopygium* indet. 5 | N | N | N | N | N | N | N | *Canal 528* (JBB) |
| *Dicranopygium* indet. 6 | N | N | N | N | N | N | N | *Canal 601* (JBB) |
| *Dicranopygium* indet. 7 | N | N | N | N | N | N | N | *Canal 602* (JBB) |
| *Dicranopygium* indet. 8 | N | N | N | N | N | N | N | *Canal 640* (JBB) |
| *Evodianthus funifer* (Poit.) Lindm. | N | N | - | N | N | N | N | *Giaretta 1512* (SPF) [a] |
| *Evodianthus funifer* (Poit.) Lindm. | N | N | N | N | N | N | N | *Canal 423* (JBB) [b] |
| *Evodianthus funifer* (Poit.) Lindm. | N | N | N | N | N | N | N | *Leal 433* (SPF) [c] |
| *Evodianthus funifer* (Poit.) Lindm. | N | N | N | N | N | N | N | *Leal 436* (SPF) [d] |
| *Ludovia bierhorstii* G.J.Wilder | N | N | - | N | - | N | N | *Canal 538* (JBB) |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| *Ludovia integrifolia* (Woodson) Harling | N | N | N | N | N | N | N | *Canal 425* (JBB) [a] |
| *Ludovia integrifolia* (Woodson) Harling | N | N | N | N | N | N | N | *LCMO 1989-6313* [b] |
| *Ludovia lancifolia* Brongn. | N | N | - | N | N | N | N | *Forzza 7106* (RB) [a] |
| *Ludovia lancifolia* Brongn. | N | N | - | N | N | N | N | *LCMO 1983-1702* [b] |
| *Ludovia lancifolia* Brongn. | N | N | - | N | N | N | N | *Leal 430* (SPF) [c] |
| *Ludovia lancifolia* Brongn. | N | N | - | N | N | N | N | *Leal 450* (SPF) [d] |
| *Schultesiophytum chorianthum* Harling | N | N | N | N | N | N | N | *Canal 717* (JBB) |
| *Sphaeradenia acutitepala* Harling | N | N | N | N | N | N | N | *Canal 424* (JBB) |
| *Sphaeradenia* aff. *buenaventurae* Harling | N | N | - | N | - | N | N | *Canal 608* (JBB) |
| *Sphaeradenia crocea* Harling | N | N | N | N | N | N | N | *Canal 554* (JBB) |
| *Sphaeradenia* aff. *distans* R.Erikss. | N | N | N | N | - | N | N | *Canal 668* (JBB) |
| *Sphaeradenia duidae* Harling | N | N | N | N | N | N | N | *Forzza 7136* (RB) |
| *Sphaeradenia* aff. *hamata* Harling | N | N | N | N | N | N | N | *Canal 642* (JBB) |
| *Sphaeradenia killipii* (Standl.) Harling | N | N | N | N | N | N | N | *Canal 426* (JBB) |
| *Sphaeradenia laucheana* (Mast.) Harling | N | N | N | N | N | N | N | *Canal 707* (JBB) |
| *Sphaeradenia* cf. *pallida* R.Erikss. | N | N | N | N | N | N | N | *Canal 655* (JBB) |
| *Sphaeradenia pterostigma* Harling | N | N | N | N | N | N | N | *Canal 666* (JBB) |
| *Sphaeradenia* aff. *stylosa* Harling | N | N | N | N | N | N | N | *Canal 662* (JBB) |
| *Sphaeradenia* indet. 1 | N | N | - | N | - | N | N | *LCMO 1982-0503* |

|  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|
| *Sphaeradenia* indet. 2 | N | N | N | N | N | N | N | *Canal 453* (JBB) |
| *Sphaeradenia* indet. 3 | N | N | N | N | N | N | N | *Canal 529* (JBB) |
| *Sphaeradenia* indet. 4 | N | N | N | N | N | N | N | *Canal 531* (JBB) |
| *Sphaeradenia* indet. 5 | N | N | N | N | N | N | N | *Canal 534* (JBB) |
| *Sphaeradenia* indet. 6 | N | N | - | N | N | N | N | *Canal 540* (JBB) |
| *Sphaeradenia* indet. 7 | N | N | N | N | N | N | N | *Canal 542* (JBB) |
| *Sphaeradenia* indet. 8 | N | N | N | N | N | N | N | *Canal 593* (JBB) |
| *Sphaeradenia* indet. 9 | N | N | N | N | N | N | N | *Canal 636* (JBB) |
| *Sphaeradenia* indet. 10 | - | N | N | N | N | N | N | *Canal 639* (JBB) |
| *Sphaeradenia* indet. 11 | N | N | N | N | N | N | N | *Canal 664* (JBB) |
| *Stelestylis stylaris* (Gleason) Harling | N | N | - | N | - | N | N | *Forzza 8149* (RB) |
| *Stelestylis surinamenis* Harling | N | N | N | N | N | N | N | *Leal 461* (SPF) |
| *Thoracocarpus bissectus* (Vell.) Harling | N | N | - | N | N | N | N | *Canal 530* (JBB) [a] |
| *Thoracocarpus bissectus* (Vell.) Harling | N | N | N | N | N | N | N | *Leal 441* (SPF) [b] |
| *Thoracocarpus bissectus* (Vell.) Harling | N | N | N | N | N | N | N | *Leal 464* (SPF) [c] |

**Morphological data.** — A morphological matrix was also compiled form same all 138 terminals used for molecular study. The final matrix was composed by 42 anatomical and morphological characters, wich were selected from phylogenetic studies that involved Cyclanthaceae and/or closely related families (Hammel & Wilder, 1989; Eriksson, 1994; Mello-Silva, 2005; Rudall & Bateman, 2006; Mello-Silva & al., 2011). Morphological and reproductive characters were coded mainly from direct observation of specimens from several herbaria: CAY, COAH, COL, CHOCO, ESA, F, GH, HAMAB, HUA, IAN, INPA, JAUM, JBB, MEDEL, MBML, MG, MO, NY, R, RB, SP, SPF, UDBC, UFACPZ, US (acronyms from Thiers, 2018) or were obtained from the literature and are described and codified below (Table 2 and 3):

*Character* 1. Habit: (0) terrestrial (1) root-climbing (2) epiphytic.

The codification of this character takes into account the predominant type of growth of the plant. Some species of Cyclanthaceae present different life forms according to the habitat or environmental conditions (Harling & al., 1998). *Aechmea bromeliifolia* is predominantly epiphytic (Faria & al., 2010). Pandanaceae, Stemonaceae, Triuridaceae and Velloziaceae are terrestrial (Duyfjes, 1992; Kubitzki, 1998a; Maas & Rübsamen, 1986; Stone & al., 1998).

*Character* 2. Root phloem sieve tube elements: (0) dispersed among fibers (1) in fascicles.

*Cyclanthus*, *Ludovia* and Asplundia group, except for *Evodianthus*, present the phloem of the first-order roots confined in discreet fascicles of numerous sieve tube elements. In contrast, the sieve tube elements and the companion cells are dispersed among fibers in *Evodianthus*, *Sphaeradenia* and *Stelestylis* (Wilder 1986b; Wilder, 1989b). This character has not been analyzed in the outgroup terminals.

*Character* 3. Crystal idioblasts in the root: (0) bundles of raphides (1) absent (2) styloid.

The crystal idioblasts of the roots store bundles of parallel raphides or a small number of styloids. Styloid idioblasts in the roots occur in *Dianthoveus* and *Evodianthus* and raphides occur in the remaining genera (Wilder 1986a, b, 1989). Silva & Scatena (2011) observed raphides in the vascular cortex and cylinder of *Aechmea bromeliifolia*. There is no information available on the presence of crystals in Velloziaceae, but raphides may be present (Dahlgren & Clifford, 1982; Prychid & Rudall, 1999). In Stemonaceae, Kauff & al. (2000) did not register the presence of calcium oxalate crystals in the roots of *Croomia* and *Stemona* and observed styloids in the roots of *Stichoneuron*. Crystal idioblasts are absent in Triuridaceae (Tomlinson, 1982; Prychid & Rudall, 1999). Raphide-shaped crystals are observed in Pandanaceae (North, 1971; Stone & al., 1998).

*Character* 4. Prefoliation: (0) supervolute (1) conduplicate (2) plicated along the primary veins (3) plicated in parallel to the primary veins.

In *Cyclanthus bipartitus* the plicae in the blade develop along the primary veins, while in Carludovicoideae they develop in parallel to the primary veins (Wilder, 1981b, c). *Aechmea bromeliifolia* has supervolute prefoliation (Smith & Till, 1998). Prefoliation in Pandanaceae (Stone & al., 1998), Stemonaceae (Ayensu, 1968) and Velloziaceae (Kubitzki, 1998a) is conduplicate. Triuridaceae does not have leaves (Mass-Van de Kamer & Weustenfeld, 1998).

*Character* 5. Phyllotaxy: (0) spiraled (1) spirotristichous (2) tristichous (3) distichous.

All monocots present alternate phyllotaxy, with only one leaf per node (Dalghren, 1985). In Cyclanthaceae, the leaf arrangement can be distichous or spiraled. These states may be fixed or variable, sometimes depending on the age of the individuals (Harling, 1958). Distichous phyllotaxy is always present in Sphaeradenia group, and spiraled in Asplundia group (Wilder, 1981b, 1981c). *Cyclanthus* may present entirely distichous or entirely spiraled phyllotaxy (Wilder, 1992b). The initial phyllotaxy of *Sphaeradenia* is spiraled, posteriorly becoming distichous. Conversely, in *Asplundia* and *Carludovica* the first leaves are distichous and the others are spiraled. In *Thoracocarpus,* the first leaves are occasionally distichous, while the other are always spiraled, grouped in the apex of the branches. In Bromeliaceae the leaf disposition is always spiraled, except in some species of *Tillandsia* (Smith & Till, 1998). In Stemonaceae, the phyllotaxy is distichous (Kubitzki, 1998a). Leaves placed in three straight rows (tristichous) or in three twisted rows (spirotristichous) occur in Pandanaceae (Stone & al., 1998) and Velloziaceae (Mello-Silva & al., 2011). Triuridaceae do not present leaves.

*Character* 6. Petiole: (0) absent (1) present. Petioles are present in Stemonaceae (Kubtizki, 1998a) and may be present in Cyclanthaceae (Wilder, 1976, 1977a, 1977b, 1981a, 1981b, 1981c, 1989a). *Aechmea bromeliifolia*, Pandanaceae and Velloziaceae do not present petiole. This character does not apply to Triuridaceae, as they do not present leaves.

*Character* 7. Leaf margin: (0) serrulate or spinescent (1) entire.

Leaf blades with spinescent margin are characteristic of Pandanaceae (Stone & al. 1998). Velloziaceae present leaf margins entire, with or without trichomes, or spinescent (Mello-Silva, 2005). *Aechmea bromeliifolia* has serrulate margin (Faria & al., 2010). In the remaining families in the analysis, the leaf margin is always entire (Rudall & Bateman, 2006). This character does not apply to Triuridaceae.

*Character* 8. Longitudinal incisions in the blade: (0) absent (1) one (2) three.

Adult leaves in Cyclanthaceae may be undivided or present one or three longitudinal incisions (Wilder, 1976, 1978, 1981b, 1981c, 1989a). Undivided leaves are present only in *Ludovia* (Wilder, 1978, 1981c). Leaf blades with one incision (bifid blades) occur in most genera in Cyclanthaceae (Wilder, 1978). Occasionally, bifid leaves can be lacerated by external mechanical pressures (Harling, 1958; Hammel, 2003). *Carludovica* present three leaf incisions, which divide the leaf in four segments, giving them a flabelliform aspect (Wilder, 1976). The blades are undivided in the remaining Pandanales that have leaves and in *Aechmea bromeliifolia* (Kubitzki, 1998a, b; Smith & Till, 1998; Stone & al., 1998). The character does not apply to Triuridaceae.

*Character* 9. Leaf blade consistency: (0) rigid (1) flexible.

The rigidity of the blade in Cyclanthaceae is caused by the bigger thickness of the cuticle and cutinized region of the epidermis, with these layers being thicker in Sphaeradenia group (Wilder, 1984, 1985a; Medina & al., 2017). Rigid blades with lustrous adaxial surface emerge as synapomorphy of Sphaeradenia group in Harling (1958) and Eriksson (1994). There is no information about this character for terminals in the outgroup. In *Aechmea bromeliifolia* the leaves are rigid (Faria & al., 2010). In Velloziaceae and Pandanaceae the leaves present epicuticular wax of the Strelitzia type, which may give a rigid consistency to the blade (Kubitzki 1998a; Stone & al., 1998). In Stemonaceae they are flexible, with membranaceous blades with thin mesophyll (Govindarajalu & Rajasekaran, 1972). Pandanaceae has a well-developed cutin (Kam, 1971). This character does not apply to Triuridaceae.

*Character* 10. Number of primary costae: (0) none (1) one (2) three.

The blades in Cyclanthaceae may be unicostate, when they present only the central costa or tricostate, when they present lateral costae in addition to the main costa, which extend through each segment of the blade (Harling, 1958). In undivided leaves, the blade is unicostate and the central costa ends close to the blade apex (Wilder, 1981c). In divided leaves, the central costa ends in the base of the division, in the end of the leaf incision. Tricostate leaves occur in *Cyclanthus*, *Carludovica*, *Schultesiophytum*, many species of *Asplundia* and in three species of *Dicranopygium* (Harling, 1958; Wilder, 1976, 1981b, 1981c). Occasionally, tricostate leaves develop in *Dianthoveus* and *Evodianthus* (Wilder, 1981c, 1989a, 1989b). Pandanaceae, Stemonaceae and Velloziaceae present one primary vein (Kubitzki, 1998a, b; Stone & al., 1998), absent in *Aechmea bromeliifolia* (Faria & al., 2010). The character does not apply to Triuridaceae.

*Character* 11. Position from where the lateral costae originate: (0) central costa apex (1) median region of the central costa (2) central costa base.

In *Cyclanthus,* the lateral costae originate from the apex of the central costa, which is extremely short (Wilder, 1981b). In other Cyclanthaceae, the lateral costae originate from the base of the central costa, except in *Schultesiophytum*, where they originate from the median region of the central costa (Wilder, 1981c). This character does not apply to the outgroup, which either does not have lateral costae or does not have leaves.

*Character* 12. Extension of the lateral costae: (0) reaching the blade apex (1) not reaching the blade apex.

In *Cyclanthus,* the lateral costae reach the apex of the leaf segments, while in the remaining genera the lateral costae reach up to 40% of the blade extension (Wilder, 1981b, c).

*Character* 13. Transversal section of the petiole: (0) flattened (1) elliptical.

The transversal section profile of the distal portion of the petiole in species of Asplundia group is flattened, except for *Carludovica*, while in Sphaeradenia group and *Cyclanthus* it is almost elliptical (Wilder, 1981b, c). In Stemonaceae the transversal section of the petiole is elliptical (Kubitzki, 1998a). This character does not apply to the Bromeliaceae, Velloziaceae, Triuridaceae and Pandanaceae terminals, which do not present petioles.

*Character* 14. Birefringent cells in the mesophyll: (0) absent (1) present.

Cells similar to those in the parenchyma, without organelles, with cell walls less stained and more birefringent, are present in all species investigated in the Sphaeradenia group and in few species of Asplundia group (Wilder, 1985b; Eriksson, 1994, 1995). In Eriksson (1994), they emerge as synapomorphy of Sphaeradenia group. There is no information available for this character in the outgroup terminals.

*Character* 15. Styloid idioblasts in the leaf mesophyll: (0) absent or unidirectional (1) oriented in all directions.

Three main types of calcium oxalate crystals are found in monocots: raphides, styloids and druses, which differ in shape and arrangement. As they are very constant, they can be codified in cladistics analysis (Prychid & Rudall, 1999). Raphide is the most common type of crystal and is present in all genera of Cyclanthaceae (Wilder, 1984, 1985d). Druse is the rarer type within the monocots and it has not been reported for Cyclanthaceae (Prychid & Rudall, 1999). Styloids occur in the mesophyll of all investigated species of *Carludovica*, *Cyclanthus*, *Dianthoveus*, *Evodianthus*, *Sphaeradenia*, *Stelestylis* and some *Asplundia* and *Dicranopygium*, while they were not observed in *Ludovia*, *Schultesiophytum* and *Thoracocarpus* (Wilder, 1984, 1985d, 1989b). Styloids are oriented in all directions only in *Dianthoveus* and *Evodianthus*, resulting in rough leaf blades when dry (Wilder, 1985b, 1989b; Harling & al. 1998). The outgroup was coded following Prychid & Rudall (1999).

*Character* 16. Inflorescence position: (0) terminal (1) lateral.

The position of the inflorescence in Cyclanthaceae is directly linked to the type of stem growth. Monopodial growth implies in lateral inflorescences, and sympodial growth results in lateral inflorescences (Wilder 1977a, b, 1979, 1981a, 1989a). In Eriksson (1994), lateral inflorescences and monopodial growth emerged as synapomorphy of Carludovicoideae, with reversal in *Carludovica*, *Dianthoveus* and *Evodianthus*. *Aechmea bromeliifolia* (Smith & Till, 1998), Triuridaceae (Maas-Van de Kamer & Weustenfeld, 1998) and Velloziaceae (Kubitzki, 1998a) present terminal inflorescence. In Stemonaceae, the inflorescences or isolated flowers are lateral (Kubitzki, 1998b) and inflorescences may be lateral or terminal in Pandanaceae (Stone & al., 1998).

*Character* 17. Inflorescence type: (0) spike (1) uniflorous (2) raceme (3) compound capitulum (4) fasciculate (5) spadix with unisexual flowers in alternate whorls (6) spadix with spirally-arranged unisexual flowers.

In Cyclanthaceae, the staminate and pistillate flowers are inserted in the same axis, differently arranged in the two subfamilies. Cyclanthoideae has extremely reduced, fused flowers, individually unidentifiable, disposed in alternate whorls, while Carludovicoideae presents spirally-disposed groups of one pistillate flower surrounded by four staminate flowers (Harling, 1958; Sajo & al., 2014). In *Aechmea bromeliifolia* the inflorescence is a spike, with bisexual flowers (Faria & al., 2010). In Velloziaceae, the inflorescences may be uniflorous, fasciculate or a compound capitulum (Kubitzki, 1998a; Mello-Silva, 2005; Kao, 2017). Stemonaceae has isolated flowers or arranged in racemes (Kubitzki, 1998a). Triuridaceae presents racemes (Maas-Van de Kamer & Weustenfeld, 1998). In Pandanaceae the inflorescences are spikes, racemes or intermediate forms between both (Stone & al., 1998).

*Character* 18. Position of inflorescence bracts: (0) distributed along the peduncle (1) clustered in the apex of the peduncle.

In Cyclanthaceae, the arrangement of the bracts in the peduncle is constant in each genus (Wilder, 1988). In *Dicranopygium* and *Evodianthus* the bracts are clustered right below the spadix, being congested and apparently originating from the same node. In *Carludovica* and *Cyclanthus*, which present more elongated peduncles than the other genera, the bracts are also clustered right below the spadix, although not so densely, being distributed in different heights of the peduncle apex. Both conditions are coded here as clustered in the apex of the peduncle. In the remaining genera, the bracts are dispersed along the peduncle, although concentrated mainly in its distal portion. In *Aechmea bromeliifolia* and Pandanaceae, the bracts are distributed along the peduncle (Faria & al., 2010; Stone & al., 1998). The bracts in Velloziaceae, Stemonaceae and Triuridaceae, when present, are positioned in the peduncle apex, right below the flowers or inflorescences (Maas & Rübsamen, 1986; Inthachub & al., 2009; Kao, 2017).

*Character* 19. Bract size: (0) decreasing towards the peduncle apex (1) increasing towards peduncle apex the (2) invariable.

In most genera, the proximal bracts are larger than the distal. The inverse condition, with the proximal bracts smaller, is observed in some species of *Asplundia* subgen. *Choanopsis*. In *Dicranopygium* and *Evodianthus*, bracts present approximately the same dimensions (Wilder, 1988). In *Aechmea bromeliifolia* and Pandanaceae, the bracts decrease in size towards the peduncle apex (Faria & al., 2009; Stone & al, 1998). In other families in Pandanales, in species that present more than one bract per flower/inflorescence, these are approximately the same size (Maas & Rübsamen, 1986; Inthachub & al., 2009; Kao, 2017).

*Character* 20. Reproductive habit: (0) hermaphroditic (1) monoecious (2) dioecious.

All Cyclanthaceae are monoecious (Harling, 1958). *Aechmea bromeliifolia* is hermaphroditic (Faria & al., 2010). Velloziaceae are hermaphroditic, except for *Barbaceniopsis,* which is dioecious (Smith, 1962; Kubitzki, 1998a). Stemonaceae are hermaphroditic (Kubitzki, 1998b). Pandanaceae are dioecious (Stone & al., 1998). In Triuridaceae the plants may be hermaphroditic, monoecious or dioecious (Rudall & Bateman, 2006), but the species used in our analysis is monoecious (Maas & Rübsamen, 1986).

*Character* 21. Symmetry of the staminate or bisexual flowers: (0) actinomorphic (1) zygomorphic.

In subfamily Carludovicoideae of Cyclanthaceae, the symmetry plane of the flowers depends on the distribution of sterile lobes, position of pedicel and shape of the receptacle. Sterile lobes, or lobes of the staminate flower, are staminodial in nature (Sajo & al., 2014) and do not derive from the perianth, as previously thought (Harling, 1958; Eriksson, 1994; Harling & al., 1998). Actinomorphic flowers do not present sterile lobes, or these completely involve the receptacle, the pedicel is centralized and the receptacle excavate, while in zygomorphic flowers the sterile lobes partially involve the receptacle, the pedicel is laterally displaced and the receptacle is flattened (Harling, 1958). In Cyclanthoideae, isolated flowers are not detectable (Sajo & al., 2014). The flowers of Pandanaceae, Stemonaceae, Triuridaceae and Velloziaceae are actinomorphic (Stone & al., 1998, Duyfjes, 1992; Maas-Van de Kamer & Weustenfeld, 1998; Kubitzki, 1998a, b).

*Character* 22. Sterile lobes in the staminate flower: (0) absent (1) in one whorl (2) in two whorls.

In some groups of Cyclanthaceae and in the whole outgroup, sterile lobes are absent (Harling, 1958; Stone & al., 1994). When present, lobes may be disposed in one whorl that partially or totally involves the receptacle. Two whorls of sterile lobes occur only in *Evodianthus* (Eriksson, 1994).

*Character* 23. Papillae in the staminate flower receptacle: (0) absent (1) present.

*Dianthoveus* has numerous multicellular papillae in the receptacle, which form a cupule in the base of each anther (Hammel & Wilder, 1989; Wilder, 1989a) and that emerge as an autapomorphy of the genus (Eriksson, 1994). These papillae are not found in the other terminals in our analysis.

*Character* 24. Stamen number: (0) four (1) five (2) six (3) numerous.

Cyclanthaceae and sometimes Pandanaceae and *Vellozia* have numerous stamens (Harling, 1958; Stone & al., 1998; Mello-Silva 2005). *Aechmea bromeliifolia* has six stamens (Smith & Till, 1998), as well as some *Vellozia* and the remaining genera in Velloziaceae (Mello-Silva & al., 2011). Stemonaceae has four stamens and Triuridaceae has from two to six stamens, with *Sciaphila densiflora* presenting six stamens (Schlechter, 1912; Rudall & Bateman, 2006; Maas-Van de Kamer & Weustenfeld, 1998; Kubitzki, 1998a, b).

*Character* 25. Filament: (0) conspicuous and slender (1) inconspicuous or absent.

In Cyclanthaceae, the filaments are usually slender and conspicuous (Harling & al., 1998), as well as in *Aechmea bromeliifolia*, Pandanaceae and most Triuridaceae and Velloziaceae (Rudall & Bateman, 2006; Stone & al., 1998; Faria & al., 2010). Sessile anthers or with inconspicuous filaments occur in *Evodianthus* and *Dianthoveus* (Eriksson, 1994), in Stemonaceae, some Triuridaceae and most *Barbacenia* (Velloziaceae, Mello-Silva & al., 2011).

*Character* 26: Basal bulb: (0) absent (1) present.

In most Cyclanthaceae, there is a spherical structure in the transition area between filament and receptacle, called "basal bulb" (Harling, 1958; Harling & al., 1998). The basal bulb is absent in the monotypic genera *Dianthoveus* and *Evodianthus* (Harling, 1958; Eriksson, 1994). Basal bulbs are not observed in the remaining terminals in this analysis.

*Character* 27. Secretion globules in the anther: (0) absent (1) present.

In some genera of Cyclanthaceae, a globose and darkened appendix is present in the anther apex, called secretion globule (Harling, 1958). Its nature and function are unknown, but they are possibly glandular (Eriksson, 1995). The presence of this anther appendix seems to be a synapomorphy of the clade (*Chorigyne* (*Sphaeradenia*, *Stelestylis*), within "Sphaeradenia group". However, this characteristic is polymorphic in *Sphaeradenia*, where the secretion globule is sometimes absent, rudimentary or inconspicuous (Eriksson, 1995). Secretion globules are not observed in the remaining terminals in this analysis.

*Character* 28. Appendix in the anther connective: (0) absent (1) present.

In Cyclanthaceae, the anther connective sometimes elongates in an apiculate laminar appendix. Hammel & Wilder (1989) coded this character together with secretion globules, in a multistate character, differently from Eriksson (1994), who coded them as distinct characters, given their doubtful homology. In the remaining terminals, the codification follows Rudall & Bateman (2006). Connective appendix is not seen in *Aechmea bromeliifolia* (Faria & al., 2010).

*Character* 29. Pollen aperture: (0) porate (1) sulcate, ulcerate or sulcoidate (2) inapertured.

Inapertured pollen is a common condition and independently arose several times within monocots (Furness & Rudall, 2006). In Cyclanthaceae, inapertured pollen grains that are functionally monoaperturate (Furness & Rudall, 2006) are observed in *Dianthoveus* and *Evodianthus* (Hammel & Wilder, 1989; Eriksson, 1994). In the other groups in Cyclanthaceae the pollen is sulcate or a variation of this (Harling & al., 1998). *Aechmea bromeliifolia* has porate pollen (Souza & al., 2017). Inapertured pollen occurs also in Pandanaceae, Stemonaceae, Triuridaceae (Furness & Rudall, 2006) and *Vellozia*; the remaining genera in Velloziaceae have sulcate pollen (Rudall & Bateman, 2006).

*Character* 30. Pollen exine: (0) verrucose (1) reticulate (2) foveolate (3) psilate (4) gemmate (5) spinulose.

Pollen with ornamentations and protuberances are common in Pandanales. In Cyclanthaceae, the exine sculpturing is foveolate, except for *Dianthoveus* and *Evodianthus*, where it is psilate (Harling & al., 1998). *Aechmea bromeliifolia* has pollen with verrucose exine (Souza & al., 2017). In Velloziaceae, the exine can be reticulate or vermiform (Kubitzki, 1998a). Spinulate pollen is a diagnostic character of many Triuridaceae, *Pentastemona* and some species of *Stemona* (Furness & Rudall, 2006). In Pandanaceae the pollen grain exine can be reticulate, spinulose or psilate (Furness & Rudall, 2006).

*Character* 31. Position of pollen aperture: (0) distal pole (1) equatorial surface.

In Cyclanthaceae, as in most monocots, pollen grain aperture is located in the distal pole surface of the pollen grain, except for *Carludovica*, in which the aperture is located in one extremity of the equatorial surface of the grain (Harling, 1958; Dalghren & al., 1985; Eriksson, 1994; Harling & al., 1998; Furness & Rudall, 2006). In the other terminals in this analysis the aperture is located in the distal pole of the pollen grain (Furness & Rudall, 2006).

*Character* 32. Perianth of the bisexual or pistillate flowers: (0) two whorls, heterochlamydeous (1) two whorls, monochlamydeous (2) one whorl (3) absent. The pistillate flowers of Carludovicoideae are monochlamydeous with four tepals (Harling, 1958; Sajo & al., 2014). In Cyclanthoideae the perianth lobes are reduced and fused, in two whorls that involve the staminodes and pistils (Sajo & al., 2014). Bromeliaceae has heterochlamydeous perianth, with three sepals and three petals (Smith & Till, 1998). Veloziaceae has six tepals distributed in two whorls, monochlamydeous (Kubitzki, 1998a). Flowers in Stemonaceae present two whorls of tepals (Kubitzki, 1998b). In Triuridaceae, the tepals are arranged in only one whorl (Maas-Van de Kamer & Weustenfeld, 1998). All Pandanaceae lack perianth (Stone & al., 1998).

*Character* 33. Staminodes in bisexual or pistillate flowers: (0) absent or inconspicuous (1) filamentous.

In Carludovicoideae, the pistillate flowers present long filamentous staminodes (Harling, 1958; Sajo & al., 2014), but in *Cyclanthus* they are little developed and fused (Sajo & al., 2014). Bromeliaceae do not present staminodes (Smith & Till, 1998). In Pandanaceae, the staminodes are reduced and ephermeral. Staminodes are also present in *Barbaceniopsis* (Velloziaceae, Smith & Ayensu 1976, Ibisch & al., 2001). The Triuridaceae sampled in this analysis do not have staminodes (Maas-Van de Kamer & Weustenfeld, 1998) and Stemonaceae do not present staminodes (Rudall & Bateman, 2006).

*Character* 34. Connation of bisexual or pistillate flowers: (0) free (1) connate.

In Cyclanthaceae, inflorescences can present connate or free pistillate flowers and, consequently, infructescences can have connate or free fruits (Harling & al., 1998). *Chorigyne*, *Dianthoveus*, *Evodianthus* and *Schultesiophytum* present pistillate flowers completely free from each other, while in the remaining genera they are connate in higher or lower degrees (Harling, 1958). There is no flower connation in the outgroup terminals.

*Character* 35. Gynoecium in relation to carpel fusion: (0) syncarpic with multilocular ovary (1) syncarpic with unilocular ovary (2) apocarpic.

Cyclanthaceae and *Pentastemona* have unilocular syncarpic gynoecium (Harling, 1958; Rudall & Bateman, 2006). Bromeliaceae and Velloziaceae present multilocular syncarpic gynoecium (Smith & Till, 1998; Kubitzki, 1998a). The remaining Stemonaceae and Triuridaceae have apocarpic gynoecium, while in Pandanaceae the three states are found (Rudall & Bateman, 2006).

*Character* 36. Carpel number in bisexual or pistillate flowers: (0) three (1) one (2) four (3) numerous.

Differently from most monocots, Carludovicoideae presents four carpels per pistillate flower and, rarely, some flowers in the same spadix can present up to eight carpels, while in Cyclanthoideae the carpels are extremely fused, not being possible to distinguish the carpel number of a single flower (Harling, 1958). Bromeliaceae, *Pentastemona* and Velloziaceae present three carpels (Smith & Till, 1998; Fukuhara & al., 2003; Kubitzki, 1998a;). Stemonaceae presents one carpel (Fukuhara & al., 2003), Triuridaceae has numerous carpels (Rudall & Bateman, 2006) and Pandanaceae has variable carpel number within and among species (Stone & al., 1998).

*Character* 37. Placenta number: (0) three (1) numerous (2) four (3) one.

In subfamily Cyclanthoideae, pistillate flowers are extremely reduced and fused, forming a sole ovarian chamber with numerous placentae (Sajo & al., 2014). All genera in Carludovicoideae have four free placentae, except for *Sphaeradenia*, where the four placentae are fused in one, apically positioned in the ovary (Harling, 1954a; Eriksson 1994, 1995), with the insertion point sometimes more or less divided in four parts (Harling, 1954a). The number of placentae coincides with carpel number in the remaining terminals.

*Character* 38. Placentation: (0) axial (1) basal (2) parietal (3) sub-apical (4) apical.

Placenta position has a great taxonomic significance in Cyclanthaceae, differentiating large group of genera. In "Asplundia group" placentation is parietal, while in "Sphaeradenia group" it is sub-apical or apical (Harling 1954a, 1958). *Ludovia* and *Chorigyne* have sub-apical placentation (Harling & al., 1998). In Bromeliaceae and Velloziaceae, placentation is axial (Smith & Till, 2008; Mello-Silva, 2005). Basal placentation is observed in Triuridaceae (Maas-

Van de Kamer & Weustenfeld, 1998). In Stemonaceae the placentation can be basal in *Stemona*, apical in *Croomia* and *Stichoneuron* and parietal in *Pentastemona* (Kubitzki, 1998b; Inthachub & al., 2009). Finally, in Pandanaceae the placentation varies between basal and parietal (Stone & al., 1998).

*Character* 39. Number of ovules per carpel: (0) more than one (1) one.
The Triuridaceae terminal sampled in this analysis has one ovule per carpel. Most Pandanaceae have one ovule per carpel, except for some species of *Freycinetia* (Stone & al., 1998). The other taxa have more than one ovule per carpel, usually numerous (Rudall & Bateman, 2006).

*Character* 40. Type of fruit or fruticule: (0) berry (1) drupe (2) capsule (3) follicle (4) division and winding of the infructescence (5) detachment of the apical hood (fleshy pyxidium) of the fruticule (6) discoid berries in two valves

The infructescences of Cyclanthaceae are formed by fruticules of the berry type, which may be free or fused (Harling & al., 1998). *Asplundia*, *Carludovica*, *Dicranopygium*, *Sphaeradenia* and *Thoracocarpus* present dehiscent syncarps when mature, while *Chorigyne*, *Evodianthus* and *Dianthoveus* have free and indehiscent berries (Harling & al., 1998). The discoid berries in *Cyclanthus* open in two valves (Harling & al., 1998). In *Carludovica* the apical region of the infructescence irregularly divides and roll over along the infructescence axis, exposing the pulp and seeds. In other genera with dehiscent infructescences, seed exposure can occur through fissures in the upper infructescence wall, in the region where fruticules join together, when each apical hood detaches, carrying the seed and/or exposing them over the infructescence axis (Harling & al., 1998). In *Aechmea bromeliifolia* the fruits are of the berry type (Faria & al., 2010). In Pandanaceae the fruits may be drupes or berries (Stone & al., 1998). The fruit can be a berry in *Stemona* (Duyfjes, 1992) or a capsule in the rest of family Stemonaceae (Kubitzki, 1998b). In the Triuridaceae sampled in this analysis the fruit is a follicle (Maas-Van de Kamer & Weustenfeld, 1998). Velloziaceae presents capsules (Kubitzki, 1998a).

*Character* 41. Seed shape: (0) fusiform (1) trapezoidal (2) flattened. (3) cylindrical (4) espherical.

Cyclanthaceae seeds present large variation in shape. Strongly flattened seed are present in *Asplundia*, *Evodianthus* and *Thoracocarpus*. The seed in the clade *Chorigyne-Stelestylis* are flattened (Eriksson, 1994). Seeds more or less spherical and not flattened are found in the remaining genera. *Aechmea bromeliifolia* has fusiform seeds (Stefanini, 2013). In Velloziaceae the seeds are more or less trapezoidal or have other shapes (Renato Mello-Silva, pers. commun.). Stemonaceae has cylindrical seeds (Van Steenis, 1982; Kubitzki, 1998b; Inthachub & al., 2009). In Triuridaceae the seeds are spherical or cylindrical (Maas & Rübsamen, 1986). Seeds in Pandanaceae present a wide range of shapes (Stone & al., 1998).

*Character* 42. Caudal appendix in the seed: (0) absent (1) present.

The chalazal region in the seeds of *Stelestylis* develops a conspicuous vermiform-subulate appendix in each extremity. According to Eriksson (1994), this would be a autapomorphy of the genus, not occurring in any other terminal in this analysis.

**Table 2.** Character analysis and coding. F&R = Furness & Rudall (2006), H&al. = Harling & al. (1998), R&B = Rudall & Bateman (2006)

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1. Habit: (0) terrestrial (1) root-climbing (2) epiphytic.

2. Root phloem sieve tube elements (Wilder, 1986a, b, 1989): (0) dispersed among fibers (1) in fascicles.

3. Crystal idioblasts in the root (Wilder, 1986a, b, 1989b): (0) bundles of raphides (1) absent (2) styloid.

4. Prefoliation (Wilder, 1981b, c): (0) supervolute (1) conduplicate (2) plicated along the primary veins (3) plicated in parallel to the primary veins.

5. Phyllotaxy: (0) spiraled (1) spirotristichous (2) tristichous (3) distichous.

6. Petiole: (0) absent (1) present.

7. Leaf margin: (0) serrulate or spinescent (1) entire.

8. Longitudinal incisions in the blade: (0) absent (1) one (2) three.

9. Leaf blade consistency (Wilder, 1984, 1985a; Medina & al., 2017): (0) rigid (1) flexible.

10. Number of primary costae: (0) none (1) one (2) three.

11. Position from where the lateral costae originate: (0) central costa apex (1) median region of the central costa (2) central costa base.

12. Extension of the lateral costae: (0) reaching the blade apex (1) not reaching the blade apex.

13. Transversal section of the petiole: (0) flattened (1) elliptical.

14. Birefringent cells in the mesophyll (Wilder, 1985b): (0) absent (1) present.

15. Styloid idioblasts in the leaf mesophyll (Wilder, 1985d, 1989b): (0) absent or unidirectional (1) oriented in all directions.

16. Inflorescence position: (0) terminal (1) lateral.

17. Inflorescence type: (0) spike (1) uniflorous (2) raceme (3) compound capitulum (4) fasciculate (5) spadix with unisexual flowers in alternate whorls (6) spadix with spirally-arranged unisexual flowers.

18. Position of inflorescence bracts: (0) distributed along the peduncle (1) clustered in the apex of the peduncle.

19. Bract size: (0) decreasing towards the peduncle apex (1) increasing towards peduncle apex the (2) invariable.

20. Reproductive habit: (0) hermaphroditic (1) monoecious (2) dioecious.

21. Symmetry of the staminate or bisexual flowers: (0) actinomorphic (1) zygomorphic.

22. Sterile lobes in the staminate flower: (0) absent (1) in one whorl (2) in two whorls.

23. Papillae in the staminate flower receptacle: (0) absent (1) present.

24. Stamen number: (0) six (1) four (2) five (3) numerous.

25. Filament: (0) conspicuous and slender (1) inconspicuous or absent.

26. Basal bulb: (0) absent (1) present.

27. Secretion globules in the anther: (0) absent (1) present.

28. Appendix in the anther connective: (0) absent (1) present.

29. Pollen aperture (H&al.; F&R; R&B): (0) porate (1) sulcate, ulcerate or sulcoidate (2) inapertured.

30. Pollen exine (H&al.; F&R): (0) verrucose (1) reticulate (2) foveolate (3) psilate (4) gemmate (5) spinulose.

31. Position of pollen aperture (Harling, 1958; D&al.; F&R): (0) distal pole (1) equatorial surface.

32. Perianth of the bisexual or pistillate flowers: (0) two whorls, heterochlamydeous (1) two whorls, monochlamydeous (2) one whorl (3) absent.

33. Staminodes in bisexual or pistillate flowers: (0) absent or inconspicuous (1) filamentous.

34. Connation of bisexual or pistillate flowers: (0) free (1) connate.

35. Gynoecium in relation to carpel fusion: (0) syncarpic with multilocular ovary (1) syncarpic with unilocular ovary (2) apocarpic.

36. Carpel number in bisexual or pistillate flowers: (0) three (1) one (2) four (3) numerous.

37. Placenta number: (0) three (1) numerous (2) four (3) one.

38. Placentation: (0) axial (1) basal (2) parietal (3) sub-apical (4) apical.

39. Number of ovules per carpel: (0) more than one (1) one.

40. Type of fruit or fruticule: (0) berry (1) drupe (2) capsule (3) follicle (4) division and winding of the infructescence (5) detachment of the apical hood (fleshy pyxidium) of the fruticule (6) discoid berries in two valves.

41. Seed shape: (0) fusiform (1) trapezoidal (2) flattened. (3) cylindrical (4) espherical.

42. Caudal appendix in the seed: (0) absent (1) present.

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**Alignment and phylogenetic analysis.** — The software Geneious 9.1.7 (Kearse & al., 2012) was used to generate contigs and edit sequences. Sequence alignments for individual markers were performed with the software MAFFT v. 7 (Katoh & Standley, 2013) as some character positions might not be homologous or present multiple substitutions that may affect the phylogenetic analysis if not removed. Low quality sequences were excluded from the analysis. The sequences were blasted against other sequences deposited in GenBank, in order to avoid including contaminated samples in the analysis. Outgroup sequences were obtained from GenBank.

Nucleotide substitution models were selected using *jModeltest v. 2.1.3* (Darriba & al., 2012). A consensus tree was used to calculate maximum likelihood results for the data under different evolution models. Later, the best model for each partition was chosen using the Akaike Information Criterion (AIC). The substitution model GTR +

G was selected for *atp*B-*rbc*L, *rpb2* and *mat*K, the model GTR + I + G was chosen for *psb*A-*trn*H, *trn*L-*trn*F and *trnQ-rps16* and model SYM + G was specific for *phyC*.

From the alignments of the individual markers, three datasets were generated for analysis: one combining the five plastidial markers (cpDNA), one combining the two nuclear markers (nrDNA) and another combining all markers (total combined matrix). These matrices were built with the software Geneious 9.1.7 (Kearse & al., 2012), which concatenates datasets and generate files for analyses with the main software available for phylogenetic analysis. For each concatenated dataset, independent phylogenetic analyses using two different approaches were conducted: Parsimony (MP) and Bayesian Inference (BI). Only BI was carried out for individual molecular markers alignments, for detection of potential causes for possible incongruences.

Parsimony analyses were carried out with program *TNT* (Goloboff & al., 2008). Heuristic searches were conducted using ten ratchet replicates coupled with tree-drifting, and a final round of tree bisection and reconnection (TBR) (Goloboff, 1999; Nixon, 1999). First, for each of the 200 ratchet iterations, a random set of characters was up-weighted and down-weighted ten-fold. One optimal tree was searched and saved using the reweighted matrix, with TBR as a tree perturbation strategy. After setting the matrix to its original weight, a new optimal tree was searched with TBR using the saved tree from the previous phase. Then tree-drifting was conducted for 200 iterations using the trees saved from the ratchet phase. This method is similar to ratchet, but instead of reweighting a random set of characters, it saves optimal or suboptimal tress per iteration based on the Raw Length Difference and Relative Fit Difference values described by Goloboff (1999). The final tree set obtained from the ratchet plus tree-drifting searches was subsequently used for a final heuristic search using TBR, saving a maximum of 10,000 trees if necessary. A strict consensus tree was generated from the final set of most parsimonious trees. Node confidence was estimated using 1000 bootstrap pseudoreplicates (BS) with similar parameters to the initial ratchet search but using only 20 iterations per pseudoreplicate.

Bayesian inference analysis was carried out with *MrBayes* 3.2.3 (Ronquist & al., 2012) also using CIPRES Science gateway (Miller & al., 2010). Substitution models selected by *jModelTest* were set for each independent partition. Two MCMC runs with 50.000.000 generations were carried out in parallel, each run containing four chains. The standard value of the temperature coefficient was used for all analysis. Trees and estimated parameter values were sampled every 1000 generations, obtaining a total of 30.000 samples, from which the first 10.000 were discarded as burn-in. Convergence between the two independent runs was analyzed using Tracer v.1.5 (Rambaut & Drummond, 2007). The posterior distributions of the independent runs were combined using LogCombiner v. 1.7.5 and summarized in the software TreeAnnotator v. 1.7.5 (Drummond & al., 2012). Data edition and analysis of phylogenetic trees were carried out in FigTree v. 1.3.1 (Rambaut, 2009). Posterior probabilities (PP) for clade support were analyzed as follows: strong, 0.95–1.0; moderate, 0.8–0.94 and weak <0.80.

The morphological dataset, as well as the combined morphological and molecular dataset (total evidence), were analyzed using the MP and BI approaches, as described for the combined molecular dataset. In the BI analysis, morphological data were coded for datatype=standard option, and only variable characters were analyzed (coding=variable). To infer morphological possible synapomorphies for the main recognized clades, morphological character trees were produced from the phylogeny.

**Table 3.** Morphological matrix. "?", missing data; "-", inapplicable; a = 0 and 1; b= 0 and 2; c = 1 and 2. Acan. = *Acanthochlamys*, Aech. = *Aechmea*, Barb. = *Barbaceniopsis*, Carl. = *Carludovica*, Chor. = *Chorigyne*, Cycl. = *Cyclanthus*, Dian. = *Dianthoveus*, Dicr. = *Dicranopygium*, Frey. = *Freycinetia*, Mart. = *Martellidendron*, Pent. = *Pentastemona*, Sch. = *Schultesiophytum*, Sph. = *Sphaeradenia*, Stel. = *Stelestylis*, Stich. = *Stichoneuron* and Thor. = *Thoracocarpus*.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Aech. bromeliifolia* | 2 | ? | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | - | - | - | ? | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Benstonea affinis* | 0 | ? | ? | 1 | 1 | 0 | 0 | 0 | 0 | 1 | - | - | - | ? | 0 | ? | 2 | 0 | 2 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 2 | 1 | ? | 3 | 1 | 0 | 1 | ? | ? | ? | 0 | 1 | ? | 0 |
| *Frey. arborea* | 1 | ? | ? | 1 | 1 | 0 | 0 | 0 | 0 | 1 | - | - | - | ? | 0 | ? | 2 | 0 | 2 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 2 | 1 | ? | 3 | 0 | 0 | 1 | ? | ? | ? | 0 | 0 | ? | 0 |
| *Mart. gallinarum* | 0 | ? | ? | 1 | 1 | 0 | 0 | 0 | 0 | 1 | - | - | - | ? | 0 | ? | 2 | 0 | 2 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 2 | 1 | ? | 3 | 0 | 0 | 1 | ? | ? | ? | 0 | 1 | ? | 0 |
| *Pandanus tectorius* | 0 | ? | ? | 1 | 1 | 0 | 0 | 0 | 0 | 1 | - | - | - | ? | 0 | ? | 2 | 0 | 2 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 2 | 1 | ? | 3 | 0 | 0 | 1 | ? | ? | ? | 0 | 1 | ? | 0 |
| *Sararanga sinuosa* | 0 | ? | ? | 1 | 1 | 0 | 0 | 0 | 0 | 1 | - | - | - | ? | 0 | ? | 2 | 0 | 2 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 2 | 1 | ? | 3 | 0 | 0 | 1 | ? | ? | ? | 0 | ? | ? | 0 |
| *Croomia pauciflora* | 0 | ? | 1 | 1 | 3 | 1 | 1 | 0 | 1 | 1 | - | - | 0 | ? | 0 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 2 | 5 | ? | 1 | 0 | 0 | 2 | 1 | 3 | 4 | 1 | 2 | 3 | 0 |
| *Pent. sumatrana* | 0 | ? | ? | 1 | 3 | 1 | 1 | 0 | 1 | 1 | - | - | 0 | ? | 0 | 1 | 2 | 1 | 2 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 2 | 5 | ? | 1 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 2 | 3 | 0 |
| *Stemona tuberosa* | 1 | ? | 1 | 1 | 3 | 1 | 1 | 0 | 1 | 1 | - | - | 0 | ? | 0 | 1 | 2 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 2 | 5 | ? | 1 | 0 | 0 | 2 | 1 | 3 | 1 | 1 | 0 | 3 | 0 |
| *Stich. caudatum* | 0 | ? | 2 | 1 | 3 | 1 | 1 | 0 | 1 | 1 | - | - | 0 | ? | 0 | 1 | b | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 2 | 5 | ? | 1 | 0 | 0 | 2 | 1 | 3 | 4 | 1 | 2 | 3 | 0 |
| *Sciaphila densiflora* | 0 | ? | 0 | - | - | - | - | - | - | - | - | - | - | - | - | 0 | 2 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 4 | ? | 2 | 0 | 0 | 2 | 3 | 1 | 1 | 0 | 3 | 4 | 0 |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Acan. bracteata* | 0 | ? | ? | 1 | 1 | 0 | 1 | 0 | 0 | 1 | - | - | - | ? | 0 | 0 | 3 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | ? | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 0 |
| *Barb. boliviensis* | 0 | ? | ? | 1 | 2 | 0 | 0 | 0 | 0 | 1 | - | - | - | ? | 0 | 0 | ? | 1 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | ? | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 0 |
| *Vellozia candida* | 0 | ? | ? | 1 | 1 | 0 | 1 | 0 | 0 | 1 | - | - | - | ? | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 2 | 1 | ? | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 0 |
| *Xerophyta elegans* | 0 | ? | ? | 1 | ? | 0 | 0 | 0 | 0 | 1 | - | - | - | ? | 0 | 0 | ? | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | ? | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 0 |
| *X. retinervis* | 0 | ? | ? | 1 | ? | 0 | 0 | 0 | 0 | 1 | - | - | - | ? | 0 | 0 | ? | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 5 | ? | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 0 |
| *Asplundia alata* | 0 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | ? | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A. aff. albicarpa* | 1 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | ? | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A. allenii* | 0 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | ? | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A. antioquiae* | 1 | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | 0 | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A. cf. aurantiaca* | 1 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | 0 | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A. brachyphylla* | 0 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | ? | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A. brachypus* | 0 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | c | 2 | 1 | 0 | ? | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 0 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A. bruneistigma* | 1 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 1 | - | - | 0 | ? | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A. callejasii* | 0 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 1 | - | - | 0 | ? | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A. cymbispatha* | 0 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | ? | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A. fanshawei* | 1 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | - | ? | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |

| | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *A.* aff. *ferruginea* | 1 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | ? | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A. flavovaginata* | 0 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | ? | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A. gamotepala* | 1 | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | 0 | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A. gardneri* | 0 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | ? | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A. glandulosa* | 0 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | 0 | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A. aff. helicotricha* | 1 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 1 | - | - | 0 | ? | 0 | 1 | 5 | 0 | 0 | 1 | 0 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A. heteranthera* | 1 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 1 | - | - | 0 | ? | 0 | 1 | 5 | 0 | 0 | 1 | 0 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A. insignis* | 0 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | ? | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A. longitepala* | 1 | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | 0 | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A. maguirei* | 0 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | ? | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A. peruviana* | 1 | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | - | - | 0 | 0 | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A. pittieri* | 0 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | ? | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A. platyphylla* | 0 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | 0 | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A. pycnantha* | 1 | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | 0 | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A. rigida* | 1 | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | - | - | 0 | 0 | 0 | 1 | 5 | 0 | 0 | 1 | 0 | 1 | 0 | 3 | 0 | 1 | ? | 0 | 1 | 2 | 0 | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A. rivularis* | 0 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | ? | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |

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| *A. sanctae ritae* | 1 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | ? | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A.* aff. *sanctae ritae* | 1 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | ? | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A. stenophylla* | 1 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 1 | - | - | 0 | ? | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A. utilis* | 1 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | ? | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A. vagans* | 1 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 1 | - | - | 0 | ? | 0 | 1 | 5 | 0 | 0 | 1 | 0 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A. vaupesiana* | 1 | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | 0 | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A. xiphophylla* | 1 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | ? | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A.* sp. nov. 1 | 1 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | ? | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A.* sp. nov. 2 | 1 | ? | ? | 2 | 0 | 1 | 1 | 0 | 1 | 2 | 2 | 1 | 0 | ? | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A.* indet. 1 | ? | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | ? | 0 | 1 | 5 | 0 | 0 | 1 | ? | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A.* indet. 2 | 1 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | ? | 0 | 1 | 5 | 0 | 0 | 1 | ? | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A.* indet. 3 | 0 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | 0 | 0 | 1 | 5 | 0 | 0 | 1 | ? | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A.* indet. 4 | 1 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 1 | - | - | 0 | ? | 0 | 1 | 5 | 0 | 0 | 1 | ? | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A.* indet. 5 | 1 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | ? | 0 | 1 | 5 | 0 | 0 | 1 | ? | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A.* indet. 6 | 0 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 1 | - | - | 0 | ? | 0 | 1 | 5 | 0 | 0 | 1 | ? | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A.* indet. 7 | 1 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | ? | 0 | 1 | 5 | 0 | 0 | 1 | ? | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |

