RESEARCH ARTICLE

Phylogeny and historical biogeography of the Panama-hat family (Cyclanthaceae, Pandanales)

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Abstract The monocot family Cyclanthaceae (Pandanales) comprises ca. 230 known species in 12 genera restricted to the Neotropics. The family has not been the subject of a species-level molecular phylogenetic study to date, with multiple evolutionary and biogeographic questions about Cyclanthaceae still unanswered. In this study, we address genus- and species-level relationships and the historical biogeography of Cyclanthaceae based on a broadly sampled molecular phylogeny. Two low-copy nuclear genes (*phyC*, *rpb2*) and five plastid regions (*atpB-rbcL*, *psbA-trnH*, *trnL-trnF*, *trnQ-rps16*, *matK*) representing 99 species and all genera of Cyclanthaceae were sampled, spanning the taxonomic and biogeographic diversity of the family. Our results strongly support the monophyly of all Cyclanthaceae genera and confirm previously proposed hypotheses of intergeneric relationships. Infrageneric relationships are generally well supported, with some exceptions in the genus *Asplundia* that may require a broader sampling to clarify. The early diversification of Cyclanthaceae is estimated to date back to the Paleocene-Eocene period in South America, where the family possibly arrived through a boreotropical route. The origin of most genera is inferred from the Paleocene of the Tumbes-Chocó-Magdalena region, possibly indicating an earlier origin for this biodiversity hotspot. The current distribution of Cyclanthaceae is likely to have been strongly influenced by major biogeographical events in the Neotropics, such as the uplift of the Andes and the opening of the South America dry diagonal. Further studies that include a broader sample of the large *Asplundia-Dicranopygium* clade and *Sphaeradenia* group are required.

Keywords ancestral area reconstruction; calibrated phylogeny; Carludovicoideae; Cyclanthoideae; monocots; Tumbes-Chocó-Magdalena hotspot

Supporting Information may be found online in the Supporting Information section at the end of the article.

INTRODUCTION

Cyclanthaceae is a monocot family placed in the order Pandanales, comprising ca. 230 species and 12 genera arranged into two subfamilies (Govaerts & Eriksson, 2020). It is endemic to the Neotropics, occurring from southern Mexico and the Caribbean, to the Atlantic Rainforest in southern Brazil (Harling, 1958). The family includes terrestrial herbs, nomadic vines (sensu Sperotto & al., 2020), and epiphytes that are highly diversified in moist habitats, ranging from lowland to montane tropical rainforests, up to elevations of 3750 m in the Andean region (Harling & al., 1998) (Figs. 1, 2). Many species of Cyclanthaceae are of cultural or economic importance, with uses as roofing material (Harling & al., 1998), basket-weaving material (Baluarte-Vásquez, 2000; Balcázar-Vargas & Van Andel, 2005), fishing tools (Oliveira & al., 2006), food (Chízmar-Fernández & al., 2009; Segura & al., 2018), ornamentals (Medina & al., 2017), and for manufacturing the traditional Panama hat from the leaves of *Carludovica palmata* Ruiz & Pav. (Bennett & al., 1992; Fadiman, 2001).

Species of Cyclanthaceae are distinguished from the remaining families in Pandanales by their open leaf sheaths and monoecious inflorescences (Harling & al., 1998). Infrafamiliar classifications of Cyclanthaceae have undergone successive changes over time, to date solely based on morphological studies (Fig. 3). The first scheme was proposed by Drude (1881),