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| *A.* indet. 8 | 1 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | ? | 0 | 1 | 5 | 0 | 0 | 1 | ? | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A.* indet. 9 | 1 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 1 | - | - | 0 | ? | 0 | 1 | 5 | 0 | 0 | 1 | ? | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A.* indet. 10 | 0 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 1 | - | - | 0 | ? | 0 | 1 | 5 | 0 | 0 | 1 | ? | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *A.* indet. 11 | 1 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | 0 | 0 | 1 | 5 | 0 | 0 | 1 | ? | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *Carl. drudei* | 0 | ? | ? | 2 | 0 | 1 | 1 | 2 | 1 | 2 | 2 | 1 | 1 | ? | 0 | 0 | 5 | 1 | 0 | 1 | 0 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | 0 | 2 | 1 | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 4 | 2 | 0 |
| *Carl. palmata* | 0 | 1 | 1 | 2 | 0 | 1 | 1 | 2 | 1 | 2 | 2 | 1 | 1 | 0 | 0 | 0 | 5 | 1 | 0 | 1 | 0 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | 0 | 2 | 1 | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 4 | 2 | 0 |
| *Carl.rotundifolia* | 0 | ? | ? | 2 | 0 | 1 | 1 | 2 | 1 | 2 | 2 | 1 | 1 | ? | 0 | 0 | 5 | 1 | 0 | 1 | 0 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | 0 | 2 | 1 | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 4 | 2 | 0 |
| *Carl. sulcata* | 0 | ? | ? | 2 | 0 | 1 | 1 | 2 | 1 | 2 | 2 | 1 | 1 | ? | 0 | 0 | 5 | 1 | 0 | 1 | 0 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 4 | 2 | 0 |
| *Chor. cyllidrica* | 2 | ? | ? | 2 | 3 | 1 | 1 | 1 | 1 | 1 | - | - | 1 | ? | ? | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 1 | 0 | 1 | 2 | 0 | 2 | 1 | 0 | 1 | 2 | 2 | 3 | 1 | 0 | 0 | 1 |
| *Chor. pendula* | 2 | ? | ? | 2 | 3 | 1 | 1 | 1 | 1 | 1 | - | - | 1 | ? | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 1 | 0 | 1 | 2 | 0 | 2 | 1 | 0 | 1 | 2 | 2 | 3 | 1 | 0 | 0 | 1 |
| *Cycl. bipartitus* | 0 | 1 | 1 | 3 | b | 1 | 1 | 1 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 6 | 1 | 0 | 1 | ? | ? | 0 | 3 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 2 | 0 | 1 | 1 | 3 | 3 | 2 | 1 | 6 | 4 | 0 |
| *Dian. cremnophilus* | 0 | 1 | 2 | 2 | 0 | 1 | 1 | 1 | 1 | a | 2 | 1 | 0 | 0 | 1 | 0 | 5 | 1 | 2 | 1 | 0 | 0 | 1 | 3 | 1 | 0 | 0 | 1 | 2 | 3 | 0 | 2 | 1 | 0 | 1 | 2 | 2 | 2 | 1 | 0 | 2 | 0 |
| *Dicr. goudotii* | 0 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 1 | - | - | 0 | ? | 0 | 1 | 5 | 1 | 2 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *Dicr. lugonis* | 0 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 1 | - | - | 0 | ? | 0 | 1 | 5 | 1 | 2 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 2 | 1 | 1 | 1 | 0 | 2 | 2 | 1 | 5 | 2 | 0 |
| *Dicr. pygmaeum* | 0 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 1 | - | - | 0 | ? | 0 | 1 | 5 | 1 | 2 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *Dicr. stenophyllum* | 0 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 1 | - | - | 0 | ? | 0 | 1 | 5 | 1 | 2 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |

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| *Dicr. aff. umbrophillum* | 0 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 1 | - | - | 0 | ? | 0 | 1 | 5 | 1 | 2 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *Dicr. wallisii* | 0 | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | - | - | 0 | 0 | 0 | 1 | 5 | 1 | 2 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *Dicr.* indet. 1 | 0 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 1 | - | - | 0 | ? | 0 | 1 | 5 | 1 | 2 | 1 | ? | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *Dicr.* indet. 2 | 0 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 1 | - | - | 0 | ? | 0 | 1 | 5 | 1 | 2 | 1 | ? | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *Dicr.* indet. 3 | 0 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 1 | - | - | 0 | ? | 0 | 1 | 5 | 1 | 2 | 1 | ? | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *Dicr.* indet. 4 | 0 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 1 | - | - | 0 | ? | 0 | 1 | 5 | 1 | 2 | 1 | ? | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *Dicr.* indet. 5 | 0 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 1 | - | - | 0 | ? | 0 | 1 | 5 | 1 | 2 | 1 | ? | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *Dicr.* indet. 6 | 0 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 1 | - | - | 0 | ? | 0 | 1 | 5 | 1 | 2 | 1 | ? | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *Dicr.* indet. 7 | 0 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 1 | - | - | 0 | ? | 0 | 1 | 5 | 1 | 2 | 1 | ? | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *Dicr.* indet. 8 | 0 | ? | ? | 2 | 0 | 1 | 1 | 1 | 1 | 1 | - | - | 0 | ? | 0 | 1 | 5 | 1 | 2 | 1 | ? | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |
| *Evodianthus funifer* | 1 | 0 | 2 | 2 | 0 | 1 | 1 | 1 | 1 | c | 2 | 1 | 0 | 0 | 1 | 0 | 5 | 1 | 2 | 1 | 0 | 2 | 0 | 3 | 1 | 0 | 0 | 0 | 2 | 3 | - | 2 | 1 | 0 | 1 | 2 | 2 | 2 | 1 | 0 | 2 | 0 |
| *Ludovia bierhorstii* | 1 | 1 | 1 | 2 | 3 | 0 | 1 | 0 | 0 | 1 | - | - | - | 1 | 0 | 1 | 5 | 0 | 0 | 1 | 0 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 3 | 1 | 5 | 4 | 0 |
| *Ludovia integrifolia* | 1 | 1 | 1 | 2 | 3 | 0 | 1 | 0 | 0 | 1 | - | - | - | 1 | 0 | 1 | 5 | 0 | 0 | 1 | 0 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 2 | 1 | 1 | 1 | 2 | 2 | 3 | 1 | 5 | 4 | 0 |
| *Ludovia lancifolia* | 2 | 1 | 1 | 2 | 3 | 0 | 1 | 0 | 0 | 1 | - | - | - | 1 | 0 | 1 | 5 | 0 | 0 | 1 | 0 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 2 | 1 | 1 | 1 | 2 | 2 | 3 | 1 | 5 | 4 | 0 |
| *Sch. chorianthum* | 0 | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 1 | 5 | 1 | 0 | 1 | 0 | 1 | 0 | 3 | 0 | 1 | 0 | 1 | 1 | 2 | 0 | 2 | 1 | 0 | 1 | 2 | 2 | 2 | 1 | 0 | 2 | 0 |
| *Sph. acutitepala* | 2 | 0 | 1 | 2 | 3 | 1 | 1 | 1 | 0 | 1 | - | - | 1 | 1 | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 1 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 3 | 4 | 1 | 5 | ? | 0 |

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| *Sph.* *aff.* *buenaventurae* | 2 | ? | ? | 2 | 3 | 1 | 1 | 1 | ? | 1 | - | - | 1 | ? | 0 | 1 | 5 | 0 | 0 | 1 | 0 | 1 | 0 | 3 | 0 | 1 | 1 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 3 | 4 | 1 | 5 | ? | 0 |
| *Sph. crocea* | 2 | 0 | 1 | 2 | 3 | 1 | 1 | 1 | 0 | 1 | - | - | 1 | 1 | 0 | 1 | 5 | 0 | 0 | 1 | ? | 1 | 0 | 3 | 0 | 1 | 1 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 3 | 4 | 1 | 5 | ? | 0 |
| *Sph.* aff. *distans* | 2 | ? | ? | 2 | 3 | 1 | 1 | 1 | 0 | 1 | - | - | 1 | ? | 0 | 1 | 5 | 0 | 0 | 1 | ? | 1 | 0 | 3 | 0 | 1 | 1 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 3 | 4 | 1 | 5 | ? | 0 |
| *Sph. duidae* | 0 | ? | ? | 2 | 3 | 1 | 1 | 1 | 0 | 1 | - | - | 1 | ? | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 1 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 3 | 4 | 1 | 5 | ? | 0 |
| *Sph.* aff. *hamata* | 2 | ? | ? | 2 | 3 | 1 | 1 | 1 | 0 | 1 | - | - | 1 | ? | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | a | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 3 | 4 | 1 | 5 | ? | 0 |
| *Sph. killipii* | 2 | 0 | 1 | 2 | 3 | 1 | 1 | 1 | 0 | 1 | - | - | 1 | 1 | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 1 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 3 | 4 | 1 | 5 | ? | 0 |
| *Sph. laucheana* | 0 | ? | ? | 2 | 3 | 1 | 1 | 1 | 0 | 1 | - | - | 1 | 1 | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 1 | 0 | 1 | 2 | 0 | 2 | 1 | 1 | 1 | 2 | 3 | 4 | 1 | 5 | ? | 0 |
| *Sph.* cf. *pallida* | 2 | ? | ? | 2 | 3 | 1 | 1 | 1 | 0 | 1 | - | - | 1 | ? | 0 | 1 | 5 | 0 | 0 | 1 | ? | 1 | 0 | 3 | 0 | 1 | 1 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 3 | 4 | 1 | 5 | ? | 0 |
| *Sph. pterostigma* | 2 | ? | ? | 2 | 3 | 1 | 1 | 1 | 0 | 1 | - | - | 1 | ? | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | a | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 3 | 4 | 1 | 5 | ? | 0 |
| *Sph.* aff. *stylosa* | 2 | ? | ? | 2 | 3 | 1 | 1 | 1 | 0 | 1 | - | - | 1 | ? | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 1 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 3 | 4 | 1 | 5 | ? | 0 |
| *Sph.* ident. 1 | 2 | ? | ? | 2 | 3 | 1 | 1 | 1 | 0 | 1 | - | - | 1 | ? | 0 | 1 | 5 | 0 | 2 | 1 | ? | 1 | 0 | 3 | 0 | 1 | ? | 0 | ? | ? | ? | 2 | 0 | 1 | 1 | 2 | 2 | 4 | 1 | 5 | ? | 0 |
| *Sph.* indet. 2 | 2 | ? | ? | 2 | 3 | 1 | 1 | 1 | 0 | 1 | - | - | 1 | ? | 0 | 1 | 5 | 0 | 0 | 1 | ? | 1 | 0 | 3 | 0 | 1 | ? | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 3 | 4 | 1 | 5 | ? | 0 |
| *Sph.* indet. 3 | 2 | ? | ? | 2 | 3 | 1 | 1 | 1 | 0 | 1 | - | - | 1 | ? | 0 | 1 | 5 | 0 | 0 | 1 | ? | 1 | 0 | 3 | 0 | 1 | ? | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 4 | 1 | 5 | ? | 0 |
| *Sph.* indet. 4 | 2 | ? | ? | 2 | 3 | 1 | 1 | 1 | 0 | 1 | - | - | 1 | ? | 0 | 1 | 5 | 0 | 0 | 1 | ? | 1 | 0 | 3 | 0 | 1 | ? | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 3 | 4 | 1 | 5 | ? | 0 |
| *Sph.* indet. 5 | 0 | ? | ? | 2 | 3 | 1 | 1 | 1 | 0 | 1 | - | - | 1 | ? | 0 | 1 | 5 | 0 | 0 | 1 | ? | 1 | 0 | 3 | 0 | 1 | ? | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 3 | 4 | 1 | 5 | ? | 0 |
| *Sph.* indet. 6 | 2 | ? | ? | 2 | 3 | 1 | 1 | 1 | 0 | 1 | - | - | 1 | ? | 0 | 1 | 5 | 0 | 0 | 1 | ? | 1 | 0 | 3 | 0 | 1 | ? | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 4 | 1 | 5 | ? | 0 |

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| *Sph.* indet. 7 | 2 | ? | ? | 2 | 3 | 1 | 1 | 1 | 0 | 1 | - | - | 1 | ? | 0 | 1 | 5 | 0 | 0 | 1 | ? | 1 | 0 | 3 | 0 | 1 | ? | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 3 | 4 | 1 | 5 | ? | 0 |
| *Sph.* indet. 8 | 2 | ? | ? | 2 | 3 | 1 | 1 | 1 | 0 | 1 | - | - | 1 | ? | 0 | 1 | 5 | 0 | 0 | 1 | ? | 1 | 0 | 3 | 0 | 1 | ? | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 3 | 4 | 1 | 5 | ? | 0 |
| *Sph.* indet. 9 | 2 | ? | ? | 2 | 3 | 1 | 1 | 1 | 0 | 1 | - | - | 1 | ? | 0 | 1 | 5 | 0 | 0 | 1 | ? | 1 | 0 | 3 | 0 | 1 | ? | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 3 | 4 | 1 | 5 | ? | 0 |
| *Sph.* indet. 10 | 2 | ? | ? | 2 | 3 | 1 | 1 | 1 | 0 | 1 | - | - | 1 | ? | 0 | 1 | 5 | 0 | 0 | 1 | ? | 1 | 0 | 3 | 0 | 1 | ? | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 3 | 2 | 1 | 5 | ? | 0 |
| *Sph.* indet. 11 | 2 | ? | ? | 2 | 3 | 1 | 1 | 1 | 0 | 1 | - | - | 1 | ? | 0 | 1 | 5 | 0 | 0 | 1 | ? | 1 | 0 | 3 | 0 | 1 | ? | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 2 | 2 | 4 | 1 | 5 | ? | 0 |
| *Stel. stylaris* | 2 | ? | ? | 2 | 3 | 1 | 1 | 1 | 0 | 1 | - | - | 1 | ? | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 1 | 0 | 1 | 2 | 0 | 2 | 1 | 1 | 1 | 2 | 2 | 4 | 1 | 5 | 0 | 1 |
| *Stel. surinamensis* | b | ? | ? | 2 | 3 | 1 | 1 | 1 | 0 | 1 | - | - | 1 | ? | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 1 | 0 | ? | ? | 0 | 2 | 1 | 1 | 1 | 2 | 2 | 4 | 1 | 5 | 0 | 1 |
| *Thor. bissectus* | 1 | 0 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | - | - | 0 | 0 | 0 | 1 | 5 | 0 | 1 | 1 | 0 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | ? | 2 | 0 | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 5 | 2 | 0 |

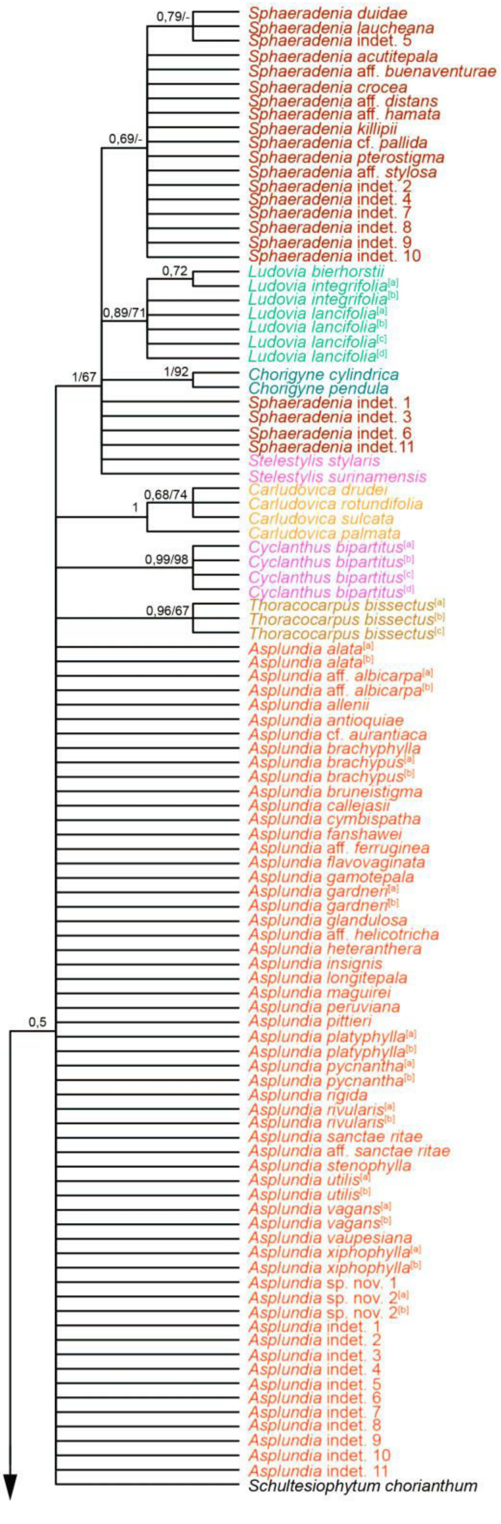
## Results

The combined matrix has 8568 aligned characters, of which 42 are non-molecular, 5695 are from the plastid genome and 2831 from nuclear DNA. From the total matrix, 540 are variable, and 2079 are parsimony-informative. Regarding topology, results from different analyses, i.e. combined DNA and total evidence, do not show strong conflicts. In the analyses of the morphological dataset alone, the topologies showed largely unresolved relationships.

**Morphological data.** — The analysis of the morphological dataset found 1000 most-parsimonious trees with a length of 150 steps, consistency index (CI) of 0.54 and retention index (RI) 0.91. Cyclanthaceae is recovered as monophyletic (BS 90%, PP 0.97). The topologies show largely unresolved relationships. Only two clades found in this analysis are also recovered in the combined analysis of morphological and molecular data. The clade *Dianthoveus* + *Evodianthus* (BS 80%, PP 0.61), which emerges as sister-group to the rest of the family, and the Sphaeradenia group (BS 67%, PP 1.0) are consistent in all analysis. The remaining genera emerge in a large polytomy. The strict consensus tree of the morphological parsimony analysis is presented in Figure 3.

**Individual markers, cpDNA e nrDNA.** — The nuclear markers exhibit the largest amount of variable and parsimony-informative sites. The nuclear low-copy *rpb*2 marker stands as the most informative region among all individual markers. In contrast, chloroplast markers show lower percentages of variable and parsimony-informative characters, with *mat*K being the most variable among them. Bayesian inference analyses of the individual markers resulted in topologies with different degrees of resolution and support (trees not shown). No significant incongruences were detected among the topologies; most of the conflict corresponds to shallow clades with low posterior probability values. In individual analyses, the intergenic spacers *psb*A-*trn*H, *trn*L-*trn*F and *trn*Q-*rps*16 did not recover the monophyly of Cyclanthaceae; the topologies obtained with each marker, however, tend to group species of a same genus in medium- to low-supported clades.

The combined chloroplast markers produced a little resolved phylogenetic hypothesis for Cyclanthaceae. The 50% majority rule consensus tree of the BI analysis shows the backbone topology as a large polytomy formed by many lineages. However, Cyclanthaceae is divided in two highly-supported clades (BS -, PP 1) representing the two subfamilies, Cyclanthoideae and Carludovicoideae. The


0,79/-
0,69/-
0,72
0,89/71
1/67
1/92
0,68/74
1
0,99/98
0,96/67
0,5
Sphaeradenia duidae
Sphaeradenia laucheana
Sphaeradenia indet. 5
Sphaeradenia acutitepala
Sphaeradenia aff. buenaventurae
Sphaeradenia crocea
Sphaeradenia aff. distans
Sphaeradenia aff. hamata
Sphaeradenia killipii
Sphaeradenia cf. pallida
Sphaeradenia pterostigma
Sphaeradenia aff. stylosa
Sphaeradenia indet. 2
Sphaeradenia indet. 4
Sphaeradenia indet. 7
Sphaeradenia indet. 8
Sphaeradenia indet. 9
Sphaeradenia indet. 10
Ludovia bierhorstii
Ludovia integrifolia[a]
Ludovia integrifolia[b]
Ludovia lancifolia[a]
Ludovia lancifolia[b]
Ludovia lancifolia[c]
Ludovia lancifolia[d]
Chorigyne cylindrica
Chorigyne pendula
Sphaeradenia indet. 1
Sphaeradenia indet. 3
Sphaeradenia indet. 6
Sphaeradenia indet.11
Stelestylis stylaris
Stelestylis surinamensis
Carludovica drudei
Carludovica rotundifolia
Carludovica sulcata
Carludovica palmata
Cyclanthus bipartitus[a]
Cyclanthus bipartitus[b]
Cyclanthus bipartitus[c]
Cyclanthus bipartitus[d]
Thoracocarpus bissectus[a]
Thoracocarpus bissectus[b]
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Asplundia aff. albicarpa[b]
Asplundia allenii
Asplundia antioquiae
Asplundia cf. aurantiaca
Asplundia brachyphylla
Asplundia brachypus[a]
Asplundia brachypus[b]
Asplundia bruneistigma
Asplundia callejasii
Asplundia cymbispatha
Asplundia fanshawei
Asplundia aff. ferruginea
Asplundia flavovaginata
Asplundia gamotepala
Asplundia gardneri[a]
Asplundia gardneri[b]
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Asplundia aff. helicotricha
Asplundia heteranthera
Asplundia insignis
Asplundia longitepala
Asplundia maguirei
Asplundia peruviana
Asplundia pittieri
Asplundia platyphylla[a]
Asplundia platyphylla[b]
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Asplundia pycnantha[b]
Asplundia rigida
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Asplundia rivularis[b]
Asplundia sanctae ritae
Asplundia aff. sanctae ritae
Asplundia stenophylla
Asplundia utilis[a]
Asplundia utilis[b]
Asplundia vagans[a]
Asplundia vagans[b]
Asplundia vaupesiana
Asplundia xiphophylla[a]
Asplundia xiphophylla[b]
Asplundia sp. nov. 1
Asplundia sp. nov. 2[a]
Asplundia sp. nov. 2[b]
Asplundia indet. 1
Asplundia indet. 2
Asplundia indet. 3
Asplundia indet. 4
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Asplundia indet. 6
Asplundia indet. 7
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Asplundia indet. 11
Schultesiophytum chorianthum

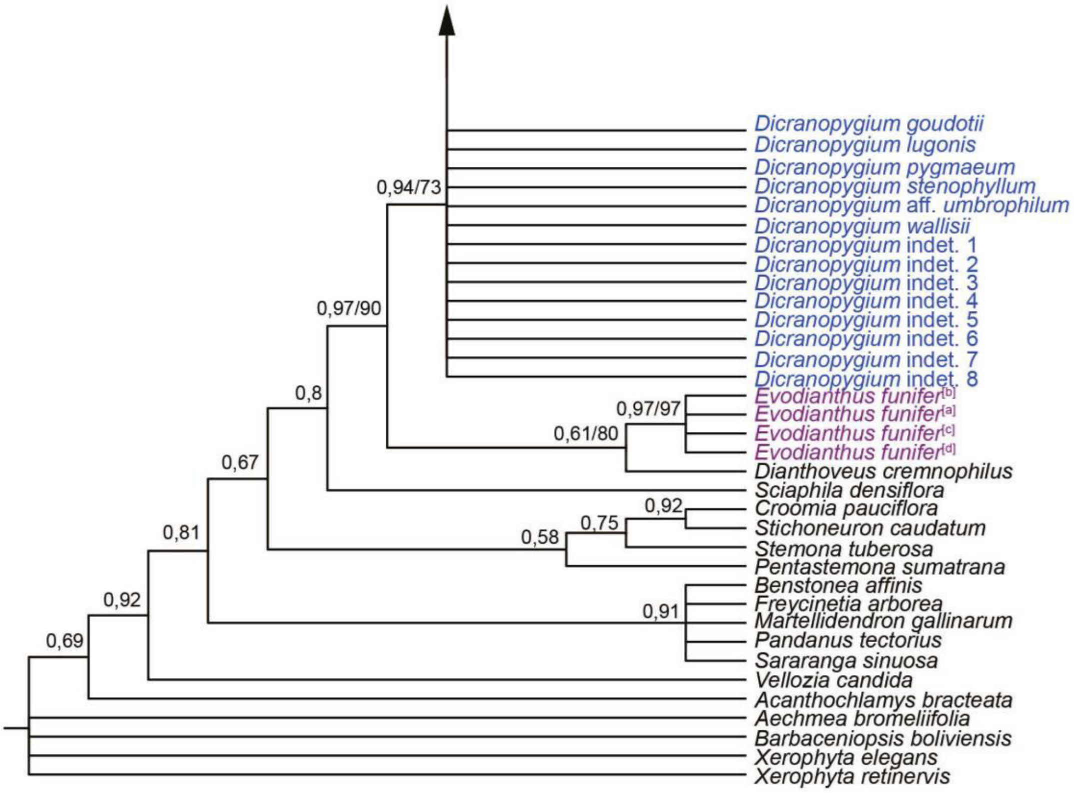


Fig. 3. Bayesian tree based on the morphology dataset. Statistical support for main clades and genera are indicated by posterior probabilities and parsimony bootstrap, respectively. Clades below generic-level only parsimony bootstrap are indicated. A dash (-) indicates branches not recovered in the corresponding analysis.

phylogenetic analyses of the cpDNA dataset did not provide enough information to resolve the generic relations in Carludovicoideae. The large genus *Asplundia* is not recovered as monophyletic in cpDNA analysis, and a clade representing the Sphaeradenia group is recovered with moderate support (BS -, PP 0.72).

**Table 4.** Sampling, matrix values and parsimony statistics of the separate and combined datasets. Variable characters and Parsimony informative characters include indel characters.

| Dataset | Terminals included | No. of total characters | No. of variable characters | No. of informative characters | No. of trees | Length of trees |
|---|---|---|---|---|---|---|
| *atp*B-*rbc*L | 121 | 1393 | 532 (38%) | 320 (23%) | 40 | 4185 |
| *mat*K | 136 | 972 | 407 (42%) | 217 (22%) | 1000 | 1731 |
| *psb*A-*trn*H | 130 | 1189 | 281 (24%) | 175 (15%) | 20 | 695 |
| *trn*L-*trn*F | 133 | 581 | 229 (39%) | 114 (20%) | 10 | 381 |
| *trn*Q-*rps*16 | 131 | 1560 | 497 (32%) | 338 (22%) | 40 | 765 |
| cpDNA | 138 | 5695 | 1946 (34%) | 1164 (20%) | 32 | 25797 |
| *phy*C | 103 | 1212 | 623 (51%) | 351 (29%) | 60 | 1180 |
| *rpb*2 | 94 | 1619 | 847 (52%) | 522 (32%) | 80 | 1678 |
| nrDNA | 113 | 2831 | 1470 (52%) | 873 (31%) | 368 | 9453 |
| Combined molecular dataset | 138 | 8526 | 3416 (40%) | 2037 (24%) | 144 | 6841 |
| Morphology | 138 | 42 | 42 | 42 | 1000 | 150 |
| Total evidence | 138 | 8568 | 3458 (40%) | 2079 (24%) | 416 | 7101 |

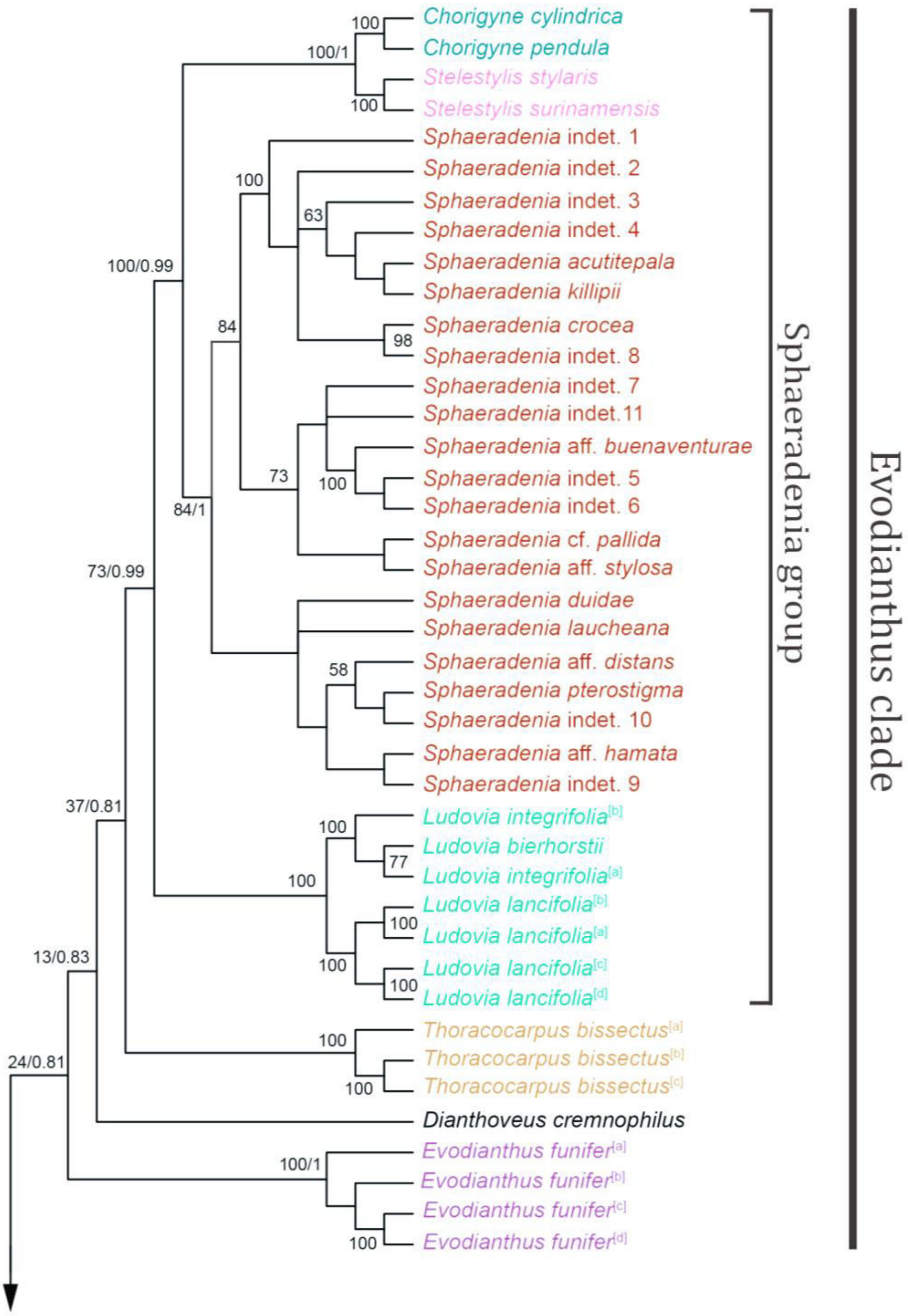
The Bayesian inference analyses of the two nuclear markers produced relatively robust overall topologies, especially at deeper nodes. The 50% majority rule consensus tree of the

Bayesian analysis shows Cyclanthaceae as monophyletic with high node confidence values (PP 0.99). The lineages of the two subfamilies are recovered (PP 1.0) and Carludovicoideae presents three well-supported clades. The genus *Carludovica* was recovered as the earliest genus to diverge within Carludovicoideae (BS 100%, PP 1.0) and the remaining genera were recovered in a strongly supported clade, divided in three lineages. In combined nrDNA analyses, all Cyclanthaceae genera were recovered as monophyletic with high support.

The main differences between the phylogenetic hypotheses obtained with the cpDNA and nrDNA datasets are mostly associated with the degree of resolution. The cpDNA dataset produced a polytomic in backbone topology whereas the nrDNA analyses resolved the deeper relationships with low to medium support. Although the polytomy in the cpDNA analysis does not provide information about the monophyly of all genera in Cyclanthaceae, it does not represent a conflicting scenario for this hypothesis. Both analyses support the same main clades across the phylogeny and present relatively low resolution within these clades. No well-supported incongruent clades were detected among the topologies generated with these datasets. All trees here invocated are available in Appendix 1.

**Combined DNA analysis.** — The combined molecular analysis found 144 most-parsimonious trees with 6841 steps, CI of 0.64 and RI of 0.78 (Figure 4). The topologies are differents in MP and BI analyses. Cyclanthaceae is recovered as monophyletic (BS 100%, PP 1.0) with *Cyclanthus* as sister to the rest. In Carludovicoideae (BS 99%), *Carludovica* is sister of the remaining genera (BS 99%), which are divided in two clades (BS 80%), the first with *Schultesiophytum* as sister (BS 56%, -) to *Asplundia* + *Dicranopygium* (BS 56%, PP 1.0) and the other with clade *Dianthoveus* + *Evodianthus* as sister to all remaining genera (BS 55%, -). All genera are recovered as monophyletic.

**Total evidence analysis.** — The total evidence analysis found 416 most-parsimonious trees with 7101 steps, CI of 0.64 and RI 0.79. Trees recovered from the MP and BI analyses for the total-evidence dataset were mostly in agreement. All major clades shown below are recovered in both total-evidence analyses. The strict consensus tree of the total evidence parsimony analysis is presented in Figure 5 and 7. The majority-rule (> 50%) consensus tree recovered from the total evidence BI analysis is shown in Figure 6, and is used to represent the estimated phylogeny of the Cyclanthaceae. Cyclanthaceae are again monophyletic (BS 100, PP 1.0), and two sister clades, Cyclanthoideae and Carludovicoideae, are recovered (BS 100%, PP 1), with *Cyclanthus* (Cyclanthoideae) recovered as sister to all remaining genera (Carludovicoideae). Three homoplastic characters, longitudinal incisions in the blade (character 8: state 0, 1 and 2), basal bulb (26:1), and fusion of the pistillate flowers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Chorigyne pendula
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Stelestylis surinamensis
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Sphaeradenia indet. 2
Sphaeradenia indet. 3
Sphaeradenia indet. 4
Sphaeradenia acutitepala
Sphaeradenia killipii
Sphaeradenia crocea
Sphaeradenia indet. 8
Sphaeradenia indet. 7
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Sphaeradenia aff. buenaventurae
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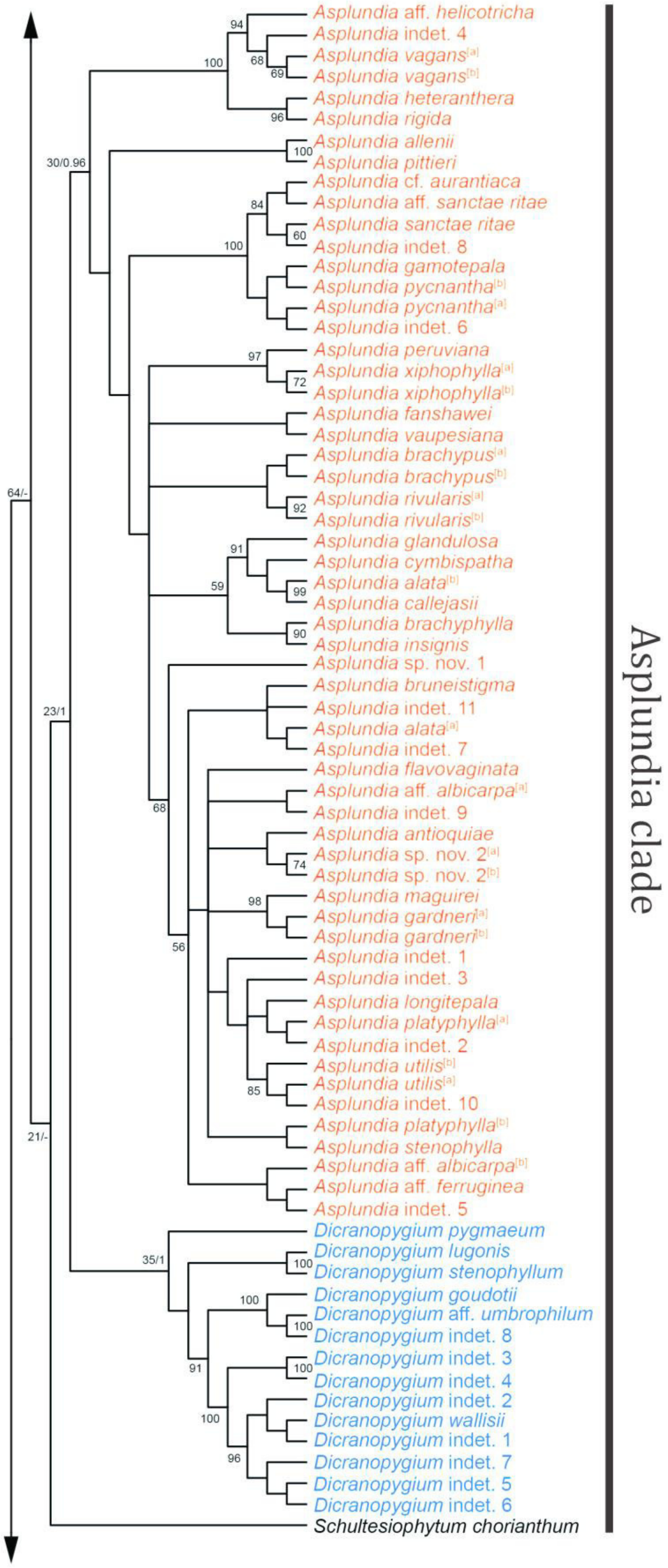
Sphaeradenia indet. 6
Sphaeradenia cf. pallida
Sphaeradenia aff. stylosa
Sphaeradenia duidae
Sphaeradenia laucheana
Sphaeradenia aff. distans
Sphaeradenia pterostigma
Sphaeradenia indet. 10
Sphaeradenia aff. hamata
Sphaeradenia indet. 9
Ludovia integrifolia[b]
Ludovia bierhorstii
Ludovia integrifolia[a]
Ludovia lancifolia[b]
Ludovia lancifolia[a]
Ludovia lancifolia[c]
Ludovia lancifolia[d]
Thoracocarpus bissectus[a]
Thoracocarpus bissectus[b]
Thoracocarpus bissectus[c]
Dianthoveus cremnophilus
Evodianthus funifer[a]
Evodianthus funifer[b]
Evodianthus funifer[c]
Evodianthus funifer[d]
100
100/1
100
100
100/0.99
84
63
98
84/1
73
100
73/0.99
58
37/0.81
100
77
100
100
13/0.83
100
100
100
24/0.81
100/1
100
Sphaeradenia group
Evodianthus clade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Asplundia pittieri
Asplundia cf. aurantiaca
Asplundia aff. sanctae ritae
Asplundia sanctae ritae
Asplundia indet. 8
Asplundia gamotepala
Asplundia pycnantha[b]
Asplundia pycnantha[a]
Asplundia indet. 6
Asplundia peruviana
Asplundia xiphophylla[a]
Asplundia xiphophylla[b]
Asplundia fanshawei
Asplundia vaupesiana
Asplundia brachypus[a]
Asplundia brachypus[b]
Asplundia rivularis[a]
Asplundia rivularis[b]
Asplundia glandulosa
Asplundia cymbispatha
Asplundia alata[b]
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Asplundia insignis
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Asplundia bruneistigma
Asplundia indet. 11
Asplundia alata[a]
Asplundia indet. 7
Asplundia flavovaginata
Asplundia aff. albicarpa[a]
Asplundia indet. 9
Asplundia antioquiae
Asplundia sp. nov. 2[a]
Asplundia sp. nov. 2[b]
Asplundia maguirei
Asplundia gardneri[a]
Asplundia gardneri[b]
Asplundia indet. 1
Asplundia indet. 3
Asplundia longitepala
Asplundia platyphylla[a]
Asplundia indet. 2
Asplundia utilis[b]
Asplundia utilis[a]
Asplundia indet. 10
Asplundia platyphylla[b]
Asplundia stenophylla
Asplundia aff. albicarpa[b]
Asplundia aff. ferruginea
Asplundia indet. 5
Dicranopygium pygmaeum
Dicranopygium lugonis
Dicranopygium stenophyllum
Dicranopygium goudotii
Dicranopygium aff. umbrophilum
Dicranopygium indet. 8
Dicranopygium indet. 3
Dicranopygium indet. 4
Dicranopygium indet. 2
Dicranopygium wallisii
Dicranopygium indet. 1
Dicranopygium indet. 7
Dicranopygium indet. 5
Dicranopygium indet. 6
Schultesiophytum chorianthum
94
100
68
69
96
30/0.96
100
84
60
100
97
72
64/-
92
91
59
99
90
23/1
68
74
98
56
85
21/-
35/1
100
100
100
91
100
100
96
Asplundia clade

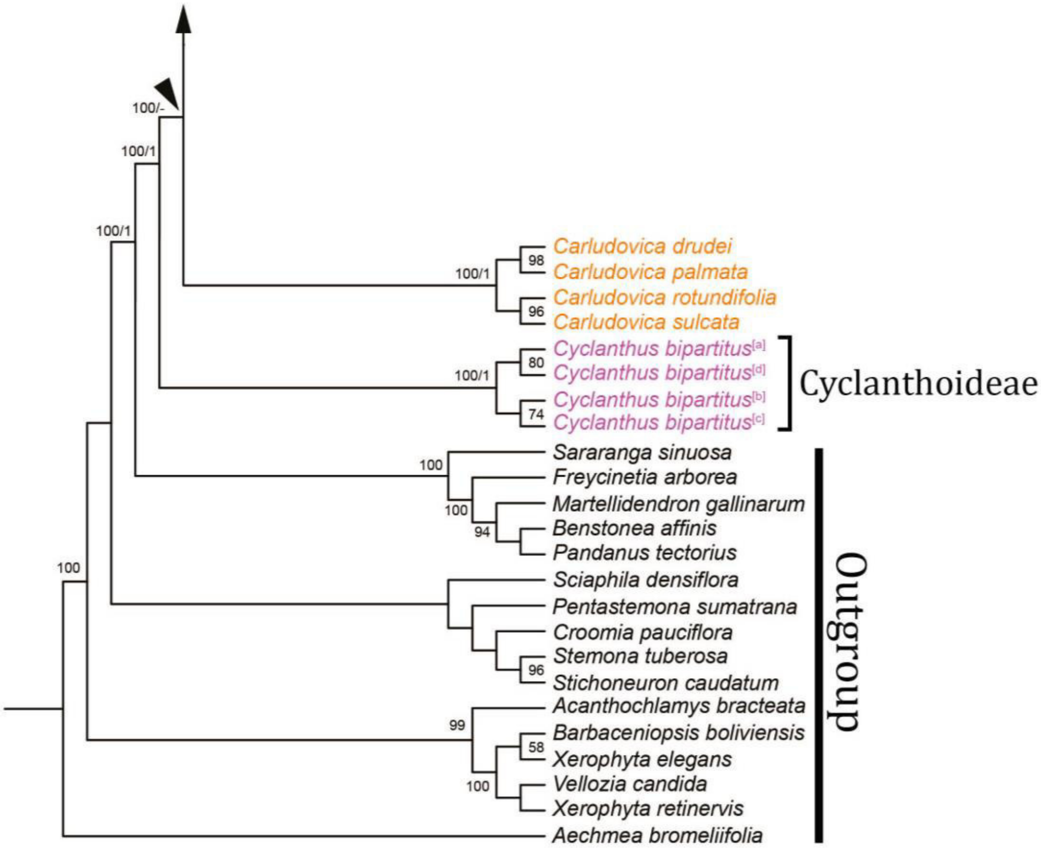


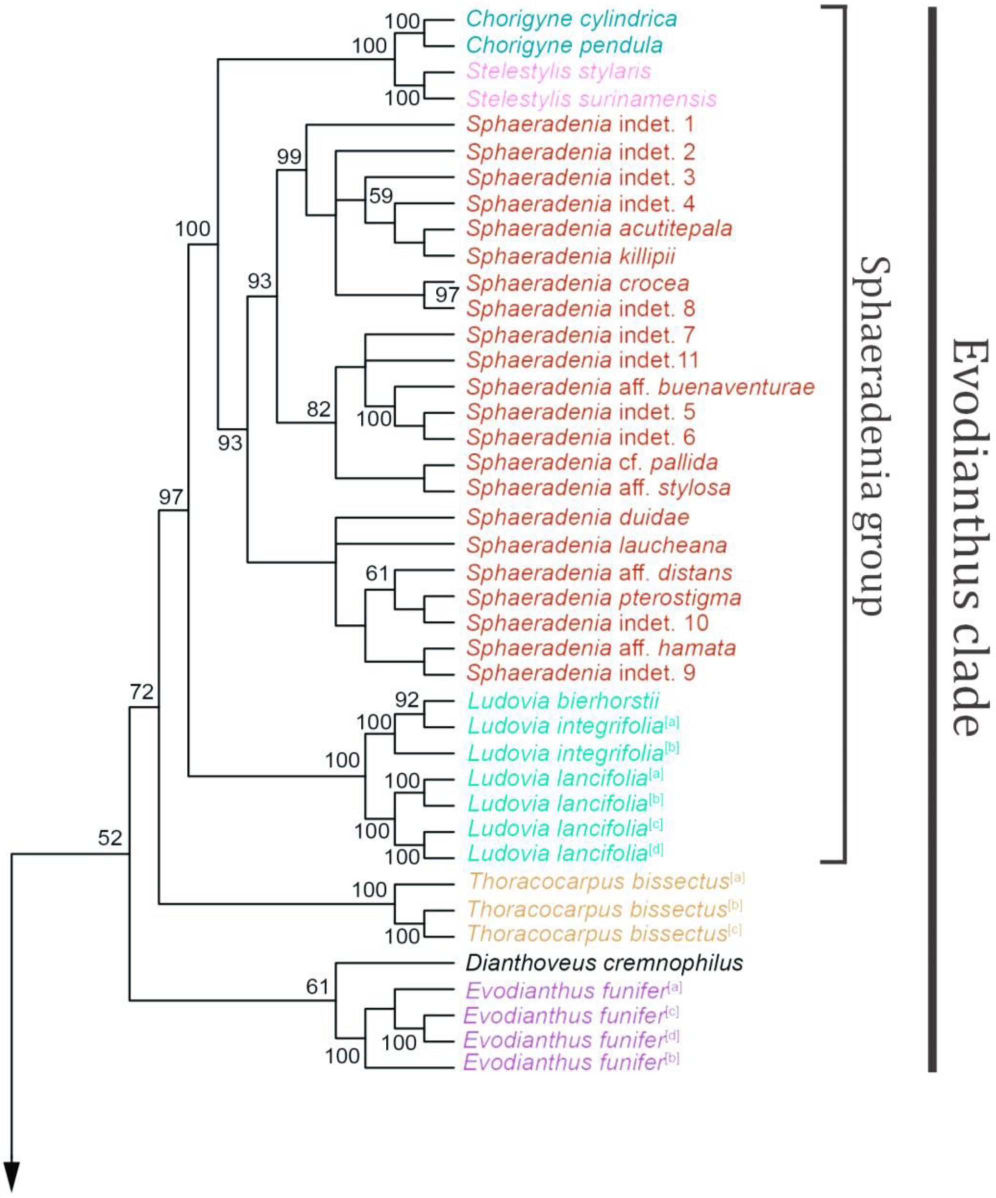
Fig. 4. Strict consensus tree of the parsimony analysis of the molecular combined dataset. Numbers near nodes indicate parsimony bootstrap values and posterior probabilities, respectvely. A dash (-) indicates branches not recovered in the corresponding analysis.

(34:1) support Cyclanthaceae. Inflorescence types are also unique in Cyclanthaceae (17:5 and 6). *Cyclanthus* is supported by autopomorphies not included in our analysis, and perhaps by unequivocal optimized characters; plications parallel to the primary veins (4:3), lateral costae originating from the central costa apex (11:0) and reaching the apex of the blade (12:0), inflorescence with unisexual flowers arranged in alternate whorls (17:5), numerous carpels (36:3), numerous placentae (37:3) fruits in discs (40:6). Subfamily Carludovicoideae is supported by a homoplastic character, unique in the family, filamentous staminodes in the pistillate flower (33:1).

There are three major lineages in Carludovicoideae, one of them represents the genus *Carludovica* (BS 100%, PP 1.0; Carludovica clade), which is supported by non-homoplastic synapomorphies once attributed to the genus; blade with two incisions (8:2), pollen aperture in the equatorial surface (31:1) and dehiscent syncarp by division and infructescence rolling over (40:5). Another character state, porate pollen (29:0) is homoplastic but unique in Cyclanthaceae. The other two lineages are moderately supported (BS 83%, PP 0.93), the first clade includes three lineages that correspond to the genera *Asplundia*, *Dicranopygium* and *Schultesiophytum* (Asplundia clade), and the other includes seven lineages, that correspond to *Chorigyne*, *Ludovia*, *Dianthoveus*, *Evodianthus*, *Sphaeradenia*, *Stelestylis* and *Thoracocarpus* (Evodianthus clade).

The Asplundia clade may be supported by a homoplastic character state, lateral inflorescence (16:1), with equivocal optimization. The monotypic genus *Schultesiophytum* is recovered as sister to *Dicranopygium* + *Asplundia*, with strong support in the BI analysis (BS 50%, PP 0.97). This is supported by lateral costae originating in the median region of the central costa (11:1), and by two additional homoplastic characters; appendix in the anther connective (28:1) and free pistillate flowers (34:0).

The large genera *Dicranopygium* and *Asplundia* are recovered as sister groups (BS 57%, PP 1.0) and are strongly supported as monophyletic in BI analysis (BS 85%, PP 1.0; BS 70%, PP 1.0, respectively). *Dicranopygium* is monophyletic and supported by one homoplastic character; bracts of the same size (19:2), and two homoplastic characters; one lateral costa (10:1), zygomorphic staminate flowers (21:1), both with equivocal optimization. *Asplundia* is supported by two homoplastic characters: predominantly terrestrial herbs or lianas (1:1 and 2) e bracts distributed along the peduncle (18:0). Its two subgenera are recovered as monophyletic groups,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Chorigyne pendula
Stelestylis stylaris
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Sphaeradenia indet. 1
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Sphaeradenia indet. 2
Sphaeradenia indet. 3
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Sphaeradenia indet. 4
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Sphaeradenia acutitepala
Sphaeradenia killipii
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Sphaeradenia crocea
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Sphaeradenia indet. 8
Sphaeradenia indet. 7
Sphaeradenia indet.11
Sphaeradenia aff. buenaventurae
82
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Sphaeradenia indet. 5
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Sphaeradenia indet. 6
Sphaeradenia cf. pallida
Sphaeradenia aff. stylosa
97
Sphaeradenia duidae
Sphaeradenia laucheana
61
Sphaeradenia aff. distans
Sphaeradenia pterostigma
Sphaeradenia indet. 10
Sphaeradenia aff. hamata
Sphaeradenia indet. 9
72
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Ludovia bierhorstii
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Ludovia integrifolia[a]
Ludovia integrifolia[b]
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Ludovia lancifolia[a]
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Ludovia lancifolia[c]
100
Ludovia lancifolia[d]
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Thoracocarpus bissectus[a]
Thoracocarpus bissectus[b]
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Thoracocarpus bissectus[c]
Dianthoveus cremnophilus
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Evodianthus funifer[a]
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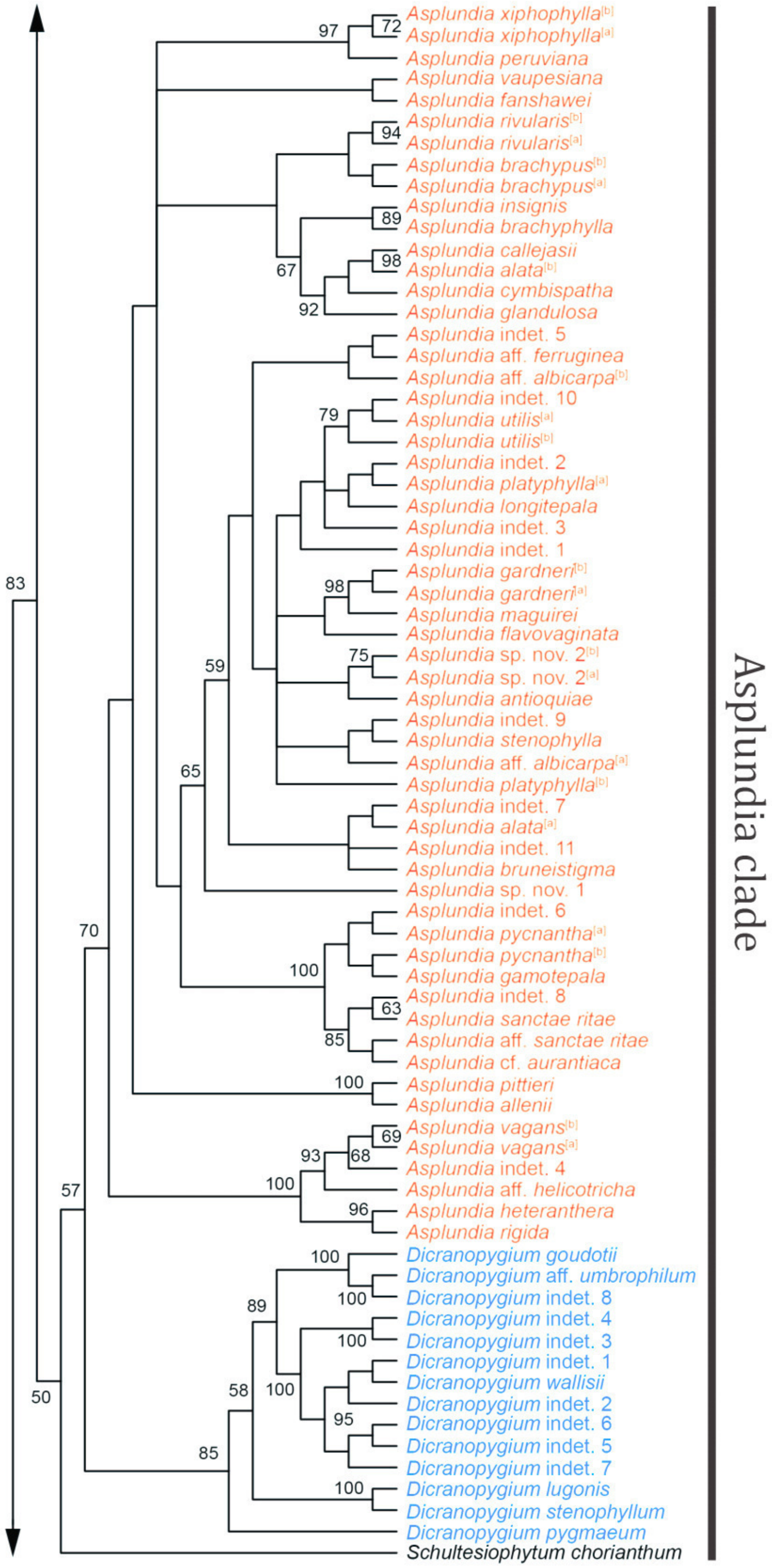
Evodianthus funifer[b]
Sphaeradenia group
Evodianthus clade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Asplundia indet. 8
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Asplundia aff. sanctae ritae
Asplundia cf. aurantiaca
Asplundia pittieri
Asplundia allenii
Asplundia vagans[b]
Asplundia vagans[a]
Asplundia indet. 4
Asplundia aff. helicotricha
Asplundia heteranthera
Asplundia rigida
Dicranopygium goudotii
Dicranopygium aff. umbrophilum
Dicranopygium indet. 8
Dicranopygium indet. 4
Dicranopygium indet. 3
Dicranopygium indet. 1
Dicranopygium wallisii
Dicranopygium indet. 2
Dicranopygium indet. 6
Dicranopygium indet. 5
Dicranopygium indet. 7
Dicranopygium lugonis
Dicranopygium stenophyllum
Dicranopygium pygmaeum
Schultesiophytum chorianthum
Asplundia clade
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92
79
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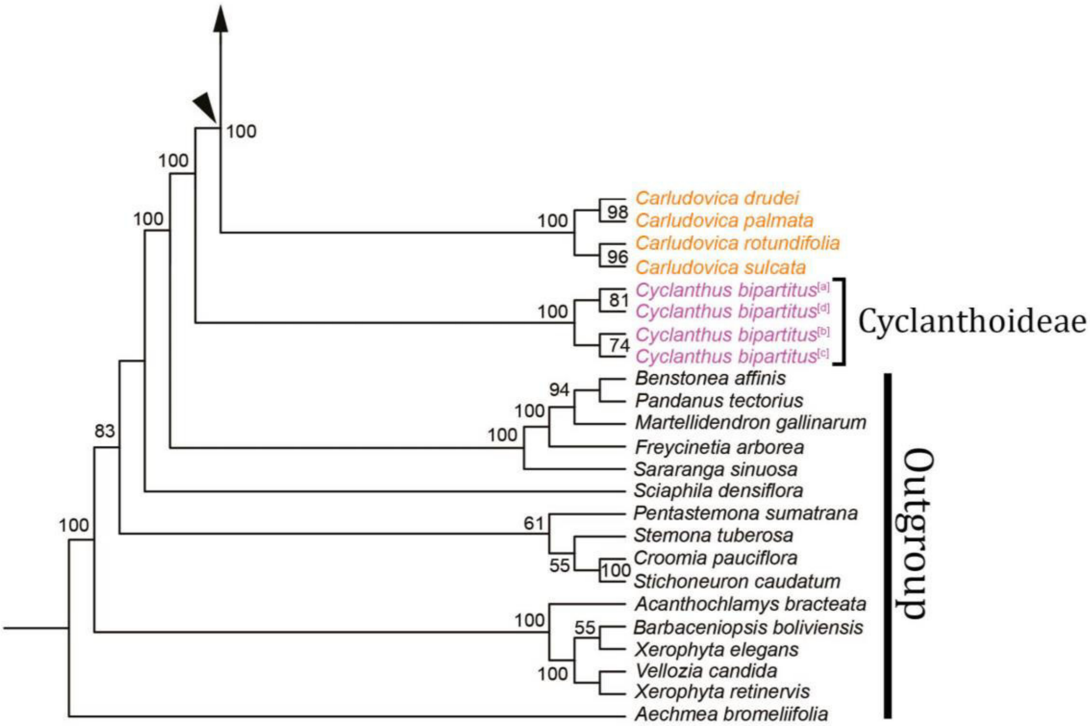


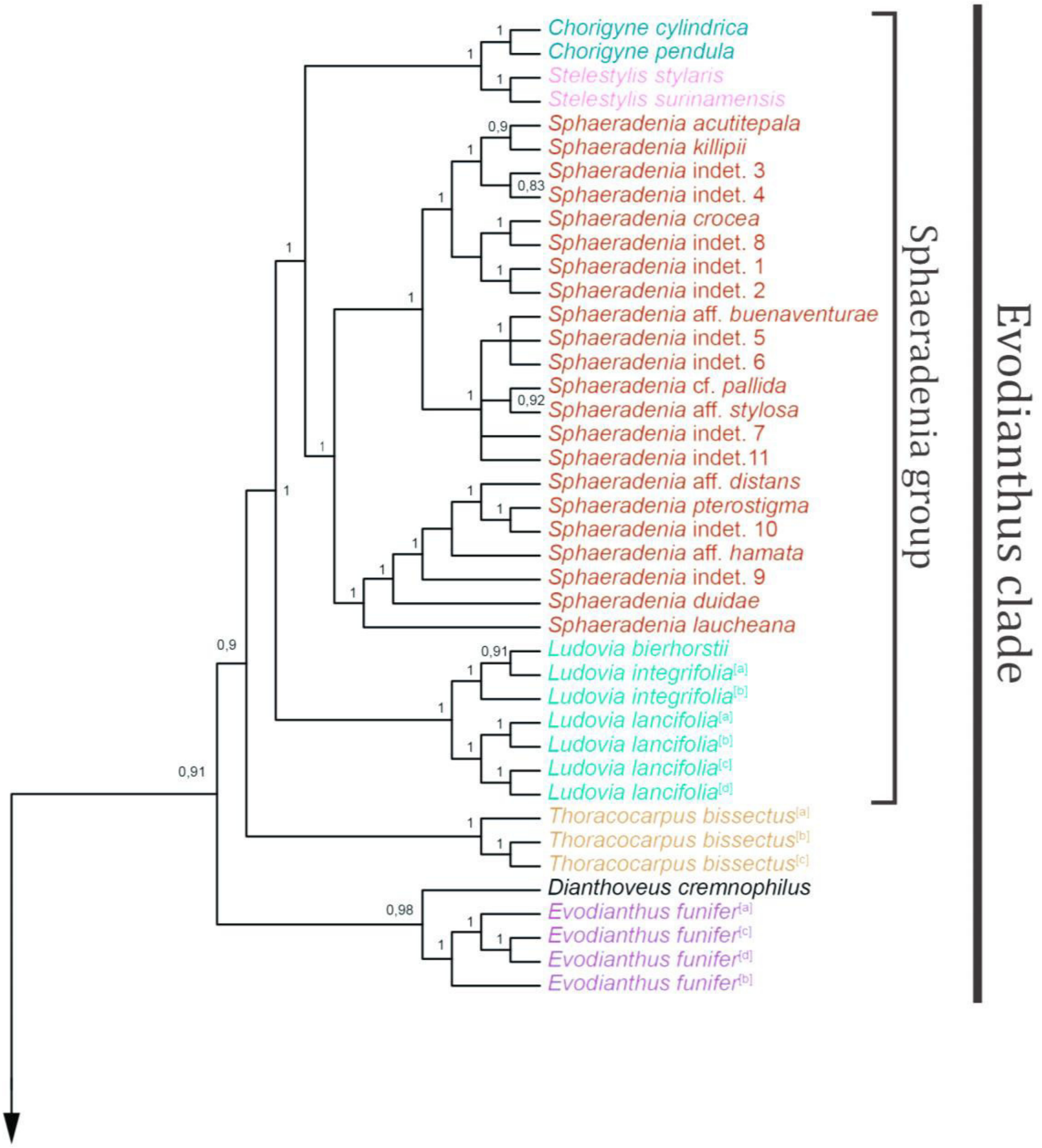
Fig. 5. Strict consensus tree of the parsimony analysis of the total-evidence dataset. Numbers near nodes indicate parsimony bootstrap values.

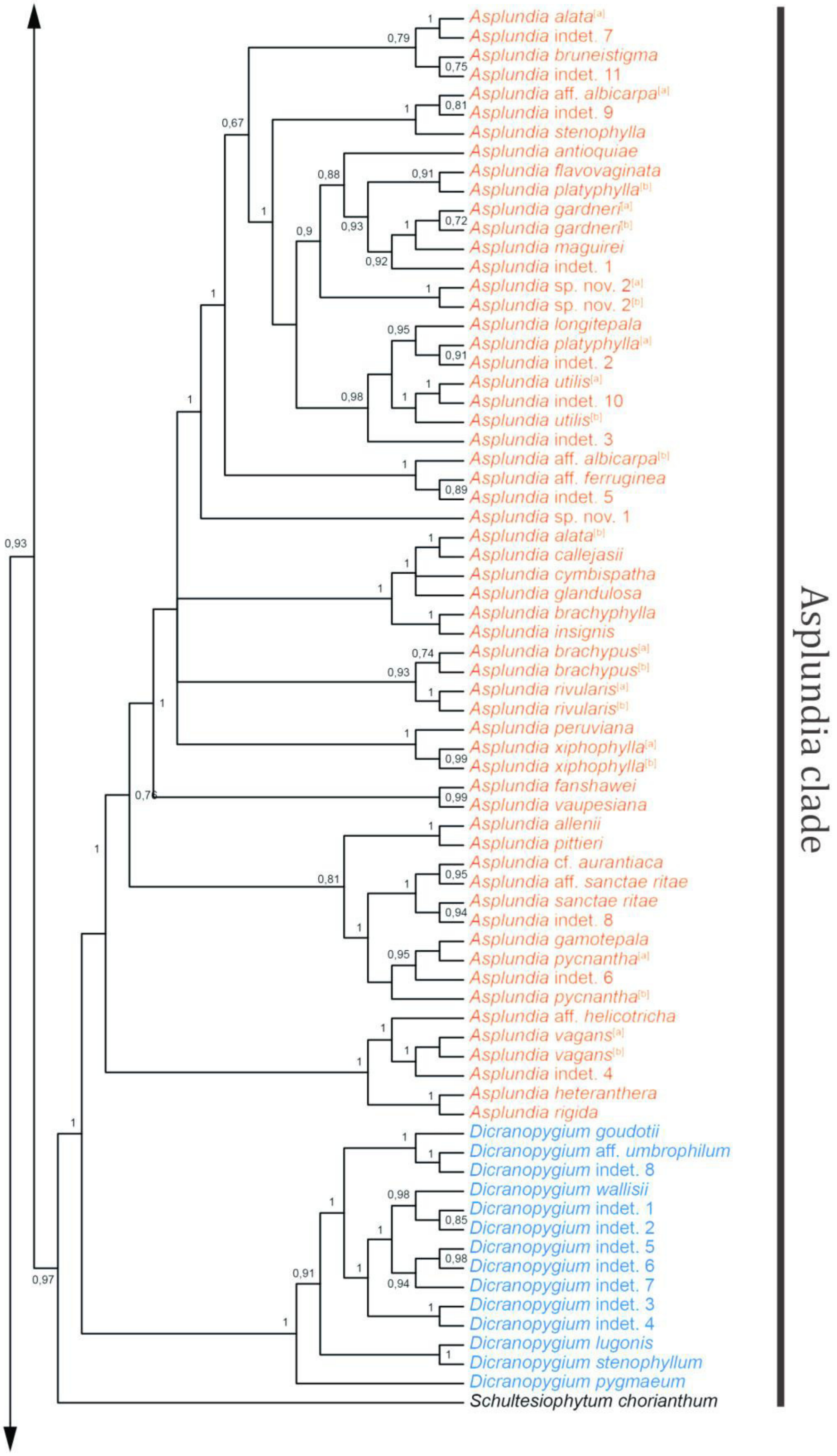
with high support values (BS 100%, PP 1.0). In *Asplundia* subg. *Asplundia* leaves have three main costae (10:2) and the staminate flowers are zygomorphic (21:1), while *Asplundia* subg. *Choanopsis* presents one main costa (10:1) and actinomorphic staminate flowers (21:0), both characters are ambiguous and appear with equivocal optimization.

The second clade in Carludovicoideae, the Evodianthus clade, is supported by the homoplastic character lianas or epiphytes, rarely terrestrial herbs (1: 1 and 2). The monophyletic group *Dianthoveus* + *Evodianthus* (BS 61%, PP 0.98) is recovered as sister to all remaining genera, with moderate support values (BS 52%, PP 0.91), and supported by two non-homoplastic characters within Cyclanthaceae, styloid idioblasts in the mesophyll oriented in several directions (15:1) and psilate pollen exine (30:3), moreover, six homoplastic characters support this group, raphides in the roots (3:2), bracts approximately of the same size (19:2), filament absent (25:1), basal bulb absent (26:0), inapertured pollen (29:2) and free pistillate flowers (34:0). *Dianthoveus* is supported by receptacle with papillae (23:1) and by one more homoplastic character, appendix in the anther connective (28:1). *Evodianthus* may be supported by sterile lobes in the staminate flowers (22:2), a character with equivocal optimization.

The monotypic genus *Thoracocarpus* emerges as sister (BS 72%, PP 0.9) to with the strongly supported Sphaeradenia group. *Thoracocarpus* is supported by bracts that decrease towards the peduncle apex (19:0), unique in Cyclanthaceae. The Sphaeradenia group is composed by *Chorigyne*, *Ludovia*, *Sphaeradenia* and *Stelestylis* (BS 97%, PP 1.0). The clade may be supported by non-homoplastic birefringent cells in the mesophyll (14:1), and two more homoplastic characters; distichous phyllotaxy (5:3) and rigid leaf blades (9:0).

*Ludovia* is recovered as monophyletic and sister to the remaining genera (BS 100%, PP 1.0; BS 97%, PP 1.0, respectively). This genus is supported by absence of leaf blade incision (6:0), unique in Cyclanthaceae, and non-petiolate leaves (8:0), homoplastic in the family. *Sphaeradenia* is monophyletic (BS 93, PP 1.0) and recovered as sister (BS 100%, PP 1.0) to the well-supported clade *Chorigyne* + *Stelestylis* (BS 100%, PP 1.0). This clade is supported by two homoplastic characters, zygomorphic staminate flowers (21:1) and anther with secretion globule (27:1) and by three ambiguously-optimized characters, plants predominantly epiphytical (1:2), petiole transversal section elliptical (13:1) and sub-apical or apical placentation (38:3 and 4). *Sphaeradenia* is supported by one placenta (37:0, homoplastic). The clade


Chorigyne cylindrica
Chorigyne pendula
Stelestylis stylaris
Stelestylis surinamensis
Sphaeradenia acutitepala
Sphaeradenia killipii
Sphaeradenia indet. 3
Sphaeradenia indet. 4
Sphaeradenia crocea
Sphaeradenia indet. 8
Sphaeradenia indet. 1
Sphaeradenia indet. 2
Sphaeradenia aff. buenaventurae
Sphaeradenia indet. 5
Sphaeradenia indet. 6
Sphaeradenia cf. pallida
Sphaeradenia aff. stylosa
Sphaeradenia indet. 7
Sphaeradenia indet.11
Sphaeradenia aff. distans
Sphaeradenia pterostigma
Sphaeradenia indet. 10
Sphaeradenia aff. hamata
Sphaeradenia indet. 9
Sphaeradenia duidae
Sphaeradenia laucheana
Ludovia bierhorstii
Ludovia integrifolia[a]
Ludovia integrifolia[b]
Ludovia lancifolia[a]
Ludovia lancifolia[b]
Ludovia lancifolia[c]
Ludovia lancifolia[d]
Thoracocarpus bissectus[a]
Thoracocarpus bissectus[b]
Thoracocarpus bissectus[c]
Dianthoveus cremnophilus
Evodianthus funifer[a]
Evodianthus funifer[c]
Evodianthus funifer[d]
Evodianthus funifer[b]
Sphaeradenia group
Evodianthus clade
0,9
0,83
0,92
0,91
0,9
0,91
0,98
1



Asplundia alata[a]
Asplundia indet. 7
Asplundia bruneistigma
Asplundia indet. 11
Asplundia aff. albicarpa[a]
Asplundia indet. 9
Asplundia stenophylla
Asplundia antioquiae
Asplundia flavovaginata
Asplundia platyphylla[b]
Asplundia gardneri[a]
Asplundia gardneri[b]
Asplundia maguirei
Asplundia indet. 1
Asplundia sp. nov. 2[a]
Asplundia sp. nov. 2[b]
Asplundia longitepala
Asplundia platyphylla[a]
Asplundia indet. 2
Asplundia utilis[a]
Asplundia indet. 10
Asplundia utilis[b]
Asplundia indet. 3
Asplundia aff. albicarpa[b]
Asplundia aff. ferruginea
Asplundia indet. 5
Asplundia sp. nov. 1
Asplundia alata[b]
Asplundia callejasii
Asplundia cymbispatha
Asplundia glandulosa
Asplundia brachyphylla
Asplundia insignis
Asplundia brachypus[a]
Asplundia brachypus[b]
Asplundia rivularis[a]
Asplundia rivularis[b]
Asplundia peruviana
Asplundia xiphophylla[a]
Asplundia xiphophylla[b]
Asplundia fanshawei
Asplundia vaupesiana
Asplundia allenii
Asplundia pittieri
Asplundia cf. aurantiaca
Asplundia aff. sanctae ritae
Asplundia sanctae ritae
Asplundia indet. 8
Asplundia gamotepala
Asplundia pycnantha[a]
Asplundia indet. 6
Asplundia pycnantha[b]
Asplundia aff. helicotricha
Asplundia vagans[a]
Asplundia vagans[b]
Asplundia indet. 4
Asplundia heteranthera
Asplundia rigida
Dicranopygium goudotii
Dicranopygium aff. umbrophilum
Dicranopygium indet. 8
Dicranopygium wallisii
Dicranopygium indet. 1
Dicranopygium indet. 2
Dicranopygium indet. 5
Dicranopygium indet. 6
Dicranopygium indet. 7
Dicranopygium indet. 3
Dicranopygium indet. 4
Dicranopygium lugonis
Dicranopygium stenophyllum
Dicranopygium pygmaeum
Schultesiophytum chorianthum
Asplundia clade
0,93
0,97

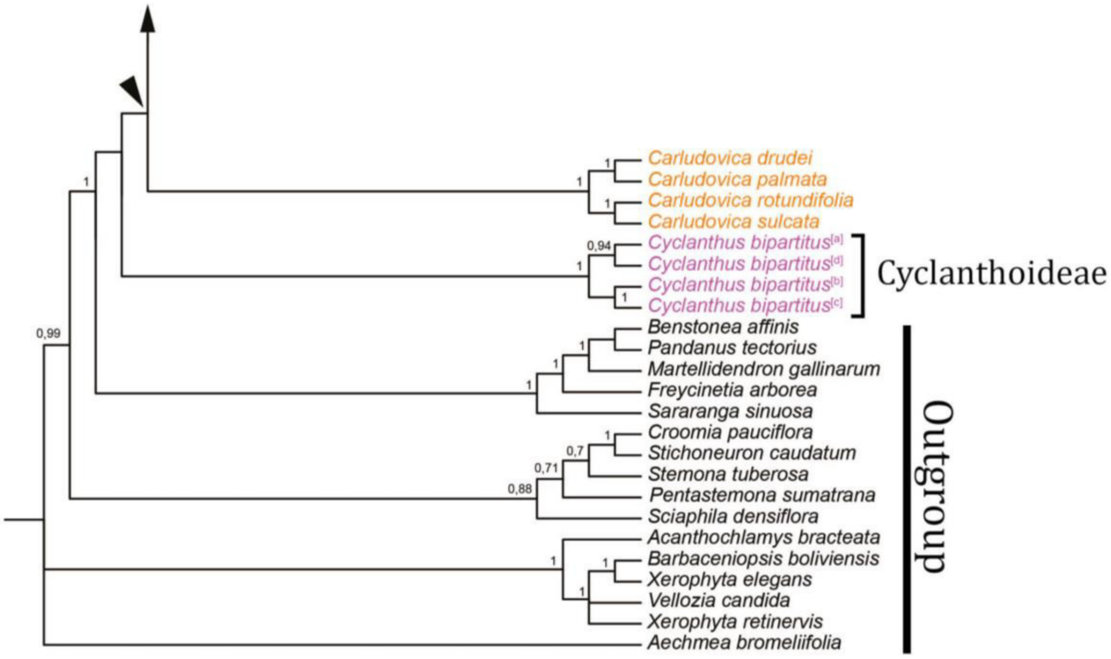


Fig. 6. Bayesian tree based on the total-evidence dataset. Numbers near nodes indicate posterior probabilities.

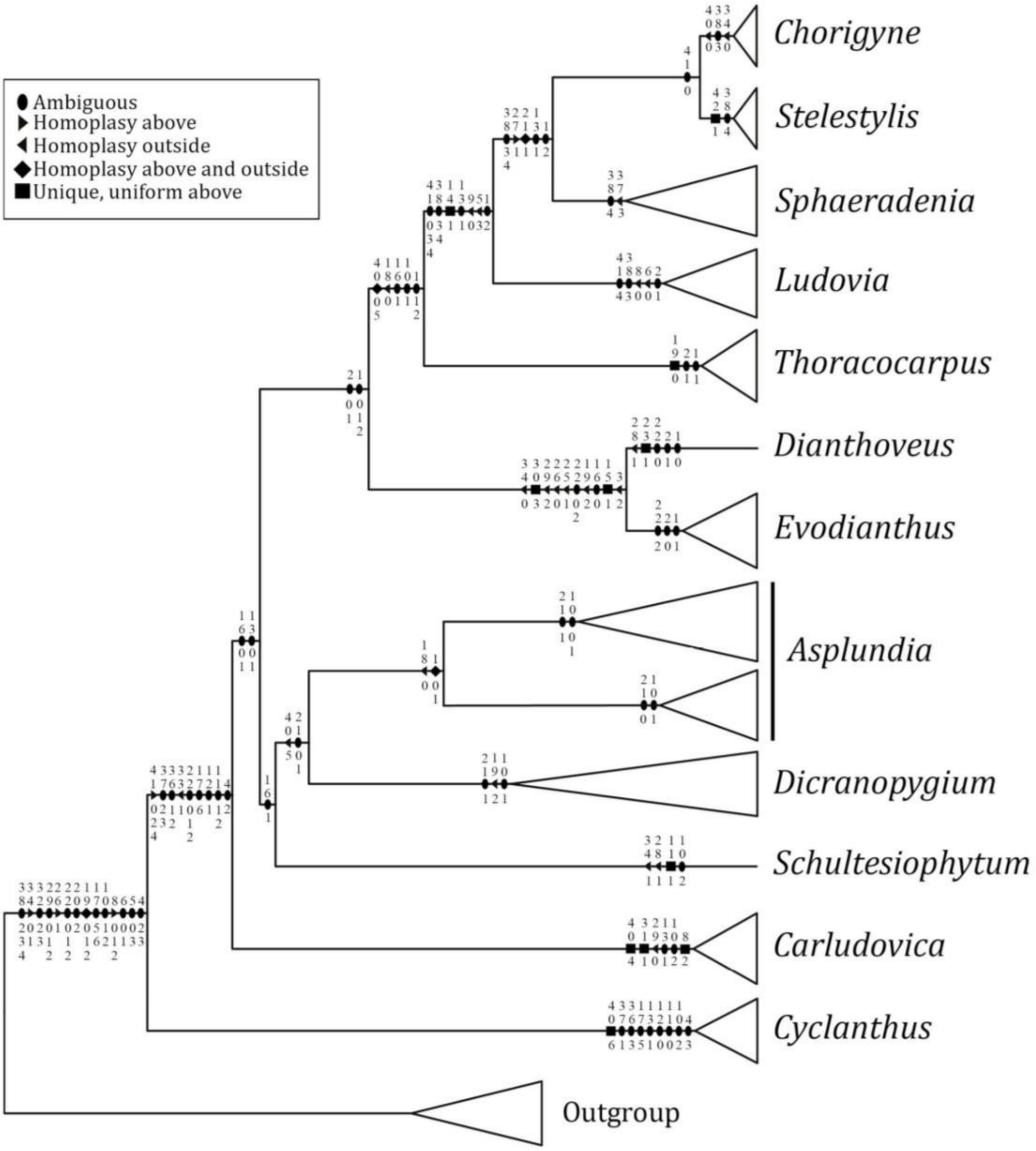


Fig. 7. Strict consensus tree produced from the combined matrix of all data. Character bars are shown in the key. Numbers above of the character bars refer to character numbers, and those at below indicate the character state.

*Chorigyne* + *Stelestylis* is supported by fusiform seeds (41:0). *Stelestylis* (BS 100%, PP 1.0) is supported by presence of caudal appendix in the seed (42:1). *Chorigyne* is supported by the homoplastic characters free pistillate flowers (34:0) and baccate fruit (40:0).

## Discussion

Cyclanthaceae emerges as monophyletic and positioned within Pandanales as sister group to the Paleotropical Pandanaceae in all wide phylogenetic analysis of monocots or related groups (Behnke & al., 2000, 2013; Buerki & al., 2012; Caddick & al., 2002; Chase & al., 2000, 2006; Davis & al., 2004; Gallaher & al., 2014; Graham & al., 2006; Hertweck & al., 2015; Janssen & Bremer, 2004; Lam & al., 2015, 2016; Mello-Silva, 2005; Mello-Silva & al., 2011; Mennes & al., 2013, 2015; Rudall & Bateman, 2006; Salatino & al., 2001; Tang & al., 2017). Our total-evidence analysis corroborates these results, with high support in all analysis (BS 100%, PP = 1.0). The close relation between Cyclanthaceae and Pandanaceae has been noted previously (Harling, 1958; Dahlgren & al., 1985). These families emerge as sister groups in morphological phylogenies, sharing conspicuous bracts, inflorescences in dense spikes and spadix, imperfect and minute flowers, besides the gigantism trend, with the plants being long ramified lianas or large arborescent herbs (Chase & al., 1995; Stevenson & Loconte, 1995; Rudall & Battemann, 2006; Soltis & al., 2017).

As currently circumscribed, Cyclanthaceae is a natural, well-delimited group, supported by petiolate (6:1; shared with Stemonaceae) and bifid leaves (8:1 and 2; except for *Ludovia*), plications along the primary veins (4:2; except for *Cyclanthus*), long filiform staminodes (33:1; except for *Cyclanthus*) and unisexual flowers arranged in alternate whorls or spirally with four staminate flowers surrounding one pistillate flower (17:5 and 6; Harling, 1958).

**Two clades in Cyclanthaceae.** — Our results allow the identification of two subfamilies,Cyclanthoideae and Carludovicoideae, as shown by Harling (1958), and in agreement with several recent authors (Behnke & al., 2000; Behnke & al., 2013; Davis & al., 2004; Chase & al., 2006; Mennes & al., 2013; Mennes & al., 2015; Gallaher & al., 2014; Hertweck & al., 2015; Lam & al., 2016), with high support in the combined molecular (BS 100%, PP 1.0) and total-evidence analyses (BS 100%, PP 1.0). Both are morphologically well-characterized.

*Cyclanthus* (Cyclanthoideae) is supported by plicate prefoliation parallel to the primary veins (4:3), one short main costa (10:1), lateral costae that originate from the apex of the main costa (11:0) and that reach the apex of the leaf segment (12:0), petiole elliptical in transversal section (13:1), pistillate and staminate flowers in alternate whorls (17:4), numerous carpels (36:3) and placentae (37:3), and infructescence where each whorl forms a syncarp of valvar discs (40:6). Besides, the presence of laticifers (Wilder & Harris, 1982), lysigenous aerenchyma (Wilder, 1985b), pollination by Scarabaeideae (Beach, 1982; Moore & Jameson, 2013) and unique floral odor chemical profile (Schultz & al., 1999) would be probable synapomorphies supporting Cyclanthoideae. The partition of the leaf in two segments depends on plant age and environmental conditions. In some individuals, the leaves do not divide, despite the presence of the abscission line between two segments, which are easily detachable (Harling, 1958; Gomes & Mello-Silva, 2006).

Carludovicoideae is supported by plications along the primary veins (4:2; Wilder, 1976), lateral costae that originate from the base of the main costa (11:2), which never reach the leaf segment apex (12:1), pistillate flowers surrounded by groups of four staminate flowers (17:6; Harling, 1958), presence of sterile lobes in staminate flowers (22: 1 and 2), long filiform staminodes (33:1; Harling & al., 1998), four carpels (36:2), one or four placentae (37: 0 and 2).

**Subfamily Cyclanthoideae.** — Schultes (1959) recognized a second species of *Cyclanthus*, ignored by some subsequent authors (Harling, 1973; Eriksson, 1994; Harling & Eriksson, 1998; Harling & al., 1998; Gomes & Mello-Silva, 2006; Leal & Forzza, 2012). Here we acknowledge two species, as well as Hammel (1986, 2003), Hammel & Wilder (1989), D’Arcy, (1987) e Correa & al. (2004), *Cyclanthus bipartitus* Poit. ex A.Rich., polymorphic and distributed from Guatemala to the northern part of South America (Harling, 1958; Harling, 1973; Brako & Zarucchi, 1993; Harling & Eriksson, 1998; Hammel, 2003; Gomes & Mello-Silva, 2006; Eriksson & Harling, 2007; Leal & Forzza, 2012), and *Cyclanthus indivisus* R.E.Schult., restricted to Southeastern Amazon (Schultes, 1959).

**Main lineages in Carludovicoideae.** — Our total-evidence analysis confirms the monophyly of all genera of Carludovicoideae, which is divided in three main lineages: (i) the genus *Carludovica*; (ii) Asplundia clade, with the genera *Asplundia*, *Dicranopygium* and *Schultesiophytum*, and (iii) Evodianthus clade, comprehending *Dianthoveus, Evodianthus* and *Thoracocarpus,* in addition to the genera attributed to Sphaeradenia group, *Chorigyne*, *Ludovia*, *Sphaeradenia*, and *Stelestylis* (Harling, 1958, Hammel & Wilder, 1989; Eriksson, 1994).

***Carludovica.*** — *Carludovica* is sister to the remaining Carludovicoideae (BS 100%; PP = 1.0), agreeing with many authors (Behnke & al., 2000; Behnke & al., 2013; Davis & al., 2004; Chase & al., 2006; Hertweck & al., 2015; Lam & al., 2016). The positioning of *Carludovica* differs from that in Harling (1958), where it emerges as sister to *Asplundia* and *Thoracocarpus*, and in Hammel & Wilder (1989) and Eriksson (1994), where it emerges as sister to *Evodianthus* + *Dianthoveus*. The internal relationships in the clade ((*Carludovica drudei*, *C. palmata*) (*C. rotundifolia*, *C. sulcata*)) differ from that in Franz (2004), which present *C. palmata* as sister to the remaining species of the genus.

*Carludovica* are always acaulescent terrestrial herbs or with very short aerial stems, inhabiting humid forests. The genus is supported by divided flabelliform leaves with three incisions, which gives them the appearance of palm leaves (8:2), three main costae (10:2), petiole elliptical in transversal section (13:1), monoporate pollen (29:0) with the pore in the equatorial surface (31:1) and infructescences that open in irregular layers that roll over along the axis (40:5). Besides that, it has the petiole 3–5 times longer than the leaf blade, a unique character in Cyclanthaceae. Flabelliform leaves are also observed in *Asplundia allenii* Hammel and in other two undescribed species in the genus, however not originating from three, irregularly lobed incisions.

Along with *Chorigyne, Carludovica* is the only Cyclanthaceae genera that are more diverse in Central America than in South America. It is distributed from Mexico to Bolivia (Harling & al., 1998) and its four species inhabit Mesoamerica, with *C. palmata* and *C. drudei* Mast. extending to Southern Panama, being distributed in the Chocó region, in the Andean slope forests and in Southwest Amazon (Hammel, 2003).

**Asplundia clade.** — The Asplundia clade, (*Schultesiophytum*, (*Asplundia*, *Dicranopygium*)), is supported by the lateral inflorescence (16:1), which is a homoplastic character. The clade is highly supported in our BI analysis (BS 50%, PP 0.97), but does not emerge in any of the previous studies (Harling, 1958; Hammel & Wilder, 1989; Eriksson, 1994). It is the more diverse lineage within the family, comprehending around 160 species. *Schultesiophytum* is monotypic and is sampled in molecular studies for the first time. The relationships among the genera in Asplundia clade obtained in our study significantly differ from those proposed by Hammel & Wilder (1989) and Eriksson (1994), which do not include more than two genera in this clade. In Harling (1958), *Schultesiophytum* presents uncertain position. In Hammel & Wilder (1989), it emerges as sister to clade (*Carludovica* (*Dianthoveus*, *Evodianthus*) and in Eriksson (1994), emerges as sister to the remaining genera in Carludovicoideae. Behnke & al. (2000) recovered *Asplundia* as sister to *Dicranopygium*, which is corroborated here. *Schultesiophytum* is supported by presenting three main costae (10:2), lateral costae that originate in the median portion of the main costa, which is an autapomorphy for the genus (11:1), anthers with apical appendix (28:1) and free pistillate flowers (34:0). The sole species, *S. chorianthum* Harling, is a terrestrial herb of up to 3 m tall, distributed from the lowlands in Southwest Amazon to elevations of around 1200 m in the Eastern slopes of the Andes in Colombia, Equator and Peru.

The most internal lineage in Asplundia clade has the two more diverse genera in Cyclanthaceae, *Asplundia* and *Dicranopygium*, with about 100 and 60 species, respectively. This clade is well supported in our total evidence BI analysis (BS 57; PP 1.0) and also in Behnke & al. (2000) and Mennes & al. (2013; 2015), and is supported by zygomorphic staminate flowers (21:1, except in *A.* subg. *Choanopsis*) and by presenting a syncarp that dehisces through an apical hood (40:5; Harling & al., 1998). This clade is not present in the analysis by Hammel & Wilder (1989) and Eriksson (1994).

*Asplundia* is the largest genus in the family, with 106 species (Govaerts & Eriksson, 2018). They are lianas or terrestrial herbs (1: 0 and 1) with spathes dispersed along the peduncle (18:0). It is an important component of Neotropical humid forests from Southern Mexico to the Atlantic Forest in Southern Brazil, including the West Indies (Harling & al., 1998; Acevedo-Rodríguez & Strong, 2012), with higher diversity in Northwest South America and Southern Central America (Harling, 1958).

Harling (1958) divided the genus into two subgenera, *A.* subgen. *Asplundia*, with 73 species and characterized by zygomorphic staminate flowers (21:1) and leaf blades with three main costae (10:2) and *A.* subgen. *Choanopsis* with 32 species and actinomorphic staminate flowers (21:0) and leaf blades with one main costa (10:1). In Eriksson (1994), *A.* subgen. *Choanopsis* emerges as sister to *Thoracocarpus*, however, our results show the two subgenera in *Asplundia* as monophyletic and corroborate that the evolution of the family occurred in two strongly supported main lineages (BS 100%; PP 1.0).

The clade ((*Asplundia*. indet. 8, *A. sanctae-ritae* Galeano & Bernal) (*A.* cf. *aurantiaca* Harling, *A.* aff. *sanctae-ritae*) (*A. pycnantha* Harling, (*Asplundia* indet. 6, (*A. pycnantha* Harling, *A. gamotepala* Harling)) has maximum support in our analyses (BS 100%, PP = 1.0) and is endemic from Chocó and the Western Andean slope. One group of species that are predominantly terrestrial herbs (1:0) with large leaves with broad segments, a character not included in the analysis, forms a cohesive clade within *Asplundia* ((*A. insignis* (Duchass. ex Griseb.) Harling, *A. brachyphylla* Harling) ((*A. alata* Harling, *A. callejasii* Tuberq. & E.S.Leal), *A. cymbispatha* Harling, *A. glandulosa* Harling)). *Asplundia brachypus* (Drude) Harling and *A. rivularis* (Lindm.) Harling, endemic to the Atlantic Forest, form a clade (BS 46%, PP = 0.93). Other clades within the subgenus emerge with low support or with few species.

*Dicranopygium* also emerges as monophyletic, supported by leaf blades with one main costa (10:1), bracts with the same size (19:2) and asymmetrical staminate flowers (21:1). The bracts are always spathes grouped right below the spadix. A possible synapomorphy is the amiliferous endosperm (Eriksson, 1994).

*Dicranopygium* is distributed from Southern Mexico to Peru and the Guiana Shield, being little diverse in the Amazon lowlands. This genus has the most complex formal subdivision within the family. The ca. 55 species are distributed in four subgenera, differentiated by the staminate flower structure. *Dicranopygium* subgen. *Dicranopygium* Harling, with about 49 species, has perianth with glandular lobes and stamens with parallel techae. *Dicranopygium* subgen. *Uribanthus* Harling (1 sp.) has funnelform receptacle, introse anthers and divergent thecae. *Dicranopygium* subgen. *Gleasonianthus* Harling (4 spp.) presents staminate flowers without perianth, flatterned receptacle and sterile lobes of the staminate flowers without glands, and *Dicranopygium* subgen. *Tomlisonianthus* G.J.Wilder (1 sp.) has a combination of characteristics from the other three subgenera (Wilder, 1978).

The subgenus *Dicranopygium* is divided in six sections, *Dicranopygium* sect. *Dicranopygium* Harling (ca. 34 spp.), *Dicranopygium* sect. *Macrostemon* Harling (6 spp.), *Dicranopygium* sect. *Adenotepalum* Harling (1 sp.), *Dicranopygium* sect. *Pterygostigma* Harling (3 spp.), *Dicranopygium* sect. *Allardia* Harling (3 spp.) and *Dicranopygium* sect. *Steyermarkiella* Harling (2 spp.).

Our sampling of 30% of the species did not allow us test the monophyly of the groups above. From the sixteen species analyzed, one belongs to *Dicranopygium* subgen. *Gleasonianthus*, seven to *Dicranopygium* subgen. *Dicranopgygium*, distributed in three sections, five species in *Dicranopygium* sect. *Dicranopygium* and one each in *Dicranopygium* sect. *Macrostemon* and *Dicranopygium* sect. *Adenotepalum.* The other eight species were not identified at specific level, evidencing the need for more collections for future taxonomic and systematic studies for *Dicranopygium*.

**Evodianthus clade.** — The Evodianthus clade is formed by the sister genera *Dianthoveus* and *Evodianthus* (BS 61%, PP 0.98), *Thoracocarpus* and the genera that compose Sphaeradenia group (Harling, 1958; Eriksson, 1994). The absence of lateral costae may be a probable synapomorphy, although this character is also observed in some representatives outside this clade. The clade (*Dianthoveus*, *Evodianthus*) is supported by the styloid sacs in the roots (3:2; Wilder, 1986a, 1989), styloid idioblasts oriented in all directions in the mesophyll (15:1; Wilder, 1985d, 1989b), terminal inflorescence (16:0), bracts approximately the same size (19:2), sterile lobes in the staminate flower absent or in two whorls (22:0 and 2), filament inconspicuous or absent (25:1), absence of basal bulb (26:0), inapertured (29:2; Furness & Rudall, 2006) and psilate pollen (30:3; Furness & Rudall, 2006) and free pistillate flowers (34:0). These morphological characteristics, allied to the results of our molecular study, allow the merging of these two genera.

*Dianthoveus*, never before sampled in molecular studies, is characterized by its terrestrial habit (1:0), phloem sieve elements in fascicles (2:1), absence of sterile lobes in the staminate flowers (22:0), papillate receptacle (23:1) and presence of appendix in the anther connective (28:1). The only species, *D. cremnophilus* Hammel & G.J.Wilder, is a robust terrestrial herb with a short stem, which grows in rocks along water bodies, being restricted to the Chocó and lowlands and slopes of the Andes in Northern Ecuador and Southern Colombia (Hammel & Wilder, 1989; Harling & al., 1998).

*Evodianthus* is supported by its lianescent habit (1:1), phloem sieve tube elements dispersed among fibers (2:0) and two imbricate whorls of sterile lobes in the pistillate flower (22:2), an autapomorphy for the genus. Behnke & al. (2000) obtained the relationship (*Evodianthus* (*Asplundia*, *Dicranopygium*) and Behnke & al. (2013) showed *Evodianthus* as sister to *Dicranopygium*, however, in none of these studies other genera from the Evodianthus clade were sampled, as the focus were the phylogenetic relationships in Velloziaceae. The sole species, the hemiepiphyte *Evodianthus funifer* (Poit.) Lindm., is distributed from Nicaragua and Trinidad e Tobago (Harling, 1958; Harling & al., 1998) to South America, in Ecuador (Harling, 1973), Peru (Brako & Zarucchi, 1993), Guiana, French Guiana and Suriname (Eriksson & Harling, 2007), Venezuela (Harling & Eriksson, 1998; Eriksson & Harling, 2007) and Brazilian Amazon (Gomes & Mello-Silva, 2006; Leal & Forzza, 2012). It also occurs in the Atlantic Forest between Southern Bahia and Northern Espírito Santo (Freitas & al., 2012).

*Thoracocarpus* emerges as sister to Sphaeradenia group (BS 72%, PP 0.9), with this clade being supported by lianescent or epiphytic plants (1:1 and 2), leaf blade with only one main costa (10:1), lateral inflorescence (16: 1), bracts distributed along the peduncle (18:0) and syncarps dehiscent due to apical hood (40:5). The genus is supported by the lianescent habit (1:2), phloem sieve tube elements in fascicles (2:1) and bracts that increase in size towards the peduncle apex (19:1).

In Hammel & Wilder (1989) and Eriksson (1994), the genus emerges as sister to *Asplundia*. In fact, *Thoracocarpus* is morphologically similar to *Asplundia* subgen. *Choanopsis*. Both have symmetrical staminate flowers (21:0), with excavate receptacle, perianth lobes distributed around the whole receptacle and unicostate leaves (Harling, 1958). However, they differ in number and size of bracts and seed testa (Harling & al., 1998). Bracts in *Thoracocarpus* are unique in Cyclanthaceae, decreasing in size towards the peduncle apex (19:0), an autapomorphy of the genus. The only species, *T. bissectus* (Vell.) Harling has wide distribution, from Costa Rica to Ecuador (Harling, 1973), Guiana, French Guiana and Suriname (Eriksson & Harling, 2007), Venezuela (Harling &

Eriksson 1998; Eriksson & Harling, 2007) and in Brazil with a distinct distribution (Gomes & Mello-Silva, 2006; Leal & Forzza, 2012; Freitas & al., 2012), occurring from the whole Amazon basin, extending to Maranhão and in the Atlantic Forest from Rio Grande do Norte to São Paulo (Gomes & Giulietti, 2003; Freitas & al., 2012).

The Sphaeradenia group. — Sphaeradenia group was proposed by Harling (1958) without formal status. The group emerges as a clade in morphological phylogenies (Hammel & Wilder, 1989; Eriksson, 1994). Sphaeradenia group is here recovered as monophyletic, having high support value (BS 97%, PP = 1.0) and being composed by four genera sister to *Thoracocarpus*, within Evodianthus clade. The relationship (*Ludovia* (*Sphaeradenia* (*Chorigyne*, *Stelestylis*))) already appears in Eriksson (1994). This relationship, without *Chorigyne*, which was not described at the time, was also obtained by Hammel & Eriksson (1989). The group is characterized by being predominantly ephiphytical plants (1:2), distichous phyllotaxy (5:3), rigid and crass leaf blades (9:0), petiole elliptic in transversal section (13:1), strongly birefringent dead cells in the parenchyma (14:1), apical or subapical placentation (38: 3 and 4) and fusiform seeds, never flattened (41:0 and 4; Harling, 1958; Eriksson, 1994). Sphaeradenia group is the better studied in Cyclanthaceae, with *Sphaeradenia* being revised by Eriksson (1995) and *Ludovia* and *Stelestylis*, with revisions being prepared (R. Eriksson, pers. commun.).

*Ludovia* is sister to the remaining lineages in Sphaeradenia group (BS 100%, PP 1.0), as shown in Hammel & Wilder (1989) and Eriksson (1994), and is supported by phloem sieve tube elements arranged in fascicles (2:1), leaf without a true petiole (6:0; homoplastic), undivided leaves (8:0; unique in Cyclanthaceae), sub-apical placentation (38:3) and spherical seeds (41:4). Few molecular studies have included *Ludovia*, all focused in other taxonomic groups and with few Cyclanthaceae representatives (Mennes & al., 2013; Mennes & al., 2015; Gallaher, 2014).

*Ludovia* has three species easily distinguishable from other Cyclanthaceae, due to the undivided leaves. They are mainly restricted to the lowlands on Northern South America, rarely occurring in elevations of up to 1000 m in the Andean slopes (Harling, 1958). The sister species (BS 92%, PP 0.91) *Ludovia bierhorstii* G.J.Wilder, which occurs from Colombia to Northern Ecuador, and *L. integrifolia* (Woodson) Harling, which occurs from Ecuador to Nicaragua, have an overlapping delimitation (Wilder, 1978), showing greatly variable leaves (Wilder, 1981c), structured in a clade without internal morphological support. *Ludovia lancifolia* Brongn., the third species in the genus, is distributed from the whole Amazon basin to the Andes and Guiana Shield (Mori, 1997; Harling & Eriksson 1998; Eriksson & Harling 2007; Leal & Forzza, 2012).

The clade (*Sphaeradenia* (*Chorigyne*, *Stelestylis*)) is well corroborated (BS 100, PP 1.0) and supported by the mainly epiphytic habit (1:2), elliptic petiole (13:1), zygomorphic staminate flowers (21:1), presence of secretion globes in the anther apex (27:1, homoplastic) and apical or sub-apical placentation (38: 3 and 4). *Sphaeradenia* (BS 93%, PP 1.0) is supported by the apical placenta (37:0; 38:4), unique in Cyclanthaceae (Eriksson, 1995). In previous molecular studies that did not sample *Stelestylis*, *Sphaeradenia* emerges as sister to *Chorigyne* (Davis & al., 2004; Chase & al., 2006; Hertwerck & al., 2014).

*Sphaeradenia* is the best studied genus among the large genus in Cyclanthaceae. It was revised by Eriksson (1995), who recognized fifty species, discussed internal relationships and created six informal morphological groups. Later, he described two additional species (Eriksson, 2007). Our sampling of 42% of the species does not include all morphological groups and does not allow their analysis.

Most of the *Sphaeradenia* are epiphytic (41 species) (Eriksson, 1995), rarely they are terrestrial or lianas, but many of these epiphytes have affinities with the terrestrial habit. They are distributed from Southern Nicaragua to Western Bolivia (Harling & al., 1998), with the main diversity center being the Western slope of the Cordillera Occidental in the Andes and in the Pacific lowlands in Colombia and Ecuador, being poorly represented in the Guiana Shield and Amazon (Eriksson, 1995).

The clade *Chorigyne*-*Stelestylis* is strongly supported (BS 100%, PP 1.0) and is also present in Eriksson (1994), being supported by its fusiform seeds (41:0). *Chorigyne* is the most recently described genus in Cyclanthaceae, comprehending seven species, two of these being segregated from *Sphaeradenia*, and five undescribed at the time (Eriksson, 1989). It is supported by the free pistillate flowers (34:0), sub-apical placentation (38:3) and baccate fruits (40:0). According to Eriksson (1994), the seed testa with several cell layers is also a synapomorphy of the genus. They are epiphytic, rarely terrestrial, restricted to Mesoamerica, in Nicaragua, Costa Rica and Panama (Eriksson, 1989; Harling & al., 1998).

*Stelestylis* is supported by the apical placentation (38:4) and long filiform appendices in the seed extremities (42:1; Drude, 1881; Eriksson, 1994). It was described by Drude (1881) with a single species, posteriorly grouped with three more (Harling, 1958). *Stelestylis anomala* Harling is restricted to Venezuela (Harling, 1958). *Stelestylis stylaris* (Gleason) Harling is found in the tepuis in Venezuela, Guiana and was recently found in Brazil (Barbosa-Silva & al., 2016). *Stelestylis surinamensis* Harling occurs in Suriname, French Guiana and probably in Brazil (Eriksson & Harling, 2007). The type species, *Stelestylis coriacea* Drude, is supposedly from the Atlantic Forest in Brazil, probably in Bahia. The holotype deposited in the Wien herbarium (W), was destroyed during World War II and its illustration was designated as type material (Harling, 1958: 393). *Stelestylis coriacea* was never recollected, neither in Bahia nor in Northern South America and its true identity remains unknown.

## Conclusions

Our broad sampling of the Cyclanthaceae allows us to elucidate phylogenetic relationships among its major lineages and compare the results obtained with generic-level morphological phylogenies (Hammel & Wilder, 1989; Eriksson, 1994). The two monotypic genera *Dianthoveus* and *Evodianthus* are well supported as sister groups in all analysis and also emerge in previous studies (Hammel & Wilder, 1989; Eriksson, 1994). To maximize phylogenetic information and to facilitate identification (Backlund & Bremer, 1998), *Dianthoveus* should be transferred to *Evodianthus*, as both can be identified by the raphides present in the root (3:1), styloid idioblasts in the mesophyll oriented in all directions (15:1), terminal inflorescence (16:0), bracts with the same size (19:2), filament inconspicuous or absent (25:1), basal bulb absent (26:0), inapertured (29:2) and psilate pollen (30:1), and free pistillate flowers (34:0). *Chorigyne*, *Ludovia*, *Sphaeradenia* and *Stelestylis* are closely related, forming the monophyletic Sphaeradenia group, which also appears in previous works (Hammel & Wilder, 1989; Eriksson, 1994). The clade (*Sphaeradenia* (*Chorigyne*, *Stelestylis*) is supported by the predominantly epiphytic habit (1:2), petiole elliptic in transversal section (13:1), zygomorphic staminate flowers (21:1), presence of secretion globule in the anther (27:1; homoplastic) and apical or sub-apical placentation (38:3 and 4). These genera present morphological characters that evolved in parallel or independently

(Eriksson, 1995) and that sometimes overlap, causing difficulty to separate them. They would be better delimited as a single entity than separately. However, as the type species of these genera were not sampled in this study, we decided not to present synonyms and new combinations in this study. Reconstruction of morphological character evolution confirms high levels of homoplasy in many of the characters that have been used in generic delimitation, explaining why it has been such a difficult task prior to the application of molecular phylogenetic analysis. Nevertheless, most genera are still readily diagnosable by combinations of these characters.

### Nomenclatural consequence

***Evodianthus cremnophilus*** (Hammel & G.J.Wilder) E.S.Leal, **comb. nov.** ≡ *Dianthoveus cremnophilus* Hammel & G.J.Wilder, Ann. Missouri Bot. Gard. 76: 113. 1989 – Holotype: Ecuador. Pichincha, río Pilatón valley, Quito to Santo Domingo de los Colorados, on steep slopes along highway, 44 km E of Santo Domingo, 1200 m, 0°23'S, 78°50'W, 18 Jun 1987, *Hammel & Wilder 16058* (MO, 2 sheets, barcodes MO-288182! & MO-288183!; isotypes: COL barcode COL000006769!, DUKE not seen, F not seen, GB barcode GB-004 7565 [digital image!], NY barcode 00039629!, QCA barcode 36034 [digital image!], US, 2 sheets, barcodes 00409685! & 00409686!).

*Distribution.* – Colombia and Ecuador.

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# Chapter 2

# Revisiting the Atlantic Forest cyclanths with a key for the species and a revision of the endemic clade of *Asplundia*

***Abstract***—A taxonomic revision of the Atlantic-endemic clade of *Asplundia* and a key for the seven species of Cyclanthaceae from the Atlantic Forest are presented. They are *Asplundia gardneri*, *Asplundia tetragonopus*, *Evodianthus funifer*, *Thoracocarpus bissectus* and a monophyletic lineage within *Asplundia*, *A. rivularis*, *A. orthostigma* sp. nov., and *A. brachypus*, including *A. glaucophylla*, *A. polymera*, and *A. polymera* subsp. *reitzii*. An overview of the morphological variation of the species of the Atlantic-endemic clade of *Asplundia*, as well as for the other species of cyclanths from Atlantic Forest. Full descriptions with comments on their taxonomy, geographical distribution, habitat, and notes on their ecology and conservation are presented.