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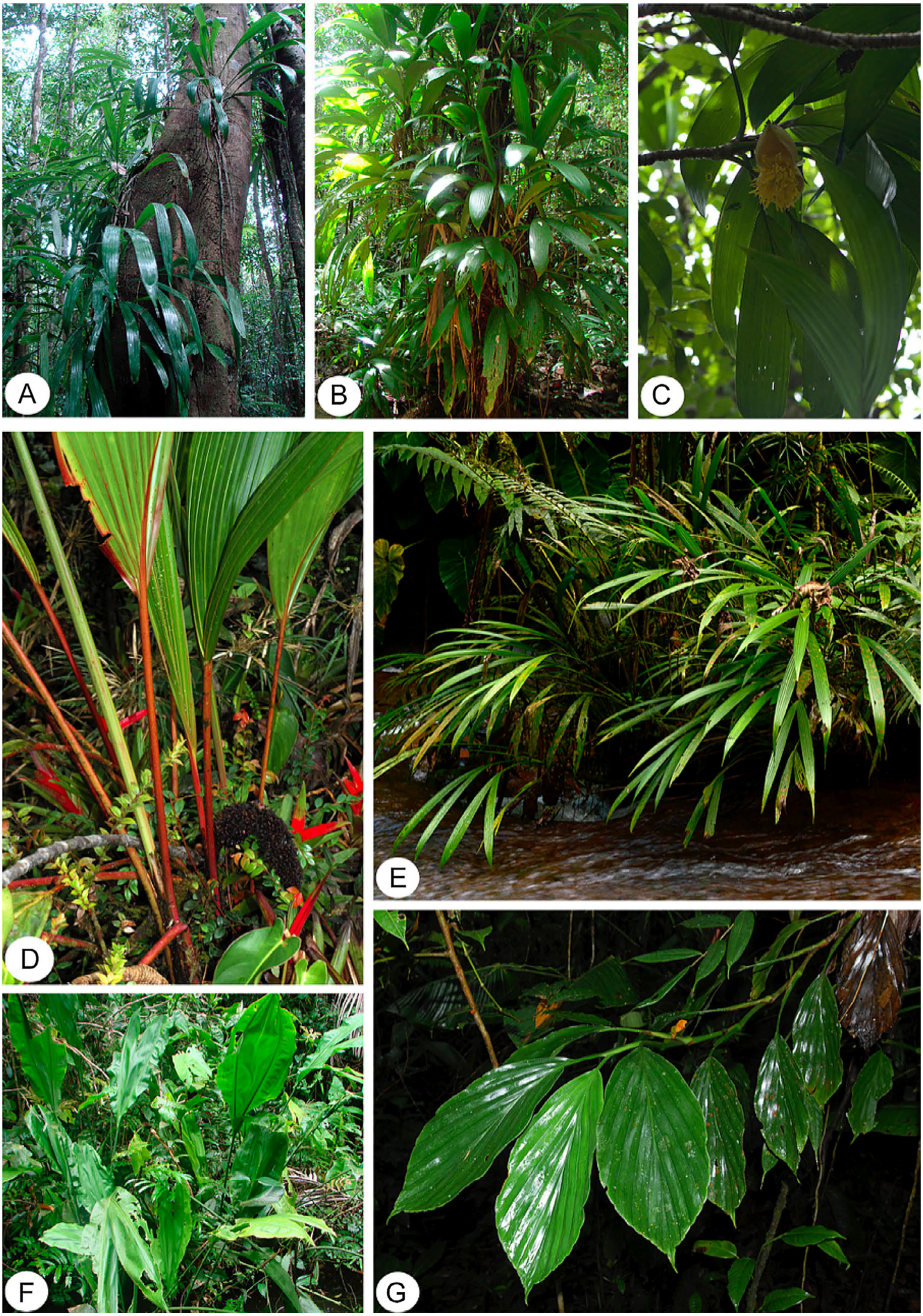

Fig. 1. Vegetative structures of Cyclanthaceae. **A**, *Evodianthus funifer*; **B**, *Asplundia* sp.; **C**, *Thoracocarpus bissectus*; **D**, *Sphaeradenia* sp.; **E**, *Dicranopygium* sp.; **F**, *Cyclanthus bipartitus*; **G**, *Ludovia integrifolia*. — Photos: Eduardo S. Leal (A, B, C, F) and David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