***Keywords***—Brazil, Cyclanthaceae, endemic flora, monocots,

Cyclanthaceae include 11 genera and about 225 species (Leal, chapter 1 and 3), distributed from southern Mexico to the Atlantic Forest in southern Brazil (Harling et al. 1998, Beck 2004). The vast maiority of the species occurs in Tropical Andes and Chocó biogeographic in northwestern South America and southern Central America (Harling et al. 1998). Harling (1958) considered ten cyclanths species occurring in the Atlantic Forest, seven of which belonging to *Asplundia*. Since then, the advance on Cyclanthaceae's knownledge in the Atlantic Forest has evolved slowly, mostly in floristic treatments and checklists (Reitz 1967, Gomes & Giulietti 2003, Leitman & Leal 2009, Freitas et al. 2012), but recent phylogenetics studies (Leal, Chapter 1) provided a framework from which the taxonomy of the group could be reviewed. Therefore, we present a review of the Atlantic Forest cyclanths, which encompass seven species, five of them belonging to *Asplundia*, including its Atlantic-endemic clade, one to *Evodianthus*, and one to

*Thoracocarpus*. This update provides valuable information for systematists, evolutionary biologists, and conservationists interested in understanding the diversity of this lineage. The present study includes a better understanding of the intraspecific morphological variation the species based on more than twice the number of specimens analyzed so far, and study of populations in the field. It presents also taxonomic novelties, more precise morphological data, and a more detailed overview on the geographic distribution and habitat of the species. Additionally, an identification key for the species of Cyclanthaceae from the Atlantic Forest is provided.

## MATERIALS AND METHODS

This revision is based on study of the 120 herbarium specimens or images from the herbaria BHCB, CEN, CESJ, CRI, ESA, EFC, FLOR, FURB, HBR, HCF, HRCB, HUCP, HUFSJ, HUSC, ICN, K, LUSC, MBM, MBML, NY, PMSP, R, RB, RFA, RFFP, SAMES, SP, SPF, SPSF, U, UEC, UPCB, UPS, US and VIES. Images of types housed in LE and S herbaria were consulted at http://plants.jstor.org and WU herbarium at http://herbarium.univie.ac.at/database/search.php (Acronyms according to Thiers, 2018). An index of all specimens analized is provided in Appendix 1. The measurement of structures were performed according Eriksson (1989: Fig. 1). The description of the leaf segments refer only to the free parts. The division of the leaf blades, expressed as a percentage, was calculated by dividing the depth of the blade partition by the size of the leaf segment. In many cases, the number of spathes in the inflorescence is given as a result of the number of scars on the peduncle after their fall. The flowers usually have difference in size and shape at the apex and base of the inflorescence. Thus, for the description of these, only flowers of the middle region of the spadix were used. The inflorescences and infructescences had their width measurements made in the middle of the structure, usually the region with the greatest extension. Colors in general are described from living material or from herbarium label data.

We constructed data sets with geographical information of the municipalities when the geographic coordinates were not available on the collections examined. Extent of Occurrence (EOO) and Area of Occupancy (AOO) were calculated using GeoCat (www.geocat.kew.org) with a 2 km$^2$ cell sizer for AOO calculation. Common names and phenological information were taken from exsiccatae labels and literature. Conservation status of each species was assessed using the criteira of the IUCN (2014) based on the GeoCat analyses (Bachman et al. 2011) combined with field knowledge. We adopted here the genotypic cluster definiton of species (Mallet, 1995), in which groups of individuals with shared features are separable from others clusters by morphological discontinuities or few intermediates when in contact. We have not recognized varieties, but have rather described the variation where present.

## RESULTS

***Morphology***—HABIT—The species of Atlantic-endemic clade of *Asplundia* are perennial terrestrial herbs, rheophytics, root-climbing lianas, with short or creeping rhizome. Sometimes are epiphytes growing on the basal branches of robust trees. The species range from 0.5 to 3.0 m tall. They are commonly found in the understory, waterfall rocks or margin of streams, in well-preserved forests or relicts of riparian vegetation.

LEAVES—The leaves in the species of Atlantic-endemic clade of *Asplundia* are clearly differentiated in sheat, petiole and blade. The sheats are broad and course, its epidermis consistence and color are variable, sometimes in the same plant. The epidermis of the petiole sheats is hard, lustrous, glossy, crumbly and showing flaws. Its color can be olive-green, pale brown, yellowish or orange. The variation of the shape and color of the epidermis sheats depends on enviromental conditions, leaf length and age of the plant. The petiole is canaliculate on its upper side and range from 20 to 90 cm length. Petioles and blades are very often of about the same length or petioles are slightly smaller. The adult leaf-blades of  are always bifid. Sometimes, the segments are frayed and secondarily splited into varying number of irregular lobes. The leaves are bifids to 50% their length or less, rarely 75% or more em *A. brachypus*, while in the other species they are 75% divided or even almost the base. Each segment range from 30 to 100 cm long and from 3 to 15 cm large, and can be broadly lanceolate, linear-lanceolate, oblonglanceolate, oblongovate or ovate, with acute, acuminate or cuspidate apex. The leaves have one (unicostate) or three (tricostate) mains ribs. The central costa appears as a continuation of the petiole, ending in the basal end of the median sinus. The lateral costae are considerably thinner than the central one. In *A. brachypus* lateral costae are absent or rather short indistinctly developed, conspicuos lateral costae being rarely present. Distinct tricostate leaves are observed in *A. rivularis* e *A. orthostigma* with the lateral costae to the largest part of their length running in the leaf margin or close to it.

INFLORESCENCE STRUCTURE—All Cyclanthaceae are monoecious, with staminate and pistillate flowers developed in one and the same inflorescence. The inflorescences are spadiciforms compound by unbrached peduncle, spathes and spadix. The peduncle arise from the leaf axils, ranging from 3 cm in flowering stage (*A. brachypus*) to 18 cm in fruiting stage (*A. rivularis*), these gradually becoming strongly lignified during infructescence development, sometimes bend, making the ripe infructescence pendulous. The peduncle is pale green or cream. Peduncle sheats are often about as long as the peduncle and may entirely cover it. In the Atlantic-clade of *Asplundia* four lanceolate, acute to acuminate cymbiforms spathes, are distributed along peduncle. The lowermost spathe is bigger, placed in about the middle of the peduncle. The others concentrated on the upper half of the peduncle or rather near the spadix. The spathes are ephemeral and fall soon after the anthesis. Rarely persistent spathes are observed in fruiting spadix. The spadices are cylindrical or ellipsoid, varying between 1.0—6.0 cm long, 0.5—2 cm width, and 5.0—12.0 cm long, 1.5—4.0 cm width, during anthesis and fruiting stage, respectly. As in all Carludovicoideae, the staminate and pistillate flowers are disposed like a chessboard mosaic. The pistillate flowers run in a flat spiral around the spadix from the basis to the apex. Each pistillate flower is surrounded by groups of four densely disposed, regularly arranged staminate flowers.

STAMINATE FLOWERS—All species of Atlantic-endemic clade of *Asplundia* have assymmetrical staminate flowers. These staminate flowers reach a maximum of 4 mm long. It consists of eccentrically attached pedicel, flat receptacle with unilaterally disposed perianth, and a varying number of stamens. The external side of each perianth lobe is provided with a glandule. The number of stamens varies from 20 to 60, densely disposed on the receptacle. The stamen is composed of a basally bulbous structure, filaments, rather thin connective and anthers. The basal bulbs in one and same receptacle are well separated from each other and the filaments are inconspicuous, of about 0.2 mm long. The anthers are elongated, rarely spherical, bithecae, of about the same length in each flower.

PISTILLATE FLOWERS—The pistillate flowers are very constant in Carludovicoideae. They are tryciclic and normally tetramerous, rarely 5-8-merous, with one perianth whorl, one whorl of staminodes and one of carpels. The staminodes are opposed to the tepals, whereas the carpels alternate with the two outer whorls. In *A. brachypus* the tepals are reduced to truncate and fleshy walls, while in *A. orthostigma* are well developed and broad.

INFRUCTESCENCE STRUCTURE—The fruits are baccate and fused to one single syncarpium, which constitute the infructescence. The uppermost parts of the berries are formed by the increase change in size and appearence of the tepals, styles and stigmas of the pistillate flowers, during fruit development. The pericarp is usually soft and the seeds are embedded in it. The infructescences are cylindrical to subcylindrical or oblong, dull brownish green, vivid green or purplish. Staminate flowers may still persist in a dried condition on the infructescence. The ripe infructescences reaching up to 12 cm long (*A. rivularis*).

SEEDS—The seeds are ellipsoid, sometimes suboblongoid, yellowish to orange. They vary from 0.7 to 2.0 mm long and from 0.3 to 0.7 mm wide.

KEY TO THE SPECIES OF CYCLANTHACEAE FROM THE ATLANTIC FOREST

1. Staminate flowers with perianth lobes in 2 whorls; spathes clustered just below spadix ........................................................................................ *Evodianthus funifer*

1. Staminate flower with perianth lobes in 1 whorl; spathes dispersed along peduncle ………………………………………………………………………………... 2

    2. Spathes 8–11, diminishing in size downwards along peduncle ...........................……………………..……………... *Thoracocarpus bissectus*

    2. Spathes 4–5, diminishing in size upwards along peduncle .................. *Asplundia*

        3. Staminate flowers symmetrical, funnel-shaped, perianth-lobes distributed all around receptacle; leaf blades always unicostate ........................................................... *A.* subg. *Choanopsis*, *A. tetragonopus*

        3. Staminate flowers asymmetrical, receptacle flat, perianth-lobes developed on one side only; leaf blades weakly or distinctly tricostate ........................................................................................ *A.* subg. *Asplundia*

            4. Leaf blades distinctly tricostate, the lateral costae entirely running far inside in the leaf margin; not endemic to the Atlantic Forest ........................................................................................ *A. gardneri*

            4. Leaf blades weakly tricostate (sometimes appears unicostate) or distinctly tricostate, the lateral costae entirely running in the leaf margin; endemic to the Atlantic Forest. ........... Atlantic-endemic clade

                5. Leaf blades bifids to 50% their lenght, rarely more, broadly

lanceolate to oblongovate, weakly tricostate or lateral costae inconspicous, when present running in the inside in the leaf margin; tepals of the pistillate flowers reduced ............................................................................ 1. *A. brachypus*

5. Leaf blades bifids to 75% their lenght or almost to the base, linear-lanceolate to lanceolate, tricostate, lateral costae conspicous, running in the leaf margin; tepals of the pistillate flowers well developed.

6. Rheophytic; epidermis of petiole sheats and peduncles bases dull, in color and consistence not diferring from epidermis in others parts of petioles and peduncles ....................................................................... 2. *A. rivularis*

6. Root-climbing lianas or terrestrial with short or creeping stems; epidermis of petiole sheats and peduncles bases hard, glossy, orange or yellowish, brittle ................................................................ 3. *A. orthostigma*

## TAXONOMIC TREATMENT FOR ATLANTIC-ENDEMIC CLADE OF ASPLUNDIA

*Asplundia* is the most diverse genus within Cyclanthaceae, with more than 97 species (Leal, unpubl. data, chapter 3), forming a monophyletic assemblage (Leal, Chapter 1). *Asplundia* are root-climbing lianas or terrestrial herbs characterized by spiral phyllotaxis, four parietal placentae, and successively smaller spathes along the peduncle (Harling 1958). Harling (1954) described it to accommodate 28 species segregated from the, at that time, highly unnatural *Carludovica* Ruiz & Pav. Four years later, Harling (1958) subdivided *Asplundia* in two subgenera and increased the number of species to 82. Since then, 22 species of *Asplundia* have been described (Harling, 1963, 1972, 1973; Grayum & Hammel, 1982; Galeano-Garcés & Bernal-González, 1984; Tuberquia, 1997; Hammel, 2003; Leal, 2011; Leal & Tuberquia 2018). Five species of *Asplundia* occur in the Mata Atlantica domain, three of them belonging to a well-supported monophyletic lineage restricted to the Atlantic Forest, nested within *Asplundia* subg. *Asplundia* (Leal, Chapter 1).

1. ASPLUNDIA BRACHYPUS (Drude) Harling, Acta Horti Berg. 17: 41. 1954. *Carludovica brachypus* Drude in Martius, Fl. bras. 3(2): 237. 1881.—TYPE: BRAZIL. Rio de Janeiro, Rio de Janeiro, Corcovado, Apr 1832, *B. Luschnath s.n.* (lectotype, designated by Harling (1958: 235), LE-00000961 (image!)).

*Carludovica schizophylla* Drude in Martius, Fl. bras. 3(2): 235. 1881.—TYPE: BRAZIL. Rio de Janeiro, Petrópolis, Serra da Estrela [Serra de Estrella], Rio de Janeiro, Corcovado, Mar 1832, *B. Luschnath s.n.* (holotype: LE-00000962 (image!)).

*Asplundia polymera* (Hand.-Mazz) Harling, Acta Horti Berg. 17: 42. 1954. *Carludovica polymera* Hand.-Mazz. in Wettstein & Schiffner, Denkschr. Kaiserl. Akad. Wiss., Wien. Math.-Naturwiss. Kl. 79: 207. 1908.—TYPE: BRAZIL. São Paulo, Rio Grande da Serra, prope rio Grande ad São Paulo Railway, 800 m, Jun 1901, *R. Wettstein & V.F. Schiffner s.n.* (holotype: WU-0038059 (image!)). Syn. nov.

*Asplundia polymera* subsp. *reitzii* Harling, Acta Horti Berg. 18: 239.—TYPE: BRAZIL: Santa Catarina, Itajaí, Luis Alves, rio Canoas, 50 m, 18 Jan 1953, *R. Reitz 5155* (holotype: HBR-0016328 (image!), isotypes: S-06-4533 (image!), US-00027157!). Syn. nov.

*Asplundia glaucophylla* Harling, Acta Horti Berg. 18: 237. 1958.—TYPE: BRAZIL: Paraná, Volta Grande, 21 Jul 1911, *P.K.H. Dusén 11968* (holotype: S, *2 sheets,* S-05-5583 (image!), S-R-514 (image!), isotypes: NY-00413610!, S-06-4529 (image!), US-00027139!). Syn. nov.

Terrestrial herb with creeping or short aerial stem or seldom root-climbing liana. Leaf blade unicostate, or indistinctly tricostate, rarely tricostate, 30–75(–90) cm long, bifid 45–50% of its length, rarely 75% or more, segments 5–20 cm broad, broadly lanceolate to oblongovate, acuminate to cuspidate, in older leaves often secondarily cleft into irregular lobes, ridge distance 10–16 mm, midrib 5–45 cm long; petiole + sheat 20–65 cm long, epidermis of sheats and peduncles bases hard, yellowish brown to olive-green, sometimes brittle cracking when dry. Peduncle 3–6 cm long during anthesis, 5–18 cm long in fruiting stage; spathes 4, ± coarse, cymbiform to ovate, acute, the lowermost one placed at about the middle of the peduncle, 7–10 x 1.5–2.0 cm, the other spathes concentrated rather near the spadix, 4–7 x 1.5–2.5 cm. Spadix ellipsoid, cylindrical to subcylindrical or oblong in fruit greenish, sometimes purplish, at anthesis 1.5–0.5 x 0.5–1.5 cm, the mature infrutescence 2.0–6.0 x 0.5–2.5 cm. Staminate flowers 2.5–4.0 mm long, receptacle 2.0–2.5 mm diam, ± flat or slightly concave; perianth lobes 4–6, abaxially glanduliferous, 0.2–0.9 x 0.2–0.5 mm; stamens 40–60, anthers 0.3–0.8 x 0.3–0.4 mm, filaments

0.1–0.2 mm long. Pistillate flowers often pleiomerous, at anthesis 2.5–4.0 mm wide; tepals strongly reduced, only developed as fleshy wales; stigmas sessile, broadly elliptical seen from above, distinctly projecting between tepals; staminodes 1.0–2.5 cm long, filiforms, white. Fruits baccate, 5–7 mm broad; tepals ca. 1 mm wide, connate only at base, apically truncate to obtuse, not bent over the stigmas, with a conspicuous elongate staminodal protuberance, with white top when dry, frequently surpassing the tepals; stigmas 1.0–2.0 x 0.7–1.5 mm, the distal apices 5–6 mm apart, linear to obovate seen from above, somewhat uncinate, surpassing and distinctly projecting between the tepals, non-receptive part swollen higher than the receptive part, the latter slightly grooved, rarely forming a central concavity, often sunken into the non-receptive part. Seeds 1.0–1.8 x 0.5–0.8 mm, ellipsoid, sometimes suboblongoid, orange. Figure 1A, B, C and Figure 2A—G.

***Distribution and Habitat***— *Asplundia brachypus* ocurrs in Atlantic Forest of the Brazilian States Espírito Santo, Minas Gerais, Rio de Janeiro, São Paulo, Paraná, Santa Catarina and Rio Grande do Sul (Figure 3), between the parallels 19°S—30°S; at from 0 to 1,600 m elevation. Gomes & Giulietti (2003) did not mention the occurrence of this species in the State of São Paulo. This species is commonly found in the understory, in the bottom of the valleys and slopes, in shady enviroments, on fairly humid ground. Sometimes it is found in rocks or as epiphyte on the base of robust trees. This species has the southernmost range of all Cyclanthaceae.

***Phenology***—Flowering November to December. Fruiting January to June.

***Vernacular name***—Bombonaça-da-terra (Reitz 1968), Timpopeba (*Völtz 1136*).

***Etymology***—The specific epithet comes from the Greek *brachy* (=short, little) and *pus* (=foot). It problably refers to short inflorescence peduncles.

***Notes About Conservation Status***—The extent of occurence (EOO) is 389,000 km$^2$. This is a widespread species, known from many collections. Throughout its distribution it is found in several protected areas. Based in criteria B2 from IUCN Standarts and Petitions Subcommitte (2014) this species should be classified as “Least Concern” (LC).

***Specimens Examined***—BRAZIL. Espírito Santo: Itaguaçu [Itaguassú] - Jatiboca, 15 May 1946, *Brade et al. 18230* (RB, SPF); Iúna, Serra do Valentim, propriedade do Sr. Aristides, próximo ao transecto 5, na grota, 1310 m, 20.3654°S, 41.4722°W, 7 Jul 2014, *Zorzanelli 1038* (VIES); Santa Teresa, Rio Saltinho, 31 May 1984, *Boone 222* (MBML, RB); Estação Biológica da Caixa d’Água, 4 Nov 1986, *Boudet Fernandes 1838* (MBM); trilha subindo o morro ao lado do country club, 25 Feb 1996, *Lombardi & Temponi 1127* (BHCB, ESA); Valão de São Lourenço, Mata Fria, terreno do Clerio Loss, 750 m, 23 Feb 1999, *Kollmann et al. 2017* (MBML, RB); estrada para João Neiva, limite norte da Estação Biológica de Nova Lombardia. Sítio do Sr. Waldir, 13 Feb 1999, *Mello-Silva et al.*

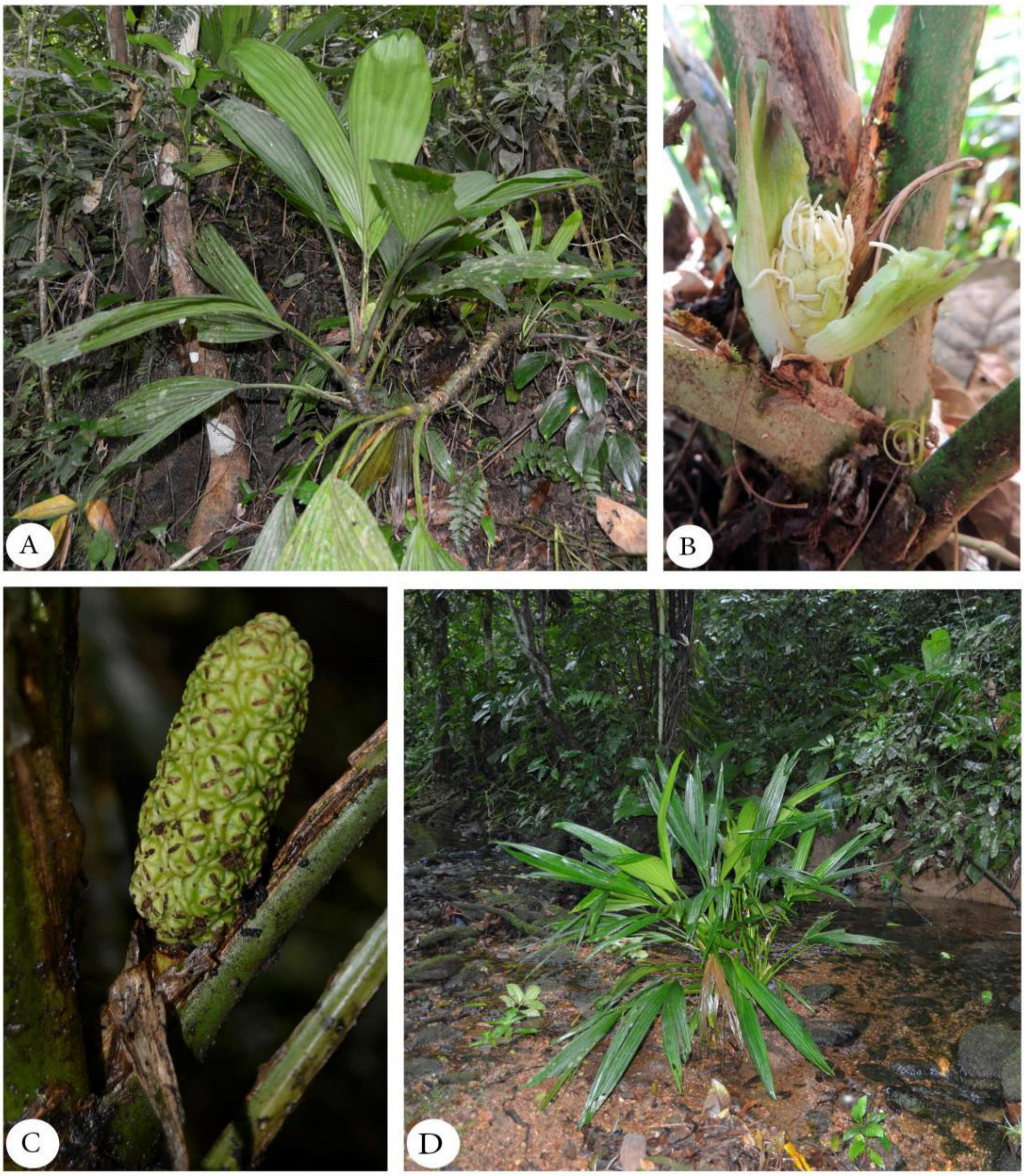

FIG. 1. A–C. *Asplundia brachypus*. A. Habit. B. Inflorescence. C. Infructescence. D. Habit of *Asplundia rivularis*. Photographs: A, C and D: Daniela Costa, B: João Braga.

*1572* (SPF *pro parte*); Nova Lombardia, terreno do Furlani, 836 m, 19°48'04"S, 40°32'14"W, 3 Fev 2011, *Souza et al. 1336* (BHCB). Minas Gerais: Conceição do Mato Dentro, Parque Natural Municipal do Ribeirão do Campo, 19°04'25.7"S, 43°36'54.6"W, 24 Dec 2002, *Mota 1886* (BHCB); Descoberto, Reserva Biológica da Represa do Gama, 23 Jan 2001, *Forzza et al. 1743* (CESJ); 550 m, 21°25.24'S, 42°57.18'W, 6 Mar 2004, *Forzza et al. 2946* (GB, RB); Itabirito, área da Serra da Moeda, 1450 m, 20°19'9.9"S, 43°56'17"W, 14 Jul 2001, *Salino et al. 7102* (BHCB, RB); Mariana, mina Fazendão, 20°09'13"S, 43°26'12"W, 29 Apr 2015, *Pivari et al. 2131* (BHCB); 881 m, 20°10'01"S, 43°26'02"W, 15 Mar 2016, *Gontijo & Tameirão Neto 987* (BHCB); Simonésia, RPPN Mata do Sossego, 1150-1600 m, 20°04'02"S, 42°04'40"W, 20 May 2006, *Salino et al. 11050* (BHCB, CESJ); Tiradentes, trilha da Mãe d'água, 3 Mar 2012, *Sobral et al. 14776* (HUFSJ). Paraná: Antonina, Estrada Cacatu-Serra Negra, 23 Mar 1966, *Hatschbach 14108* (MBM); Areia Branca, 10 m, 7 Mar 1974, *Hatschbach 34294* (MBM); Cachoeira, 15 Jan 1976, *Hatschbach 37950* (MBM); Guaraqueçaba, Serrinha, 13 Apr 1967, *Hatschbach 16321* (MBM); Rio do Costa, 9 Feb 1971, *Hatschbach 29130* (MBM); RPPN Salto Morato, 100 m, 25°10'37"S, 48°18'08"W, 5 Feb 2017, *Völtz 1204* (UPCB); Guaratuba, Serra da Prata, encosta ocidental, 8 Aug 1993, *Hatschbach & Ribas 58515* (MBM); Matinhos, Estrada para a comunidade do Paranti, 2 Apr 2016, *Völtz 1136* (EFC); Morretes, Parque Estadual do Pico do Marumbi, 22 Aug 1999, *Kozera & Kozera 1180* (UEC); 4 Apr 2009, *Keller 54* (HUCP); 11 Mar 2013, *Engels 651* (FURB, MBM, RB); Paranaguá, Serra da Prata, 20 m, 26 Dec 1962, *Hatschbach 9831* (MBM, US); Rio Cambará, 50 m, 28 May 1968, *Hatschbach 19255* (MBM); Floresta do Palmito, 10 m, 2 Apr 2016, *Kersten 1647* (HUCP). Rio de Janeiro: Cachoeiras de Macacu, Km 61.5 da RJ 116, Parada Modelo-Nova Friburgo, 780 m, 22°24'S, 42°36'W, 5 Apr 1986, *Bianchetti 356* (CEN); Caxias, Reserva da Petrobrás, Km 94 descida da Rio-Petrópolis, trilha em direção ao marco PN, 22°31'S, 43°16'W, 31 Mar 1999, *Paula et al. 161* (RB); Guapimirim, Granja Monte Olivete, trilha das Andorinhas, 500 m, 18 Jan 1995, *Braga et al. 1708* (RB); 20 Dec 1995, *Vieira et al.*

*789* (RB); Estação Ecológica Estadual de Paraíso, Serra dos Brejos, 28 Jan 1992, *Sylvestre et al. 795* (RB); Parque Nacional da Serra dos Órgãos, trilha do poço verde, 390 m, 22°29'38.2"S, 43°00'04.9"W, 15 Apr 2011, *Lombardi et al. 8446* (HRCB); Macaé, Sana, sítio São Bento, trilha para a caixa d'água, 9 May 2006, *Didonet 2* (RB); Magé, Santo Aleixo, Rua Antero Quental, após Monjolo, 19 April 2007, *Santos et al. 2163* (RFFP); trilha para Três Torres (ou travessia para Petrópolis), mata após segunda torre e capinzal, 15 Jan 2008, *Santos et al. 2280* (RFFP); Rua Capitão Antero, toca do índio, próximo às margens do Rio do Pico, 220 m, 22°32'50.26"S, 43°34'54.3"W, 20 Nov 2012, *Greco et al. 29* (RFFP); Nova Friburgo, Rio Bonito de Lumiar, estrada do sertão, sítio São Jeronimo, 779 m, 22°25.48'S, 42°25.81'W, 1 Mar 2004, *Forzza et al. 2774* (K, RB); Nova Iguaçu, Trilha para o rio São Pedro, 17 Jan 2002, *Silva Neto et al. 1644* (RB); Paty dos Alferes, estrada da Água Fria – APA Palmares, 22°26'54"S, 43°22'39"W, 20 Feb 2012, *Carina 1060* (RFA). Petrópolis, Rocio, estrada para Vargem-Grande, propriedade particular, 970 m, 22°28'24"S, 43°14'40"W, 3 Apr 2004, *Bovini 2414* (RB); Queimados, trilha para o Rio d'Ouro, 420 m, 22°37'67"S, 43°30'62"W, 9 Feb 2007, *Fraga et al. 1736* (RB). Rio Bonito, Braçanã, Faz. das Cachoeiras, 10 July 1976, *Laclette 117* (R). Rio das Ostras, Reserva Biológica União, 1 Apr 2000, *Costa et al. 767* (R). Rio de Janeiro, córrego da mata atrás do Jardim Botânico do Rio de Janeiro, s.d., *Didonet 1* (RB); Campo Grande, Parque Natural Municipal da Serra do Mendanha, trilha para Cachoeira, próxima ao córrego, *Santos 2245* (RFFP); Parque Nacional da Tijuca, trilha para o Morro da Cocanha (Alto da Boa Vista), 700 m, 10 Jun 1997, *Braga & Loureiro 4143* (RB, SPF); Floresta Nacional da Tijuca, trilha para a Cachoeira dos Primatas, 10 Mar 2012, *Leal et al. 423* (RB); Mata do Horto, Represa (atrás da ENBT/JBRJ), proximidades da Cachoeira do Solar da Imperatriz (Cachoeira dos Macacos), 230 m, 22°58'09"S, 43°14'51"W, 18 Apr 2016, *Braga et al. 16-004* (RB); Parque Estadual da Pedra Branca, Jacarepaguá, Pau-da-Fome, Cachoeira do Campo, 332 m, 22°56'11"S, 43°27'22"W, 22 Dec 2016, *Braga et al. 16-082* (RB); [Morro do] Sumaré, 10 Aug 1950, *Kuhlmann s.n.* (RB 479378); Serra da Carioca, 10 Mar

1952, *Duarte 4118* (RB); Estrada da Vista Chinesa Km 2, 7 Nov 1977, *Carauta 2751* (GB, NY, RB); Maciço da Tijuca, near entrance of building of FEEMA, 400 m, 17 Oct 1977, *Maas & Carauta 3280* (RB, U *2 sheets*). Rio Grande do Sul: Torres, Perdida, 27 Jan 1991, *Waechter 2472* (ICN). Santa Catarina: Biguaçu, Amâncio, 440 m, 27°21'36"S, 48°46'48"W, 30 Mar 2010, *Cadorin et al. 1762* (CRI); Bombinhas, Cachoeira da Praia Triste, 80 m, 27°11'34"S, 48°33'39"W, *Silva et al. 692* (HCF); Blumenau, Morro do Sapo, 388 m, 27°03'51.99"S, 49°05'54.19"W, 21 Jan 2013, *Funez et al. 1605* (FURB); Brusque, Azambuja, 50 m, 17 Jul 1948, *Reitz 2181* (US); Corupá, RPPN Emílio Fiorentino Battistella, trilha da rota das cachoeiras, 250-400 m, 26°24'01"S, 49°20'49"W, 3 Feb 2018, *Schwirkowski 2650* (FURB); Florianópolis, morro Costa da Lagoa, 300 m, 22 Jun 1966, *Klein et al. 6769* (BHCB, FLOR); Parque Municipal da Lagoa do Peri, 317 m, 27°43'27"S, 48°32'06"W, 10 Mar 2010, *Cadorin et al. 1474* (SAMES); Garuva, Mina Velha, 10 m, 21 Jan 1958, *Reitz & Klein 6256* (HBR, US); Ibirama, Horto Florestal do I.N.P., 250 m, 6 Feb 1956, *Reitz & Klein 2670* (HBR); Ilhota, Parque Botânico Morro do Baú, 340 m, 26°48'15"S, 48°56'36"W, 3 Mar 2014, *Caglione et al. 347* (FURB); Indaial, Warnou Alto, 357 m, 27°00'00"S, 49°13'51", 14 May 2010, *Korte & Kniess 3248* (CRI, FURB); Jacinto Machado, Sanga da Areia, 250 m, 30 Oct 1959, *Reitz & Klein 9267* (HBR); Jaraguá do Sul, Grota Funda, 340 m, 26°19'18"S, 49°08'43"W, 1 May 2011, *Cadorin & Oliveira 3193* (FURB); Joinville, 13 Jan 1951, *Reitz 3743* (HBR); Luiz Alves, Braço Serafim, 200 m, 26°45'49"S, 48°59'47"W, 14 Feb 2014, *Gasper & Funez 3520* (FURB); Orleans, Rio Novo, 300 m, 18 May 1993, *Citadini-Zanette et al. 1602* (CRI-3150); Palhoça, Pilões, 200 m, 24 Feb 1956, *Reitz & Klein 2734* (HBR); 200 m, 7 Jun 1956, *Reitz & Klein 3264* (HBR); São Bento do Sul, braço esquerdo, 417 m, 26°21'54.01"S, 49°14'08.12"W, 10 May 2010, *Cadorin et al. 2234* (FURB, LUSC); Sombrio, *2 Feb 1946*, *Rambo 31574* (PACA). São Paulo: Barra do Turvo, cachoeira Dito Salu, 27 Feb 2004, *Barbosa et al. 890* (US); Cananéia, Ilha do Cardoso, trilha de acesso à captação de água, próximo ao rio Pareque, 22 Feb 1979, *Grande et al. 254 b* (SP); Cubatão, Parque Estadual da Serra do Mar, núcleo Itutinga-Pilões, 5 Mar 2018, *Leal & Costa 467* (SPF); Iguape, Estação Ecológica Juréia-Itatins, trilha do imperador, 115 m, 24°34.213'S, 47°13.743'W, 29 Jan 2016, *Leal & El Ottra 462* (SPF); Miracatu, Reserva Particular da Votorantim, UHE Barra, trilha da vila dos moradores em direção à caixa d'água (aprox. 2 km), 24.0306°S, 47.3447°W, 31 Mar 2013, *Cabral et al. 905* (ESA, RB); Pindamonhangaba, fazenda São Sebastião do Ribeirão Grande, 3 Apr 1994, *Nicolau & Souza Franco 843* (SP); 8 Sep 1995, *Nicolau et al. 925* (SP); 6 Apr 1997, *Rapini & Nicolau 259* (SP); Parque Natural Municipal Trabiju, trilha encosta, paralela a da caixa d'água (captação), 24 Dec 2008, *Nicolau et al. 3625* (SP); Ribeirão Grande, Parque Estadual Intervales, trilha para Cachoeira da Água Comprida, 7 May 1997, *Wanderley et al. 2203* (SP); Santo André, Reserva Biológica do Alto da Serra de Paranapiacaba, 12 Apr 1988, *Kirizawa & Lopes 2026* (SP); 23 Apr 2014, *Vieira 198* (SP); São Miguel Arcanjo, Parque Estadual Carlos Botelho, 5 Jun 1992, *Lombardi 107* (BHCB, UEC); Sete Barras, Paruqe Intervales, base Saibadela, trilha do rio, ponto 4, 17 Mar 1997, *Izar & Zipparro 1682* (HRCB); Ubatuba, Parque Estadual da Serra do Mar, fazenda Picinguaba, 23 Apr 1991, *Kirizawa & Lopes 2468* (SP); 23 Apr 1991, *Kirizawa & Lopes 2470* (SP).

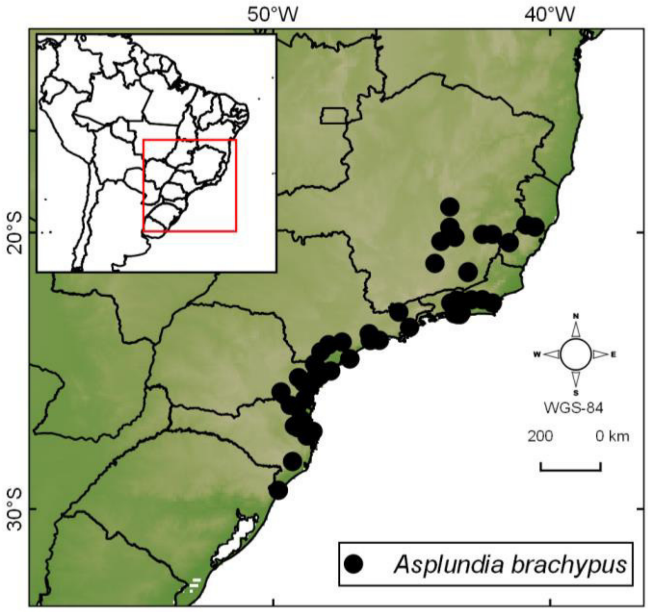

Fig. 3. Distribution map of *Asplundia brachypus*.

***Notes***—*Carludovica schizophylla*, was described by Drude (1881) concomitantly with *Carludovica brachypus* (=*Asplundia brachypus*), both from the same locality in the Rio de Janeiro state. As pointed by Harling (1958), the main reason for Drude to describe the species separately, was the frayed and secondarily deeply cleft into many irregular lobes leaf segments of *C. schizophylla*. Many broad-leaved *Asplundia* species may have the foliar segments random lacerated by phisical damages, therefore not ontogenic and common in large-old leaves (Harling 1958; Hammel 2003). In additon, the fruiting spadix of the collection cited by Drude as type of *C. schizophylla* is clearly conspecific with the type material of *A. brachypu*s, which also shows lacerated leaves. Here, we agree with Harling's view and hold *C. schizophylla* as synonymous of *A. brachypus*.

When describing *C. polymera* from São Paulo State, Handel-Mazzetti (1908) compared his new species with *C. gardneri* from northeastern Brazil, wich is differentiated by minor features of leaves, shorter inflorescence and epiphytic habit. The characteristics that made it different from previously described species of the Atlantic Forest's *Carludovica* were the probable leaf dimorphism, with both bifid and palmate leaves, and pleiomerous pistillate flowers. According to Harling (1958), all statements about leaf dimorphism in this species are unfounded, and Handel-Mazzetti analysed a strongly deformed leaf in the type collection. The pleiomerous pistillate flowers, the apical flowers being penta- or hexamerous, firstly found in the type specimen of *C. polymera*, are common in species distributed at southernmost border of the range of the Cyclanthaceae (Harling 1958). Harling (1954) transferred *C. polymera* to *Asplundia* and posteriorly differed *A. polymera* from other related species by their mode of growth, smaller leaves and spadices, and fewers stamens (Harling 1958). He also justified the description of a new subspecies, *A. polymera* subsp. *reitzii*, from Santa Catarina state; by spadix size, number of pleiomerous pistillate flowers, and geographical distribuition (Harling 1958). The original description, illustration, as well as the type material of *C. polymera* agrees perfectly with our concept of *A. brachypus*. Moreover, the characters used to separate these species are very plastic and variable. Therefore, *C. polymera* and its subspecies are considered as synonyms of *A. brachypus*.

*Asplundia glaucophylla*, from Paraná State, was compared by Harling (1958) with *A. rivularis*. Nevertheless, the fruiting spadix of the holotype of *A. glaucophylla* is obviously conspecific with the lectotype of *A. brachypus*, and the glaucous leaves used by Harling as a diagnostic character of his new species are an artifact of the drying process.

As circumscribed here, *A. brachypus* is a polymorphic taxon, which extends throughout the Atlantic Forest of Southern Brazil. The mode of growth depends on the environmental conditions and age of the plant. The size, form, lateral costae, the degree of bipartition of the leaf blades, as well as spadix size, are also variable characters.

2. ASPLUNDIA RIVULARIS (Lindm.) Harling, Acta Horti Berg. 17: 43. 1954. *Carludovica rivularis* Lindm., Bih. Kongl. Svenska Vetensk.-Akad. Handl. 26, Afd. 3, no. 8: 4. 1900.—TYPE: BRAZIL: São Paulo, Santos [São Vicente], Sororocaba, inter saxa rivuli umbrosi, 10 Dec 1874, *C.W.H. Mosén 2946* (lectotype, designated by Harling (1958: 236): S-R-525 (image!), isolectotypes: S-14-45666 (image!), UPS-V226072 (image!)).

Reophytic or terrestrial herb with short aerial stem. Leaf blade tricostate, 45–90 cm long, bifid to 75% of its length or almost to base, segments 5–11 cm broad, linear lanceolate to oblanceolate, acute, in older leaves often secondarily cleft into irregular lobes, ridge distance 0.6–1.2 mm, midrib 10–20 cm long; petiole + sheat 35–70 cm long, epidermis of petiole sheats and peduncles bases dull, in color and consistence not diferring from epidermis in others parts of petioles and peduncles. Peduncle during anthesis 4.5–8.0 cm long, 8–20 cm long in fruiting stage; spathes 4, ± coarse, lanceolate, acute to acuminate, the lowermost one placed at about the middle of the peduncle, 7–10 x 1.5–2.0 cm, the other spathes concentrated rather near the spadix, 5–8 x 1.5–2.0

cm. Spadix cylindrical to subcylindrical, at anthesis 2.0–6.0 x 0.5–1.5 cm, the mature infrutescence 3.0–12 x 1.0–4.0 cm, greenish. Staminate flowers 3.0–4.0 mm long, receptacle 2.0–2.5 mm diam, flat; perianth lobes 5–6, abaxially glanduliferous, 0.2–0.9 x 0.2–0.4 mm; stamens 40–50, anthers 0.6–0.8 x 0.3–0.4 mm, filaments 0.1–0.2 mm long. Pistillate flowers often pleiomerous, 3.0–4.0 mm wide at anthesis; tepals reduced, only developed as fleshy walls; stigmas sessile, linear to elliptical seen from above, wholly encircled by the tepals; staminodes unknown. Fruits baccate, 6–7 mm broad; tepals, 3.0–4.0 mm wide, connate only at base, apically truncate, not bend over the stigmas, with a elongate staminodal protuberance, with white top when dry, smaller or equal to the tepals; stigmas 1.5–2.0 x 1.5–2.0 mm, the distal apices 5–6 mm apart, obovate to quadrangular seen from above, equal to or slightly surpassing the tepals, non-receptive part swollen higher than the receptive part, the latter broadly grooved, sometimes forming a deep central concavity. Seeds 1.5–2.0 x 0.7–1.0 mm, ellipsoid, orange. Figure 1D and Figure 2 H, I.

***Distribution and Habitat***—. *Asplundia rivularis* is restricted to the coast of Rio de Janeiro and São Paulo States (Fig. 4), between the parallels 23°—25°S, at 0 to 850 m elevation, although Gomes & Giulietti (2003) considered it distributed from Rio de Janeiro to Santa Catarina. It is a rheophyte, solely found on waterfalls or stream margins, always associated with rocky and humid places and may be simpatric with *A. brachypus*.

***Phenology***—Flowering November; Fruiting November to March.

***Etymology***—The specific epithet refers to its riverside preference.

***Notes About Conservation Status***— The Area of Occupancy (AOO) is 36 km$^2$. It is found in protected areas and generally forms large populations. Based in criteria B2 from IUCN Standards and Petitions Subcommitte (2014), *A. rivularis* may be considered as “Endangered” (EN).

***Specimens Examined***—BRAZIL. Rio de Janeiro: Paraty, Morro de Várzea, mata de encosta, acesso pela praia Negra, 24 Mar 1992, *Marques et al. 302* (RB); Patrimônio, trilha para a aldeia Araponga, 200 m, 8 Aug 1995, *Bovini et al. 929* (RB); estrada em direção à comunidade indígena, 19 Dec 2007, *Bovini et al. 2705* (NY, RB); trilha de Parati-Mirim para Mamanguá, 22 Jan 2001, *Fiaschi & Lobão 603* (RB, SPF); trilha para a Serra de Parati, após a estrada que vai à localidade do Corisco, mata pluvial atlântica no vale do Rio do Corisco, trilha na encosta à margem esquerda do rio, após atravessá-lo, 28 Sep 1996, *Mello-Silva & Santos 1237* (RB, SPF); estrada nova para a Praia do Sonho, 15 Nov 1993, *Barros 2869* (SP); 1 Jan 2007, *Didonet 4* (RB). São Paulo: Cubatão, Raiz Nova da Serra, num córrego, mata virgem, Dec 1898, *Edwall CGG4229* (SP); Serra do Cubatão, inter São Paulo et Santos, Jan 1901, *Schwacke 14159* (RB); Iguape, Estação Ecológica Juréia-Itatins, caminho do imperador, 10 Feb 1993, *Rossi et al. 1274* (SP); 12 Dec 1995, *Cordeiro et al. 1615* (SP, SPSF); 6 Jan 1999, *Alves et al. 1757* (NY, SP); 75 m, 24°34.213'S, 47°14.077'W, 29 Jan 2016, *Leal & El Ottra 463* (SPF); Santo André, Alto da Serra, sobre pedras nas correntezas das cabeceiras do rio Grande [Pinheiros], 14 Apr 1898, *Edwall CGG3853* (SP); Santos, Parque Estadual da Serra do Mar

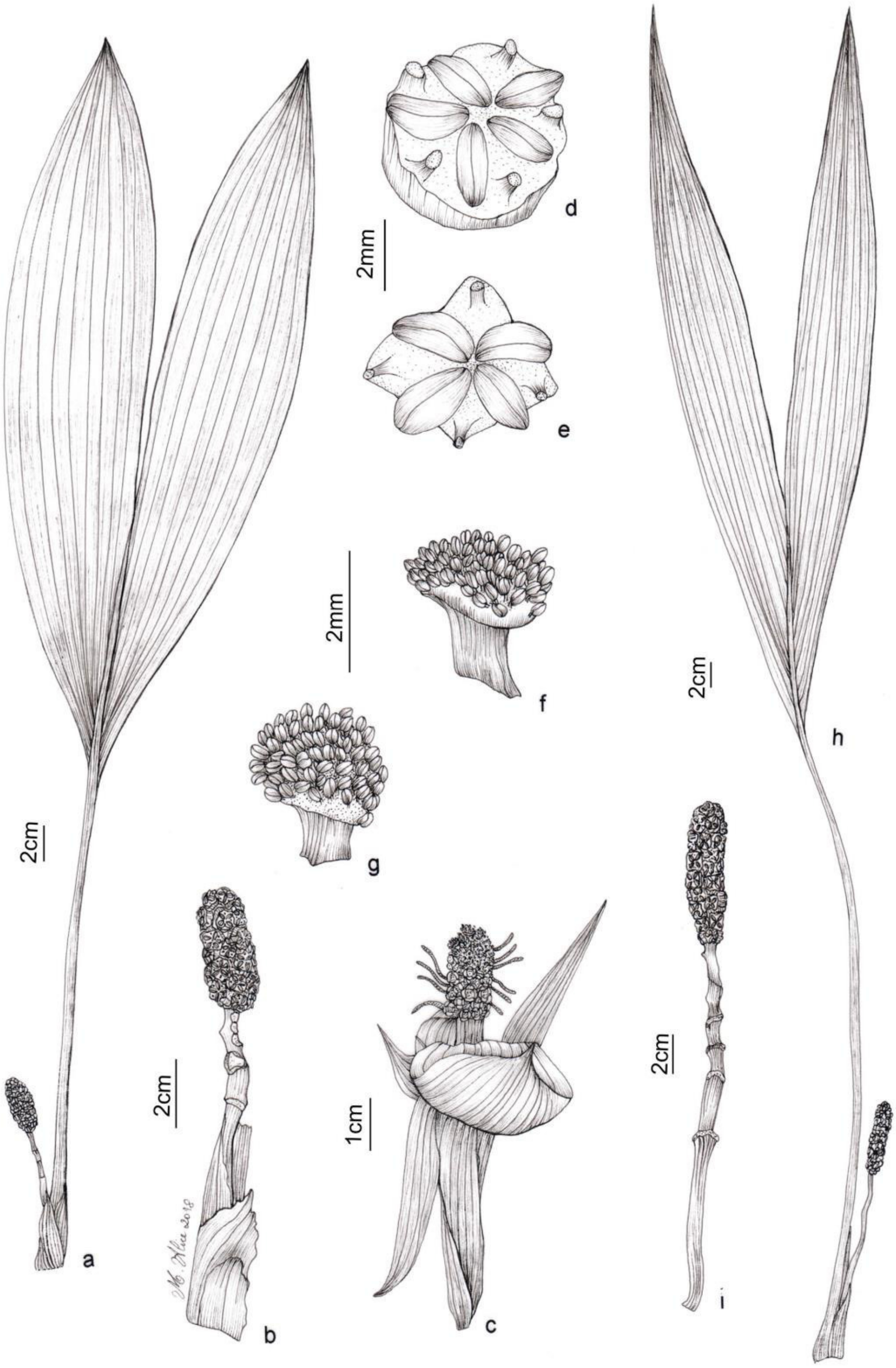

FIG. 2. A–G. *Asplundia brachypus*. A. Leave. B. Infructescence C. Inflorescence. D and E. Fruits (upper view). F and G. Staminate flowers (side view). H–I. *Asplundia rivularis*. H. Leave. I. Infructescence. (A, C, D, E, F and G. *Vieira 789;* RB barcode 00685299; B. *Forzza 2946;* RB barcode 00478893; H and I. *Didonet 4;* RB barcode 00492505; Drawn by M.A. Rezende).

Núcleo Itutinga-Pilões, na cachoeira escondida, próximo à divisa entre Santos e Paranapiacaba (Santo André), no vale do Rio Quilombo, 815 m, 23°47'S, 46°17'W, 7 Mar 2017, *Prudêncio & Marins 553* (HUSC); São Paulo, Distrito do Grajaú, fazenda Castanheiras, 21 Mar 2003, *Garcia et al. 2178* (PMSP); Ubatuba, Núcleo de Picinguaba, Trilha do Corisco, 23°20'48"S, 44°50'59"W, 9 Nov 1993, *Sanchez et al. 29951* (SP, UEC); Vila Atlântica, Cachoeira, 25 Nov 1949, *Joly 803* (SPF); Serra do Mar, Dec 1930, *Hoehne s.n.* (SP 25029).

***Notes***— The type-locality of *A. rivularis* has been given as "S. Paulo, Santos, Sororocaba" (Lindman, 1900) or "São Paulo, Santos, Sorocaba ("Sororocaba")" (Harling, 1958). Sorocaba is a municipality of the State of São Paulo, interior to the coastal forest system, where no ocurrence of Cyclanthaceae has been found or expected. The original label, however, agree with Lindman's information. It is hand-writing by Mosén and reads "Prov. S. Paulo. Santos. Sororocaba.". Very probably, Sororocaba is distinct from Sorocaba and was a place on the left margin of the rio Branco or Boturoca, on the slopes of the Serra do Mar Range, nearly -23.951747, -46.486141, in the current municipality of São Vicente, near Santos, in the State of São Paulo (Moreira, 1903; Caramaschi & Caramaschi, 1991). This locality has been visited by another botanist, Hemmendorf, in the beginning of the 20th century, and plant specimens collected by him, housed in R herbarium, came from the same locality "Sororocaba, prope Santos" (Caramaschi & Caramaschi, 1991). Also many other Mosén's collections made at the same time, bring that locality in their labels. Sororocaba is, however, often treated by botanists, taxonomic indexes, and databases as Sorocaba, a municipality about 115 km NW from there.

When Lindman (1900) described *Carludovica rivularis* (the basionym of *A. rivularis*), he cited only the specimen *Mosén 2946* housed at S herbarium. However, two sheets of *Mosén 2946* are found in this herbarium. In one of these sheets (S-R-525), Harling wrote *holotypus*, in this manner effecting the lectotypification, although he did not convey that. Both sheets at S bear no fertile parts, which were preserved in spirit collection, but not found there anymore (Karin Santos, pers.

comm.). Nevertheless, it was probably the base for the excelent illustrations of the reproductive parts provided by Lindman (1900) and Harling (1946). The rheophyte *A. rivularis* is superficially similar to *A. brachypus*, being distinguished by its longer, narrower and more deeply bifid leaf blade and almost linear segments (Harling, 1958).

Fig. 4. Distribution map of *Asplundia rivularis* and *A. orthostigma*.

3. ASPLUNDIA ORTHOSTIGMA E.S.Leal, sp. nov.—TYPE: BRAZIL: Espírito Santo, Linhares, Reserva Florestal de Linhares, às margens do córrego Rancho Alto, após o viveiro, 6 Oct 1993, fl., *D.A. Folli 2031* (holotype: RB-00479019!; isotype: CVRD (image!)).

*Asplundia orthostigma* resembles *A. rivularis*, but is distinguished by its root-climbing liana habit (vs. rheophytic), epidermis of sheats and peduncles bases hard, glossy, orange or yellowish, brittle cracking when dry (vs. dull), stigmas in ripe fruiting stage completely turned upwards (vs. not turned upwards), encircled by the tepals (vs. projecting between tepals), and not grooved (vs. broadly grooved).

Root climbing liana or seldom terrestrial herb, short aerial stem. Leaf blade tricostate, lateral costae running at the leaf margin, 70–90 cm long, bifid to 75–80% of its length, segments 9–14 cm broad, lanceolate, acuminate, ridge distance 10–20 mm, midrib 17–20 cm long; petiole + sheath 30–55 cm long, epidermis of sheaths and peduncles bases hard, glossy, orange or yellowish, brittle cracking when dry. Peduncle during anthesis 12–14 cm long; 8–15 cm long in fruiting stage, spathes 4–5, ± coarse, cymbiform to ovate, 7–12 x 2–3 cm. Spadix cylindrical to subcylindrical, in fruit greenish, at anthesis 2.5–4.0 x 1.2–2.0 cm, the mature infrutescence 4.5–7.0 x 1.5–2.5 cm. Staminate flowers persisting as wilted in fruit 3.0–3.5 mm long, pedicel 1.2–2.0 mm long, receptacle ca. 2.0 mm wide, flat; perianth lobes 5–7, abaxially glanduliferous, 0.5–1.0 x 0.2–0.5 mm; stamens 20–40, anthers 0.6–1 x 0.2–0.4 mm, filaments up to 0.3 mm long. Pistillate flowers at anthesis 4–6 mm wide; tepals 1.0–1.5 x 1.0–1.5 mm, 0.8–1.0 mm thick, free, truncate, incurved, bent over stigmas; staminodes unknown; styles 4, 1.0–1.5 mm long, free; stigmas 1.0–1.5 x 1.0–1.5 mm (the distal apices 4.4–5 mm apart), widely obovate to almost square seen from above or quadrangular, wholly encircled by the tepals, slightly elevated towards the distal end, non-receptive part higher than the sterile part. Fruits baccate, 4–5 mm broad; tepals 4–6 x 3–5 mm, 0.5–0.8 mm thick, free, apically truncate to obtuse, no conspicuous elongate staminodal protuberance; styles 4–5 mm long, free; stigmas 2.5–4.0 x 1.5–3.7 mm, obovate seen from above, wholly encircled by the tepals, strongly turned towards the distal end, almost vertical, sometimes forming a central concavity, non-receptive part swollen smaller than the receptive part, the latter slightly grooved. Seeds 1.5–2 x 0.3–0.7 mm, ellipsoid, yellow. Figure 5.

***Distribution and Habitat***—*Asplundia orthostigma* ocurrs in the north and central parts of Espírito Santo State, in the municipalities of Linhares and Santa Teresa (Fig. 4). Most populations were found in Santa Teresa, within three different conservation units and private properties. The species inhabits montane forest’s tree trunks, reaching up to 5 m on the forophyte.

***Phenology***—Flowering October; Fruiting February to May.

***Vernacular name***—timbopeba (*Folli 2031*).

***Etymology***—The specific epithet is referred to its stigmas straight, turned upwards, encircled by the tepals, in ripe fruiting stage.

***Notes About Conservation Status***— The AOO = 20 km$^2$ and EOO = 375 km$^2$. Based in both criteria B1 and B2 from IUCN Standards and Petitions Subcommitte (2014), this new species may be considered as “Endangered” (EN). Although ocurring in protected areas, it is known for few collections and their populations are small and scattered.

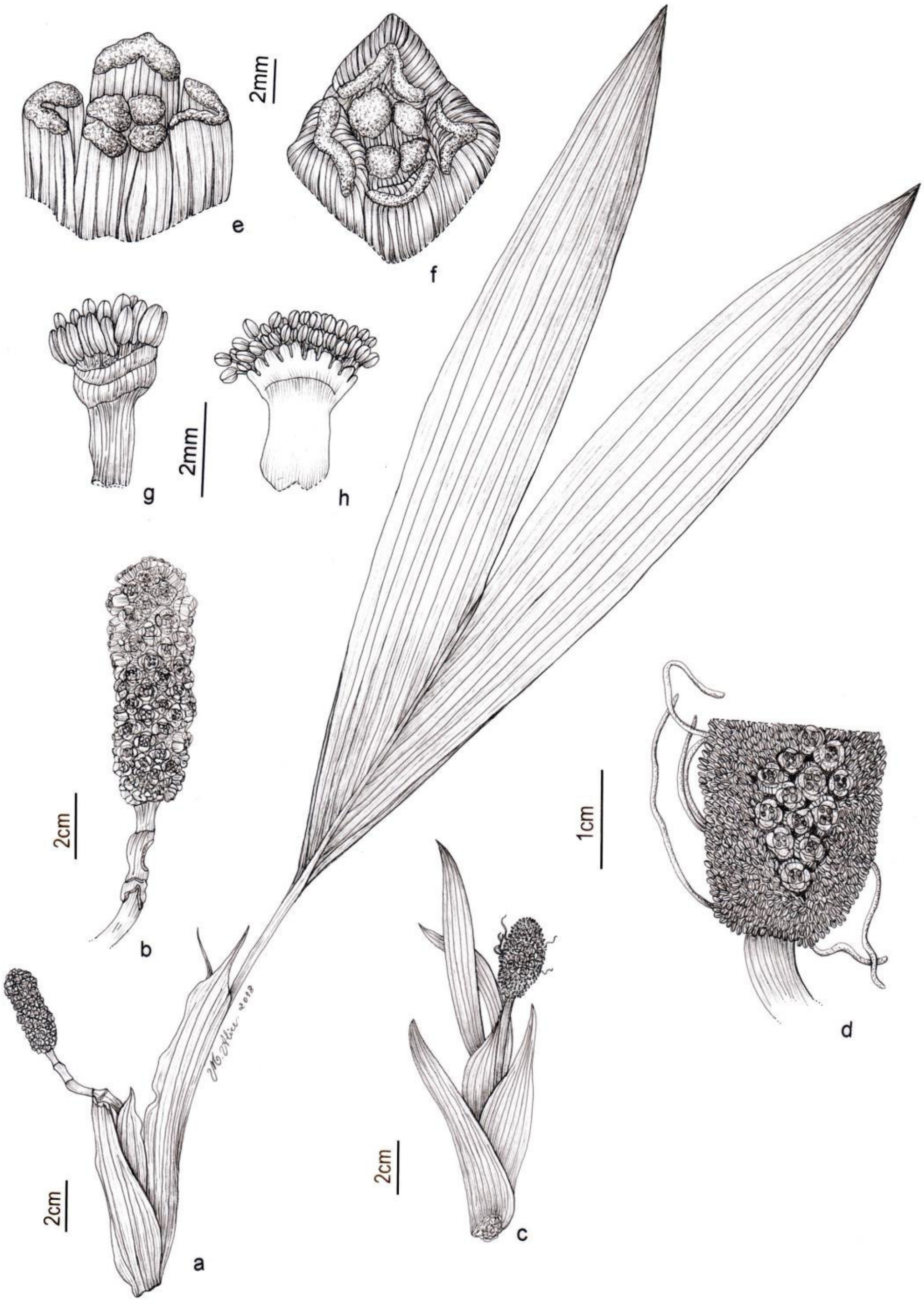

FIG. 5. A–H. *Asplundia orthostigma*. A. Leave. B. Infructescence C. Inflorescence. D. Detail of inflorescence. E. Fruit (side view). F. Fruit (upper view). G. Staminate flower (lateral view). H. Staminate flower (adaxial view). (A, C–H. *Folli 2031*; RB barcode 00479019; B. *Kollmann 8833*; RB barcode 00604454; Drawn by M.A. Rezende).

***Additional Specimens (Paratypes) Examined***—BRAZIL. Espírito Santo, Santa Teresa, estrada para João Neiva, limite norte da Estação Biológica de Nova Lombardia, sítio do Sr. Waldir, 13 Feb 1999, *Mello-Silva et al. 1572* (K, RB-00478896, SPF-135079 *pro parte*); Reserva Biológica Augusto Ruschi, estrada para Goiapabo-açu, parte final, 800 m, 24 Oct 2002, *Vervloet et al. 1269* (MBML-00016749, RB-00604436); trilha da cachoeira, partindo da nova sede, 11 Mar 2003, *Vervloet & Bausen 1959* (MBML-00016722); estrada para João Neiva, parte inicial, 14 May 2003, *Vervloet & Pizziolo 2450* (MBML-00016683); Santo Antônio, terreno de J. Dalmaschio, 4 Feb 2006, *Kollmann & Krause 8833* (MBML, RB-00604454); Estação Biológica de Santa Lúcia, mata de encosta na margem direita do rio Timbuí, 600 m, 12 Feb 1999, *Mello-Silva et al. 1558* (SPF-135078); estrada Fundão-Santa Teresa, 30 May 2001, *Kollmann et al. 3777* (MBML-00016734).

***Notes***—Floral morphology places *A. orthostigma* in subgenus *Asplundia*, which is characterized by asymmetric staminate flowers with a flattened receptacle and perianth lobes developed on one side only (Harling, 1958). This subgenus is supported as monophyletic (Leal, chapter 1). Besides the *Asplundia orthostigma*'s aforementioned similarities to *A. rivularis*, it also shares similarities with *A. gardneri* (Hook.) Harling, both with epidermis of sheaths and peduncles bases hard, glossy, orange or yellowish, brittle cracking when dry, and distinctly tricostate leaves. However, *A. orthostigma* shows lateral costae running at the leaf margin (vs. the lateral costae entirely running far inside in the leaf in *A. gardneri*), the plants are predominantly root-climbing lianas (vs. predominantly terrestrial herbs in *A. gardneri*) and differs in many features of the stigma in fruiting stage.

A distinctive feature of *Asplundia orthostigma* are their stigmas wholly encircled by the tepals, completely turned upwards, straight, vertical or erect in ripe fruiting stage. This condition, not observed in any other species of Atlantic Forest's *Asplundia*, is found in the Central American *A. euryspatha* Harling, and *A. labela* (R.E.Schult.) Harling, and in Ecuadorian *A. fagerlindii* Harling.

*Asplundia orthostigma* occurs simpatrically with the widespread *A. brachypus*, but with no overlap in the divergent morphological characters, and the two species are easily differentiated. Morphological traits differing *A. orthostigma* from its nearest relatives, such as orientation of the stigma in fruting stage, are frequently used as important characteristics to distinguish taxa of *Asplundia* (Harling 1958).

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# Chapter 3

# Nomenclator botanicus of the Cyclanthaceae

**Abstract.** All published names of Cyclanthaceae are treated here. We indicate 225 currently accepted names, 60 heterotypic synonyms, 36 doubtful names, and 1 excluded name. We also designate four new lectotypes, two neotypes and for four names a second-step lectotypes are given. Twelve names are newly treated as synonyms.

## Introduction

Cyclanthaceae includes terrestrial plants, root-climbing lianas and epiphytes distributed in 12 genera, with the estimated number of species varying between 180 (Beck, 2004) to 230 species (Harling et al., 1998), distributed from southern Mexico to the Atlantic Forest in southern Brazil (Harling et al., 1998). The main purpose of this paper is to provide a comprehensive nomenclatural index of the published names of Cyclanthaceae and to indicate their current taxonomic and nomenclatural status, based on our results on taxonomic and phylogenetic work with the family.

Until 1958, 64 species were known in 8 genera. In a magnificient taxonomic treatement of the Cyclanthaceae, Harling (1958) described three new genera, 114 new species, eight new subspecies and one variety, recognizing 178 species and 11 genera. During 60 years after that, two genera (Hammel & Wilder, 1989; Eriksson, 1989), 70 species (Schultes, 1959; Harling, 1963; Harling, 1972; Harling, 1973; Grayum & Hammel, 1982; Galeano & Bernal, 1984; Hammel, 1986a; Hammel & Wilder, 1989;

Eriksson, 1989; Eriksson, 1995; Tuberquia, 1997; Hammel, 2003a; Eriksson, 2007; Leal, 2011), and one subspecies (Eriksson, 1995) have been described. Besides that, two species have changed status to subspecies (Eriksson, 1995), and one genera was synonymized (Eriksson, 1993). Leal (chapter 1) based in morphological and molecular data reassessed the circumscription of the genera in Cyclanthaceae and synonymized *Dianthoveus* under *Evodianthus*. In total, 246 specific and 12 subspecific names were distributed in 11 genera. All of these names have been here evaluated, and our assessment of their current taxonomic status is presented.

## Matherial and Methods

Scanned images of types from all names of Cyclanthaceae available on JSTOR Global plants (http://plants.jstor.org/) were consulted. Type material housed in COL, F, GH, HUA, IAN, MEDEL, MG, MO, NY, R, and US herbaria (acronyms according to Thiers, 2018) were examined. All original literature sources were also reviewed. The nomenclatural data assembled here are based on Index Kewensis and Gray Herbarium Card Index (both available at *International Plant Names Index* [IPNI], http://www.ipni.org/), and Tropicos (http://www.tropicos.org). Authors and original publications were checked for each species and corrected when necessary. Abbreviate authors of scientific names are in accordance with Brummitt & Powell, *Authors of Plant Names* (Kew, 1992; also incorporated in IPNI), abbreviate book titles according to Stafleu & Cowan, *Taxonomic Literature* (ed. 2 and supplements) but with capital initial letters, and journal titles according to *BPH-2: Periodicals with Botanical Content* (available online at http://huntbotanical.org/databases/). Validly published species and synonyms were extracted from the last monograph for the genus (Harling, 1958), then complemented with all new taxa and nomenclatural changes published subsequently.

Specimens are considered holotypes when a single gathering in a particular herbarium is cited in the protologue, and there is only one specimen of that gathering housed there, or if there was a single gathering with no herbarium mentioned in the protologue, or else a single specimen exists in the herbarium where the author was based (ICN Art. 9.1, McNeill et al., 2012; McNeill, 2014). In some works, the protologue indicates a holotype, but there is more than one sheet of that collection at the herbarium cited. In such cases, we rely on the notations on the sheets and we observe whether the materials mounted on the different sheets are complementary (eg. a leaf and a flower and/or fruit) to determine whether a holotype can be identified; if not, a lectotype was designated, using our informed assessment of the most appropriate specimen. Epitypes have not been designated.

Type locality information is taken directly from the type specimen labels, in its original language, even if it does not entirely agree with the location given in the protologue. Information not present on the specimen labels, such as the province, state or departmente name, or a more modern or accepted spelling of a place name, is placed within brackets. Barcode numbers of type specimens are cited when available. For names that were considered synonyms after 1958, we indicate the author that first presented this point of view. Whenever we newly treat a taxon as a synonym, we include the annotation "**syn. nov.**" at the end of the entry.

Each distributional record was based on protologue, flora or checklist compiled by family specialists (listed in the introduction, plus Reitz, 1968; Hammel, 1986b; Brako & Zarucchi, 1993; Boggan et al., 1997; Eriksson & Harling, 2007; Harling & Eriksson, 1998; Eriksson, 2009; Hammel 2003b; Gomes & Giulietti, 2003; Gomes & Mello-Silva, 2006, Tuberquia, 2015; Leal & Forzza, 2012; Freitas et al., 2012), and also confirmed by voucher specimens examined. Distributional records were not accepted in cases of uncertainty about species reports or specimens determinations.

## Results and discussion

In the present treatment we recognize 227 accepted names to Cyclanthaceae, being 226 species and one subspecies. Widespread species, in many cases, have an extensive synonymy list. The greatest species richness is found in genus *Asplundia* (97 spp.), followed by *Dicranopygium* (53 spp.), *Sphaeradenia* (52 spp.), *Chorigyne* (7 spp.), *Carludovica* (4 spp.), *Stelestylis* (4 spp.), *Cyclanthus* (2 spp.), *Evodianthus* (2 spp.), *Ludovia* (2 spp.), and the monotypic *Schultesiophytum* and *Thoracocarpus*. The family occurs from Mexico (7 spp.) to Brazil (33 spp.), and attains the highest richness in Colombia (100 spp.) and the lowest in Trinidad and Tobago (4 spp., Table 1).

**TABLE 2.** Number of native species of Cyclanthaceae by country.

| Country or region | Total | Endemic species | Rate of endemism |
|---|---|---|---|
| Colombia | 100 | 40 | 40% |
| Ecuador | 67 | 22 | 32.83% |
| Costa Rica | 48 | 6 | 12.5% |
| Panama | 48 | 6 | 12.5% |
| Peru | 35 | 11 | 31.43% |

| | | | |
|---|---|---|---|
| Venezuela | 35 | 16 | 45.72% |
| Brazil | 33 | 11 | 33.33% |
| Nicaragua | 14 | 0 | 0% |
| Guyana | 13 | 2 | 15.38% |
| Suriname | 12 | 0 | 0% |
| French Guiana | 10 | 0 | 0% |
| Honduras | 8 | 0 | 0% |
| Bolivia | 7 | 2 | 28.57% |
| Mexico | 7 | 0 | 0% |
| Guatemala | 6 | 0 | 0% |
| Belize | 5 | 0 | 0% |
| Lesser Antilles | 5 | 3 | 60% |

The species richness in Cyclanthaceae is concentrated along the tropical Andes, biogeographical region of Chocó, in southern Central America, and northwestern South America. Five species, *Carludovica palmata* Ruiz & Pav., *Cyclanthus bipatitus* Poit. ex A. Rich., *Evodianthus funifer* (Poit.) Lindm, *Ludovia lancifolia* Brong. and *Thoracocarpus bissectus* (Vell.) Harling, are widespread in Central and South America. The genus *Chorigyne* is restrict to Central America and *Stelestylis* is found in Guyana Shield, with a doubious species in the Atlantic Forest in Brazil. The second species of the *Evodianthus*, *E. cremnophilus* (Hammel & G.J.Wilder) E.S.Leal, is found in premontane forest in Cordillera Occidental in Colombia and Ecuador, while the monotypic *Schultesiophytum* is found only in the southwestern Amazon basin. Species of *Ludovia* occurs below 1200 m in Central and South tropical America except in the Atlantic Forest. The medium-sized genus *Sphaeradenia* occurs preferably at high altitudes in the Andean region, but some species are observed in lowland forests in pacific and western Amazon. Many species of *Dicranopygium* are found associated with rocks in rapids and streams, occur in lowland and premontane forests, predominantly in Chocó region, with few species found in the Amazonian lowlands. Two species of *Carludovica* are restricted to Central America and other two reach South America. Finally, the genus *Asplundia* is the most widespread of the Cyclanthaceae, delimiting its northern and southern distribuition. It ocurrs from Mexico to southern Brazil being, together with *Evodianthus* and *Thoracocarpus*, the three Cyclanthaceae native genera found in Atlantic Forest.

All the genera considered here are well delimited and monophyletic (Leal, chapter 1). This work, along with that phylogenetic hypothesis, aims to provide the taxonomic framework for future studies in the family, since the two largest genera, *Asplundia* and *Dicranopygium*, still require a considerable taxonomic review. Many species have been poorly understood in the past, sometimes known only from poor descriptions and/or type material, and numerous taxa are based on only one or a few specimens. The flowers of a large number of species remain little known or unknown, and ripe and inmature infructescence can bear different stages of tepals, styles and stigmas, which can lead to spurious delimitations or misidentifications.

## Nomenclator botanicus

1. **Asplundia acuminata** (Ruiz & Pav.) Harling, Acta Horti Berg. 17: 41. 1954 ≡ *Carludovica acuminata* Ruiz & Pav., Fl. Peruv. [Ruiz & Pavon] 1: 293. 1798 ≡ *Ludovia acuminata* (Ruiz & Pav.) Pers., Syn. Pl. [Persoon] 2: 576. 1807 ≡ *Salmia*

*acuminata* (Ruiz & Pav.) Willd., Mag. Neuesten Entdeck. Gesammten Naturk. Ges. Naturf. Freunde Berlin 5: 401. 1811. Type: Peru. [Huánuco], Pozuzo et Muña nemoribus, s.d., *H. Ruiz & J. A. Pavon s.n.* (lectotype: first-step lectotype designated by Harling (1958: 166), second-step, designated here: MA 810364 [digital image seen]; isolectotypes: G 00098242 [digital image seen], MA 810363 [digital image seen]).

*Habit and distribution.*—Root-climbing liana; endemic to Central Peru and probably Ecuador where it grows in mountain forests at high elevations.

*Notes*.—Ruiz & Pavón (1798) described *Carludovica acuminata* (= *Asplundia acuminata*) based on three sterile collections. Harling (1958) designated the material housed in MA herbarium as a lectotype, however two sheets of Ruiz & Pavón's collections are found in this herbarium without any evidence of which, or if both, Harling chose as lectotype. We complete the lectotypification here by desiginating MA 810363 as a second-step lectotype.

2. **Asplundia ahlneri** Harling, Acta Horti Berg. 18: 176. 1958, as '*Ahlneri'*. Type: Colombia. Cundinamarca, Sasaima, vereda San Bernardo; La María entre las quebradas La María y La Victoria, 1750–1940 m, 23 Jan 1948, *H. García-Barriga 12558* (holotype: US 00027128; isotype: COL 000006754).

*Habit and distribution.*—Root-climbing liana; occurs in Central Colombian and Venezuelan mountain forests at high elevations.

3. **Asplundia alata** Harling, Acta Horti Berg. 18: 223. 1958. Type: Panama. Colón [Canal Zone], Mojinga [Mohinga] swamp, 15 Jul 1931, *L. H. Bailey & E. Z. Bailey 579* (holotype: F V0092226F).

*Habit and distribution.*—Terrestrial short-stemmed herb, seldom root-climbing liana of wide distribution, known from Central America, in Costa Rica and Panama, to Colombia. It is restricted to rainy forests, below 1000 m of altitude, rarely more.

4. **Asplundia albicarpa** Hammel, Novon 13: 52. 2003. Type: Costa Rica. San José: Parque Nacional Braulio Carrillo, Estácion Carrillo, 400 m, 28 Jul 1985, *B. E. Hammel & J. Trainner 14253* (holotype: MO 2 sheets (MO 2805673, MO 2805638); isotypes: COL n.v., CR n.v., GB n.v., INB n.v., PMA n.v., QCNE n.v., US n.v.).

*Habit and distribution.*—Root-climbing liana and also often scandent terrestrial herb; wet forests of Central Costa Rica to Ecuador, up to 1800 m altitude.

5. **Asplundia allenii** Hammel, Novon 13: 55. 2003. Type: Panama. Coclé, El Valle de Antón, vicinity finca Tomás Arias, 600 m, 5 Aug 1946, *P. H. Allen 3623* (holotype: G n.v.; isotypes: F 2 sheets (F V0360282F, F V0360283), GH 00404550).

*Habit and distribution.*—Not stoloniferous terrestrial herb; pacific lowland forest from Panama to Colombia, mainly in region of Chocó region.

6. **Asplundia antioquiae** Harling, Acta Horti Berg. 18: 184. 1958, as '*Antioquiae*'. Type: Colombia. Antioquia, [Mutatá] selva pluvial; carretera al mar cerca de Villa Arteaga, precipitácion pluvial 3750–5000 mm anuales, 150 m, 4–8 Aug 1947, *W. H. Hodge 7063* (holotype: US 00027129; isotype: MEDEL 000333).

*Habit and distribution.*—Root-climbing liana; pacific lowland and montane forest from Costa Rica to Colombia, below 1000 m altitude.

7. **Asplundia aulacostigma** Harling, Acta Horti Berg. 18: 174. 1958. Type: Ecuador. Napo-Pastaza, Mera, ca. 1100 m, 3 Mar 1956, *E. Asplund 19568* (holotype: S R-505 [digital image seen]; isotypes: NY 00888365, S 06-4613 [digital image seen], UPS V-226141 [digital image seen]).

*Habit and distribution.*—Root-climbing liana; forests from pacific lowland and Andes's west slopes in Ecuador, below 1500 m altitude.

8. **Asplundia aurantiaca** Harling, Opera Bot., B 1: 24. 1973. Type: Ecuador. Esmeraldas, río San Miguel, 28 Mar–6 Apr 1959, *G. Harling 4683* (holotype: S R-506 [digital image seen]).

*Habit and distribution.*—Root-climbing liana; pacific lowland and Andes' west slopes forest, from Colombia to Ecuador, below 1000 m altitude.

9. **Asplundia australis** Harling, Acta Horti Berg. 18: 192. 1958. Type: Bolivia. La Paz, San Carlos, Mapiri river, 800 m, 5 Feb 1927, *O. Buchtien 349* (holotype: US 00027130; isotype: US 01013914).

*Habit and distribution.*—Root-climbing liana; known only from Bolivia.

*Notes*.—Two sheets are found in US herbarium. Only the sheet US 00027130 was annotated "holotype" by Harling and this one owns the original label of the Buchtien's collections. The sheet US 01013914 was annotated as "isotype" and "sheet 2" in unknown hand (certainly not Harling's) and does not have the original label of the Buchtien's collections. The sheets do not appear to be complementary; the protologue neither specifies a single sheet as holotype, nor cites an isotype at US. By not having noted "sheet 1" and being the sheet that certainly Harling analyzed, we considered as holotype only the sheet US 00027130.

10. **Asplundia brachyphylla** Harling, Acta Horti Berg. 18: 231. 1958. Type: Guyana. Anandabaru, Kopinang river, 549 m, Apr 1926, *R. A. Altson 471* (holotype: K, 2 sheets (K 000400087 [digital image seen], K 000400086 [digital image seen]); isotype: NY 00688968).

*Habit and distribution.*—Terrestrial herb with creeping stem; known in Guyana, Suriname, French Guyana and Brazilian Amazon.

11. **Asplundia brachypus** (Drude) Harling, Acta Horti Berg. 17: 41. 1954 ≡ *Carludovica brachypus* Drude in Martius & Eichler, Fl. Bras. 3: 237. 1881. Type: Brazil. Rio de Janeiro, Rio de Janeiro, Corcovado, Apr 1832, *B. Luschnath s.n.* (lectotype, designated by Harling (1958: 235): LE 00000961 [digital image seen]).

= *Carludovica schizophylla* Drude in Martius & Eichler, Fl. Bras. 3: 235. 1881. Type: Brazil. Rio de Janeiro, Petrópolis, Serra da Estrela [Serra de Estrella], Rio de Janeiro, Corcovado, Mar 1832, *B. Luschnath s.n.* (holotype: LE 00000962 [digital image seen]).

= *Asplundia polymera* (Hand.-Mazz.) Harling, Acta Horti Berg. 17: 42. 1954 ≡ *Carludovica polymera* Hand.-Mazz., Denkschr. Kaiserl. Akad. Wiss., Wien. Math.-Naturwiss. Kl. 79: 207. 1908. Type: Brazil. São Paulo, Rio Grande da Serra, prope rio Grande ad São Paulo Railway, 800 m, Jun 1901, *R. Wettstein & V. F. Schiffner s.n.* (holotype: WU 0038059 [digital image seen]).

= *Asplundia polymera* subsp. *reitzii* Harling, Acta Horti Berg. 18: 239. 1958. Type: Brazil. Santa Catarina, Itajaí, Luis Alves, rio Canoas, 50 m, 18 Jan 1953, *R. Reitz 5155* (holotype: HBR 0016328 [digital image seen]; isotypes: S 06-4533 [digital image seen], US 00027157).

= *Asplundia glaucophylla* Harling, Acta Horti Berg. 18: 237. 1958. Type: Brazil. Paraná, Volta Grande, 21 Jul 1911, *P. K. H. Dusén 11968* (holotype: S, 2 sheets (S 05-5583 [digital image seen], S R-514 [digital image seen]); isotypes: NY 00413610, S 06-4529 [digital image seen], US 00027139).

*Habit and distribution.*—Terrestrial herb with creeping stem, sometimes epiphytic on the base trees trunks; endemic to the Atlantic Forest in eastern Brazil.

*Notes*.—Morphological variation, ecological aspects and detailed geographic distribuition of *A. brachypus* are found in Leal (chapter 2).

12. **Asplundia brasiliensis** Harling, Acta Horti Berg. 18: 214. 1958. Type: Brazil. Amazonas, 5° 12’S, rio Jutahi, 29 Jan 1875, *J. W. H. Trail 1127* (holotype: K n.v.; isotype: P02085552 [digital image seen]).

*Habit and distribution.*—Habit unknown; known only from type locality in Brazil.

13. **Asplundia brunneistigma** Hammel, Novon 13: 57. 2003. Type: Costa Rica. Heredia, Parque Nacional Braulio Carrillo, primary forest between río Pejo and río Sardinaltio, Atlantic slope of volcán Barva, 10°17.5’N, 84°04.5’W, 700–800 m, 3 Apr 1986, *M. Grayum 6709* (holotype: MO 2632897; isotype: CR n.v., GB n.v., US n.v.).

*Habit and distribution.*—Root-climbing liana; found in Atlantic lowlands in Costa Rica, Panama and Colombia.

14. **Asplundia cabrerae** Harling, Acta Horti Berg. 18: 198. 1958, as ‘*Cabrerae*’. Type: Colombia. Amazonas, at border of Vaupés, río Apaporis, raudal Yayacopi (La playa) and vicinity, quarzite base, ca. 260 m, 0°5’S, 70°30’W, 18 Feb 1952, *R. E. Schultes & I. Cabrera 15506* (holotype: US 00027131).

*Habit and distribution.*—Root-climbing liana, seldom terrestrial herb; western Amazon in Colombia, Peru, Ecuador and probably Brazil.

15. **Asplundia callejasii** Tuberq. & E.S. Leal, Brittonia, *in press*. Type: Colombia. Antioquia: Amalfi, vereda El Jardín, quebrada La Quebradona, 7°04′34″N, 74°57’22.2’’W, 800–900 m, 25 July 2007, *D. Tuberquia, J. Cardona, C. Robles, E. Suarez, J. Lázaro Toro & D. Preciado 2944* (holotype: HUA; isotype: COL).

16. **Asplundia caput-medusae** (Hook.f.) Harling, Acta Horti Berg. 17: 42. 1954, as ‘*Caput-Medusae*’ ≡ *Carludovica caput-medusae* Hook.f., Bot. Mag. 116, ser. 3, v. 46: tab. 7118. 1890, as ‘*Caput-Medusae*’. Type: Unknown origin, probably from Venezuela, cultivated in Hort. Kewensis, 23 Dec 1887, *s.c. s.n.* (lectotype: K n.v., designated by Harling (1958: 218)).

*Habit and distribution.*—Terrestrial herb; Venezuela (Harling, 1958).

17. **Asplundia cayapensis** Harling, Opera Bot., B 1: 22. 1973. Type: Ecuador. Esmeraldas, Rio Grande, 70 m, 28 Mar–6 Apr 1959, *G. Harling 4633* (holotype: S 2 sheets, (S R-507 [digital image seen]; S 05-5573 [digital image seen]).

*Habit and distribution.*—Terrestrial herb; Ecuador (Harling, 1973).

18. **Asplundia ceci** Hammel, Novon 13: 59. 2003. Type: Costa Rica. San Jose, Braulio Carrillo Park, along road from near the entrance down to the río Sucio and in the vicinity of Estación Carrillo, 400–1500 m, 10°05–10'N, 84°57–69'W, *B. E. Hammel & J. Trainer 14260* (holotype: MO 2632940; isotypes: COL n.v., CR n.v., GB n.v., PMA n.v., US n.v.).

*Habit and distribution.*—Root-climbing liana, sometimes terrestrial from long stem; Costa Rica and Colombia.

19. **Asplundia clementinae** Harling, Acta Horti Berg. 18: 210. 1958, as '*Clementinae*'. Type: Ecuador. Los ríos, Hacienda Clementina on río Pita, 23 Mar 1939, *E. Asplund 5460* (holotype: S R-508 [digital image seen]).

*Habit and distribution.*—Root-climbing liana; known only from the type locality.

20. **Asplundia cupulifera** Harling, Acta Horti. Berg. 18: 168. 1958. Type: Colombia. Valle del Cauca, Sabaletas, km 29 on highway from Buenaventura to Cali, 25 m, 4 Jun 1944, *E. P. Killip & J. Cuatrecasas 38767* (holotype: F V0092230F; isotypes: COL 000006755, F V0092231F, US, 2 sheets (US 00027132, US 00027133)), VALLE 000230 [digital image seen]).

*Habit and distribution.*—Root-climbing liana; Pacific lowlands from Ecuador.

21. **Asplundia cuspidata** Harling, Acta Horti Berg. 18: 156. 1958. Type: Ecuador. Napo-Pastaza, Mera, in Rastrojo, ca. 1100 m, 3 Feb 1956, *E. Asplund 19192* (holotype: S R-509 [digital image seen]).

*Habit and distribution.*—Root-climbing liana; western Ecuador.

22. **Asplundia cymbispatha** Harling, Acta Horti Berg. 18: 220. 1958. Type: Bolivia. Tumupasa, 12 Dec 1901, *R. S. Williams 460* (holotype: NY 00688967).

*Habit and distribution.*—Terrestrial herb; southweast of Amazonian basin in Brazil, Bolivia, Colombia, and Peru.

23. **Asplundia divergens** (Drude) Harling, Acta Horti Berg. 17: 42. 1954 ≡ *Carludovica divergens* Drude in Martius & Eichler, Fl. Bras. 3: 241. 1881. Type: Brazil. Amazonas, rio Japurá, Dec 1819–Jan 1820, *C. F. P. Martius s.n.* (lectotype: M 0219253 [digital image seen], designated by Harling (1958: 201)).

*Habit and distribution.*—Root-climbing liana; found on Brazilian Amazon.

24. **Asplundia domingensis** Harling, Opera Bot., B 1: 25. 1973. Type: Ecuador. Santo Domingo, Hac. Zaracay, 500 m, 29 Mar 1967, *B. Sparre 15166* (holotype: S, 2 sheets (S R-510 [digital image seen], S 09-44070 [digital image seen])).

*Habit and distribution.*—Root-climbing liana; Pacific lowlands up to 1000 m in Colombia and Ecuador.

25. **Asplundia dussii** Harling, Acta Horti Berg. 18: 226. 1958, as '*Dussii*'. Type: Guadeloupe. Bains-Jaunes, 1896, *P. E. Duss 3804* (holotype: NY 00688966; isotypes: F V0092229F, US 00027134).

*Habit and distribution.*—Terrestrial herb; restrict to Lesser Antilles.

26. **Asplundia ecuadoriensis** (Harling) Harling, Acta Horti Berg. 17: 42. 1954 ≡ *Carludovica ecuadoriensis* Harling, Acta Horti Berg. 15: 199. 1950. Type: Ecuador. Los ríos, Hacienda Clementina, virgin forest, Samama, 750 m, 24 Mar 1947, *G. Harling 548* (holotype: S, 2 sheets (S A-4048 n.v., S A-4056 n.v.); isotype: S, 2 sheets (S 06-4630 [digital image seen], S R-511 n.v.).

*Habit and distribution.*—Root-climbing liana; known only from Ecuador.

27. **Asplundia euryspatha** Harling, Acta Horti Berg. 18: 248. 1958. Type: Costa Rica. Guanacaste, Vicinity of Tilarán, 500–650 m, 10–31 Jan 1926, *P. C. Standley & J. Valerio 44556* (holotype: US 00027135).

*Habit and distribution.*—Terrestrial herb; Costa Rica and Panama.

28. **Asplundia ewanii** Harling, Acta Horti Berg. 18: 154. 1958, as '*Ewanii*'. Type: Colombia. Putumayo, Cordillera Oriental (e. slope), Rio Afiladores drainage, vic. of Auroras near Llorente, 2195 m, 2 Oct 1944, *J. A. Ewan 16263* (holotype: US 00027136; isotype: US 01268613).

*Habit and distribution.*—Root-climbing liana; high altitudes in mountains of Central Colombia.

29. **Asplundia fagerlindii** Harling, Acta Horti Berg. 18: 247. 1958, as '*Fagerlindii*'. Type: Ecuador. Napo-Pastaza, Tiputini-Lagartococha, 20 Jan–5 Feb 1953, *F. Fagerlind & G. Wibom 2361* (holotype: S, 2 sheets (S 05-5578 [digital image seen]; S R-512 [digital image seen]); isotype: S 06-4636 [digital image seen]).

*Habit and distribution.*—Root-climbing liana; endemic from Ecuador.

30. **Asplundia fanshawei** (Maguire) Harling, Acta Horti Berg. 17: 42. 1954, as '*Fanshawei*' ≡ *Carludovica fanshawei* Maguire, Bull. Torrey Bot. Club 75: 189. 1948. Type: Guyana. Kaituma river, 12 miles up in marsh forest, 14 Mar 1945, *Forest Dept. 5140 (Field 2404)* (holotype: NY 00688962; isotype: K 000632670 [digital image seen]).

*Habit and distribution.*—Root-climbing liana; occurs in north of the South America, in Guiana Shield and adjacent parts of Brazil.

31. **Asplundia fendleri** Harling, Acta Horti Berg. 18: 221. 1958, as '*Fendeleri*'. Type: Venezuela. [Aragua], prope Coloniam Tovar, 1800–2000 m, 1856–1857, *A. Fendler 1348* (holotype: GH 00028601; isotype: GH, 2 sheets (GH 00112907, GH 00112908)).

*Habit and distribution.*—Terrestrial herb; known only from type locality in Venezuela.

32. **Asplundia ferruginea** Grayum & Hammel, Syst. Bot. 7: 225. 1982. Type: Costa Rica. Heredia, Finca La Selva, the OTS field station on the río Puerto Viejo just E of its junction with the río Sarapiquí, about 800 m S near loop, ca. 100 m, 28 May 1981, *B. E. Hammel & J. Trainner 10759* (holotype: DUKE 10000072 [digital image seen]; isotypes: MO 102950, NY 00133654).

*Habit and distribution.*—Root-climbing liana; known from Nicaragua to Panama.

33. **Asplundia flavovaginata** Harling, Acta Horti Berg. 18: 194. 1958. Type: Peru. Huánuco, Prov. Huanúco, Tingo Maria, 10 Aug 1940, *E. Asplund 12943* (holotype: S 05-5581 [digital image seen]; isotype: S R-513 [digital image seen]).

*Habit and distribution.*—Root-climbing liana; found in mountains of Central Peru, Colombia, Venezuela to Costa Rica.

34. **Asplundia gamotepala** Harling, Acta Horti Berg. 18: 250. 1958. Type: Colombia. Valle del Cauca, North shore of Buenaventura Bay; near sea level, 3 Jun 1944, *E. P.*

*Killip & J. Cuatrecasas 38736* (holotype: F, 2 sheets (F V0092232F, F V0092233F); isotype: VALLE 000228 [digital image seen]).

*Habit and distribution.*—Root-climbing liana; Pacific lowlands from Colombia.

35. **Asplundia gardneri** (Hook.) Harling, Acta Horti Berg. 17: 42. 1954, as '*Gardneri*' ≡ *Carludovica gardneri* Hook., J. Bot. (Hooker) 2: 29. 1840. Type: Brazil. Ceará, Serra do Araripe, Sep 1838, *G. Gardner 1866* (lectotype: first-step designated by Harling (1958: 206), second-step, designated here: K 000632673; isolectotypes: BM 000938232 *pro parte* [digital image seen], CGE n.v., FI n.v., G, 2 sheets (G 00098243 [digital image seen], G 00098244 [digital image seen]), K 000632672 *pro parte* [digital image seen], L 0041991 [digital image seen], NY 00133658, OXF n.v., P, 3 sheets (P 000726022 [digital image seen], P 000726023 *pro parte* [digital image seen], P 000726024 [digital image seen]), US 00027126).

*Habit and distribution.*—Terrestrial herb with creeping stem, seldom inhabits rocky and humid places; known only from Brazil. This is the only species of Cyclanthaceae that occurs in mountain relictual rainforest enclaves in Caatinga vegetation, localy known as *brejos*, and in riparian forests in Central Brazilian Cerrado.

*Notes.*—Harling (1958) designated the material housed in K herbarium as lectotype. Nevertheless, at least two sheets of *Gardner 1866* are found in K herbarium, without any evidence of Harling's lectotypification. Here, we complete the lectotypification by desiginating K 000632673, with a leaf and two infructescences, as a second-step lectotype because the remanescent sheet (K 000632672) is a mixed collection, composed of an *Asplundia gardneri* infructescence and a palm leaf.

36. **Asplundia gigantea** Tuberq., Caldasia 19: 182. 1997. Type: Colombia. Chocó, Nuquí, Corregimiento de Arusí, región del Cabo Corrientes, Estación Biológica "El Amargal", 0-50 m, 05°30'-05°37'N, 77°30'W, 6 May 1994, *D. Tuberquia 265* (holotype: HUA n.v.; isotype: COL 000006756).

*Habit and distribution.*—Terrestrial herb with creeping stem or root-climbing liana; known from Colombian Pacific lowlands, below 1000 m, in the Departments of Chocó and Antioquia.

37. **Asplundia glandulosa** (Gleason) Harling, Acta Horti Berg. 17: 42. 1954 ≡ *Carludovica glandulosa* Gleason, Bull. Torrey Bot. Club 56: 8. 1929. Type: Guyana. Mt. Russell District, Mar 1886, *G. S. Jenman 2105* (holotype: K 000400088 [digital image seen]).

*Habit and distribution.*—Terrestrial plant; known from Guyana, Suriname, French Guyana, and Brazil.

38. **Asplundia gleasonii** Harling, Acta Horti Berg. 18: 234. 1958, as '*Gleasonii*'. Type: Guyana. Potaro River, [in forest near the] Kaieteur savannah, Sep–Oct 1881, *G. S. Jenman 900* (holotype: K 000400093 [digital image seen]).

*Habit and distribution.*—Root-climbing liana; known only from Guyana.

39. **Asplundia goebelii** (J. Weiss & R. Wagner) Harling, Acta Horti Berg. 17: 42. 1954, as '*Goebelii*' ≡ *Carludovica goebelii* J. Weiss & R. Wagner, Allg. Bot. Z. Syst. 5: 138. 1899. Type: Venezuela. Carabobo, San Esteban [cultivated in Hortus Bot. Monacensis], Dec 1903, *s.c. s.n.* (neotype: M 0219252 [digital image seen], designated by Harling (1958: 219)).

*Habit and distribution.*—Terrestrial herb with creeping stem, seldom root-climbing liana; this is a poorly known species, found only in Venezuela.

*Notes*.—Apparently this species was described on living material garden, which has probably not been preserved. Two sheets, collected in 1903, from cultivated plants in the Hortus Botanicus Monacencis are housed at M herbarium, one of which (M 0219252) Harling (1958) designated as neotype.

40. **Asplundia guianensis** Harling, Acta Horti Berg. 18: 206. 1958. Type: Guyana. Kaituma river, 12 miles up in marsh forest, 14 Mar 1945, *Forest Dept. 5141 (Field 2405)* (holotype: U 0001484 [digital image seen]; isotypes: K, 2 sheets (K 000632674 [digital image seen], K 000622675 [digital image seen]), NY 00688965, US 00027140).

= *Asplundia altiscandens* E.S.Leal, Nordic J. Bot. 29: 687. 2011 [2012]. Type: Brazil. Pará, Curuça, Ilha do Mutucal, Capoeirão, 7 Apr 2007, *J. Oliveira, S. Almeida, A. S. Silva & C. Rosário 896* (holotype: MG, 2 sheets). **syn. nov.**

*Habit and distribution.*—Root-climbing liana; known from Guyana and Brazil in the states of Amazonas, Amapá and Pará.

*Notes.*—*Asplundia altiscandens*, described by Leal (2011), is conspecific with *A. guianensis*, till recently known only by few collections that did not reflect its morphological variation. Analysis of more collections from the Brazilian states of Amazonas, Pará and Amapá made it clear that *A. guianensis* presents both wide distribution and morphological variation, encompassing *A. altiscandens*.

41. **Asplundia harlingiana** Galeano & R.Bernal, Caldasia 14: 27. 1984. Type: Colombia. Antioquia, El Retiro, ca. 4 km al NO de la cabecera municipal, cerca de la quebrada La Agudelo, ca. 2200–2300 m, 12 Apr 1980, *R. Bernal & G. Galeano 150* (holotype: COL 000006757).

*Habit and distribution.*—Terrestrial herb or root-climbing liana; known exclusively from nothern Cordillera Central in the Department of Antioquia, Colombia, between 1900 and 2300 m.

42. **Asplundia helicotricha** (Harling) Harling, Acta Horti Berg. 17: 42. 1954 ≡ *Carludovica helicotricha* Harling, Acta Horti Berg. 15: 194. 1950. Type: Ecuador.

Napo-Pastaza, Mera, 1160 m, 27 Mar 1940, *M. Lugo 133* (holotype: S, 2 sheets (S R-515 [digital image seen], S 05-5586 [digital image seen]).

*Habit and distribution.*—Root-climbing liana; known only from Ecuador.

43. **Asplundia heteranthera** Harling, Acta Horti Berg. 18: 152. 1958. Type: Brazil. [Pará, Igarapé-açu], Colônia do Prata [Santo Antônio do Prata], 24 Sep 1903, *J. Huber 3831* (holotype: G 00016546 [digital image seen]; isotype: MG 003831).

*Habit and distribution.*—Root-climbing liana; known from Suriname, French Guyana, and Brazil.

44. **Asplundia hookeri** (H.Wendl. ex Kuntze) Harling, Acta Horti Berg. 17: 42. 1954, as ‘*Hookeri*’ ≡ *Carludovica hookeri* H.Wendl. ex Kuntze, Revis. Gen. Pl. 2: 738. 1891 Type: Unknown origin, probably Venezuela, cultivated in Hort. Kewensis, *s.c. s.n.* (lectotype: K 001097482 [digital image seen], designated by Harling (1958: 222)).

*Habit and distribution.*—Terrestrial herb; known only from Venezuela (Harling, 1958).

45. **Asplundia humilis** (Poepp. & Endl.) Harling, Acta Horti Berg. 17: 42. 1954 ≡ *Carludovica humilis* Poepp. & Endl., Nov. Gen. Sp. Pl. (Poeppig & Endlicher) 2: 37. 1838 ≡ *Salmia humilis* (Poepp. & Endl.) Steud., Nomencl. Bot. [Steudel], ed. 2, 2: 501.

1841. Type: Peru. Maynas, in sylvis udis ad Yurimaguas, 1831, *E. F. Poeppig 2412* (holotype: W, probably destroyed during World War II; F photo negative 29801).

*Habit and distribution.*—Terrestrial plant; species known only from the type collection.

46. **Asplundia insignis** (Duchass. ex Griseb.) Harling, Acta Horti Berg. 17: 42. 1954 ≡ *Carludovica insignis* Duchass. ex Griseb., Fl. Brit. W. I. [Grisebach]: 513. 1864. Type: Guadeloupe. s.l., 1851, *E. P. Duchassaing s.n.* (lectotype: P 00726025 [digital image seen], designated by Harling (1958: 224); isolectotypes: GOET 002348 [digital image seen], P 00726026 [digital image seen]).

= *Carludovica caribaea* J.F.Cowell, Torreya 3: 103. 1903. Type: Saint Kitts and Nevis. Molyneaux Estate, in a forest ravine, 13 Sep 1901, *N. L. Britton & J. F. Cowell 326* (holotype: NY, 3 sheets (NY 00073055, NY 00073056, NY 00563954)).

*Habit and distribution.*—Terrestrial plant; endemic to Lesser Antilles.

47. **Asplundia isabellina** Harling, Acta Horti Berg. 18: 173. 1958. Type: Ecuador. Napo-Pastaza, Mera, in rastrojo, ca. 1100 m, 10 Dec 1955, *E. Asplund 18778* (holotype: S R-516 [digital image seen]; isotype: S 06-4642 [digital image seen]).

= *Asplundia leptospatha* Harling, Acta Horti Berg. 18: 164. 1958. Type: Costa Rica. Puntarenas, between Golfo Dulce and río Térraba, 30 m, Dec 1947, *A. F. Skutch 5352* (holotype: US 00027141).

*Habit and distribution.*—Root-climbing liana; known from Costa Rica, Panama and Ecuador.

*Notes.*—Hammel (2003) synonymized *Asplundia leptospatha* under *Asplundia isabellina*.

48. **Asplundia krukoffii** Harling, Acta Horti Berg. 18: 196. 1958, as ‘*Krukoffii*’. Type: Brazil. Amazonas; Basin of rio Juruá, near mouth of Rio Embira [Envira] (tributary of rio Tarauacá), 7°30’S, 70°15’W, *B. A. Krukoff 4926* (holotype: NY 00688964).

*Habit and distribution.*—Root-climbing liana; known only to the southweastern Amazon basin in Brazil.

49. **Asplundia labela** (R.E.Schult.) Harling, Acta Horti Berg. 17: 42. 1954, as ‘*Labela*’ ≡ *Carludovica labela* R.E.Schult., Bot. Mus. Leafl. 9: 166. 1941. Type: Mexico. Oaxaca, District Choapan, on floor of dark rain-forest or on rotten logs, summit of the mountains between Santa María Yahuivé and Santiago Yaveo, 1000 m, 17°20’N, 95°45’W, 15 May 1939, R. E. *Schultes & B. P. Reko 920* (holotype: GH, 2 sheets (GH 00028595, GH 00028596); isotype: GH 00028594).

= *Asplundia chiapensis* (Matuda) Harling, Acta Horti Berg. 17: 42. 1954 ≡ *Carludovica chiapensis* Matuda, Bull. Torrey Bot. Club 76: 210. 1949, Type: Mexico. Chiapas, finca Córcega, Pueblo Nuevo Comaltitlán, in wet forest, 900 m, 14 Apr 1948, *E. Matuda 17697* (neotype, designated here: MEXU, 3 sheets (MEXU 00007372 [digital image seen], MEXU 00007753 [digital image seen], MEXU 00007754 [digital image seen]); isoneotypes: CAS 000135 [digital image seen], CHIP n.v., F V0092237F, NY 00133655, S G-8278 [digital image seen], US 00027150).

*Habit and distribution.—*Terrestrial herb, seldom root-climbing liana; a widespread species in in Belize, Guatemala, Honduras, Mexico and Nicaragua.

*Notes.—*Matuda (1949) indicates the type of *Carludovica chiapensis* being collection *Matuda 17694*, collected on 19 April 1948, as "type in Matuda Herbarium, isotypes in the Instituto de Biología of Mexico, Museo de Dirección General de Agricultura of Mexico, and the Chicago Natural History Museum". However, this collection is not found in these mentioned herbaria. Harling (1958) abbreviated the Matuda herbarium as MAT, and indicated the collection *Matuda 17697*, collected on 14 April 1948, as holotype housed in this herbarium, with many duplicates. The MAT herbarium no longer exists and the collections of Eizi Matuda are distributed in several herbaria. The collection *Matuda 17694* was not found, and at that time not possible to know if it exists or if it is a typographical error. We choose *Matuda 17697*, in MEXU herbarium, as neotypus of the *C. chiapensis*. Hammel (2001) synonymized *Asplundia chiapensis* under *Asplundia labela*.

50. **Asplundia latifolia** (Ruiz & Pav.) Harling, Acta Horti Berg. 17: 41. 1954 ≡ *Carludovica latifolia* Ruiz & Pav., Fl. Peruv. [Ruiz & Pavon] 1: 292. 1798 ≡ *Ludovia latifolia* (Ruiz & Pav.) Pers., Syn. Pl. [Persoon] 2: 576. 1807 ≡ *Salmia latifolia* (Ruiz & Pav.) Willd., Mag. Neuesten Entdeck. Gesammten Naturk. Ges. Naturf. Freunde

Berlin 5: 401. 1811. Type: Peru. Huánuco, Chinchao, Muña, Pozuzo et Cuchero nemoribus calidissimis, s.d., *H. Ruiz & J. A. Pavon s.n.* (lectotype: G 00098245, designated by Harling (1958:189); isolectotypes: FI n.v., MA 810367 [digital image seen], MA 810368 [digital image seen], MA 810369 [digital image seen]).

*Habit and distribution.*—Terrestrial herb or root-climbing liana; known only from the mountain forests of Central Peru.

51. **Asplundia latifrons** (Drude) Harling, Acta Horti Berg. 17: 42. 1954 ≡ *Carludovica latifrons* Drude in Martius & Eichler, Fl. Bras. 3: 237. 1881. Type: Brazil. [Amazonas], São Gabriel [da Cachoeira], in ditione vallis Amazonum occidental ad flum. Rio Negro, Mar 1852, *R. Spruce 2294* (lectotype: K 000632676 [digital image seen], designated by Harling (1958: 204); isolectotype: P 00726021 [digital image seen]).

*Habit and distribution.*—Root-climbing liana; known only from Brazil.

52. **Asplundia liebmannii** Harling, Acta Horti Berg. 18: 232. 1958, as '*Liebmannii*' ≡ *Carludovica mexicana* Liebm., nom. in sched. Type: Mexico. Oaxaca, Baranca de la Hacienda de Jovo, May 1941, *F. M. Liebmann 10802* (holotype: C 10009986 [digital image seen]; isotype: US, 3 sheets (US 00027142, US 00027143, US 00027144).

*Habit and distribution.*—Terrestrial herb; known from south Mexico, Honduras and Nicaragua.

53. **Asplundia lilacina** Harling, Opera Bot., B 1: 20. Type: Ecuador. Pastaza, Mera, 27–28 Mar 1968, *G. Harling, G. Storm & B. Ström 7854* (holotype: GB, 3 sheets (GB 0047561 [digital image seen], GB 0047562 [digital image seen], GB 0047563 [digital image seen]).

*Habit and distribution.*—Root-climbing liana; found only in Ecuador.

54. **Asplundia longicrura** (Drude) Harling, Acta Horti Berg. 17: 42. 1954 ≡ *Carludovica longicrura* Drude in Martius & Eichler, Fl. Bras. 3: 240. 1881. Type: Brazil. [Amazonas], in Brasiliae aequatorialis silvis ad. flum. Taruma [Tarumã], Mar 1855, *R. Spruce s.n.* (holotype: K 000632677 [digital image seen]).

*Habit and distribution.*—Root-climbing liana; found only in Brazilian Amazon.

*Notes.*—Both Drude (1881) and Harling (1958) testified the type locality of this species as *flum. Jaruma* or “rio Jaruma”. However, this is a typographical error. Spruce (1908: 495) reports a short excursion “from Barra [Barra do Rio Negro, currently Manaus] to rio Taruma [Tarumã]” in which the holotype from *Asplundia longicrura* was collected.

55. **Asplundia longitepala** Harling, Acta Horti Berg. 18: 195. 1958. Type: Colombia. Valle del Cauca, Cordillera Occidental, vertiente oriental; Hoya del río Cali, vertiente derecha: Baga de la Tulia, 1850–2000 m, 30 Oct 1944, *J. Cuatrecasas 18381* (holotype: VALLE, 2 sheets (VALLE 000236 [digital image seen], VALLE 000237 [digital image seen]).