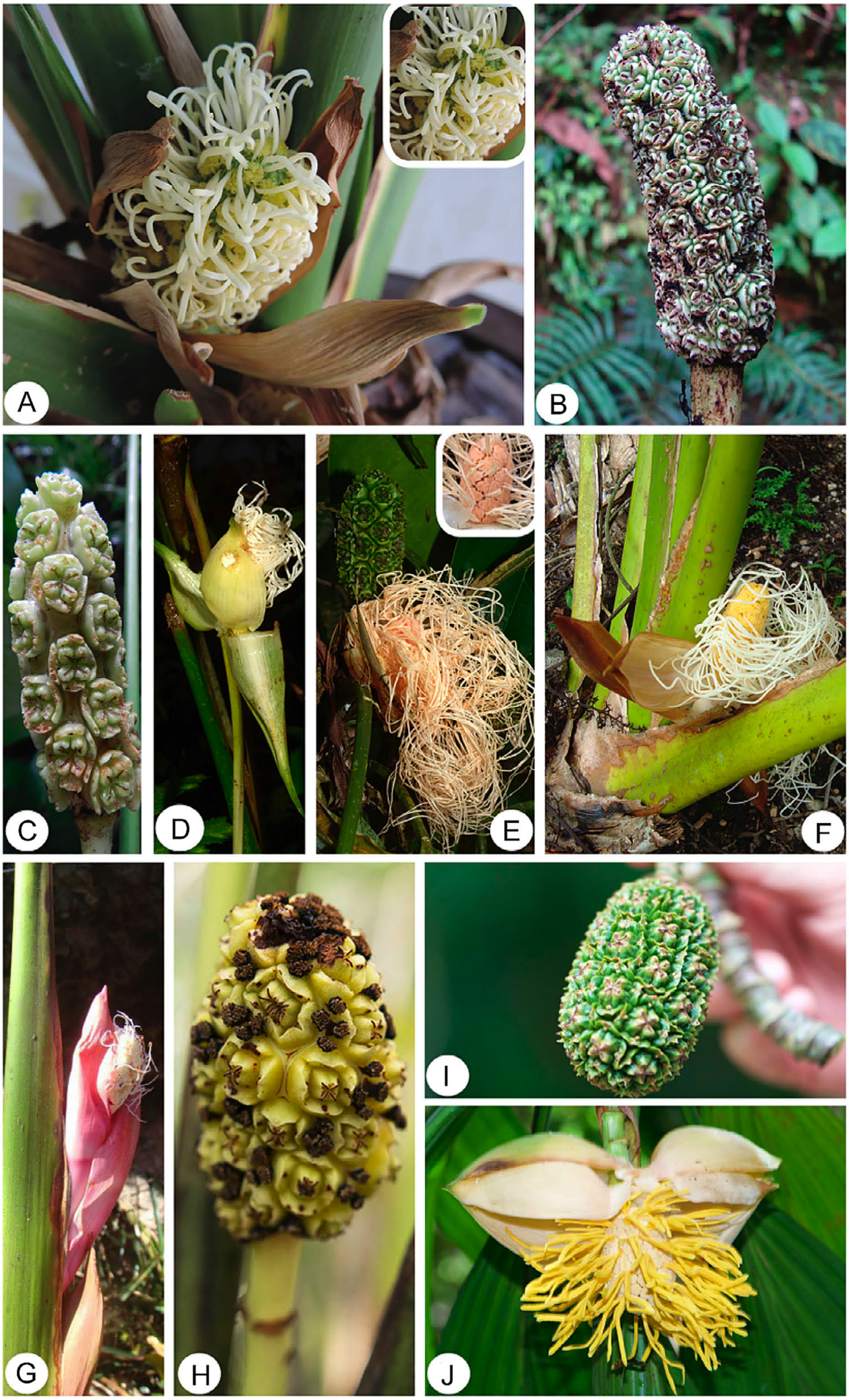

Fig. 2. Reproductive structures of Cyclanthaceae. **A**, Inflorescence of *Asplundia gardneri*; **B**, Infructescence of *A. callejasii*; **C**, Infructescence of *Dicranopygium* sp.; **D**, Inflorescence of *Dicranopygium* sp.; **E**, Inflorescence and infructescence of *Evodianthus funifer*; **F**,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

who recognized two tribes: Cyclantheae (including only *Cyclanthus* Poit. ex A.Rich.) and Carludoviceae (including the remaining three genera recognized at the time: *Carludovica* Ruiz & Pav., *Ludovia* Brongn., *Stelestylis* Drude). Subsequently, Harling (1954a,b) made extensive taxonomic changes to *Carludovica*, splitting it into *Asplundia* Harling, *Dicranopygium* Harling, and *Sphaeradenia* Harling apart from *Carludovica*. Later, Harling (1958) elevated the two tribes recognized by Drude (1881) to subfamilies, mainly based on inflorescence structure: Cyclanthoideae, with alternating whorls of pistillate and staminate flowers, and Carludovicoideae, with pistillate flowers surrounded by four staminate flowers. Harling (1958) also placed the genera of Carludovicoideae into two informal groups: the *Sphaeradenia* group (comprising four genera, indicated with asterisks in Fig. 3), and the *Asplundia* group (comprising the remaining genera). Hammel & Wilder (1989) recovered the *Asplundia* and *Sphaeradenia* groups as monophyletic in a morphology-based phylogenetic analysis, and additionally placed their newly described genus *Dianthoveus* Hammel & G.J.Wilder in the former group. An additional phylogenetic study of morphological data recovered the *Sphaeradenia* group as monophyletic (Eriksson, 1994), including the genus *Chorigyne* R.Erikss., which had been recently described (Eriksson, 1989), with support from multiple morphological synapomorphies: a predominantly epiphytic habit, distichous phyllotaxy, coriaceous leaf blades, and apical or subapical placentation. However, the monophyly of the *Asplundia* group was not corroborated, and affinities among its genera remained uncertain (Eriksson, 1994).