*Habit and distribution.*—Root-climbing liana; known from Costa Rica to western Colombia.

56. **Asplundia luetzelburgii** Harling, Acta Horti Berg. 18: 228. 1958, as '*Luetzelburgii*'. Type: Brazil. [Amazonas, São Gabriel da Cachoeira], Tunuy [Tunuí], rio Içana, ufer am fall sehr feucht, 28 Oct 1926, *P. Luetzelburg 22667* (holotype: M 0219250 [digital image seen]; isotype: R 000044713, mixture with *Sphaeradenia amazonica* Harling).

*Habit and distribution.*—Terrestrial herb; ocurrs in northwestern Amazonian basin, in Brazil, Colombia, and Venezuela.

57. **Asplundia lutea** Harling, Opera Bot., B 1: 14. 1973. Type: Ecuador. Esmeraldas, río San Miguel, virgin forest, 28 Mar–6 Apr 1959, *G. Harling 4697* (holotype: S R-517 [digital image seen]).

*Habit and distribution.*—Root-climbing liana; known only from Ecuador.

58. **Asplundia maguirei** Harling, Acta Horti Berg. 18: 228. 1958, as '*Maguirei*'. Type: Guyana. Potaro River Gorge, 17 May 1944, *B. Maguire & D. B. Fanshawe 23533* (holotype: NY 00688963; isotypes: GH 00028602, K 000632671 [digital image seen]).

*Habit and distribution.*—Root-climbing liana; known from Guyana and Suriname.

59. **Asplundia meraënsis** Harling, Opera Bot., B 1: 13. Type: Ecuador. Pastaza, Mera, virgin forest, 1400 m, 29 Dec 1958, *G. Harling 3772* (holotype: S R-518 [digital image seen]).

*Habit and distribution.*—Root-climbing liana; endemic to the Ecuador.

60. **Asplundia microphylla** (Oerst.) Harling, Acta Horti Berg. 17: 42. 1954 ≡ *Carludovica microphylla* Oerst., Vidensk. Meddel. Naturhist. Foren. Kjøbenhavn 1857: 197. 1857. Type: Costa Rica. [Cartago], in sylvis umbrosis circa Turialvam [Turrialba], May 1847, *A. S. Oersted s.n.* (holotype: C 10021530 [digital image seen]; isotype: MO photo negative MO 370010).

= *Asplundia microphylla* subsp. *panamensis* Harling, Acta Horti Berg. 18: 161. 1958. Type: Panama, Chiriquí, río Chriquí Viejo valley, 8 Apr 1938, *G. White 75* (holotype: MO 123149; isotypes: F n.v., GH 00028596).

= *Asplundia sphaerocephala* Harling, Acta Horti Berg. 18: 164. 1958. Type: Nicaragua. [Granada], Mombacho Volcano, 900 m, 5 Jul 1923, *W. R. Maxon, A. D. Harvey & A. T. Valentine 7756* (holotype: US 00027159; isotype: BM n.v.).

*Habit and distribution.*—Root-climbing liana; ocurrs in Central America from Nicaragua to Panama.

*Notes.*—Barry Hammel synonymized *Asplundia sphaerocephala* (Hammel, 2001) and *Asplundia microphylla* subsp. *panamensis* (Hammel, 2003b) under *Asplundia microphylla*.

61. **Asplundia moritziana** (Klotzsch) Harling, Acta Horti Berg. 17: 42. 1954. as '*Moritziana*' ≡ *Carludovica moritziana* Klotzsch, Linnaea 20: 468. 1847. Type: Venezuela. [Aragua], Col. Tovar, ad trunc scandens in sylvis humidis umbrosis, 1846, *J. W. K. Moritz 325 b* (neotype: LE 00000958 [digital image seen], designated by Harling (1958: 144); isoneotypes: F photo negative 4293, HBG, 2 sheets (HBG 514486 [digital image seen], HBG 514487 [digital image seen]), LE 00000959 [digital image seen]).

= *Carludovica macropoda* Klotzsch, Linnaea 20: 469. 1847. Type: Venezuela. [Aragua], Col. Tovar, in sylvis humidis umbrosis, 1846, *Moritz 5* (neotype: BM n.v., designated by Harling (1958: 144); isoneotype: F photo negative 4294, HBG, 2 sheets (HBG 514484 [digital image seen], HBG 514485 [digital image seen]), P 00726020 [digital image seen]).

*Habit and distribution.*—Root-climbing liana; known only in Venezuela.

62. **Asplundia multistaminata** Harling, Acta Horti Berg. 18: 158. 1958. Type: Costa Rica. Limón, Jiménez, Llanuras de Santa Clara, 200 m, Apr 1894, *J. D. Smith 4985* (holotype: US 00027155; isotype: GH 00028599).

*Habit and distribution.*—Root-climbing liana; known from Nicaragua, Costa Rica, and Panama.

63. **Asplundia neblinae** Harling, Mem. New York Bot. Gard. 23: 108. 1972. Type: Venezuela. Amazonas, Cerro de la Neblina, río Yatua, frequent in forest between camps 3 and 4, elev. 1100 m, 10 Nov 1957, *B. Maguire, J. J. Wurdack & C. K. Maguire 42019* (holotype: GB 0047564 [digital image seen]; isotypes: NY 02350154, US 00890130).

*Habit and distribution.*—Root-climbing liana; known only from Brazil-Venezuela border.

64. **Asplundia nilssonii** Harling, Bol. Soc. Venez. Ci. Nat. 25: 59. 1963, as '*Nilssonii*'. Type: Venezuela. Bolívar, Cerro Uananapan, soth of Uei-tepui, [2] kms from campamento 132, between Luepa and Cerro Venamo, 1330–1450 m, 25 Apr 1960, *J. A. Steyermark & S. Nilsson 763* (holotype: VEN 45143 [digital image seen]; isotypes: NY 02350155, S R-519 [digital image seen], UPS n.v.).

*Habit and distribution.*—Root-climbing liana; known only to the type locality.

65. **Asplundia nonoënsis** Harling, Acta Horti. Berg. 18: 211. 1958. Type: Ecuador. Pichincha, Los Puentes (near Nanegal towards Nono), forest, ca. 1200 m, 11 Aug 1955, *E. Asplund 17290* (holotype: S R-520 [digital image seen]; isotypes: NY, 2 sheets (NY 02361386, NY 02361387), S 06-4643 [digital image seen]).

*Habit and distribution.*—Root-climbing liana; known only from the type locality.

66. **Asplundia pariensis** Harling, Bol. Soc. Venez. Ci. Nat. 25: 60. 1963. Type: Venezuela. Sucre, Peninsula de Paria, Cerro Patao, Norte de Puerto de Hierro, noroeste de Güiria; Selva nublada por debajo de la cumbre, 800–825 m, 19 Jul 1962, *J. A. Steyermark & G. Agostini 91108* (holotype: S R-521 [digital image seen]; isotype: K 000632668, VEN 55047 [digital image seen]).

*Habit and distribution.*—Root-climbing liana; known only from type locality.

67. **Asplundia parviflora** Harling, Acta Horti Berg. 18: 158. 1958. Type: Peru. Huánuco, Huamalies, Monzon et Huallaga, 700–800 m, 1906, *A. Weberbauer 3689* (holotype: G, 2 sheets (G 00098246 [digital image seen]; one sheet without barcode).

*Habit and distribution.*—Root-climbing liana; known only from type locality.

68. **Asplundia pastazana** Harling, Acta Horti Berg. 18: 212. 1958. Type: Ecuador. Napo-Pastaza, 10 Mar 1956, *E. Asplund 19685* (holotype: S R-522 [digital image seen]).

*Habit and distribution.*—Root-climbing liana; known only from lower Andine slopes of eastern Ecuador.

69. **Asplundia peruviana** Harling, Acta Horti Berg. 18: 190. 1958. Type: Peru. Junín, Puerto Yessup; ca. 400 m, dense forest, 10–12 Jul 1929, *E. P. Killip & A. C. Smith 26240* (holotype: NY 00688978; isotype: US 00027156).

*Habit and distribution.*—Root-climbing liana; common species in southweast Amazon, in Colombia, Peru, and Brazil.

70. **Asplundia pittieri** (Woodson) Harling, Acta Horti Berg. 17: 42. 1954, as '*Pittieri*' ≡ *Carludovica pittieri* Woodson in Woodson & Schery, Ann. Missouri Bot. Gard. 29: 323. 1942. Type: Panama. San Blas, high hills back of Puerto Obaldía; 50–200 m, Aug 1911, *H. Pittier 4312* (holotype: US 00027147; isotypes: GH 00028600, NY 00688961).

*Habit and distribution.*—Terrestrial herb; ocorrus in lowlands forests from Costa Rica to Colombia's pacific coast.

71. **Asplundia platanthera** Harling, Acta Horti Berg. 18: 176. 1958. Type: Peru. Huánuco, Huánuco, La divisora, forest, ca. 1600 m, 28 Jul 1940, *E. Asplund 12589* (holotype: S R-523 [digital image seen]; isotype: S 05-5599 [digital image seen]).

*Habit and distribution.*—Root-climbing liana; known moutains forests from Central Peru.

72. **Asplundia platyphylla** Harling, Acta Horti Berg. 18: 241. 1958. Type: Colombia. Valle del Cauca, Costa del Pacífico; río Cajambre: Barco, 5–80 m, 23 Apr 1944, *J. Cuatrecasas 17020* (holotype: VALLE, 4 sheets (VALLE 000218 [digital image

seen], VALLE 000219 [digital image seen], VALLE 000220 [digital image seen], VALLE 000221 [digital image seen]).

= *Asplundia longistyla* Harling, Acta Horti Berg. 18: 242. 1958. Type: Colombia. Nariño, Quebrada La Toma, on Rio Telembi, between Rio Pimbi and Rio Cuembí, above Barbacoas, ca. 70 m, 4 Feb 1945, *J. A. Ewan 16863* (holotype: US, 2 sheets (US 00027152, US 00027153)). **syn. nov.**

*Habit and distribution.*—Terrestrial plant, seldom root-climbing-liana; known exclusively from Colombia's pacific lowlands and western slopes of Cordillera Occidental, below 1800 m.

*Notes.*—This is a very distinctive species from western Colombia with leaf segment broad, subcuneate and rotundate. Type material of *Asplundia platyphylla* and *A. longistyla* are indistinguishable and, since the two names have been published together, we have chosen *A. platyphylla* as the correct name for its more complete type collection and for being a name more commonly used.

73. **Asplundia ponderosa** R.E.Schult. ex Harling, Acta Horti Berg. 18: 217. 1958. Type: Colombia. [Amazonas], Comisaria del Amazonas, río Apaporis, raudal de Jerijerimo, extensive white-sand savannah or caatinga on right bank, Mar 1951, *R. E. Schultes 12093* (holotype: COL 000006768; isotype: GH 00028603).

*Habit and distribution.*—Terrestrial herb; known from western Amazon in Colombia and Brazil.

74. **Asplundia pycnantha** Harling, Acta Horti Berg. 18: 208. 1958. Type: Colombia. Valle del Cauca, Costa del Pacífico; río Cajambre: Silva, 5–80 m, 5–15 May 1944, *J. Cuatrecasas 17588* (holotype: F V0092234F, isotype: VALLE 000225 [digital image seen]).

*Habit and distribution.*—Root-climbing liana; common species in Pacific region from Colombia and Ecuador, below 1300 m.

75. **Asplundia quinindensis** Harling, Acta Horti Berg. 18: 209. 1958. Type: Ecuador. Esmeraldas, Quinindé (Rosa Zárate), dense forest, 13 May 1955, *E. Asplund 16299* (holotype: S 05-5600 [digital image seen]; isotypes: NY 02350156, S R-524 [digital image seen]).

*Habit and distribution.*—Root-climbing liana; ocurrs in lowland of northwestern Ecuador.

76. **Asplundia rhodea** R.E.Schult. ex Harling, Acta Horti Berg. 18: 214. 1958. Type: Colombia. Meta, Cordillera La Macarena (extreme nordeste), macizo Renjifo, cumbre y alrededores, 1300–1900 m, 6–20 Jan 1951, *J. M. Idrobo & R. E. Schultes 953* (holotype: COL 000006758; isotype: MO 1515097, US 00027158).

*Habit and distribution.*—Terrestrial herb; known only from the Sierra de La Macarena's mountain forests.

77. **Asplundia rigida** (Aubl.) Harling, Acta Horti Berg. 17: 43. 1954 ≡ *Pothos rigidus* Aubl., Hist. pl. Guiane 2: 839. 1775 ≡ *Carludovica plumerii* Kunth, Enum. Pl. [Kunth] 3: 106. 1841, nom. illeg. ≡ *Carludovica rigida* (Aubl.) Urban, Repert. Spec. Nov. Regni Veg. 15: 397. 1919. Type: Martinique, s.l., 1689–1690, *J. D. Surian s.n.* (lectotype: P n.v., designated by Harling (1958: 146); isolectotype: L n.v.).

= *Carludovica angustifolia* Seem. ex Griseb., Fl. Brit. W. I. [Grisebach]: 513. 1864, *nom. inval.*

= *Carludovica scandens* J.F.Cowell, Torreya 3: 103. 1903. Type: Saint Kitts and Nevis. Buckely Estate, in the forest, 8 Sep–5 Oct 1901, *N. L. Britton & J. F. Cowell 164* (holotype: NY, 3 sheets (NY 00073057, NY 00073058, NY 00073059)).

*Habit and distribution.*—Root-climbing-liana, seldom terrestrial herb; ocurrs in Lesser Antilles and Trinidad and Tobago.

78. **Asplundia rivularis** (Lindm.) Harling, Acta Horti Berg. 17: 43. 1954 ≡ *Carludovica rivularis* Lindm., Bih. Kongl. Svenska Vetensk.-Akad. Handl. 26, Afd. 3, no. 8: 4. 1900. Type: Brazil. São Paulo, Santos [São Vicente], Sororocaba, inter saxa rivuli umbrosi, 10 Dec 1874, *C. W. H. Mosén 2946* (lectotype: S R-525 [digital image seen], designated by Harling (1958: 236); isolectoypes: S 14-45666 [digital image seen], UPS V226072 [digital image seen]).

*Habit and distribution.*—Rheophytic herb along streams and rocky places; endemic to the Atlantic Forest in Brazil.

79. **Asplundia sanctae-ritae** Galeano & R. Bernal, Caldasia 14: 28. 1984. Type: Colombia. Antioquia, Guatapé, Vereda Santa Rita, ca. 12 km al E de la Cabecera Municipal, ca. 1900 m, *R. Bernal & G. Galeano 196* (holotype: COL, 3 sheets (COL 000006759, COL 000006760, COL 000006761); isotype: HUA n.v.).

*Habit and distribution.*—Root-climbing liana; mountain forests from Costa Rica, Panama and Colombia, between 800 to 2000 m.

80. **Asplundia sarmentosa** Galeano & R. Bernal, Caldasia 14: 29. 1984. Type: Colombia. Antioquia, Vereda Santa Elena, 12 km al E de Medellín, 2400 m, 27 Dec 1980, *R. Galeano & G. Bernal 339* (holotype: COL, 4 sheets (COL 000006762, COL 000006763, COL 000006764, COL 000006765); isotype: HUA n.v.).

*Habit and distribution.*—Root-climbing liana; known only from Colombia, on the Cordillera Central, in the Departments of Antioquia, Caldas and Risaralda, between 1880 and 2500 m altitude.

81. **Asplundia schizotepala** Harling, Acta Horti Berg. 18: 155. 1958. Type: Ecuador. Napo-Pastaza, NE, Tiputini-Lagartococha, 20 Jan–5 Jan 1953, *F. Fagerlind & G. Wibom 2360* (holotype: S R-526 [digital image seen]).

*Habit and distribution.*—Root-climbing liana; occurs in southwestern Amazon in Brazil, Colombia, Ecuador, and Peru.

82. **Asplundia sleeperae** Grayum & Hammel, Syst. Bot. 7: 222. 1982. Type: Costa Rica. Heredia, Finca La Selva, the OTS field Station on the río Puerto Viejo just E of its junction with the río Sarapiquí, ca. 100 m, 5 May 1980, *M. Grayum 2791* (holotype: DUKE 10000074 [digital image seen]).

*Habit and distribution.*—Terrestrial herb; known from Nicaragua to Colombia; below 1300 m.

83. **Asplundia sparrei** Harling, Opera Bot., B 1: 21. 1973, as ‘*Sparrei*’. Type: Ecuador. Zamora-Chinchipe, road Loja to Zamora, km 54, deep ravine with dense (sub-) tropical vegetation, ca. 1000 m, 17–18 May 1967, *B. Sparre 16358* (holotype: S R-527 [digital image seen]; isotype: MEL 2376181 [digital image seen]).

*Habit and distribution.*—Root-climbing liana; known only of the type locality.

84. **Asplundia spectabilis** Harling, Acta Horti Berg. 18: 240. 1958. Type: Venezuela. Yaracuy, Aroa, Los Canelitos, cerca del caserío de San José, 3–4 Jul 1953, *L. Aristeguieta & F. Pannier 1903* (holotype: S R-528 [digital image seen]; isotype: VEN 43974 [digital image seen]).

*Habit and distribution.*—Terrestrial herb; known only from northwestern Venezuela.

85. **Asplundia stenophylla** (Standl.) Harling, Acta Horti Berg. 17: 43.1954 ≡ *Carludovica stenophylla* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 130. 1937. Type: Costa Rica. Cartago, El Muñeco, south of Navarro, ca. 1400 m, 8-9 Feb 1924, *P. C. Standley 33829* (holotype: US 00027145).

*Habit and distribution.*—Root-climbing liana; common species in mountain forests from Costa Rica to Ecuador, between 500 and 1800 m.

86. **Asplundia tetragona** (Kunth) Harling, Acta Horti Berg. 17: 43. 1954 ≡ *Carludovica tetragona* Kunth in Humboldt, Bonpland & Kunth, Nov. Gen. Sp. 1: 79. 1815 ≡ *Salmia tetragona* (Kunth) Roem. & Schult., Syst. Veg., ed. 15 bis 3: 496. 1818. Type: [Colombia. Quindío or Tolima], in montanis Ibaguensium. Crescit locis subtemperatis montis Quindiu, juxta La Cuesta de Tolima, 700 hexapodarum, s.d., *F. W. H. A. Humboldt & A. J. A. Bonpland s.n.* (lectotype, designated here: P 00669328 [digital image seen]; isolectotype: P 00726019 [digital image seen])).

*Habit and distribution.*—Root-climbing liana; known only from type locality.

*Notes.*—Harling (1958) indicates the holotype of *A. tetragona* as housed in P herbarium. Two sheets of Humboldt and Bonpland collection are found there, one with fruits, and the other sterile. We choose here the the frutiferous sheet (P 00669328) as the lectotype.

87. **Asplundia tetragonopus** (Mart. ex Drude) Harling, Acta Horti Berg. 17: 43. 1954 ≡ *Carludovica tetragonopus* Mart. ex Drude in Martius & Eichler, Fl. Bras. 3: 238. 1881. Type: Brazil. Bahia, prope flumen Itahypé, in arboribus et Geonomae truncis epiphytica, Nov 1818, *C. F. P. Martius s.n.* (holotype: M 0219249 [digital image seen], mixture with *Evodianthus funifer*).

= *Asplundia maximiliani* Harling, Acta Horti Berg. 18: 153. 1958, as '*Maximiliani*'. Type: Brazil. Bahia, s.l., 1816, *M. A. P. Wied-Neuwied s.n.* (holotype: GOET 000774 [digital image seen], isotype: MEL 2353472 [digital image seen]). **syn. nov.**

*Habit and distribution.*—Root-climbing liana; endemic to the Atlantic Forest from Brazil.

*Notes.*—Even without analyzing the staminate flowers, Harling (1958) considered that *A. tetragonopus* belongs to subgenus *Asplundia*. However, the two infructescences of the holotype agree with some materials of *A. maximiliani*, described only with flowers, which belongs to the subgenus *Choanopsis*. The morphology of the infructescence undergoes changes during its development and we consider that those of the holotype of *A. tetragonopus* represents the immature phase of the infructescences of *A. Maximiliani*. Some collections of *Asplundia maximiliani* shows great resemblance in the structure of the young fruiting pistillate flowers.

88. **Asplundia trilobulata** Tuberq., Caldasia 19: 179. 1997. Type: Colombia. Chocó, Nuquí, Corregimiento de Arusí, región del Cabo Corrientes, alrededores de la Estación

Biológica El Amargal, 150 m, 2 Mar 1994, *D. Tuberquia 252* (holotype: HUA 0000840; isotype: COL 000006766).

*Habit and distribution.*—Root-climbing liana; known only from type locality.

89. **Asplundia truncata** Harling, Acta Horti Berg. 18: 193. 1958. Type: Ecuador. Azuay, dense rich jungle between río Blanco and río Norcay on road between Chacanceo and Molleturo, 1520 m, 4 Jun 1943, *J. A. Steyermark 52817* (holotype: F V0092235F; isotype: F V0092236F).

*Habit and distribution.*—Root-climbing liana; little known species, found only in the type locality.

90. **Asplundia ulei** Harling, Acta Horti Berg. 18: 175. 1958, as '*Ulei*'. Type: Peru. Madre de Dios, río Acre, Seringal Auristella, Aug 1911, *E. Ule 9180* (holotype: K 0006362669 [digital image seen]; isotype: MG 014042).

*Habit and distribution.*—Root-climbing liana; known from Amazon in Peru.

91. **Asplundia uncinata** Harling, Acta Horti Berg. 18: 249. 1958. Type: Costa Rica. Limón, forest near farmhouse at Finca Castilla, 30 m, 26 Jul 1936. *C. W. Dodge & V. F. Goerger 9412* (holotype: F V0092228F; isotype: MO 123148).

*Habit and distribution.*—Terrestrial herb; known in Central America from Costa Rica and Panama.

92. **Asplundia urophylla** Harling, Acta Horti Berg. 18: 167. 1958. Type: Colombia. Valle del Cauca, cordillera Occidental, vertiente oriental; hoya del río Cali; río Pichindé, entre Los Cárpatos y El Olivo, 2025–2920 m, 26 Jul 1946, *J. Cuatrecasas 21731* (holotype: VALLE 000245 [digital image seen], isotype: VALLE 000246 [digital image seen]).

*Habit and distribution.*—Root-climbing liana; this species is known only for Colombia, in the Central and Occidental Cordilleras, in the Departments of Valle del Cauca, Antioquia, and Quindío, on mountain forests between 1800 and 2900 m.

93. **Asplundia utilis** (Oerst.) Harling, Acta Horti Berg. 17: 43. 1954 ≡ *Sarcinanthus utilis* Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1857: 197. 1857 ≡ *Carludovica utilis* (Oerst.) Benth. & Hook.f. ex Hemsl., Biol. Cent.-Amer., Bot. 3: 416. 1855 ≡ *Asplundia costaricensis* Harling, Acta Horti Berg. 18: 186. 1958. nom. superfl. ≡ *Carludovica costaricensis* (Harling) L.O.Williams, Fieldiana, Bot. 29: 345. 1961. nom. illeg. Type: Costa Rica. In sylvis umbrosis circa Pacaca, Dec 1847, *A. S. Oersted s.n.* (holotype: C 10021529 [digital image seen]).

*Habit and distribution.*—Root-climbing liana; common species in lowland and moutain forests from Mexico to Ecuador, below 1500 m altitude.

*Notes.*—For detailed nomenclatural comments see Hammel (1989).

94. **Asplundia vagans** Harling, Acta Horti Berg. 18: 170. 1958. Type: Colombia. Chocó, río San Juan, margen derecha, Quebrada del Taparal, 5–20 m, 30 May 1946, *J. Cuatrecasas 21440* (holotype: VALLE 000242 [digital image seen]).

*Habit and distribution.—*Root-climbing liana; widespread species from Guatemala to Bolivia.

95. **Asplundia vaupesiana** Harling, Acta Horti Berg. 18: 202. 1958. Type: Colombia. Amazonas-Vaupés, río Apaporis, Jino-Gojé, entre los ríos Piraparaná y Popeyaká, 250 m, 3–11 Sep 1952, *H. García-Barriga 14425* (holotype: COL 000006767).

*Habit and distribution.—*Root-climbing liana; common species in western Amazon, in Brazil, Colombia and Venezuela.

96. **Asplundia venezuelensis** Harling, Acta Horti Berg. 18: 203. 1958. Type: Venezuela. Bolívar, río Torono, Indian camp above junction with río Paragua, 280 m, dense forest, 11–12 Apr 1943, *E. P. Killip 37383* (holotype: US 00027160; isotype: VEN 43691 [digital image seen]).

*Habit and distribution.—*Root-climbing liana; found in lowland to montane forests in Venezuela, in the states of Bolívar, Amazonas, Aragua, Distrito Federal and adjacent parts of Brazil.

97. **Asplundia xiphophylla** Harling, Acta Horti Berg. 18: 199. 1958. Type: Peru. Loreto, vicinity of Iquitos, Mishuyacu, on the ground in forest, 2 Nov 1940, *E. Asplund 14223* (holotype: S R-529 [digital image seen]).

*Habit and distribution.*—Root-climbing liana, rarely terrestrial herb; common species of the western Amazon, found in Brazil, Colombia, Peru, and Venezuela.

98. **Carludovica drudei** Mast., Gard. Chron. 8: 714. 1877, as '*Drudei*'. Type: Colombia. Cultivated in Hort. Kewensis, 1890, *s.c. s.n.* (neotype: K n.v., designated by Harling (1958: 137)).

= *Carludovica speciosa* Linden, Gard. Chron. 8: 753. 1877. nom. nud.

= *Carludovica tabascana* Matuda, Anales Inst. Biol. Univ. Nac. México 22: 395. 1952. Type: Mexico. Tabasco, Teapa, en bosque denso, Jul 1945, *C. L. Gilly & E. I. Xolocotzi 183-A* (holotype: MEXU, 2 sheets (MEXU 00007370 [digital image seen], MEXU 00007371 [digital image seen]; isotype: ENCB 003174 [digital image seen]).

*Habit and distribution.*—Terrestrial herb; known from Mexico, Costa Rica, Panama, and Colombia.

99. ***Carludovica palmata*** Ruiz & Pav. Fl. Peruv. [Ruiz & Pavon] 291. 1798 ≡ *Ludovia palmata* (Ruiz & Pav.) Pers., Syn. Pl. [Persoon] 2: 576. 1807 ≡ *Salmia palmata* (Ruiz & Pav.) Willd., Mag. Neuesten Entdeck. Gesammten Naturk. Ges. Naturf. Freunde Berlin 5: 401. 1811. Type: Peru. Huánuco, in Pozuzo et Cuchero nemoribus, s.d., *H.*

*Ruiz & J. A. Pavón s.n.* (lectotype: first-step designated by Harling (1958: 128), second-step: designated here, MA 810370 [digital image seen]; isolectotypes: F photo negative 4280, G 00098241 [digital image seen], MA, 15 sheets (MA 810371 [digital image seen], MA 810372 [digital image seen], MA 810373 [digital image seen], MA 810375 [digital image seen], MA 810376 [digital image seen], MA 817217 [digital image seen], MA 817218 [digital image seen], MA 817219 [digital image seen], MA 817220 [digital image seen], MA 817221 [digital image seen], MA 817222 [digital image seen], MA 817223 [digital image seen], MA 817225 [digital image seen], MA 817226 [digital image seen], MA 817227 [digital image seen]).

= *Carludovica gigantea* Kuntze, Revis. Gen. Pl. 2: 737. 1891. Type: Panama. [Colón], Matachín, 8 Jun 1874, *C. E. O. Kuntze* (lectotype: K n.v., designated by Harling (1958: 128); isolectotype: NY, n.v.).

= *Carludovica jamaicensis* Lodd. ex Sweet, Hort. Brit. [Sweet], ed. 3: 630. 1839 ≡ *Carludovica jamaicensis* Lodd., Cat. Pl. (Loddiges), ed. 14. 1826, nom. nud. ≡ *Salmia jamaicensis* Steud., Nomencl. Bot. [Steudel], ed. 2, 2: 501. 1841. nom. inval. ≡ *Carludovica jamaicensis* Lodd. ex Fawc. & Harris, Bull. Bot. Dept. Jamaica 9: 146. 1902, nom. illeg. Type: Not designated, described on living material (lectotype: tab. 7 in Bull. Bot. Dept. Jamaica 9 (1902), designated by Harling (1958: 128)).

*Habit and distribution.*—Large terrestrial herb; widespread species from Guatemala to Central Bolivia. Widely cultivated in tropical countries and botanical gardens around the world.

*Notes.—Carludovica palmata* is the most known and economicly important species of Cyclanthaceae, its fibers being the source for the traditional Panama-hat. This species was described from H. Ruiz and J. A. Pavón collection in Central Peru. Harling (1958) designated the material housed in MA herbarium as lectotype, nevertheless at least sixteen sheets of Ruiz & Pavón's collections of this species are found in this herbarium, without any evidence of which Harling chose as lectotype. Here, we complete the lectotypification by desiginating MA 810370 as a second-step lectotype. This sheet, with a leaf, an inflorescence and an infructescence, is the most complete among those available in the type collection.

100. **Carludovica rotundifolia** Schaedtler, Hamburger Garten- Blumenzeitung 31: 301. 1875. Type: (neotype, designated here: plate 7083 of Hooker, J.D., Curtis's Bot. Mag. 115, ser. 3, v. 45: tab. 7083. 1889).

= *Carludovica rotundifolia* H.Wendl. ex Hook.f., Bot. Mag. 115, ser. 3, v. 45: tab. 7083. 1889. Type: Costa Rica. Cultivated in Hort. Kewensis, 24 Nov 1888, *s.c. s.n.* (lectotype: K n.v., designated by Harling (1958: 135)). nom. illeg.

= *Carludovica rotundifolia* subsp. *pachyspadix* Harling, Acta Horti Berg. 18: 136. 1958. Type: Panama. Chiriquí, vicinity of Bajo Chorro, 1900 m, 20–22 Jul 1940, *R. E. Woodson & R. W. Schery 675* (holotype: MO n.v.; isotype: GH 00028597).

*Habit and distribution.*—Terrestrial herb; found in Costa Rica and Panama.

*Notes.*—This species was originally described from plants collected in Costa Rica by H. Wendland, between 1856 and 1857, and cultivated in Herrenhausen Gardens, Germany. The first time that the name *Carludovica rotundifolia* apperared in botanical literature was in 1862, in three works almost simultaneous, as a *nomen nudum*, with autorship destined to Wendland (Herrich-Schaeffer, 1862: 236; Seemann, 1862: 163; Skofitz, 1862: 159). Two years later, it was quoted as being cultivated in Botanical Garden of Berlin, but without description, remaining as invalidly published name (Koch, 1864: 28). In the following years the name has appeared in horticultural or gardening catalogues (Dean, 1870: 267; Croucher, 1872: 461). Schaedtler (1875) described formally and validated the name, being the autorship credited to him. Hooker (1889) described and illustrated *C. rotundifolia* of material received from Wendland and cultivated in Kew gardens. Many authors credit the autorship of the name for Hooker (Standley, 1937; Woodson & Schery, 1943; Hammel, 1986a; 1986b; 2003b). However, as evidenced by Reveal (2012) the correct autorship of the name should be given to Schaedtler. We used the Hooker's plate as neotype for Schaedtler's name.

101. **Carludovica sulcata** Hammel, Phytologia 60: 8. 1986. Type: Costa Rica. Heredia, Finca LA Selva, the OTS Field Station on the río Puerto Viejo just E of its junction with the río Sarapiquí, elev. 150 m, 7 Aug 1983, *B. E. Hammel 13330* (holotype: DUKE n.v.; isotypes: CAS 0001336 [digital image seen], CR 110325 [digital image seen], F, 2 sheets (F V0045378F, F V0045379F), MO 123150).

    *Habit and distribution.*—Terrestrial herb; found in Nicaragua and Costa Rica.

102. **Chorigyne cylindrica** R.Erikss., Nordic J. Bot. 9: 44. 1989. Type: Panama. Colón, Santa Rita ridge road, ca. 22 km from Transisthmian highway, in forest on ridges,

slopes and draws near end of road, 500 m, 9°25’N, 79°40’W, 17–18 Feb 1986, *B. E. Hammel, G. McPherson & D. Roubik 14493* (holotype: GB 0047598 [digital image seen]; isotypes: MO, 3 sheets (MO 123151, MO 123152, MO 123153], PMA, 2 sheets (PMA 28219 [digital image seen], PMA 28220 [digital image seen])).

*Habit and distribution.*—Epiphyte, seldom terrestrial herb; known from Costa Rica and Panama.

103. **Chorigyne densiflora** R.Erikss., Nordic J. Bot. 9: 35. 1989. Type: Panama. Bocas del Toro-Chiriquí, Cerro Colorado. Road along top, 1500–1700 m, 13 Aug 1977, *J. P. Folsom, G. Small & R. Robbins 4697* (holotype: MO 2624251; isotype: GB 0047590 [digital image seen]).

*Habit and distribution.*—Epiphyte; known only from Panama.

104. **Chorigyne ensiformis** (Hook.f.) R.Erikss., Nordic J. Bot. 9: 37. 1989 ≡ *Carludovica ensiformis* Hook.f., Bot. Mag. 105, ser. 3, v. 35: tab. 6418. 1879 ≡ *Sphaeradenia ensiformis* (Hook.f.) Harling, Acta Horti Berg. 17: 3. 1954. Type: Costa Rica. Cultivated in Hort. Kewensis, 11 Aug 1877, *s.c. s.n.* (lectotype: K n.v., designated by Eriksson (1989: 37)).

*Habit and distribution.*—Epiphyte; known from Costa Rica and Panama.

105. **Chorigyne paucinervis** R.Erikss., Nordic J. Bot. 9: 40. 1989. Type: Panama. Chiriquí, along road between Gualaca and the Fortuna Dam site, at 16 km NW of Los Planes de Hornito, 1260 m, 10 Apr 1980, *T. Antonio 4200* (holotype: GB 0047591 [digital image seen]; isotype: PMA 28224 [digital image seen]).

*Habit and distribution.—*Epiphyte; known only from type locality.

106. **Chorigyne pendula** (Hammel) R.Erikss., Nordic J. Bot. 9: 39. 1989 ≡ *Sphaeradenia pendula* Hammel, Phytologia 60: 11. 1986. Type: Costa Rica. Heredia, Finca LA Selva, the OTS Field Station on the río Puerto Viejo just E of its junction with the río Sarapiquí, ca. 100 m, 14 Aug 1980, *B. E. Hammel 9528* (holotype: DUKE n.v.; isotype: CR n.v., MO n.v.).

*Habit and distribution.—*Epiphyte; known from Costa Rica and Panama.

107. **Chorigyne pterophylla** R.Erikss., Nordic J. Bot. 9: 40. 1989. Type: Costa Rica. Limón, río Segundo, Asunción, 28 Apr 1985, *L. D. Gómez & G. Herrera 23522* (holotype: MO 107951; isotype: GB 0047592 [digital image seen]).

*Habit and distribution.—*Epiphyte; known from Costa Rica and Panama.

108. **Chorigyne tumescens** R.Erikss., Nordic J. Bot. 9: 44. 1989. Type: Panama. Veraguas, NW of Santa Fe, 4.2 km from Escuela Agrícola Alto de Piedra, 25 Feb 1976, *S. A. Mori & J. A. Kallunki 4821* (holotype: MO 123155).

*Habit and distribution.—*Epiphyte; known only from type locality.

109. **Cyclanthus bipartitus** Poit. ex A. Rich., Dict. Class. Hist. Nat. 5: 222. 1824 ≡ *Cyclanthus bipartitus* Poit., Mém. Mus. Hist. Nat. 9: 36, t. 2. 1822, nom. illeg. Type: French Guiana. s.l., 1819–1821, *P. A. Poiteau s.n.* (lectotype: P 00310138 [digital image seen], designated by Harling (1958: 400); isolectotypes: G 00098240 [digital image seen], K 000632660 [digital image seen]).

= *Cyclanthus plumierii* Poit. ex A. Rich., Dict. Class. Hist. Nat. 5: 222. 1824. *Cyclanthus plumierii* Poit., Mém. Mus. Hist. Nat. 9: 37. 1822, nom. illeg. Type: not designated (lectotype: Plate 3 of Poiteau, Mém. Mus. Hist. Nat. t. 9: Pl. 3. 1822, designated by Harling (1958: 400)).

= *Cyclanthus cristatus* Klotzsch, Linnaea 20: 469. 1847. Type: Colombia. s.l., s.d., *G. C. W. H. Karsten s.n.* (lectotype: B, fruit in alcohol, n.v.; designated by Harling (1958: 400)).

= *Discanthus odoratus* Spruce, J. Linn. Soc., Bot. 3: 196. 1859. Type: Peru. [San Martín], Tarapoto, 1868, *R. Spruce 60* (holotype: K, 2 sheets (K 000632658 [digital image seen], K 000632659 [digital image seen])).

= *Cyclanthus bipartitus* var. *gracilis* Drude in Martius & Eichler, Fl. Bras. 3: 246. 1881. Type: [Colombia], Provinciae Rio Negro, in sylvis humidis primaervis ad flum. Japurá, prope Porto dos Miranhas, Jan 1820, *C. F. P. Martius 3177* (holotype: M 0219245 [digital image seen]).

= *Cyclanthus glaucus* Klotzsch, nom. in shed.

*Habit and distribution.*—Terrestrial herb; widespread species, occurs from Mexico to Brazilian Amazon.

110. **Cyclanthus indivisus** R.E.Schult., Bot. Mus. Leafl. 18: 305. 1959. Type: Colombia. Amazonas-Vaupés, río Apaporis, Soratama (entre el río Pacoa y el río Kananarí), 20 Aug 1951, *R. E. Schultes & I. Cabrera 13680* (holotype: GH n.v.; isotype: ECON 00112910).

*Habit and distribution.*—Terrestrial herb; restrict to the western Amazon, in Colombia, Ecuador, and Peru.

111. **Dicranopygium angustissimum** (Sandwith) Harling, Acta Horti Berg. 17: 44. 1954 ≡ *Carludovica angustissima* Sandwith, Bull. Misc. Inform. Kew 18: 497. 1933. Type: Guyana. Holmia, Potaro River, on wet rocks in a creek, Nov 1907, *A. W. Bartlett 8740* (lectotype, designated by Harling (1958: 332): K 000400090 [digital image seen]; isolectotype: K 000400091 [digital image seen]).

*Habit and distribution.*—Terrestrial herb; known only from Guyana.

*Notes.*—When Sandwith (1933) described *Carludovica angustissima* (the basionym of *C. angustissima*), he cited only the specimen *Bartlett 8740* housed at K herbarium. However, two sheets of *Bartlett 8740* are found in this herbarium. In one of these sheets (K 000400090), Harling wrote *holotypus*, in this manner effecting the lectotypification, although he did not convey that.

112. **Dicranopygium aristeguietae** Harling, Acta Horti Berg. 18: 305. 1958, as '*Aristeguietae*'. Type: Venezuela. Barinas, cerca de ciudad Bolivia (Pedraza) comienzos de la serrania Andina, Feb 1953, *L. Aristeguieta 1655* (holotype: VEN, 4 sheets (VEN 43688 [digital image seen], all sheets with the same barcode number); isotype: NY 00688960).

*Habit and distribution.*—Terrestrial herb; known only from Venezuela.

113. **Dicranopygium arusisense** Tuberq., Caldasia 19: 184. 1997. Type: Colombia. Chocó, Nuquí, Corregimiento de Arusí, región del Cabo Corrientes, Quebrada Arusisito, 0–20 m, 3 May 1994, *D. Tuberquia 262* (holotype: HUA 0000477; isotype: COL 000006771).

*Habit and distribution.*—Terrestrial herb, occasionaly climbing; known only from the type locality.

114. **Dicranopygium atrovirens** (H.Wendl.) Harling, Acta Horti Berg. 17: 44. 1954 ≡ *Carludovica atrovirens* H.Wendl., Index Palm. 67. 1854. Type: Uncertain origin. Cultivated in Atkins [Cienfuegos] Botanical Garden, Cuba, 13 Jul 1930, *J. G. Jack 8008* (neotype: A 00112909, designated by Harling (1958: 306)).

*Habit and distribution.*—Terrestrial herb; known only from cultivated plants.

115. **Dicranopygium aurantiacum** (R.E.Schult.) Harling, Acta Horti Berg. 17: 44. 1954

≡ *Carludovica aurantiaca* R. E. Schult., Bot. Mus. Leafl. 16: 58. 1953. Type: Colombia. [Guainía], río Guainía basin, río Naquieni, vicinity of Cerro Monachí, June 1948, *R. E. Schultes & F. López 10085* (holotype: GH, 3 sheets (GH 00028607, GH 00028608, GH 00028609)).

= *Dicranopygium amazonicum* Harling, Acta Horti Berg. 18: 299. 1958. Type: [Colombia], Bacia do Rio Negro, s.d., *R. E. Schultes 10085* (holotype: IAN 060292). nom. illeg.

*Habit and distribution.*—Terrestrial herb; known from northwestern Amazon in Colombia.

*Notes.*—Harling (1958: 299) probably described *Dicranopygium amazonicum* from an isotype of *D. aurantiacum* (*Schultes 10085*), but the label of the type material housed at IAN herbarium is clearly modified from the original in GH. Some parts of it are translated into portuguese and informations such as precise location, collection date and collector are absent. Besides, the sheets agree perfectly being thoroughly conspecific.

116. **Dicranopygium bolivarense** Harling, Acta Horti Berg. 18: 304. 1958. Type: Venezuela. Bolívar, Salto de Pará, medio Caura, 250 m, 5 Mar 1939, *Ll. Williams 11382* (holotype: VEN 31172 [digital image seen]; isotype: F, 2 sheets (F V0092242F, F V0092243F), US 00027161).

*Habit and distribution.*—Terrestrial herb; known only from Bolivar and Amazonas States in Venezuela.

117. **Dicranopygium calimense** Harling, Acta Horti Berg. 18: 292. 1958. Type: Colombia. Valle del Cauca, río Calima (región del Chocó), La Trojita, 5–50 m, 19 Feb 1944, *J. Cuatrecasas 16244* (holotype: VALLE 000210 [digital image seen]).

*Habit and distribution.*—Terrestrial or rarely epiphytic herb; common in Pacific lowlands from Colombia to Ecuador.

*Notes.*—Harling (1958), when describing *D. calimense*, indicated the holotype as housed in the herbarium of the Superior School of Tropical Agriculture at Cali, Colombia (CALI, nowadays designating the herbarium of the University of Calicut, Kerala, India [Thiers, 2018]). Later, the holotype sheet was transferred to the herbarium VALLE.

118. **Dicranopygium callithrix** Silverst., Novon 14: 337. 2004. Type: Colombia. Risaralda, Pereira, hacienda Alejandria, km 7 carretera Cerritos-La Virginia, lomas, bosque de galleria en una quebrada encañonada, 950–960 m, 4°51’S, 75°53’W, 12 Nov 2001, *P. A. Silverstone-Sopkin, N. Paz, H. Sanint & al. 8813* (holotype: CUVC, 2 sheets (CUVC 33394 n.v., CUVC 33395 n.v.; isotype: COL 00029614).

*Habit and distribution.*—Terrestrial herb; known only from the type locality.

119. **Dicranopygium campii** Harling, Opera Bot., B 1: 36. 1973, as ‘*Campii*’. Type: Ecuador. Morona-Santiago, Cordillera Cutucú, junction of río Itzintza and Chupiasa, ca. 1000 m, 2°40’S, 78°W, *W. H. Camp E-1412* (holotype: S R-7463 [digital image seen]; isotypes: GB 0047593 [digital image seen], NY 00133660, US 00027162).

*Habit and distribution.*—Terrestrial herb; known only from the type locality.

120. **Dicranopygium coma-pyrrhae** (Harling) Harling, Acta Horti Berg. 17: 44. 1954, as ‘*Coma-Pyrrae*’ ≡ *Carludovica coma-pyrrhae* Harling, Acta Horti Berg. 15: 197. 1950, as ‘*Coma-Pyrrae*’. Type: Ecuador. Napo-Pastaza, Tena, ca. 500 m, 17 Oct 1939, *E. Asplund 9408* (holotype: S R-1485 [digital image seen]; isotypes: S 06-4664 [digital image seen], S 06-4665 [digital image seen]).

*Habit and distribution.*—Terrestrial herb; known only from the type locality.

121. **Dicranopygium crinitum** Harling, Acta Horti Berg. 18: 316. 1958. Type: Panama. [Colón], drowned forest of Quebrada Ancha, 70 m, 21 Dec 1934, *J. A. Steyermark & P. H. Allen s.n.* (holotype: S R-1486 [digital image seen]; isotype: G 00098237 [digital image seen], MO 371064).

*Habit and distribution.*—Terrestrial herb; known only from Panama.

122. **Dicranopygium cuatrecasasianum** Harling, Acta Horti Berg. 18: 312. 1958, as ‘*Cuatrecasanum*’. Type: Colombia. Valle del Cauca, río Calima (region del Chocó),

margem derecha, lomas frente a Quebrada de la Brea, 30–50 m, 18 May 1946, *J. Cuatrecasas 21096* (holotype: VALLE 000240 [digital image seen]).

*Habit and distribution.*—Terrestrial herb; known from Panama, Colombia and Ecuador.

123. **Dicranopygium dolichostemon** Harling, Acta Horti Berg. 18: 314. 1958. Type: Colombia. Antioquia, north of Dabeiba, along road to Turbo, 300–350 m, 25 Feb–1 Mar 1942, *R. D. Metcalf & J. Cuatrecasas 30170* (holotype: UC 687149 [digital image seen]; isotype: US 00811090).

*Habit and distribution.*—Terrestrial herb; known only from Antioquia, Colombia.

124. **Dicranopygium euryphyllum** (Harling) Harling, Acta Horti Berg. 17: 44. 1954 ≡ *Carludovica euryphylla* Harling, Acta Horti Berg. 15: 197. 1950. Type: Ecuador. Santiago-Zamora, Patuca, steep thickets on the bank of río Namangoza, immediately below the confluence of río Upano and río Paute, 600 m, 11 Jun 1947, *G. Harling 1130* (holotype: S R-1487 [digital image seen]; isotypes: S 06-4666 [digital image seen], S 06-4667 [digital image seen]).

*Habit and distribution.*—Terrestrial herb; known only from Ecuador.

125. **Dicranopygium fissile** Galeano & R. Bernal, Caldasia 14: 31. 1984. Type: Colombia. Antioquia, San Carlos, quebrada La Chorrera, 3 km al NO de la cabecera

municipal, 1100 m, 31 Dec 1980, *L. Henao & L. Tobón 173* (holotype: COL, 2 sheets (COL 000006779, COL 000006780)).

*Habit and distribution.*—Terrestrial herb; known only from the type locality.

126. **Dicranopygium globosum** Harling, Acta Horti Berg. 18: 321. 1958. Type: Colombia. Chocó, headwaters of río Tutunendo, east of Quibdó, 20–21 May 1931, *W. A. Archer 2180* (holotype: US 00027164).

*Habit and distribution.*—Terrestrial herb; known only from the type locality.

127. **Dicranopygium goudotii** Harling, Acta Horti Berg. 18: 301. 1958, as '*Goudotii*'. Type: [Colombia]. Magdalena, de las frias à Santa Ana, s.d., *J. Goudot s.n.* (holotype: K 000632661 [digital image seen]; isotypes: G 00098238 [digital image seen], K 000632662 [digital image seen]).

*Habit and distribution.*—Terrestrial herb; widespread species in Colombia, occurs in the Pacific coast plains, region of the Andes and Valle del Cauca del Magdalena.

128. **Dicranopygium gracile** (Liebm. ex Matuda) Harling, Acta Horti Berg. 17: 44. 1954 ≡ *Carludovica gracilis* Liebm. ex Matuda, Anales Inst. Biol. Univ. Nac. México 22: 387. 1952. Type: Mexico. Oajaca [Oaxaca], Chinantla, in sylvis inter Lacoba et Jacotepec, Jun 1842, *F. M. Liebmann 10801* (holotype: C 10009987 [digital image

seen]; isotypes: C, 2 sheets (C 10009988 [digital image seen], C 10009989 [digital image seen]), K 000632666 [digital image seen], US 00027127).

= *Dicranopygium gracile* (Liebm. ex Matuda) Harling ssp. *hondurense* Harling, Acta Horti Berg. 18: 284. 1958. Type: Honduras. Atlántida, Lancetilla valley, near Tela, 20–600 m, 6 Dec 1927–20 Mar 1928, *P. C. Standley 54832* (holotype: A 00028605 [digital image seen]; isotype: F V0092239F). **syn. nov**.

= *Dicranopygium izabalense* Harling, Acta Horti Berg. 18: 285. 1958. Type: Guatemala. Izabal, along trail beginning from mile 33.23 betwenn Dartmouth and Morales towards Lago Izabal, Montaña del Mico, 35–150 m, *J. A. Steyermark 39041* (holotype: F, 2 sheets (F V0092240F, F V0092241F)).

*Habit and distribution.*—Terrestrial herb; known from Mexico, Guatemala, Honduras and Nicaragua.

*Notes.*—The different subspecies described by Harling (1958) appear to be just minor variants within the normal variability of this species. Hammel (2001) treated *Dicranopygium izabalense* as a synonym of *D. gracile*.

129. **Dicranopygium grandifolium** Harling, Acta Horti Berg. 18: 291. 1958. Type: Colombia. Valle del Cauca, río Digua valley, Chorrera La Elsa, 975 m, 2–3 Apr 1939, *E. P. Killip 34796* (holotype: F, 2 sheets (F V0092244F, F V0092245F); isotypes: BM 000938234 [digital image seen], COL 000006772, US 00027165).

*Habit and distribution.*—Terrestrial herb; known from western Colombia, Ecuador, and Costa Rica.

130. **Dicranopygium harlingii** G.J.Wilder, J. Arnold Arbor. 59: 75. 1978, as '*Harlingii*'. Type: Panama. East of Cerro Jefe, from La Eneida, 29 Apr 1973, *G. J. Wilder & R. Dressler s.n.* (holotype: F V0045382F).

*Habit and distribution.*—Terrestrial herb; known from Costa Rica to Colombia.

131. **Dicranopygium idrobonis** Harling, Acta Horti Berg. 18: 322. 1958, as '*Idrobonis*'. Type: Colombia. Nariño, Costa del Pacífico, selva pluvial y rastrojos en la Cuenca del río Telembí, Barbacoas y alrededores, 30 m, 6–10 May 1953, *J. M. Idrobo & H. Weber 1457* (holotype: COL 000006773; isotype: US 00027166).

*Habit and distribution.*—Terrestrial herb; known only from the type locality.

132. **Dicranopygium imeriense** Harling, Acta Horti Berg. 18: 302. 1958. Type: Venezuela. [Amazonas], Brazilian-Venezuelan boundary, western foothills of Serra Imeri, near Salto de Huá, 27 Nov–8 Dec 1930, *E. G. Holt & E. R. Blake 480* (holotype: NY 00688959; isotypes: F V0092246F, US 00027167, VEN 10459 [digital image seen]).

*Habit and distribution.*—Terrestrial herb; known from northwestern Amazon in Brazil and Venezuela.

133. **Dicranopygium insulare** (Gleason) Harling, Acta Horti Berg. 17: 44. 1954 ≡ *Carludovica insularis* Gleason, Bull. Torrey Bot. Club 56: 4. 1929. Type: Trinidad and Tobago. Castasa woods, 30 Sep 1911, *W. E. Broadway 4066* (holotype: K 000632665 [digital image seen]; isotype: NY 00688954, mixture with leaf of *Asplundia* sp., S n.v.).

*Habit and distribution.*—Terrestrial herb; known only from Trinidad and Tobago.

134. **Dicranopygium latissimum** Harling, Acta Horti Berg. 18: 293. 1958. Type: Peru. Huánuco, San Martín, tingo María, 625–1100 m, 30 Oct 1949–19 Feb 1950, *H. A. Allard 21559* (holotype: US 00027168).

*Habit and distribution.*—Terrestrial herb; known only from Peru.

135. **Dicranopygium lugonis** Harling, Acta Horti Berg. 18: 319. 1958, as '*Lugonis*'. Type: Ecuador. Napo-Pastaza, Mera, rocky wall of Mangayacu river canyon, ca. 1100 m, 8 Dec 1955, *E. Asplund 18734* (holotype: S R-1488 [digital image seen]; isotypes: B 100347234 [digital image seen], NY, 2 sheets (NY 00133661, NY 00133662), R, 2 sheets (R 000195647, both sheets under same barcode number), S, 2 sheets (S 06-4668 [digital image seen], S 06-4669 [digital image seen])).

*Habit and distribution.*—Terrestrial herb; known only from Ecuador and Peru.

136. **Dicranopygium macrophyllum** Harling, Bol. Soc. Venez. Ci. Nat. 25: 63. 1963. Type: Venezuela. Sucre, Península de Pria, Cerro Patao, Norte de Puerto Hierro, Noreste de Güiria, Quebarada Pedregosa (esquisto de Mica), 100–300 m, 23 Jul 1962, *J. A. Steyermark & G. Agostini 91273* (holotype: S R-1489 [digital image seen]; isotype: VEN 55123 [digital image seen]).

*Habit and distribution.*—Terrestrial herb; known only from the type locality.

137. **Dicranopygium microcephalum** (Hook.f.) Harling, Acta Horti Berg. 17: 44. 1954 ≡ *Carludovica microcephala* Hook.f., Bot. Mag. 118, ser. 3, v. 48: t. 7263. 1892. Type: Costa Rica, Cultivated in Hort. Kewensis, 23 Mar 1892, *s.c. s.n.* (holotype: K n.v.).

*Habit and distribution.*—Terrestrial herb; known only from Costa Rica.

138. **Dicranopygium mirabile** Harling, Acta Horti Berg. 18: 326. 1958. Type: Colombia. Antioquia, Urabá, cerca a Dabeiba, carretera a Mutatá, sitio “La Cerrazón”, en los bordes del camino, ca. 400 m, 9 Jan 1950, *L. Uribe 2060* (holotype: COL 000006781).

*Habit and distribution.*—Terrestrial herb; known from Antioquia, Colombia.

139. **Dicranopygium nanum** (Gleason) Harling, Harling, Acta Horti Berg. 17: 44. 1954 ≡ *Carludovica nana* Gleason, Bull. Torrey Bot. Club 56: 5. 1929. Type: Guyana. Serra Mey, s.d., *R. H. Schomburgk s.n.* (holotype: K 000400092 [digital image seen]).

*Habit and distribution.*—Terrestrial herb; known from Venezuela and Guyana.

140. **Dicranopygium novogranatense** Harling, Acta Horti Berg. 18: 318. 1958. Type: Colombia. Valle del Cauca, río Calima (región del Chocó), entre La Trojita y Guadualito, 0 – 5 m, *J. Cuatrecasas 16864-G* (holotype: VALLE 000216 [digital image seen]).

*Habit and distribution.*—Terrestrial herb; common species in Pacific lowlands from Colombia.

*Notes.*—Harling (1958), when describing *D. novogranatense*, also indicated the holotype as housed in the herbarium CALI, in that time designating the herbarium of the Superior School of Tropical Agriculture at Cali, but nowaday designating the herbarium of the University of Calicut, Kerala, India (Thiers 2018). Later, the holotype sheet was transferred to the herbarium VALLE.

141. **Dicranopygium odoratum** Tuberq., Caldasia 19: 187. 1997. Type: Colombia. Chocó, Nuquí, Corregimiento de Arusí, región del Cabo Corrientes, Estación Biológica "El Amargal", 40 m, 05°30'–05°37'N, 77°30'W, 6 May 1994, *D. Tuberquia & Y. Martínez 267* (holotype: HUA 0000478; isotype: COL 000006774).

*Habit and distribution.*—Terrestrial herb; known only from the type locality.

142. **Dicranopygium omichlophilum** R.E.Schult. ex Harling, Acta Horti Berg. 18: 294. 1958. Type: Colombia. Meta, Cordillera La Macarena, troche entre el río Güejar y el caño Guapayita, 500–600 m, 20–28 Dec 1950, *J. M. Idrobo & R. E. Schultes 731* (holotype: COL 000006775; isotype: COL 000006782).

*Habit and distribution.*—Terrestrial herb; known from Colombia and Venezuela.

143. **Dicranopygium pachystemon** Harling, Acta Horti Berg. 18: 323. 1958. Type: Peru. Santa Martín, Boquerón pass, 92 km from Tingo María on highway to Pucallpa, ca. 400 m, 16 Dec 1949–5 Jan 1950, *H. A. Allard 22123* (holotype: US 00027169).

*Habit and distribution.*—Terrestrial herb; known from Peru.

144. **Dicranopygium parvulum** (Harling) Harling, Acta Horti Berg. 17: 44. 1954 ≡ *Carludovica parvula* Harling, Acta Horti Berg. 15: 195. 1950. Type: Colombia. Cundinamarca, Regius Panche, s.d., *E. André 3320 a* (holotype: NY 00688957; isotype: F V0092247F, K n.v.).

= *Dicranopygium parvulum* var. *macarense* Harling, Acta Horti Berg. 18: 298. 1958. Type: Colombia. Meta, Cordillera La Macarena (extremo nordeste), macizo Renjifo, cumbre y alrededores, 1300–1900 m, 6–20 Jan 1951, *J. M. Idrobo & R. E. Schultes 1164* (holotype: COL 000006776; isotypes: COL 000006777, COL 000006778, NY 00688958, US 00027170). **syn. nov**.

*Habit and distribution.*—Terrestrial herb; known only from Central Colombia.

*Notes.*—Harling (1958) used only the length of the leaves to describe *D. parvulum* var. *macarense*, but this is a weak character to support taxonomic status, given its wide variation.

145. **Dicranopygium polycephalum** Harling, Acta Horti Berg. 18: 290. 1958. Type: Colombia. Santander, region about La Paz, 25 km NE of Vélez, ca. 1900 m, 6 May 1944, *N. C. Fassett 25190* (holotype: US 00027171).

*Habit and distribution.*—Terrestrial herb; known only from the type locality.

146. **Dicranopygium pygmaeum** (Gleason) Harling, Acta Horti Berg. 17: 44. 1954 ≡ *Carludovica pygmaea* Gleason, Bull. Torrey Bot. Club 56: 4. 1929. Type: Guyana. Tumatumari, Potaro river, 05°20'N, 3–5 Jan 1920, *A. S. Hitchcock 17388* (holotype: NY 00688956; isotypes: GH 00028611, K 000632664 [digital image seen], S R-1490 [digital image seen], US 00027146).

= *Carludovica fimbriata* Maguire, Bull. Torrey Bot. Club 75: 189. 1948 ≡ *Dicranopygium fimbriatum* (Maguire) Harling, Acta Horti Berg. 17: 44. 1954 ≡ *Dicranopygium pygmaeum* (Gleason) Harling subsp. *fimbriatum* (Maguire) Harling, Acta Horti Berg. 18: 330. 1958. Type: Suriname. Coppenam river headwaters, 23 Jul 1944, *B. Maguire 24159* (holotype: NY, n.v.; isotypes: GH 00028610, NY 00133657, US00027148). **syn. nov**.

*Habit and distribution.*—Terrestrial herb; known from Guiana Shield plateau.

*Notes.*—This is a very variable species in relation to the dimensions of the vegetative parts. Maguire (1948) pointed out the close relationship of *C. fimbriata* with *C. pygmaea* (= *Dicranopygium pygmaeum*). Harling (1958), based on the width of the leaf segments, treated it as a subspecies of *D. pygmaeum*. Here we consider the subspecies as a synonym for understanding that the characteristics used by Harling to separate the taxons are very variable, even within the same population.

147. **Dicranopygium rheithrophilum** (Harling) Harling, Acta Horti Berg. 17: 44. 1954 ≡ *Carludovica rheithrophila* Harling, Acta Horti Berg. 15: 195. 1950. Type: Ecuador. Los ríos, hacienda Clementina, Samana Montain, virgin forest in brook, 300 m, 19 Jan 1947, *G. Harling 100* (holotype: S R-1491 [digital image seen]; isotypes: S 06-4671 [digital image seen], S 06-4672 [digital image seen]).

*Habit and distribution.*—Terrestrial herb; known from Colombia and Ecuador.

148. **Dicranopygium robustum** Harling, Mem. New York Bot. Gard. 23: 111. 1972. Type: Venezuela. Amazonas, ríos Pacimoni-Yatua, Casiquiare, along río Yaciba above mouth, 160 m, 4 Dec 1953, *B. Maguire, J. J. Wurdack & G. S. Bunting 36511* (holotype: GB 0047567 [digital image seen]; isotype: NY 02851813).

*Habit and distribution.*—Terrestrial herb; known only from the type locality.

149. **Dicranopygium rupestre** (Klotzsch) Harling, Acta Horti Berg. 17: 44. 1954 ≡ *Carludovica rupestris* Klotzsch, Linnaea 20: 469. 1847. Type: [Venezuela. Carabobo], inter Valencianum et Puerto Cabello, in rupibus locis humidis, *J. W. K. Moritz 391* (holotype: B n.v. [probably destroyed], F photo negative 4288).

*Habit and distribution.*—Terrestrial herb; poorly known species, found only Venezuela.

150. **Dicranopygium sanctae-martae** Harling, Acta Horti Berg. 18: 296. 1958, as '*Sanctae-martae*'. Type: Colombia. Magdalena, [Sierra Nevada de] Santa Marta, 1845, *W. Purdie s.n.* (holotype: K 000632663 [digital image seen]).

*Habit and distribution.*—Terrestrial herb; known from nothern Colombia.

151. **Dicranopygium sararense** Harling, Acta Horti Berg. 18: 310. 1958. Type: Colombia. Norte de Santander, Cordillera Oriental, región del Sarare, hoya del río Cubugón entre El Caraño y El Indio, 470–600 m, 12 Nov 1941, *J. Cuatrecasas 13042* (holotype: COL 000006783; isotypes: F V0092248F, US, 2 heets (US 00027172, US 00027173).

*Habit and distribution.*—Terrestrial herb; known only from the type locality.

152. **Dicranopygium schultesii** Harling, Acta Horti Berg. 18: 286. 1958, as '*Schultesii*'. Type: Colombia. Amazonas, trapecio amazónico, Loretoyacu river, ca. 100 m, Sep

1946, *R. E. Schultes & G.A. Black 8337* (holotype: US 00027174; isotype: GH 00028612).

*Habit and distribution.*—Terrestrial herb; known from southwestern Amazon in Colombia, Ecuador, and Peru.

153. **Dicranopygium scoparum** Galeano & R.Bernal, Caldasia 14: 32. 1984. Type: Colombia. Chocó, El Carmen, vereda El Doce (carretera Medellín-Quibdó, km 150, Cordillera Occidental, vertiente occidental, río El Aguilón, 680 m, 10 Jul 1979, *G. Galeano & R. Bernal 130* (holotype: COL 000006784; isotype: HUA 0000029).

*Habit and distribution.*—Terrestrial herb; known only from the type locality.

154. **Dicranopygium stenophyllum** Harling, Acta Horti Berg. 18: 300. 1958. Type: Ecuador. Napo-Pastaza, 8 km N of Puyo, 6 Nov 1952, *F. Fagerlind & G. Wibom 1086* (holotype: S R-1492 [digital image seen]).

*Habit and distribution.*—Terrestrial herb; known from eastern Ecuador and Peru.

155. **Dicranopygium tatica** Hammel, Novon 13: 62. 2003. Type: Costa Rica. Limón, Cuenca del Bananito, Selva Bananito Lodge, 50 m, 9°49’30”N, 83°03’50”W, 24 Mar 2001, *B. E. Hammel & J. Morales 22357* (holotype: INB n.v.; isotype: COL n.v., CR n.v., MO 2772134).

*Habit and distribution.*—Terrestrial herb; known only from Caribbean lowlands in Costa Rica.

156. **Dicranopygium testaceum** Harling, Acta Horti Berg. 18: 316. 1958. Type: Panama. [Darién], Paca, below Cana, 15 Apr 1908, *R. S. Williams 787* (holotype: NY 00688955).

*Habit and distribution.*—Terrestrial herb; known from Panama and Colombia's Pacific lowlands.

157. **Dicranopygium trianae** Harling, Acta Horti Berg. 18: 312. 1958, as '*Trianae*'. Type: Colombia. Nariño, Barbacoas, en la via de Túquerres, 1800 m, May 1953, *J. J. Triana 1713* (holotype: US 00027175; isotype: COL 000006785).

*Habit and distribution.*—Terrestrial herb, sometimes climbing; known only from sothwestern Colombia.

158. **Dicranopygium umbrophilum** Hammel, Phytologia 60: 9. 1986, as '*umbrophila*'. Type: Costa Rica. Heredia, Finca La Selva, 20 May 1982, *B. E. Hammel 12386* (holotype: DUKE n.v.; isotype: CR n.v.).

*Habit and distribution.*—Terrestrial herb, sometimes climbing; known from Nicaragua to Panama.

159. **Dicranopygium venezuelanum** Harling, Acta Horti Berg. 18: 324. 1958. Type: Venezuela. Mérida, between Hacienda Agua Blanca above La Azulita and río Capaz, 975 m, 26 Apr 1944, *J. A. Steyermark 56130* (holotype: F V0092249F).

*Habit and distribution.*—Terrestrial herb; known only from western Venezuela.

160. **Dicranopygium wallisii** (Regel) Harling, Acta Horti Berg. 17: 44. 1954, as ‘*Wallisii*’ ≡ *Carludovica wallisi* Regel, Gartenflora 28: 325. 1879. Type: [Colombia. Chocó], cultivated in Hort. Petropolitano, Jul 1879, *s.c. s.n.* (holotype: LE 00000955).

*Habit and distribution.*—Terrestrial herb; known from Costa Rica to Colombia.

161. **Dicranopygium wedelii** Harling, Acta Horti Berg. 18: 282. 1958, as ‘*Wedelii*’. Type: Panama. Bocas del Toro, Water valley, 23 Sep 1940, *H. Wedel 921* (holotype: MO 123156; isotypes: GH 00028606, US 00027176).

*Habit and distribution.*—Terrestrial herb; known from Nicaragua to Panama.

162. **Dicranopygium williamsii** (Standl.) Harling, Acta Horti Berg. 17: 44. 1954, as ‘*Williamsii*’ ≡ *Carludovica williamsii* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 11: 146. 1936. Type: Peru. San Martín, San Roque, 1350–1500 m, Jan–Feb 1930, *Ll. Williams 7477* (holotype: F V0092238F; isotype: G 00098239 [digital image seen]).

*Habit and distribution.*—Terrestrial herb; known in eastern Ecuador and Peru.

163. **Dicranopygium yacusisa** Harling, Acta Horti Berg. 18: 288. 1958, as '*Yacu-Sisa*'. Type: Peru. San Martín, Chazuta, río Huallaga, ca. 260 m, Mar 1935, *G. Klug 4026* (holotype: S R-1493 [digital image seen]; isotypes: F V0092250F, MO 302540, NY 00688953, GH 00028613, UC n.v., US 00027177).

*Habit and distribution.*—Terrestrial herb; known from southwestern Amazon in Ecuador, Peru and Brazil. Registered from Venezuela Amazon (Harling & Eriksson, 1998).

164. **Evodianthus cremnophilus** (Hammel & G.J.Wilder) E.S.Leal, (pending publication) ≡ *Dianthoveus cremnophilus* Hammel & G.J.Wilder, Ann. Missouri Bot. Gard. 76: 113. 1989. Type: Ecuador. Pichincha, Quito to Santo Domingo de los Colorados, 44 km E of Santo Domingo, on steep slopes along highway, 1200 m, 0°23'S, 78°50'W, 18 Jun 1987, *B. E. Hammel & G. J. Wilder 16058* (holotype: MO, 2 sheets (MO 288182, MO 288183); isotypes: COL 000006769, DUKE n.v., F n.v., GB 0047565 [digital image seen], NY 00039629, QCA 36034 [digital image seen], US, 2 sheets (US 00409685, US 00409686)).

*Habit and distribution.*—Terrestrial herb; known from southwestern Colombia to nothern Ecuador.

165. **Evodianthus funifer** (Poit.) Lindm., Bih. Kongl. Svenska Vetensk.-Akad. Handl.

26: 8. 1900 ≡ *Ludovia funifera* Poit., Mém. Mus. Hist. Nat. 9: 28. 1822 ≡ *Salmia funifera* (Poit.) Spreng., Syst. Veg. 3: 772. 1826 ≡ *Carludovica funifera* (Poit.) Kunth, Enum. Pl. 3: 106. 1841. Type: Type: French Guiana. s.l., 1819–1821, *P. A. Poiteau s.n.* (lectotype: K 000400097 [digital image seen], mixed with *Thoracocapus bissectus* (Vell.) Harling, designated by Harling (1958: 265)).

= *Ludovia subacaulis* Poit., Mém. Mus. Hist. Nat. 9: 31. 1822 ≡ *Salmia subacaulis* (Poit.) Schult & Schult. f., Mant. 3 (Schult & Schult. f.): 341. 1827 ≡ *Carludovica subacaulis* (Poit.) Kunth, Enum. Pl. [Kunth] 3: 107. 1841. Type: not designated.

= *Evodianthus angustifolius* Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 195. 1857 ≡ *Carludovica oerstedii* Hemsl., Biol. Cent.-Amer., Bot. 3: 416. 1885. Type: Orig. coll. lacking (lectotype: L'Amer. Centrale t. I. 1863, designated by Harling (1958: 265).

= *Carludovica chelidonura* Drude in Martius & Eichler, Fl. bras. 3: 238. 1881. Type: Brazil. [Bahia]. In sylvis umbrosis pr. Ilheos [Ilhéus], Sep 1827, *L. Riedel s.n.* (lectotype: LE 00000964 [digital image seen], designated by Harling (1958: 265)).

= *Carludovica heterophylla* Mart. ex Drude in Martius & Eichler, Fl. bras. 3: 242. 1881. Type: Brazil. [Amazonas], Provinciae Rio Negro, in montibus Serra Araracoara ad. flum. Japura, 1819–1820, *C. F. P. Martius s.n.* (holotype: M 0219246 [digital image seen]).

= *Evodianthus freyreissii* Lindm., Bih. Kongl. Svenska Vetensk.-Akad. Handl. 26: 9. 1900, as '*Freyreissii*'. Type: Brazil. s.l., 1815, *G. H. Freyreiss s.n.* (holotype: S R-2220 [digital image seen]).

= *Carludovica coronata* Gleason, Bull. Torrey Bot. Club 56: 5. 1929. Type: Guyana. Kaieteur falls, Potaro river, 23 Oct–3 Nov 1923, *J. S. de La Cruz 4444* (holotype: NY n.v.; isotypes: GH 00028604, US 00027149).

= *Evodianthus funifer* subsp. *trailianus* (Drude) Harling, Acta Horti Berg. 18: 271. 1958, as '*Trailianus*' ≡ *Carludovica trailiana* Drude in Martius & Eichler, Fl. bras. 3: 241. 1881. Type: Brazil. s.l., s.d., *C. F. P. Martius s.n.* (lectotype: M 0219247 [digital image seen], designated by Harling (1958: 271). **syn. nov**.

= *Evodianthus funifer* subsp. *peruvianus* Harling, Acta Horti Berg. 18: 272. 1958. Type: Peru. Loreto, vicinity of Iquitos, hacienda Soledad on río Itaya, 15 Nov 1940, *E. Asplund 14528* (holotype: S R-2221 [digital image seen]). **syn. nov.**

= *Evodianthus funifer* subsp. *fendleranus* Harling, Acta Horti Berg. 18: 274. 1958, as '*Fendleranus*'. Type: Venezuela. [Aragua], prope Coloniam Tovar, 22 Apr 1858, *A. Fendler 2617* (holotype: GOET 002349 [digital image seen]; isotypes: GH 00028614, K n.v.). **syn. nov.**

*Habit and distribution.*—Root-climbing liana; a widespread species, in Central America from Nicaragua to Panama, and in Trinidad and Tobago (Harling, 1958; Harling et al., 1998). Widely distributed in South America, in Ecuador (Harling, 1973), Peru (Brako & Zarucchi, 1993), Guyana, French Guiana, and Suriname (Eriksson & Harling, 2007), Venezuela (Harling & Eriksson, 1998; Eriksson & Harling, 2007), and Brazilian Amazon (Gomes & Mello-Silva, 2006; Leal & Forzza, 2012). It occurs also in the Atlantic Forest, eastern Brazil, restricted between southern Bahia and northern Espírito Santo States (Freitas & al., 2012).

*Notes.*—We consider all subspecies proposed by Harling (1958) as synonyms of *Evodianthus funifer*. The vegetative parts size used by him to separate the taxa in this widely distributed species are quite variable, even within one same population.

166. **Ludovia integrifolia** (Woodson) Harling, Acta Horti Berg. 18: 338. 1958 ≡ *Carludovica integrifolia* Woodson in Woodson & Schery, Ann. Missouri Bot. Gard. 29: 322. 1942. Type: Panama. [Darién], southerm Darién, along the Sambú river, above tide limit, Feb 1912, *H. Pittier 5560* (holotype: US 00087785, isotype: GH n.v.).

= *Ludovia bierhorstii* G. J. Wilder, J. Arnold Arbor. 59: 87. 1978, as '*Bierhorstii*'. Type: Colombia. Nariño, near Altaquer, from cultivated material at the University of Illinois at Chicago Circle (lacking collection number) preserved in FPA, originally collected 28–30 Jul 1974, *G. J. Wilder & E. Hernandez s.n.* (holotype: F V1764556). **syn. nov.**

*Habit and distribution.*—Root-climbing liana; lowland forests from Nicaragua to western Colombia and Ecuador.

167. **Ludovia lancifolia** Brongn., Ann. Sci. Nat., Bot., sér. 4: 362. 1861, as '*lancaefolia*' ≡ *Carludovica lancifolia* H.Wendl., nom. nudum, Index Palm. 43. 1854, as '*lancaefolia*' ≡ *Carludovica lancifolia* (Brongn.) Schaedtler, Hamburger Garten-Blumenzeitung 31: 301. 1875, as '*lancaefolia'*. Type: French Guyana. s.l., s.d., cultivated in Hortus Parisiensis, Jan 1959, *R. Boullet s.n.* (holotype: P 00303334 [digital image seen]).

= *Carludovica disticha* Neumann, Rev. Hort. [Paris], sér. 3, 1: 86. 1847. Type: Original collection lacking, name based on cultivated individuals in Hort. Parisiensis.

= *Ludovia crenifolia* Drude in Martius & Eichler, Fl. bras. 3: 243. 1881. Type: Brazil. [Colombia], Provinciae Rio Negro, in horridis silvis ad Araracoara et ad Porto dos Miranhas, Jan. 1820, *C. F. P. Martius s.n.* (lectotype, designated here: M 0111302 [digital image seen]; isolectotypes: M 0111301 [digital image seen], M 0111303 [digital image seen]).

*Habit and distribution.*—Root-climbing liana, epiphyte or seldom terrestrial; widely distributed in tropical South America and Panama.

*Notes.*—Drude (1881) indicates the type of *Ludovia crenifolia* as Martius's collections. This collections are found in M herbarium. There are at least two sheets that agree with the informations of the protologue and were collected by Martius, all unfertiles and without any indication of which is the holotype. We choose here the sheet (M 0111302) as the lectotype.

168. **Schultesiophytum chorianthum** Harling, Acta Horti Berg. 18: 261. 1958. Type: Colombia. Amazonas, Trapecio amazónico, Loretoyacu river, ca. 100 m, Oct 1946, *R. E. Schultes & G. A. Black 8539* (holotype: US 00087789, isotype: NY 00133667).

*Habit and distribution.*—Terrestrial herb; southwestern Amazonian species, ocurrs in Colombia, Peru, and Ecuador.

169. **Sphaeradenia acutitepala** Harling, Acta Horti Berg. 18: 354. 1958. Type: Colombia. Valle del Cauca, Cordillera occidental, vertiente occidental, hoya del río Anchicayá, entre Sabaletas y la Quebrada del Tátabro, 30–60 m, 28 Sep 1946, *J. Cuatrecasas 22035* (holotype: VALLE, 2 sheets (VALLE 000247 [digital image seen], VALLE 000248 [digital image seen]); isotype: GB 0047594 [digital image seen]).

= *Sphaeradenia carrilloana* Grayum & Hammel, Syst. Bot. 7: 227. 1982. Type: Costa Rica. Heredia, Finca La Selva, the OTS field station on the río Puerto Viejo just E of its junction with the río Sarapiquí, ca. 100 m, 1 Jun 1981, *B. E. Hammel & J. Trainer 10782* (holotype: DUKE 10000079 [digital image seen]; isotype: MO 107950).

*Habit and distribution.*—Epiphyte; known from Caribbean lowlands of estern Panama, Costa Rica, southeast Nicaragua, Pacific lowlands of Colombia and Panama.

170. **Sphaeradenia alba** R.Erikss., Opera Bot. 126: 87. 1995. Type: Panama. Panamá, Cerro Jefe, premontane rain forest, ca. 1000 m, 11 Jun 1975, *S. A. Mori 6518* (holotype: GB 0047595 [digital image seen]).

*Habit and distribution.*—Terrestrial herb or epiphyte; known only from Panama.

171. **Sphaeradenia alleniana** Harling, Acta Horti Berg. 18: 362. 1958, as '*Alleniana*'. Type: Panama. Coclé, Cerro Pajita, region north of El valle de Anton, ca. 1050 m, 12

May 1947, *P. H. Allen 4511* (holotype: S R-5833 [digital image seen]; isotype: G 00098235 [digital image seen]).

*Habit and distribution.*—Epiphyte, seldom terrestrial herb; known from Costa Rica and Panama.

172. **Sphaeradenia amazonica** Harling, Acta Horti Berg. 18: 358. 1958. Type: Colombia. Vaupés, río Vaupés, Circasia, sandy savannah, quartzite base, ca. 260 m, 0°45'S, 70°30'W, Nov 1951, *R. E. Schultes & I. Cabrera 19675* (holotype: S R-5834 [digital image seen]; isotypes: COL 000006787, GH 00046418, NY, 2 sheets (NY 00022524, NY 00022525), US, 2 sheets (US 00433584, US 00433585)).

*Habit and distribution.*—Terrestrial herb; lowland forests from Colombia, Venezuela and northwestern Brazil.

173. **Sphaeradenia angustifolia** (Ruiz & Pav.) Harling, Acta Horti Berg. 17: 3. 1954 ≡ *Carludovica angustifolia* Ruiz & Pav., Fl. Peruv. [Ruiz & Pavon] 292. 1798 ≡ *Ludovia angustifolia* (Ruiz & Pav.) Pers., Syn. Pl. [Persoon] 2: 576. 1807 ≡ *Salmia angustifolia* (Ruiz & Pav.) Willd., Mag. Neuesten Entdeck. Gesammten Naturk. Ges. Naturf. Freunde Berlin 5: 401. 1811. Type: Peru. Huánuco, Muña et Chinchao nemoribus, s.d., *H. Ruiz & J. A. Pavon s.n.* (lectotype: first-step lectotype designated by Harling (1958: 346), second-step, designated here: MA 810365 [digital image seen]; isolectotypes: G n.v., MA 810366 [digital image seen], OXF n.v., K n.v., F n.v.).

*Habit and distribution.*—Terrestrial herb or epiphyte; known from the Cordillera Oriental in Peru (Eriksson, 1995).

174. **Sphaeradenia asplundii** (Harling) Harling, Acta Horti Berg. 17: 3. 1954, as ‘*Asplundii*’ ≡ *Carludovica asplundii* Harling, Acta Horti Berg. 15: 201. 1950, as ‘*Asplundii*’. Type: Ecuador. Pichincha, valley of rio Saloya, El Cuello, ca. 2000 m, 11 Nov 1939, *E. Asplund 10099* (holotype: S 05-5637 [digital image seen]; isotype: S R-5835 [digital image seen]).

*Habit and distribution.*—Terrestrial herb; known from montane forests in western Colombia and Ecuador.

175. **Sphaeradenia brachiolata** R.Erikss., Opera Bot. 126: 71. 1995. Type: Ecuador. Cotopaxi, Tenefuerste, río Pilalo, km 52–53 Quevedo-Latacunga, 750–900 m, 29 Oct 1981, *C. H. Dodson & P. M. Dodson 11978* (holotype: SEL 001538 [digital image seen]; isotype: MO 289876).

*Habit and distribution.*—Epiphyte or terrestrial herb; known only from Cordillera Central in Ecuador (Eriksson, 1995).

176. **Sphaeradenia buenaventurae** Harling, Acta Horti Berg. 18: 389. 1958, as ‘*Buenaventurae*’. Type: Colombia. Valle del Cauca, Costa del Pacífico, bahía de Buenaventura, Quebrada de San Joaquín, 0–10 m, 20–23 Feb 1946, *J. Cuatrecasas*

*19898* (F, 2 sheets (F V0045365F, F V0045366F); isotype: VALLE, 2 sheets (VALLE 000238 [digital image seen], VALLE 000239 [digital image seen])).

*Habit and distribution.*—Epiphyte; Pacific lowlands from Colombia.

177. **Sphaeradenia carnosa** R.Erikss., Opera Bot. 126: 64. 1995. Type: Colombia. Valle del Cauca & Chocó, finca Las Amarillas c. 10 km W of El Cairo, 2100–2150 m, 4°47'N, 76°17'W, 29 Mar 1988, *R. Eriksson & J. T. Knudsen 152* (holotype: GB 0047596 [digital image seen]; isotypes: CUVC n.v., MO n.v., NY 00073929).

*Habit and distribution.*—Terrestrial herb; known from Cordillera Occidental in Colombia.

178. **Sphaeradenia chiriquensis** Harling, Acta Horti Berg. 18: 376. 1958. Type: Panama. Chiriqui, trail from Cerro Punta to headwaters of río Caldera, 2250–2500 m, 14 Jan 1939, *P. H. Allen 1460* (holotype: MO 123145, isotypes: F V0045361F, GH 00046415).

*Habit and distribution.*—Terrestrial herb; occurs in Panama and Costa Rica.

179. **Sphaeradenia columnaris** R.Erikss., Opera Bot. 126: 74. 1995. Type: Colombia. Valle del Cauca, Yatacué, Alto Anchicaya, near CVC hydroelectric plant headquarters, valley of río Dagua (tributary of río Anchicaya), 710–880 m, 3°38'N, 76°45'W, 17 Jul 1984, *A. Gentry & M. Monsalve 48249* (holotype: MO 1358350).

*Habit and distribution.*—Epiphyte; known only in Colombia and Ecuador.

180. **Sphaeradenia compacta** R.Erikss., Opera Bot. 126: 54. 1995. Type: Colombia. Nariño, Reserva Natural La Planada, S of Ricaurte, 1800–1850 m, 1°05'N, 77°57'W, 18 Mar 1988, *R. Eriksson & J. T. Knudsen 134* (holotype: GB 0047597 [digital image seen]; isotype: PSO 0000057 [digital image seen]).

*Habit and distribution.*—Epiphyte; known from Colombia and Ecuador.

181. **Sphaeradenia crassiceps** R.Erikss., Opera Bot. 126: 54. 1995. Type: Peru. Huánuco, SW slope of the río Yuya Pichis watershed, on the ascent of Cerros del Sira, ca. 1850 m, 9°25'N, 74°42'W, 31 Jul 1969, *T. R. Dudley 13556* (holotype: NA, 2 sheets (NA 0027489 [digital image seen], NA 0027490 [digital image seen])).

*Habit and distribution.*—Epiphyte or seldom terrestrial; known only from the type locality.

182. **Sphaeradenia crocea** Harling, Acta Horti Berg. 18: 387. 1958. Type: Colombia. Chocó, headwaters of río Tutunendo, east of Quibdó, 20–21 May 1931, *W. A. Archer 2194* (holotype: US 00433590).

*Habit and distribution.*—Epiphyte; Caribbean lowlands of Panama and Costa Rica and Pacific lowlands of Colombia.

183. **Sphaeradenia cuatrecasasiana** Harling, Acta Horti Berg. 18: 359. 1958, as '*Cuatrecasana*'. Type: Colombia. Valle del Cauca, Cordillera Occidental, Mares, 1970– 2000 m, 13 Mar 1947, *J. Cuatrecasas 23769* (holotype: F, 4 sheets (F V0092111F, all sheets with the same barcode number); isotype: VALLE, 3 sheets (VALLE 000253 [digital image seen], VALLE 000254 [digital image seen], VALLE 000255 [digital image seen])).

*Habit and distribution.*—Epiphyte or seldom terrestrial; known only from western Colombia.

184. **Sphaeradenia danielii** Harling, Acta Horti Berg. 18: 384. 1958, as '*Danielii*'. Type: Colombia. Antioquia, Capiro de la Ceja, 21 Jan 1937, *H. Daniel 2008* (holotype: US 00433594; isotype: MEDEL 000140).

*Habit and distribution.*—Terrestrial herbs; occurs in montane forests from Central Colombia.

185. **Sphaeradenia distans** R.Erikss., Opera Bot. 126: 72. 1995. Type: Colombia. Valle del Cauca, finca Las Amarillas W of El Cairo, 2100–2200 m, 4°47’N, 76°17’W, 2 Apr 1988, *R. Eriksson & J. T. Knudsen 184* (holotype: GB 0047599 [digital image seen]; isotype: CUVC n.v.).

*Habit and distribution.*—Terrestrial herb; known only from the Cordillera Occidental in western Colombia.

186. **Sphaeradenia duidae** Harling, Acta Horti Berg. 18: 364. 1958. Type: Venezuela. [Amazonas], summit of Mount Duida, Desfiladero, ca. 1800 m, Aug 1928–Apr 1929, *G. H. H. Tate 697* (holotype: NY 00038534).

= *Sphaeradenia rubescens* Harling, Bol. Soc. Venez. Ci. Nat. 25: 66. 1963. Type: Venezuela. Bolívar Massif, vicinity of camp 3, northwestern part of Abácapa-tepuí. 1300 m, 20 Apr 1953, *J. A. Steyermark 75204* (holotype: VEN 55973 [digital image seen]; isotypes: F, 3 sheets (F V0045371F, F V0045372F, F V0360281F), NY, 2 sheets (NY 00133665, NY 00133666)).

= *Sphaeradenia maguirei* Harling, Mem. New York Bot. Gard. 23: 112. 1972. Type: Venezuela. Amazonas, Cerro Sipapo (Paráque), south terraces, peak IV, 2000 m, 3 Jan 1949, *B. Maguire & L. Politi 28132* (holotype: NY 00038533).

*Habit and distribution.*—Terrestrial herb or epiphyte; known from tepuis in Venezuela and Brazil.

*Notes.*—Eriksson (1995) synonimized *Sphaeradenia rubescens* and *S. maguirei* under *S. duidae.*

187. **Sphaeradenia fosbergii** Harling, Acta Horti Berg. 18: 353. 1958, as '*Fosbergii*'. Type: Colombia. Huila, above finca la Estrella on ridge S of Quebrada Cucaracha, one

of headwaters of Quebrada Damas, 12 Km ESE of Garzón, 2200–2700 m, 2°8’N, 75°33’W, 31 Jan 1943, *F. R. Fosberg 19896* (holotype: US, 3 sheets (US 00433587, US 00433588, US 00433589)).

*Habit and distribution.—*Terrestrial herb; occurs only in the southern Colombia in Cordillera Oriental .

188. **Sphaeradenia garciae** Harling, Acta Horti Berg. 18: 389. 1958, as ‘*Garcíae*’. Type: Colombia. Chocó, Bahía Solano, dense forest along Quebrada Jellita, 50–150 m, 22 Feb 1939, E. P. *Killip & H. García 33501* (holotype: US 00433586; isotype: COL 000006788).

= *Sphaeradenia cuadrosii* Galeano & R. Bernal, Caldasia 14: 33. 1984. ≡ *Sphaeradenia garciae* subsp. *cuadrosii* R.Erikss., Opera Bot. 126: 92. 1995. Type: Colombia. Antioquia, Município de Cocorná, autopista Medellín-Bogotá, km 63, Quebrada El Bihao, ca. 1900 m, 26 Apr 1980, *R. Bernal & G. Galeano 173* (holotype: COL 000006789). **syn nov**.

*Habit and distribution.—*Epiphyte; widespread from Costa Rica to Ecuador.

*Notes.—*Galeano & Bernal (1984) described *Sphaeradenia cuadrosii* and vaguely indicated his close affinities with *S. angustifolia* from Central Peru. Eriksson (1995), based on form and width of the leaf segments decreases the species to subspecies of *Sphaeradenia garciae*, which is a widespread and variable species in relation to the dimensions of the vegetative parts. Therefore, *Sphaeradenia cuadrosii* is synonymized to *S. garciae*.

189. **Sphaeradenia gigantea** R.Erikss., Opera Bot. 126: 49. 1995. Type: Colombia. Valle del Cauca, Alto Anchicayá, S of campamentos de Yatacué (CVC), 400–500 m, 3°34’N, 76°52’W, 4 Mar 1988, *R. Eriksson & J. T. Knudsen 99* (holotype: GB, 2 sheets (GB 0047600 [digital image seen], GB 0047601[digital image seen]); isotype: CUVC n.v.).

*Habit and distribution.*—Terrestrial herb; known only from the type locality.

190. **Sphaeradenia hamata** Harling, Acta Horti Berg. 18: 351. 1958. Type: Ecuador. Pichincha, El Volante on road between Chiriboga and Santo Domingo de los Colorados, ca. 1900 m, 19 Aug 1955, *E. Asplund 17381* (holotype: S 05-5639 [digital image seen]; isotype: S R-5836 [digital image seen]).

*Habit and distribution.*—Epiphyte; occurs in Cordillera Occidental in Ecuador and Colombia.

191. **Sphaeradenia horrida** (Harling) Harling, Acta Horti Berg. 17: 3. 1954 ≡ *Carludovica horrida* Harling, Acta Horti Berg. 15: 202. 1950. Type: Ecuador. Pichincha, valley of río Pilatón below Garretas, 2200–2400 m, 4 Nov 1939, *E. Asplund*

*9680* (holotype: S 05-5643 [digital image seen]; isotypes: S R-5837 [digital image seen], UPS V064198 [digital image seen], US 00087784).

= *Sphaeradenia quitoënsis* (Harling) Harling, Acta Horti Berg. 17: 3. 1954 ≡ *Carludovica quitoënsis* Harling, Acta Horti Berg. 15: 202. 1950. Type: Ecuador. Pichincha of río Saloya, El Cuello, ca. 2000 m, 11 Dec 1939, *E. Asplund 10097* (holotype: S, 2 sheets (S R-5840 [digital image seen], S 05-5646 [digital image seen]).

*Habit and distribution.*—Terrestrial herb or epiphyte; known from Ecuador and Colombia.

*Notes.*—Eriksson (1995) synonymized *Sphaeradenia quitoënsis* into *S. horrida*.

192. **Sphaeradenia killipii** (Standl.) Harling, Acta Horti Berg. 17: 3. 1954, as '*Killipii*' ≡ *Carludovica killipii* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 65. 1940. Type: Colombia. Valle del Cauca, Buanaventura bay, 13 Apr 1939, *E. P. Killip 34975* (lectotype: F (F V0045380F, vegetative parts with attached peduncle and infructescence fragments in envelope), designated by Harling (1958: 380); isolectotypes: BC 623378 [digital image seen], COL 000006791, US, 3 sheets (US 00087786, US 00087787, US 00087788)).

*Habit and distribution.*—Epiphyte; Pacific lowlands from Colombia and Ecuador.

193. **Sphaeradenia laucheana** (Sander ex Mast.) Harling, Acta Horti Berg. 17: 3. 1954, as '*Laucheana*' ≡ *Salmia laucheana* Sander ex Mast., Gard. Chron. 13: 442. 1893 ≡

*Carludovica laucheana* (Sander ex Mast.) Hook.f., Bot. Mag. 125, ser. 3, v. 5: tab. 7683. 1899. Type: Colombia. Antioquia, cultivated in Hort. Kewensis, 27 May 1897, *s.c. s.n.* (neotype: K n.v., designated by Eriksson (1993: 459).

= *Sphaeradenia chelidonura* Harling, Acta Horti Berg. 18: 366. 1958. Type: Colombia. Meta, Cordillera Oriental, ridge between río Manzanares and Quebrada Playón, 30 km W of La Esperanza, 52 km W of Villavicencio. 1850 m, 3 Sep 1944, *M. L. Grant 10128* (holotype: US 00433583; isotype: US 01013915).

= *Sphaeradenia sneidernii* Harling, Acta Horti Berg. 18: 370. 1958, as '*Sneidernii*'. Type: Colombia. Caldas, Laguneta, Salento, 2800 m, 10 Apr 1942, *K. Sneirdern 3190* (holotype: S, 2 sheets (S R-5843 [digital image seen], S 05-5648 [digital image seen]; isotypes: A 00046419 [digital image seen], LL 00370208 [digital image seen], MICH 1192182 [digital image seen]).

= *Pseudulodovia andreana* Harling, Acta Horti Berg. 18: 340. 1958, as '*Andreana*'. Type: Colombia. Tolima, Quindió or Risaralda, Las Cruces, Quindió, 9 Mar 1876, *E. André 2298* (lectotype: K n.v. [only infructescence], designated by Eriksson (1993: 459); isolecotype: NY 00133664, only leaves from *Ludovia* sp.]).

= *Carludovica irazuensis* Cufod., Arch. Bot. Sist. 9: 180. 1933 ≡ *Sphaeradenia izaruensis* (Cufod.) Harling, Acta Horti Berg. 17: 3. 1954. ≡ *Sphaeradenia laucheana* subsp. *irazuensis* (Cufod.) R.Eriksson, Opera Bot. 126: 40. 1995. Type: Costa Rica. San José, volcán de Irazú, SW slope, near Guayabilos, 2250 m, 26 May 1930, *G. Cufodontis 466* (lectotype: F n.v., designated by Eriksson (1995:40); isolectotypes: GB n.v., F n.v., MO n.v.). **syn. nov**.

*Habit and distribution.*—Epiphyte or terrestrial herb; widespread in montane forests from Costa Rica to Ecuador and Venezuela .

*Notes.*—Eriksson (1993) synonimized *Pseudoluvia andreana* and, after (Eriksson, 1995) *Sphaeradenia chelidonura* and *Sphaeradenia sneidernii* to *Sphaeradenia laucheana*. Based on minor details also considered *Sphaeradenia irazuensis* a subspecies of *Sphaeradenia laucheana* (Eriksson, 1995). *Sphaeradenia laucheana* is a widespread and variable species and here also *S. irazuensis* is considred a synonym of *S. laucheana*.

194. **Sphaeradenia lemaënsis** Harling, Bol. Soc. Venez. Ci. Nat. 25: 65. 1963. Type: Venezuela. Bolívar, Sierra de Lema, cabeceras de río Chicanán, 80 km (en línea recta) al suroeste de El Dorado, 700 m, 6°05'N, 62°W, 29 Aug 1961, *J. A. Steyermark 89611* (holotype: VEN 55974 [digital image seen], isotype: S R-5838 [digital image seen]).

*Habit and distribution.*—Terrestrial herb; known only from the type locality.

195. **Sphaeradenia magniglobula** R.Erikss., Opera Bot. 126: 87. 1995. Type: Panama. Chiriquí or Boca del Toro, near top of continental divide ridge near Cerro Pate Macho NE of Boquete, ca. 2150 m, 15 Mar 1982, *B. E. Hammel, W. J. Kress, S. Knapp, J. Trainer & T. Will 11407* (holotype: DUKE n.v.; isotype: MO, 2 sheets (MO-107921, MO-107922)).

*Habit and distribution.*—Terrestrial herb or epiphyte; occurs in Costa Rica and Panama (Eriksson, 1995).

196. **Sphaeradenia marcescens** R.Erikss., Novon 17: 158. 2007. Type: Ecuador. Guayas, Reserva Ecológica Manglares Churute, Cerro Pancho Diablo, 250 m, 2°25’N, 79°39’W, 3 May 1996, *X. Cornejo & C. Bonifaz 5107* (holotype: GB 0048941 [digital image seen]; isotype: GUAY 214793 [digital image seen]).

*Habit and distribution.*—Terrestrial herb or epiphyte; known only from the type locality.

197. **Sphaeradenia meridionalis** R.Erikss., Opera Bot. 126: 55. 1995. Type: Bolivia. La Paz, Noryungas, 13.7 km NW of San Pedro on road through Incahuara-Mejilones, and along trail to 12 de Octubre, 1500 m, 15°58’S, 67°37’W, 12–14 Feb 1983, *J. C. Solomon 9490* (holotype: MO, 2 sheets (MO 104467, MO 104468); isotype: GB 0047602 [digital image seen]).

*Habit and distribution.*—Epiphyte; occurs in montane forest from Peru and Bolivia (Eriksson, 1995).

198. **Sphaeradenia occidentalis** R.Erikss., Opera Bot. 126: 80. 1995. Type: Costa Rica. Puntarenas, La Reserva Biológica de Monte Verde, NW part of reserve, 1500–1600 m, 10°18’N, 84°48’W, 9 Feb 1988, *R. Eriksson & J. T. Knudsen 60* (holotype: GB n.v.; isotype: CR 171245 [digital image seen]).

*Habit and distribution.*—Epiphyte; montane forests from Central Costa Rica.

199. **Sphaeradenia oligostemon** Harling, Acta Horti Berg. 18: 356. 1958. Type: Colombia. Valle del Cauca, Cordillera Occidental, vertiente occidental, hoya del río Dígua, Quebrada del San Juan, subiendo a Paragüita desde Quemeral, 1570–1740 m, 17 Mar 1947, *J. Cuatrecasas 23798* (holotype: F, 2 sheets (F V0045367F, F V0045368F)).

*Habit and distribution.*—Terrestrial vine or seldom epiphyte; knowm from northwestern Colombia.

200. ***Sphaeradenia oxystigma*** R.Erikss., Opera Bot. 126: 42. 1995. Type: Ecuador. Zamora-Chinchipe, Yangana-Valladolid road, just after the pass, 2750 m, 22 Jan 1991, *R. Eriksson, Y. Andersson, B. Nordenstam & R. Lundin 208* (holotype: GB 0047605 [digital image seen]; isotype: QCA 36188 [digital image seen]).

*Habit and distribution.*—Terrestrial herb or epiphyte; occurs in Ecuador e Peru.

201. **Sphaeradenia pachystigma** Harling, Acta Horti Berg. 18: 378. 1958. Type: Panama. Chiriquí, vicinity of Bajo Chorro, 1900 m, 20–22 Jul 1940, *R. E. Woodson & R. W. Schery 625* (holotype: MO 123147; isotype: GH 00046416).

= *Sphaeradenia davidsoniae* Harling, Acta Horti Berg. 18: 379. 1958, as '*Davidsoniae*'. Type: Panama. Chiriquí, Boquete District, Bajo Chorro, ca. 2000 m, 5 Jan 1938, *M. E. Davidson 35* (holotype: MO 123146; isotype: F V0045362F, US 00087790).

*Habit and distribution.*—Epiphyte; occurs in Costa Rica and Panama (Eriksson, 1995).

*Notes.*—Eriksson (1995) synonymized *Sphaeradenia davidsoniae* under *S. pachystigma*.

202. **Sphaeradenia pallida** R.Erikss., Opera Bot. 126: 76. 1995. Type: Colombia. Valle del Cauca, Alto Anchicayá, N of campamentos de Yatacué (CVC), 400–500 m, 3°35'N, 76°52'W, 4 Mar 1988, *R. Eriksson & J. T. Knudsen 99* (holotype: GB, 2 sheets (GB 0047606 [digital image seen], GB 0047607 [digital image seen]); isotypes: CUVC n.v., MO 104466).

*Habit and distribution.*—Terrestrial plant; known only from western Colombia (Eriksson, 1995).

203. **Sphaeradenia perangusta** R.Erikss., Opera Bot. 126: 47. 1995. Type: Peru. Amazonas, trail above Quebrada Cikan Inci to Shimpuntz W of Huampami, 200–275 m, 18 Dec 1972, *B. Berlin 630* (holotype: MO 200351).

*Habit and distribution.*—Epiphyte; known only from the type locality.

204. **Sphaeradenia praetermissa** R.Erikss., Opera Bot. 126: 79. 1995. Type: Costa Rica. Heredia, 12 km NE northeast of San Rafael, mostly between río Las Vueltas and Quebrada Grande, ca. 2000 m, 5 Jan 1972, *R. L. Wilbur, F. Almeda & J. Luteyn 15985* (holotype: DUKE 10000083 [digital image seen]; isotype: F, 2 sheets (F V0045363F, F V0045364F)).

*Habit and distribution.*—Epiphyte, seldom terrestrial; known only from Costa Rica (Eriksson, 1995).

205. **Sphaeradenia proboscidifera** R.Erikss., Opera Bot. 126: 74. 1995. Type: Colombia. Valle del Cauca, 3–4 km W of El Queremal, along the old Buenaventura road, 1250– 1380 m, 3°32'N, 76°43–44'W, 11 Mar 1988, *R. Eriksson & J. T. Knudsen 113* (holotype: GB 0047608 [digital image seen]; isotypes: CUVC n.v., MO 104465).

*Habit and distribution.*—Epiphyte, seldom terrestrial; known only from the type locality.

206. **Sphaeradenia pterostigma** Harling, Acta Horti Berg. 18: 355. 1958. Type: Colombia. Nariño, Barbacoas, Corregimiento Santander (Buenavista) a Barbacoas (vertiente del río Telembí), 200–840 m, 3–5 Aug 1948, *H. García-Barriga 13210* (holotype: US 00433582; isotype: COL 000006792).

*Habit and distribution.*—Epiphyte, seldom terrestrial; known from western Colombia and Ecuador.

207. **Sphaeradenia pulchra** R.Erikss., Opera Bot. 126: 92. 1995. Type: Colombia. Valle del Cauca, Cerro del Inglés, W of El Cairo, trail from finca Las Amarillas to summit, 2100–2400 m, 4°47'N, 76°17'W, 30 Mar 1988, *R. Eriksson & J. T. Knudsen 160* (holotype GB 0047609 [digital image seen]; isotypes: CUVC n.v., MO 104464).

*Habit and distribution.*—Epiphyte; known from Colombia and Ecuador.

208. **Sphaeradenia purpurea** Harling, Acta Horti Berg. 18: 385. 1958. Type: Colombia. Valle del Cauca, Cordillera Occidental, vertiente oriental, hoya del río Cali, Pichindé, Morro Pelado, 2270–2320 m, 17 Oct 1944, *J. Cuatrecasas 18187* (holotype: F, 2 sheets (F V0045369F, F V0045370F); isotypes: US, 2 sheets (US 00087791, US 00087792), VALLE, 2 sheets (VALLE 000234 [digital image seen], VALLE 000235 [digital image seen]).

= *Sphaeradenia longepedunculata* Harling, Acta Horti Berg. 18: 390. 1958. Type: Colombia. Cauca, Chisquio, ca. 1700 m, 7 Feb 1940, *E. Asplund 10692* (holotype: S R-5839 [digital image seen]).

*Habit and distribution.*—Epiphyte, seldom terrestrial; known only from Colombia.

*Notes.*—Eriksson (1995) synonymized *Sphaeradenia longepedunculata* under *S. purpurea*.

209. **Sphaeradenia rhodocephala** (Harling) Harling, Acta Horti Berg. 18: 391. 1958 ≡ *Carludovica rhodocephala* Harling, Acta Horti Berg. 15: 200. 1950. Type: Ecuador. Pastaza, Mera, 3 Apr 1940, *M. Lugo 168* (holotype: S R-5841 [digital image seen]; isotypes: MO 289877, NY 00038535, S 06-4721 [digital image seen]).

*Habit and distribution.*—Epiphyte, seldom terrestrial; occurs in Ecuador and Central Peru.

210. **Sphaeradenia rostellata** R.Erikss., Novon 17: 156. 2007. Type: Costa Rica. Limón, Cantón de Talamanca, P.N. Cordillera de Talamanca, Cerro El Codo, izquierda del río Lori, entre Ujarrás y San José Cabécar, 1500 m, 09°21’23”N, 83°13’40”W, 19 Mar 1993, *A. Fernandéz 741* (holotype: CR INB0001574609 [digital image seen]; isotype: CR INB0001595279 [digital image seen]).

*Habit and distribution.*—Epiphyte; known only from the type locality.

211. **Sphaeradenia sanctae-barbarae** Harling, Opera Bot., B 1: 42. 1973, as ‘*Sanctae-Barbarae*’. Type: Ecuador. Sucumbíos, Santa Barbara de Sucumbíos, valley of río Chingual, 2400 m, 10–15 Feb 1959, *G. Harling 4178* (holotype: S R-5842 [digital image seen]).

= *Sphaeradenia sanctae-barbarae* subsp. *monostyla* R.Erikss., Opera Bot. 126: 46. 1995. Type: Ecuador. Zamora-Chinchipe, Romerillo, trail at limit of Parque Nacional Podocarpus, 1650–1700 m, 4°13’S, 78°56’W, *J. E. Madsen & J. T. Knudsen 86842* (holotype: AAU, 2 sheets, n.v.). **syn. nov.**

*Habit and distribution.*—Terrestrial herb; known from Ecuador and probably Colombia.

212. **Sphaeradenia scandens** R.Erikss., Opera Bot. 126: 82. 1995. Type: Colombia. Valle del Cauca, Cerro del Inglés, W of El Cairo, trail from finca Las Amarillas to

summit, 2100 – 2400 m, 4°47’N, 76°17’W, 30 Mar 1988, *R. Eriksson & J. T. Knudsen 158* (holotype: GB 0047610 [digital image seen]; isotype: CUVC n.v.).

*Habit and distribution.*—Terrestrial herb or epiphytic vine; known only from western Colombia.

213. **Sphaeradenia sphagnicola** Harling, Acta Horti Berg. 18: 361. 1958. Type: Costa Rica. San José, vicinity of El General, 1500 m, Dec 1936, *A. F. Skutch 2962* (holotype: MO 123157; isotype: US 00087793).

*Habit and distribution.*—Terrestrial herb; known only from Costa Rica (Eriksson, 1995).

214. **Sphaeradenia stenosperma** Harling, Acta Horti Berg. 18: 388. 1958. Type: Colombia. Chocó, south of río Condoto, between Quebrada Guarapo and Mandinga, 120–180 m, 22–28 Apr 1939, *E. P. Killip 35189* (holotype: US 00433591).

*Habit and distribution.*—Terrestrial herb or epiphyte; Pacific lowland forests in Colombia.

215. **Sphaeradenia steyermarkii** (Harling) Harling, Acta Horti Berg. 17: 3. 1954, as ‘*Steyermarkii*’ ≡ *Carludovica steyermarkii* Harling, Acta Horti Berg. 15: 203. 1950, as ‘*Steyermarkii*’. Type: Ecuador. Azuay or Morona-Santiago, slopes above and

bordering, río Tintas, above Campanas campamento, southeast of El Pan, 2860–2985 m, *J. A. Steyermark 53510* (holotype: F V0045381F).

= *Sphaeradenia andina* Harling, Acta Horti Berg. 18: 374. 1958. Type: Colombia. Cauca, between La Cumbre and Quebrada La Isla, headwaters of río Dinde, ca. 2700 m, 28 Aug 1944, *E. L. Core 1108* (holotype: US 00433592).

= *Sphaeradenia silvestris* Harling, Acta Horti Berg. 18: 372. 1958. Type: Colombia. Valle del Cauca, Cordillera Occcidental, Los Farallones, vertiente oriental, bosques sobre el río Pichindé (hoya del río Cali), El Roblal, 2640 m, 25 Jul 1946, *J. Cuatrecasas 21720* (holotype: F, 3 sheets (F V0045373F, F V0045374F, F V0045375F); isotypes: VALLE, 2 sheets (VALLE 000243 [digital image seen], VALLE 000244 [digital image seen]).

*Habit and distribution.*—Terrestrial herb or seldom epiphyte; occurs in Andes from Colombia to Peru.

*Notes.*—Eriksson (1995) synonymized *Sphaeradenia andina* and *S. silvestris* to *S. steyermarkii*.

216. **Sphaeradenia stylosa** Harling, Acta Horti Berg. 18: 352. 1958. Type: Colombia. Nariño, NW slope of Volcán de Chiles, 2560–3350 m, 6–8 Sep 1944, *J. A. Ewan 16085* (holotype: US 00433593; isotype: NO 0109915 [digital image seen]).

*Habit and distribution.*—Terrestrial herb or epiphyte; occurs in Andes from Colombia to Peru.

217. **Sphaeradenia vallensis** Harling, Acta Horti Berg. 18: 391. 1958. Type: Colombia. Valle del Cauca, Cordillera occidental, vertiente occidental, monte La Guarida, filo de la cordillera sobre La Carbonera (entre Las Brisas y Albán), 1950–2000 m, 17 Oct 1946, *J. Cuatrecasas 22205* (holotype: F, 2 sheets (F V0045376F, F V0045377F); isotype: VALLE, 2 sheets (VALLE 000249 [digital image seen], VALLE 000250 [digital image seen]).

*Habit and distribution.*—Terrestrial herb or epiphyte; known only from western Colombia.

218. **Sphaeradenia versicolor** R.Erikss., Opera Bot. 126: 51. 1995. Type: Ecuador. Napo, Baeza-Tena road, 2 km S of Cosanga, 2100 m, 3 Feb 1991, *R. Eriksson, Y. Andersson, B. Nordenstam & R. Lundin 258* (holotype: GB 0047611 [digital image seen]; isotype: QCA 36209 [digital image seen]).

*Habit and distribution.*—Terrestrial herb; known only from eastern Ecuador.

219. **Sphaeradenia virella** R. Erikss., Opera Bot. 126: 99. 1995. Type: Panama. Panamá, Altos de Pacora, 650–750 m, 2 Sep 1974, *P. J. M. Maas, R. L. Dressler & H. Kennedy 1556* (holotype: U 0001485 [digital image seen]; isotype: F n.v., MO 123159).

*Habit and distribution.*—Terrestrial herb; known only from Panama.

220. **Sphaeradenia woodsonii** Harling, Acta Horti Berg. 18: 363. 1958, as '*Woodsonii*'. Type: Panama. Coclé, north rim of El Valle de Antón, near Cerro Turega, 650–700 m, 30 Jun 1940, *R. E. Woodson & R. W. Schery 192* (holotype: GH n.v.; isotype: MO 123158, US 00087794).

*Habit and distribution.*—Epiphyte; lowland forests from Panama.

221. **Stelestylis anomala** Harling, Acta Horti Berg. 18: 398. 1958. Type: Venezuela. Aragua, Parque Nacional de Rancho Grande, ca. 900 m, 29 Jun 1951, *J. García 93* (holotype: VEN 43690 [digital image seen]).

*Habit and distribution.*—Probably epiphyte; known only from Venezuela.

222. **Stelestylis coriacea** Drude in Martius & Eichler, Fl. Bras. 3: 231. 1881. Type: Brazil. Eastern Brazil, s.d., *H. Wawra s.n.* (holotype: W, lost; lectotype, designated by Harling (1958: 393): plate 53 of Martius & Eichler, Fl. Bras. 3 (1881)).

*Habit and distribution.*—Habit unknown; only from eastern Brazil.

223. **Stelestylis stylaris** (Gleason) Harling, Acta Horti Berg. 18: 394. 1958 ≡ *Carludovica stylaris* Gleason, Bull. Torrey Bot. Club 56: 7. 1929. Type: Guyana. Potaro river, Kaieteur savannah, Sep–Oct 1881, *G. S. Jenman 898* (holotype: K 000400089 [digital image seen]).

*Habit and distribution.*—Terrestrial herb, rarely epiphytic; known from Venezuela, Guyana and adjacents parts of Brazil.

224. **Stelestylis surinamensis** Harling, Acta Horti Berg. 18: 396. 1958 ≡ *Carludovica stahelii* Maguire, nom. in sched. Type: Suriname. Tafelberg (table mountain), north of savanna II, vicinity camp I, 17 Aug 1944, *B. Maguire 24407* (holotype: NY 00133659; isotypes: U 0001486 [digital image seen], US 00087795).

*Habit and distribution.*—Terrestrial herb; known from Suriname and French Guiana.

225. **Thoracocarpus bissectus** (Vell.) Harling, Acta Horti Berg. 18: 255. 1958 ≡ *Dracontium bissectum* Vell., Fl. Flum. Icon. 9: t. 118. 1831 ≡ *Philodendron bissectum* (Vell.) Stellfeld, Tribuna Farm. 12: 202. 1944. Type: Brazil. Original collection lacking (lectotype: Flora Fluminensis. Icon. 9: t. 118, designated by Harling (1958: 255)).

= *Carludovica kegeliana* Lem., Ill. Hort. 2: 23. 1855. Type: Suriname. Ad ripas fl. Cassepoere Creek, Nov 1845, *H. Kegel 1183* (lectotype: GOET 002350 [digital image seen], designated by Harling (1958: 255)).

= *Carludovica sarmentosa* Sagot ex Drude, in Martius & Eichler, Fl. bras. 3: 239. 1881. Type: Brazil. *L. Riedel s.n.* (lectotype: LE n.v., designated by Harling (1958: 255); isolectotype: LE n.v.).

= *Carludovica mattogrossensis* Lindm., Bih. Kongl. Svenska Vetensk.-Akad. Handl. 26:

6. 1900. Type: Brazil. Mato [Matto] Grosso, in silva primaeva uda territorii “Poaia”, ad traiectum amnis rio Macoco, affluentis fluminis Alto Paraguay, 11 Apr 1894, *C. A. M. Lindman A2897* (lectotype, designated here: S 06-4540 [digital image seen]; isolectotypes: S 06-4541 [digital image seen], S R-6098 [digital image seen]).

= *Carludovica bracteosa* Gleason, Bull. Torrey Bot. Club 56: 6. 1929. Type: Guyana. Upper Rupununi river, near Dadanawa, 2°45’N, 14 Jun 1922, *J. S. de la Cruz 1505* (holotype: NY 00133656; isotype: US 00027151).

*Habit and distribution.*—Root-climbing liana; widely distributed, with Costa Rica as its northern limit. In South America, in Ecuador (Harling, 1973), Guyana, French Guiana and Suriname (Eriksson & Harling, 2007), Venezuela (Harling & Eriksson 1998, Eriksson & Harling, 2007) and Brazil (Gomes & Mello-Silva, 2006; Leal & Forzza, 2012), where it presents a disjunct distribution, occurring throughout Amazon and in the Atlantic Forest.

*Notes.*—Lindman (1900) indicates the type of *Carludovica mattogrossensis* as housed in S herbarium. Three sheets of *Lindman A2897* are found there, all with fruits and without any indication of which is the holotype. We choose here the sheet (S 06-4540) as the lectotype.

## Doubtful names

*Carludovica atropurpurea* hort., Wiener Illustr. Garten-Zeitung 10: 77. 1885.

*Carludovica caulescens* hort., Wiener Illustr. Garten-Zeitung 10: 17. 1885.

*Carludovica dentata* hort., Wiener Illustr. Garten-Zeitung 10: 76. 1885.

*Carludovica discolor* L.Gentil, Liste Pl. Cult. Serres Chaudes Jard. Bot. État 46. 1907, *nom. nud.*

*Carludovica elegans* Dammer ex Huber, Bol. Mus. Goeldi Hist. Nat. Ethnogr. 4: 538, 1906.

*Carludovica elegans* L.Gentil, Liste Pl. Cult. Serres Chaudes Jard. Bot. État 538. 1907, *nom. nud.*

*Carludovica elegans* B.S.Williams, New Gen. Pl. Cat. 23: 1889. ≡ *Carludovica elegans* B.S.Williams ex L.H.Bailey, Cycl. Amer. Hort., ed. 2 [L. H. Bailey]: 665. 1917. *Nom. illeg.*

*Carludovica flabellata* H.Wendl., Index Palm. 43. 1854, *nom. nud.*

*Carludovica incisa* H.Wendl., Index Palm. 67. 1854. Type: Probably a sheet from Herrenhausen Gardens, "ex Am. Centr.", 1856, *s.c. s.n.* (lectotype (?): C n.v.).

Harling (1958) considered *Carludovica incisa* as a possible synonym of *Carludovica palmata*. *Carludovica incisa* was described on sterile and cultivated material in the Herrenhausen Gardens from Central America. A sheet collected in 1856 and by Wendland determined as *C. incisa*, may probably originate from the same individual upon which the diagnosis was founded (Harling, 1958). Nevertheless, this sheet presents only a tipical *Carludovica* leaf, which may belong to any species of the genus.

*Carludovica incisa* unranked *wendlandi* hort., Wiener Illustr. Garten-Zeitung 10: 19. 1885.

*Carludovica jonghei* Schaedtler, Hamburger Garten-Blumenzeitung 31: 101. 1875. Type: Not designated.

*Carludovica longicomans* Lem., Ill. Hort. 2: 22. 1855.

*Carludovica longifolia* hort., Wiener Illustr. Garten-Zeitung 10: 77. 1885, *nom. nud.*

*Carludovica loretensis* Standl. ex Ll. Williams, Publ. Field Mus. Nat. Hist., Bot. Ser. 15: 566. 1936. *nom. nud.*

*Carludovica marceana* hort., Wiener Illustr. Garten-Zeitung 10: 17. 1885, *nom. nud.*

*Carludovica mauritiana* Staub, Bot. Jarhesber. (Just) 9: 425. 1881, *nom. nud.*

*Carludovica nobilis* hort., Wiener Illustr. Garten-Zeitung 10: 77. 1885, *nom. nud.*

*Carludovica nobilis* L.Gentil, Liste Pl. Cult. Serres Chaudes Jard. Bot. État 46. 1907, *nom. nud.*

*Carludovica palmata* unranked *humilis* Wawra & Bermann, Wiener Illustr. Garten-Zeitung 10: 16. 1885, *nom. nud.* ≡ *Carludovica humilis* Kuntze, Revis. Gen. Pl. 2: 738. 1891, *nom. inval.*

*Carludovica palmifolia* (Willd.) Sweet, Hort. Brit. [Loudon], ed. 3.: 630. 1839 ≡ *Salmia palmaefolia* Willd., Mag. Neuesten Entdeck. Gesammten Naturk. Ges. Naturf. Freunde Berlin 5: 401. 1811 ≡ *Carludovica palmifolia* (Willd.) Griseb., Fl. Brit. W. I. [Grisebach]: 513. 1864. *nom. illeg*.

*Carludovica palmifolia* has been considered a very uncertain synonym of *Asplundia rigida* by Harling (1958). The type collection of this species is missing.

*Carludovica plicata* Klotzsch, Linnaea 20: 468. 1847. Type: Colombia. s.l., s.d., *J. W. K. Moritz s.n.* (holotype: B, probably lost).

*Carludovica plicata* has been considered a very uncertain synonym of *Asplundia moritziana* by Harling (1958), but it cannot be identified due to poor description and absence of original collection.

*Carludovica pumila* Domin, Ann. Jard. Bot. Buitenzorg 24: 234. 1911, *nom. nud.*

*Carludovica purpurascens* Linden, Ill. Hort. 28: 64. 1881, *nom. nud.*

*Carludovica purpurata* Linden ex Otto, Allg. Gartenzeitung (Otto & Dietrich) 23: 3. 1855, *nom. nud.*

*Carludovica purpurea* Domin, Ann. Jard. Bot. Buitenzorg 24: 234. 1911, *nom. nud.*

*Carludovica sartoni* Teijsm. & Binn., Cat. Hort. Bot. Bogor. (Teijsmann & Binnendijk) 381. 1886. *nom. nud.*

*Carludovica sartorii* hort., Wiener Illustr. Garten-Zeitung 10: 17. 1885, *nom. nud.*

*Carludovica serrata* hort., Wiener Illustr. Garten-Zeitung 10: 76. 1885, *nom. nud.*

*Cyclanthus angustifolius* Linden & Van Houtte ex Otto, Allg. Gartenzeitung (Otto & Dietrich) 23: 3. 1855, *nom. nud.*

*Cyclanthus bifolius* Perr., Mém. Soc. Linn. Paris 3: 112. 1825, *nom. nud.*

*Cyclanthus discolor* hort., Gard. Chron. 19: 510. 1883, *nom. nud.*

*Cyclanthus estaba* Schaedtler, Hamburger Garten- Blumenzeitung 31: 302. 1875. Type: Not designated.

*Cyclanthus godseffianus* Sander, Gard. Chron. ser 3, 11: 731. 1892, *nom. nud.*

*Cyclanthus longicomans* Van Houtte ex Otto, Allg. Gartenzeitung (Otto & Dietrich) 23: 3. 1855, *nom. nud.*

*Cyclanthus nobilis* Domin, Ann. Jard. Bot. Buitenzorg 24: 235. 1911, *nom. nud.*

*Sphaeradenia imperialis* (Linden & André) Harling, Acta Horti Berg. 18: 392. 1958 ≡ *Carludovica imperialis* Linden & André, Ill. Hort. 21: 57. 1874. Type: Lacking, described on cultivated material in Hort. Linden from Ecuador (lectotype, designated here: tab. 165 [coloured plate, habit of sterile plant] in Ill. Hort. 21 (1874)).

*Carludovica imperialis* was described from living material and no original collection is known. The original illustration is here selected as lectotype. Harling (1958) transferred it to *Sphaeradenia* based on this illustration and details of the description. Eriksson (1995) disagreed with Harling's view and excluded the species from his taxonomic revision of *Sphaeradenia*, arguing that the description brings details that would not place the species in *Sphaeradenia* and that the illustration it is not clear enough to associate it to any other genus, opinion shared here.

## Excluded names

*Carludovica trigona* Ruiz & Pav., Syst. Veg. Fl. Peruv. Chil.: 293. 1798 ≡ *Ludovia trigona* (Ruiz & Pav.) Pers., Syn. Pl. [Persoon] 2: 576. 1807 ≡ *Salmia trigona* (Ruiz & Pav.) Willd., Mag. Neuesten Entdeck. Gesammten Naturk. Ges. Naturf. Freunde Berlin 5: 401. 1811 ≡ **Geonoma trigona** (Ruiz & Pav.) A. H. Gentry, Ann. Missouri Bot. Gard. 73: 161. 1986 [Palmae].

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# Final Considerations

We newly presented a consistent phylogeny of Cyclanthaceae combining molecular and morphological datasets in species level and broad sampling. We recovered a monophyletic Cyclanthaceae using combined and total-evidence trees in both Parsimony and Bayesian analysis. Morphological analysis showed that Cyclanthaceae is widely supported by longitudinal incisions in the blade (except *Ludovia*), basal bulb in the filament base, and connate pisitillate flowers. Also the inflorescence morphology is unique in the family.

A new perspective of the phylogenetic relationship of Cyclanthaceae was provided. All genera and the subdivision of Cyclanthoideae and Carludovicoideae were supported, however one of the informal categories of Carludovicoideae was recovered non-monophyletic. The subfamily Carludovicoideae is divided into three lineages: i) *Carludovica*; ii) *Asplundia*, *Dicranopygium* and *Schultesiophytum*, named Asplundia Clade; and iii) *Dianthoveus*, *Evodianthus*, *Thoracocarpus* and the Sphaeradenia group, named Evodianthus Clade. Our results recovered a monophyletic *Evodianthus* including *Dianthoveus* supported by styloid idioblasts in the mesophyll oriented in all directions, terminal inflorescence, bracts of the same size, filament absent or inconspicuous, basal bulbs absent, psilate and inaperturate pollen. Sphaeradenia group was recovered as monophyletic strongly supported by molecular and morphological dataset, however, morphological circumscription of its genera should be revaluated in future studies.

The morphological circumscription of *Asplundia* from Atlantic forest were reassessed and reduced to three endemic species including the species newly described. The exceptional sampling, a robust phylogeny, and the nomenclator botanicus brings an avenue for future studies on biogeography, diversification and evolution of Cyclanthaceae as well as it can give insights on further systematics studies on the poorly known and rich species genera *Asplundia* e *Dicranopygium*.

# Appendix

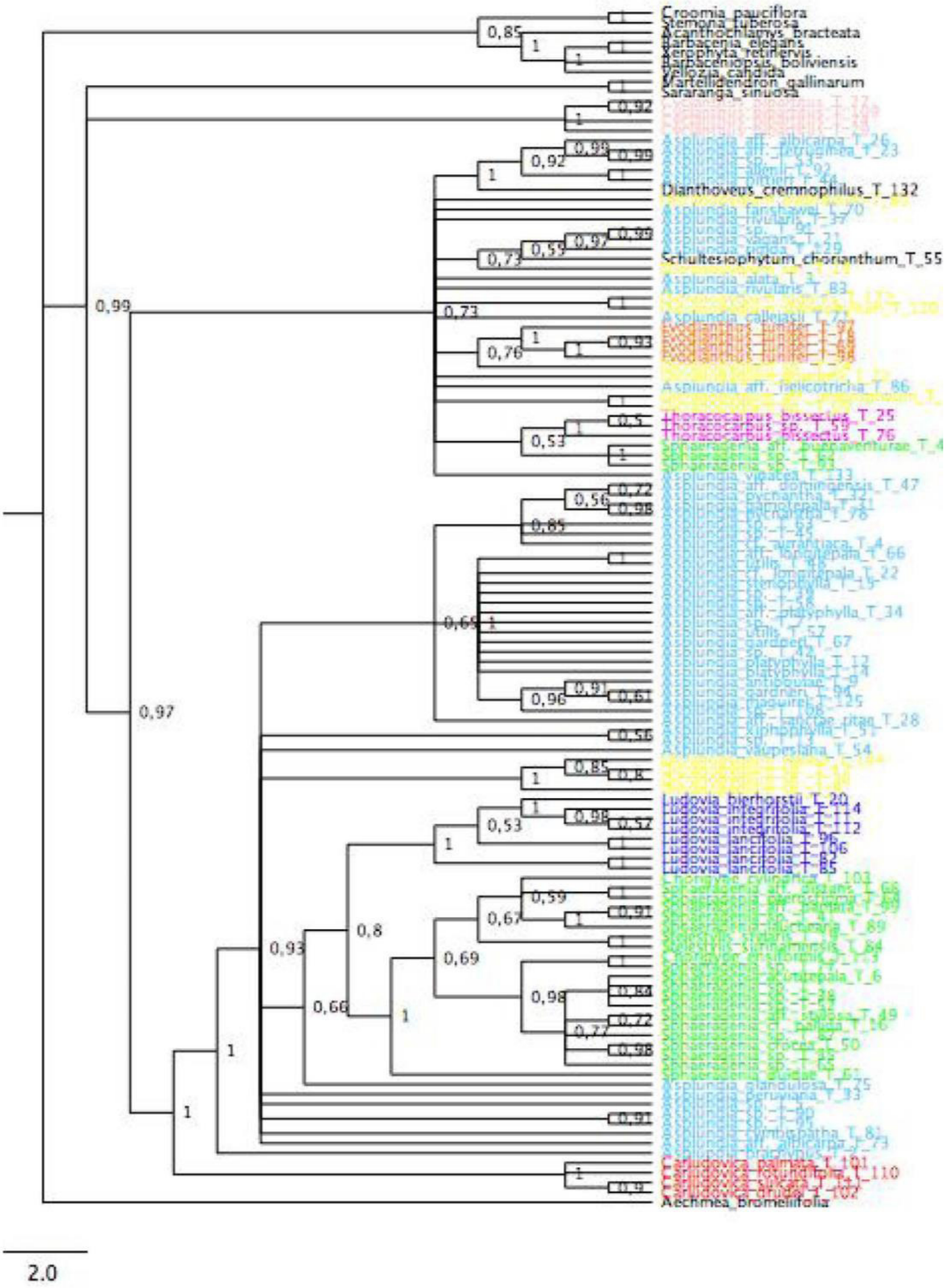

Fig. 1. Bayesian tree of the atpB-rbcL. Numbers on the branches indicate the posterior probabilities.

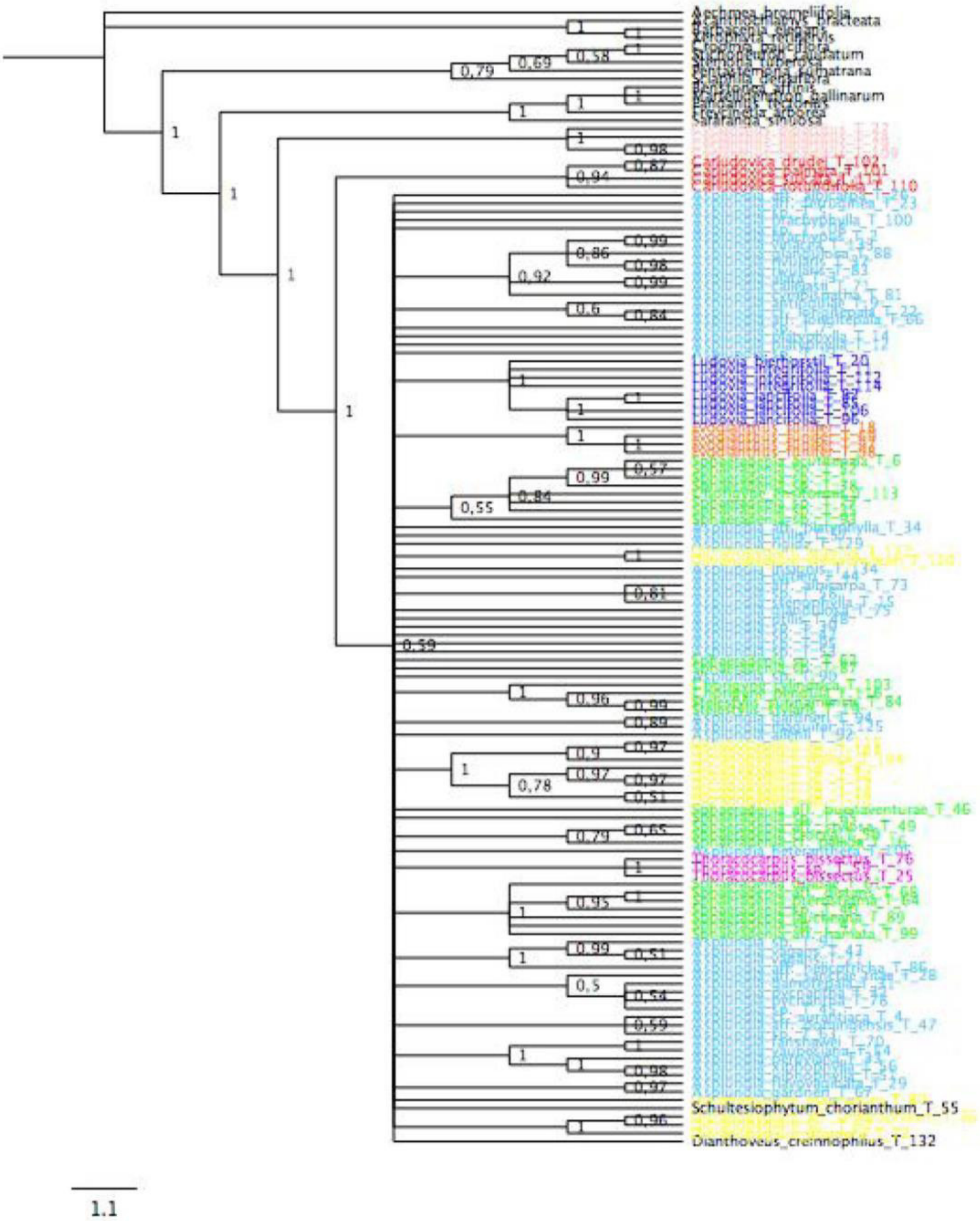

Fig. 2. Bayesian tree of the matK. Numbers on the branches indicate the posterior probabilities.

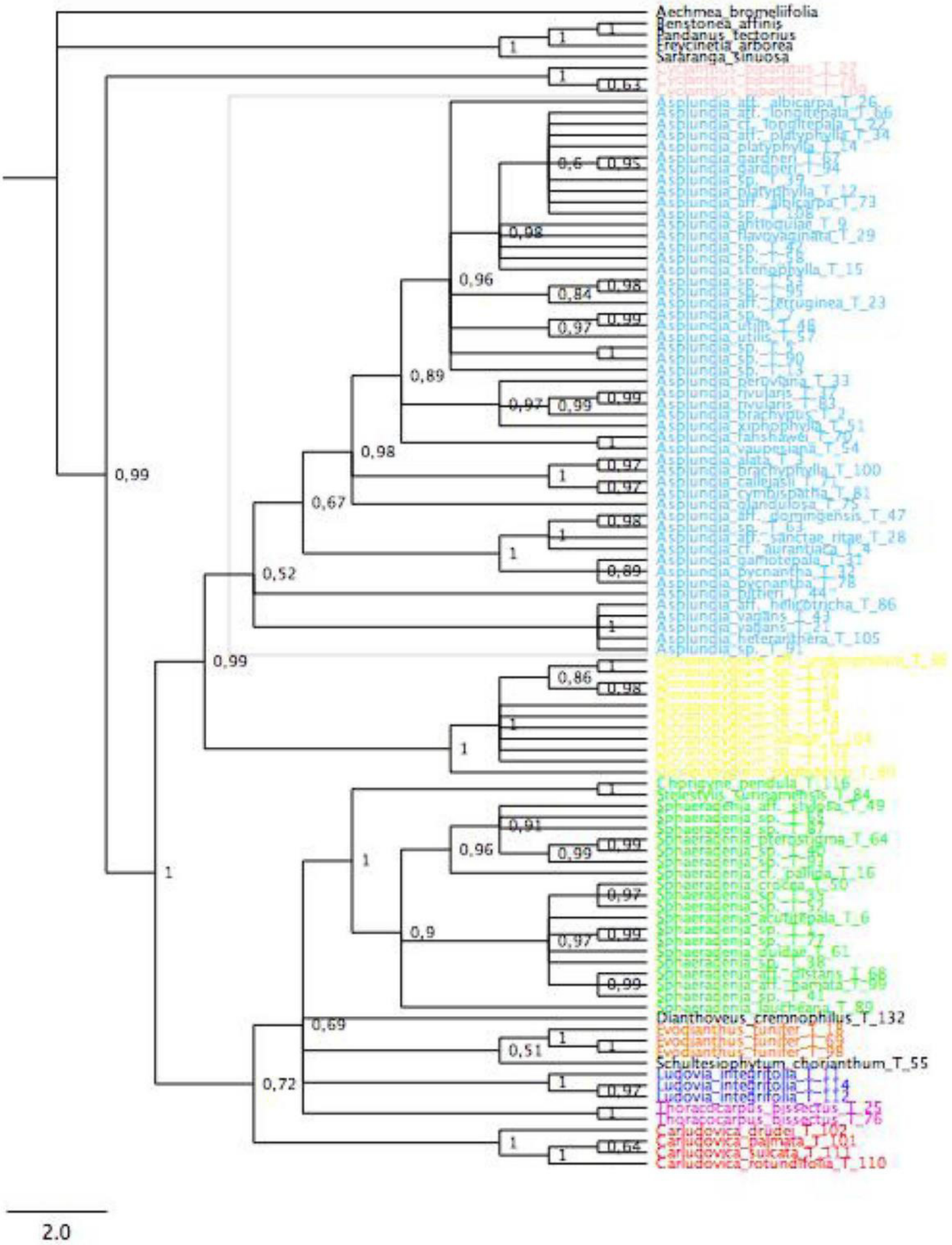

Fig. 3. Bayesian tree of the phyC. Numbers on the branches indicate the posterior probabilities.

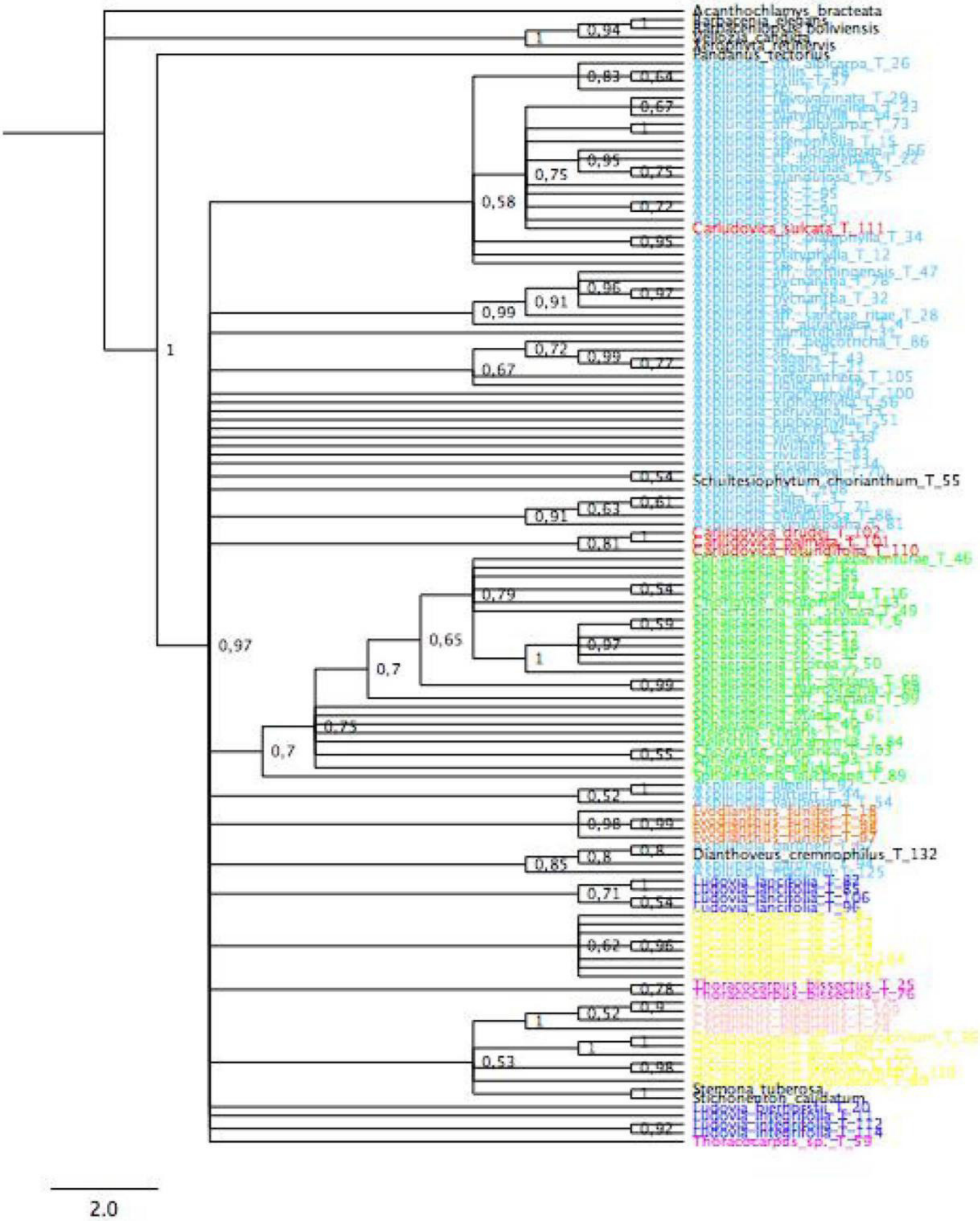

Fig. 4. Bayesian tree of the psbA-trnH. Numbers on the branches indicated the posterior probabilities.

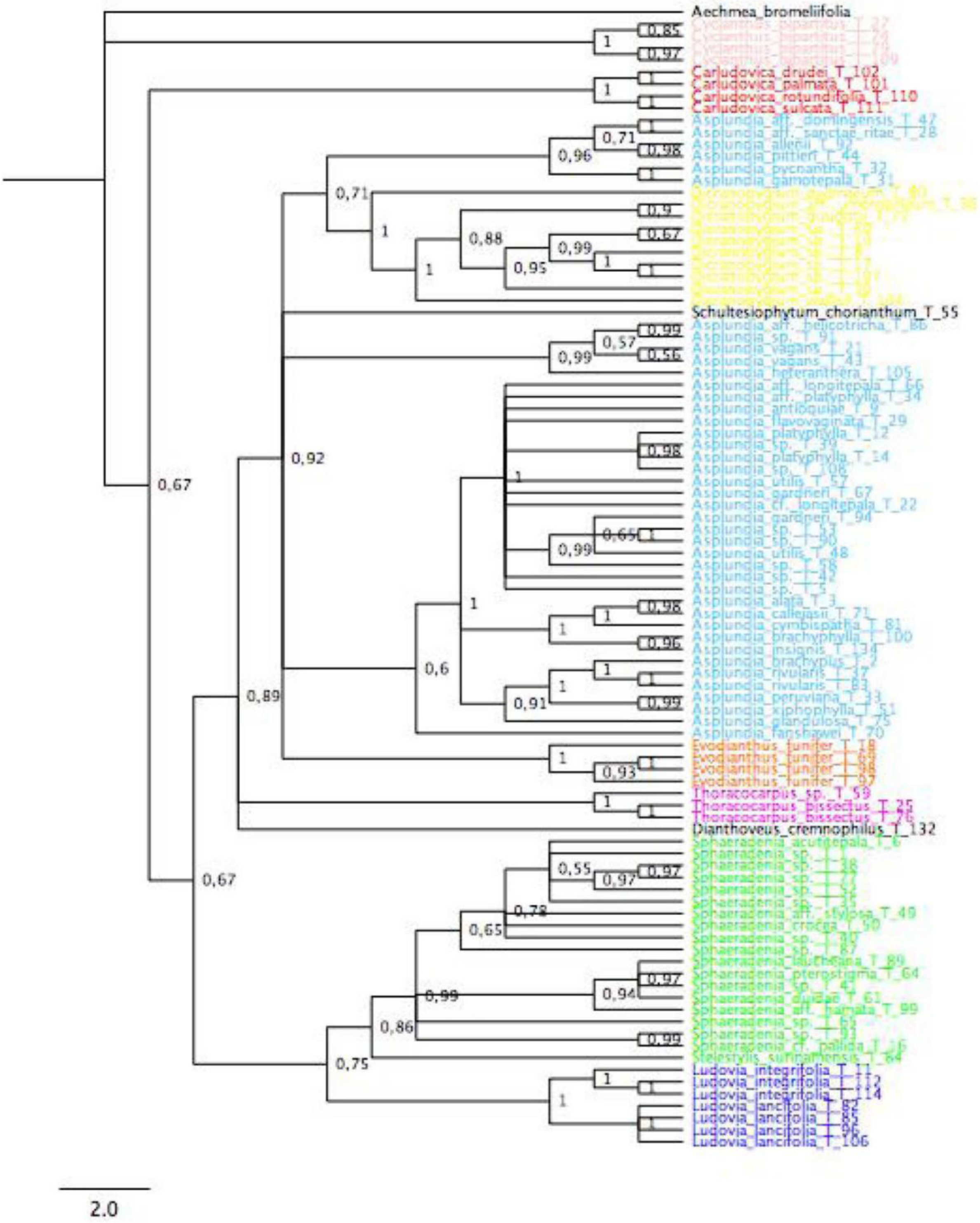

Fig. 5. Bayesian tree of the rpb2. Numbers on the branches indicated the posterior probabilities.

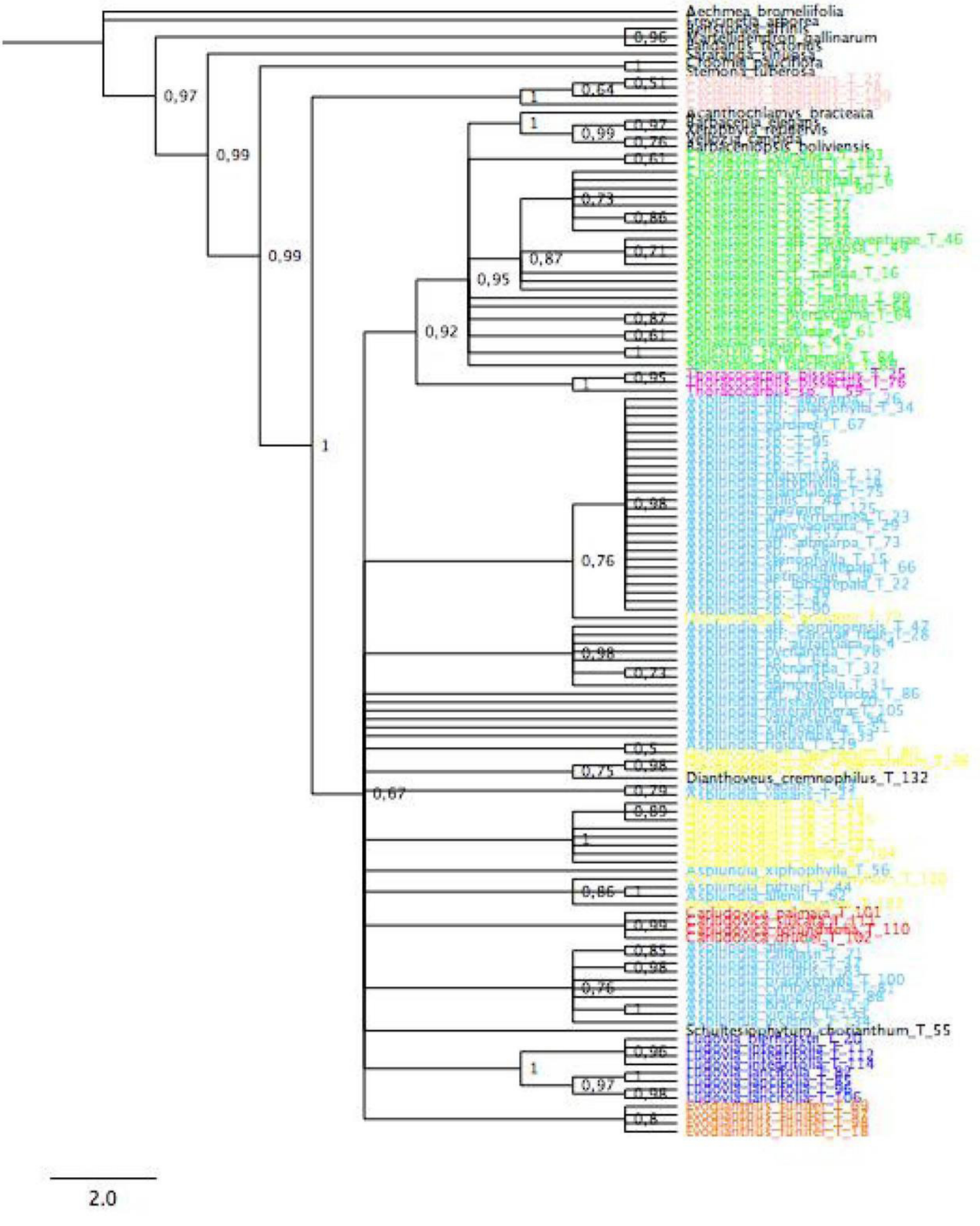

Fig. 6. Bayesian tree of the trnL-trnF. Numbers on the branches indicated the posterior probabilities.

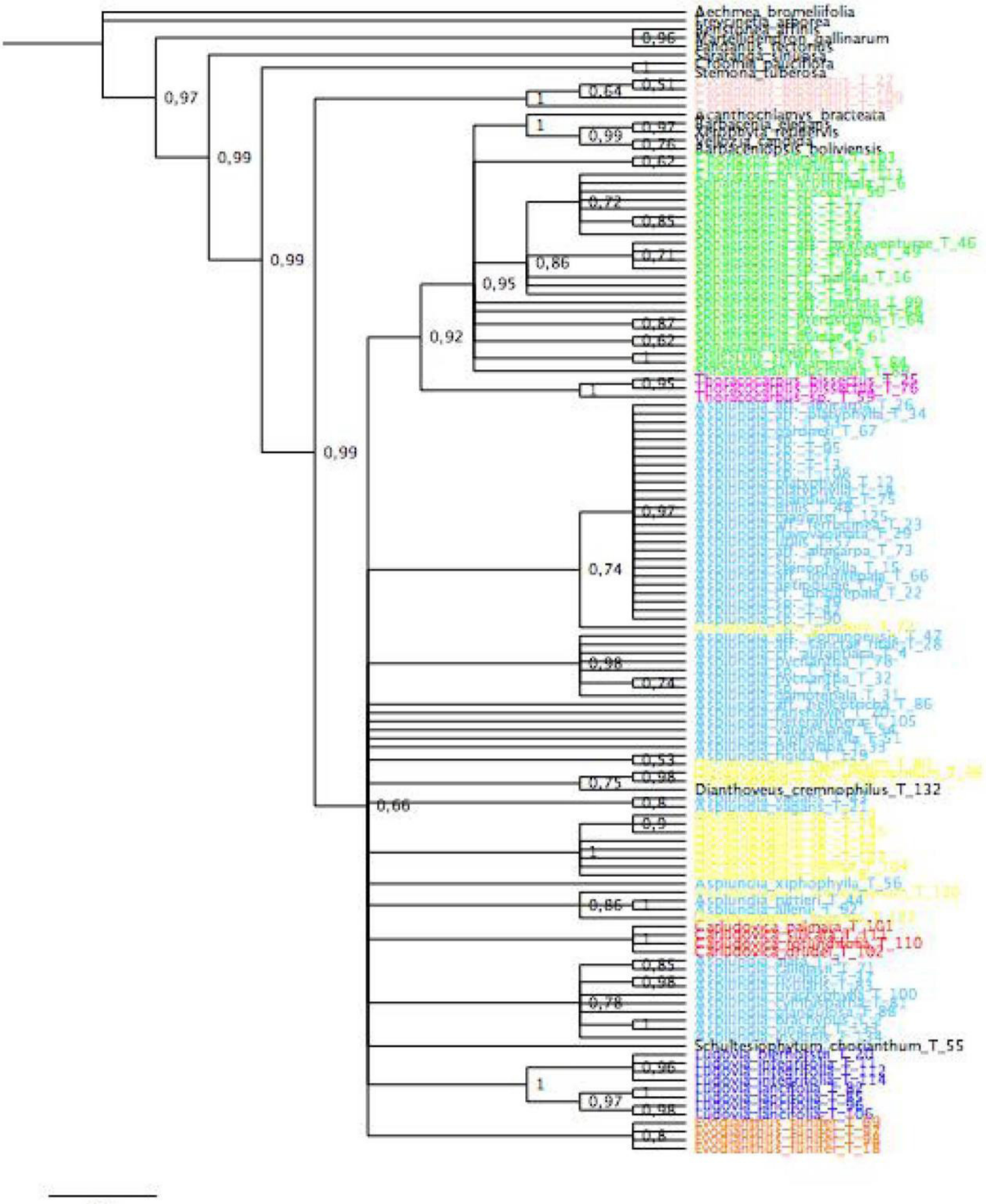

Fig. 7. Bayesian tree of the trnQ-rps16. Numbers on the braches indicated the posterior probabilities.

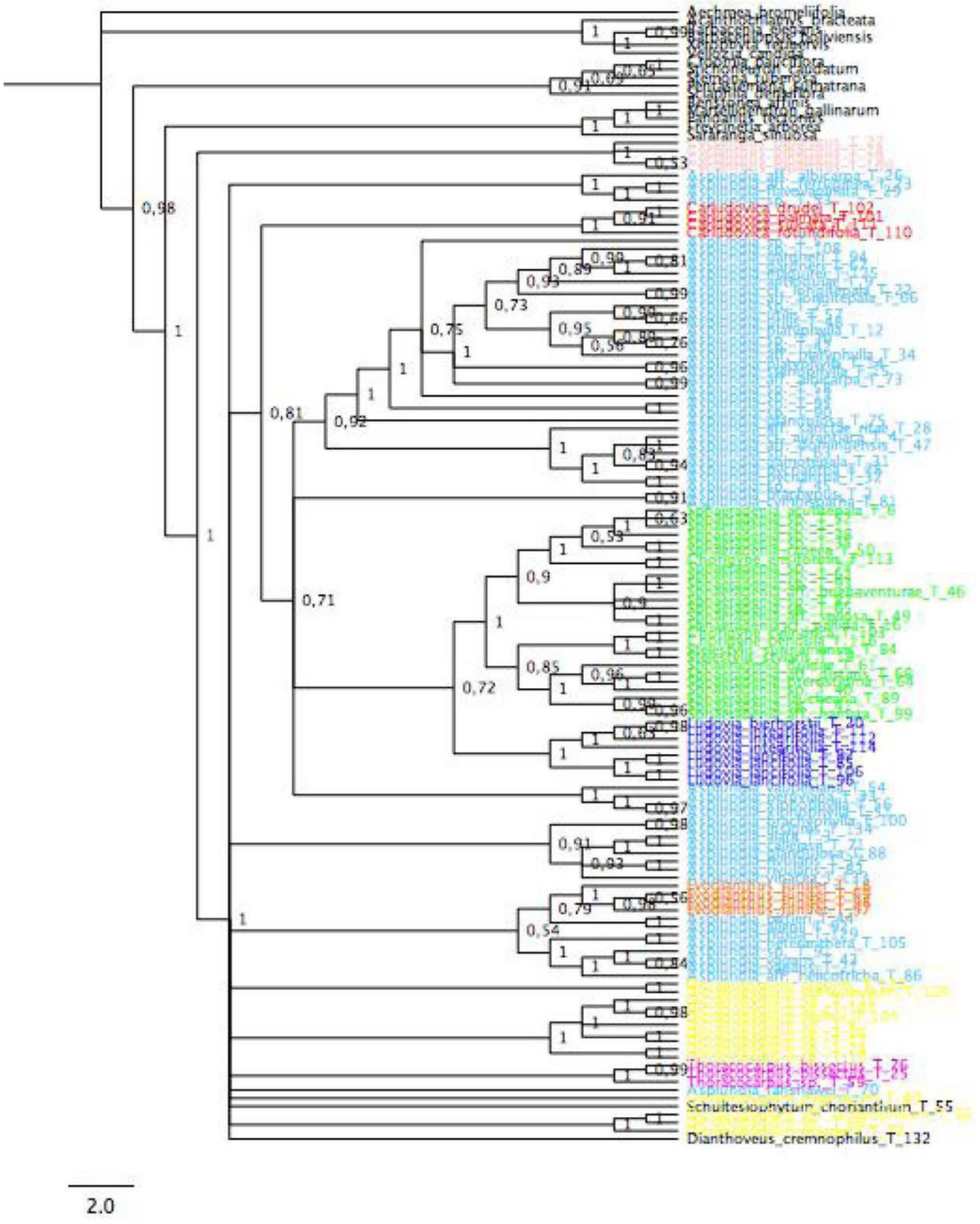

Fig. 8. Bayesian tree of combined cpDNA. Numbers on the braches indicated the posterior probabilities.

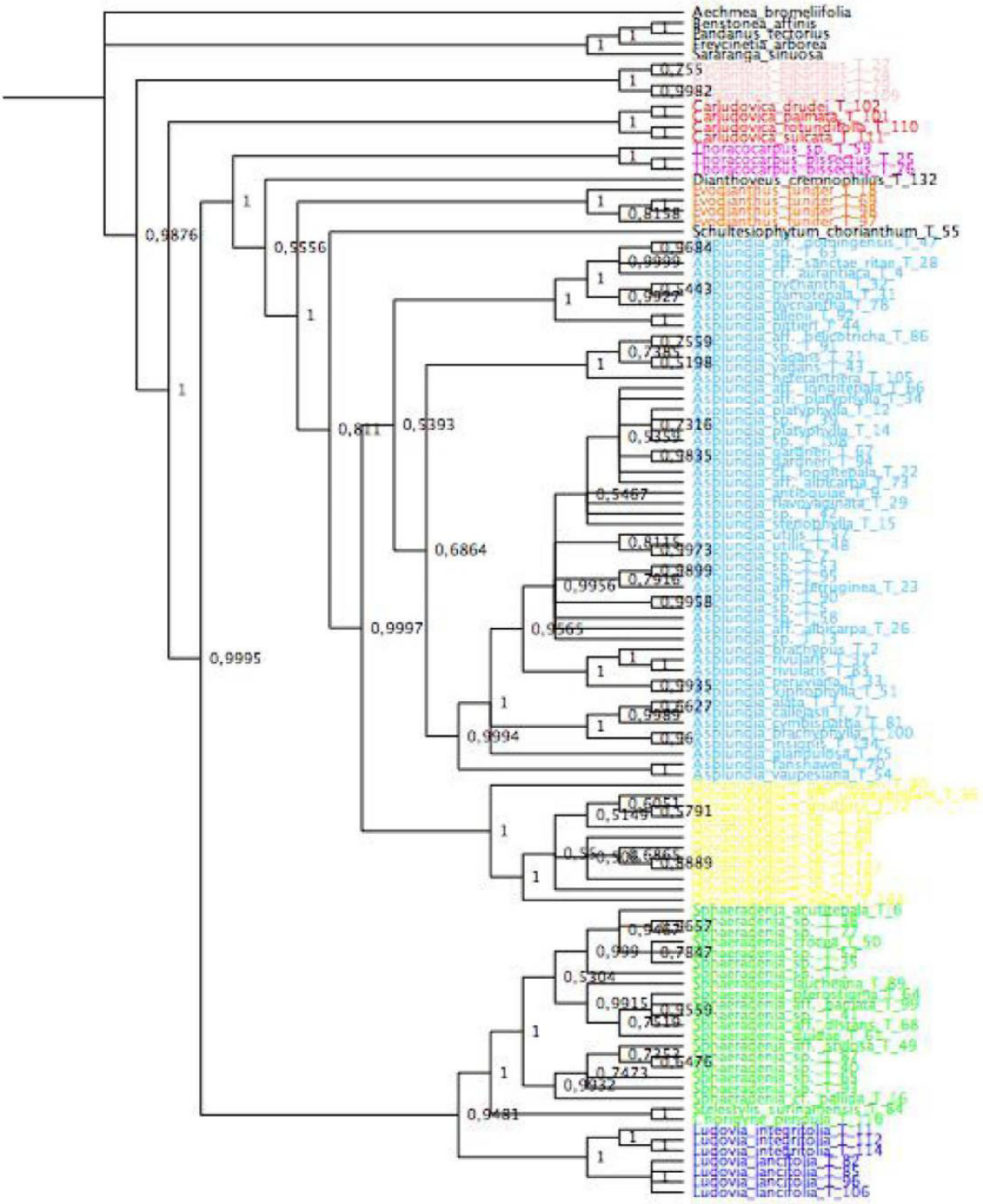

Fig. 9. Bayesian tree of combined nrDNA. Numbers on the braches indicated the posterior probabilities.