Mobilizing molecular data to address the phylogenetic history of Cyclanthaceae represents an opportunity for further refining relationships that could not be inferred based on morphology alone. Recently, Soto Gomez & al. (2020) recovered genus-level relationships across Pandanales using biorganellar phylogenomic data, but taxon sampling in Cyclanthaceae was limited to a single species per genus. Therefore, generating molecular data from multiple species per genus will permit more comprehensive exploration of generic delimitations and the development of a species-level evolutionary framework for the family.

A well-resolved species-level phylogeny of Cyclanthaceae would also be useful for testing biogeographical hypotheses. Given the relatively old age of Cyclanthaceae (crown age 45–72 Ma in Gallaher & al., 2014; 55 Ma in Soto Gomez & al., 2020) and its strong preference for low- to mid-elevation rainforests (Eriksson, 1994), the family may be a useful model group for understanding biogeographical patterns in Neotropical rainforests. Neotropical rainforests are dated to the mid-Cretaceous (Davis & al., 2005) and are not continuously distributed throughout in the continent, being often separated by alpine (e.g., Andean Puna) and drier (e.g., Cerrado and Caatinga) biomes (Antonelli & Sanmartín, 2011). Environmental conditions in these adjacent biomes restrict the occurrence of many Cyclanthaceae lineages, resulting in disjunct distributions that parallel those of modern Neotropical rainforests. For instance, very few species (to our knowledge, only the widely distributed *Carludovica palmata*, *Cyclanthus bipartitus* Poit. ex A.Rich., *Evodianthus funifer* (Poit.) Lindm., and *Thoracocarpus bissectus* (Vell.) Harling, in addition to *Ludovia integrifolia* (Woodson) Harling) are found on both sides of the Andes. Similarly, few species occur on both sides of the dry diagonal of South America, which to our knowledge

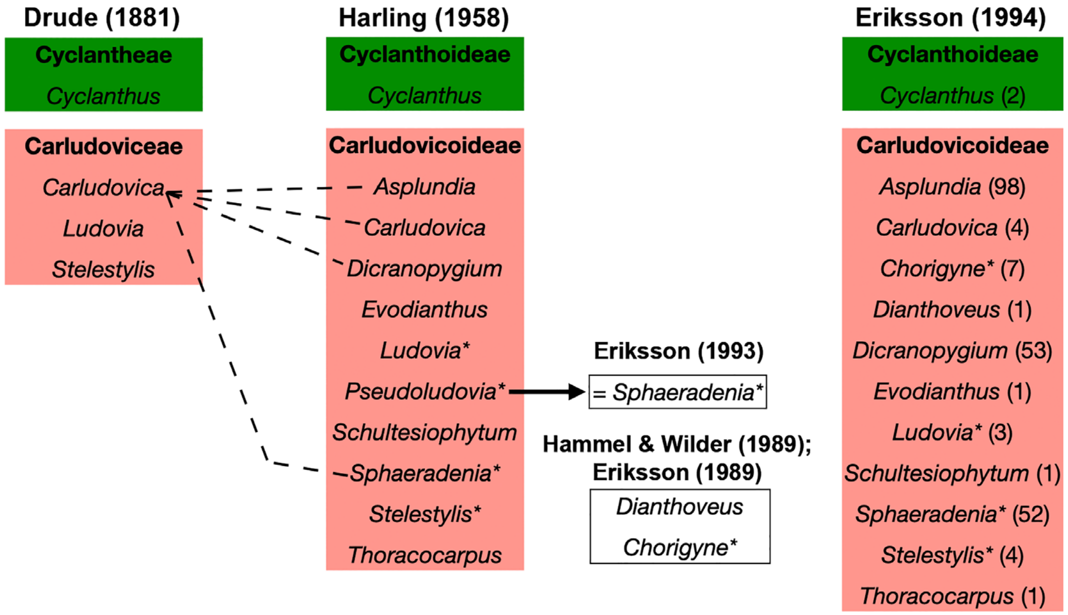

Fig. 3. Summary of taxonomic rearrangements in Cyclanthaceae. Asterisks indicate members of the *Sphaeradenia* group; the remaining genera in the subfamily Carludovicoideae belong to the *Asplundia* group. Numbers in brackets under the current circumscription indicate the estimated number of recognized species for each genus. Different colored backgrounds indicate different subfamilies within Cyclanthaceae. Dashed lines indicate splitting, whereas the arrow indicates synonymization.

only include *Asplundia gardneri* (Hook.) Harling, *A. guianensis* Harling, *E. funifer*, and *T. bissectus*. Except for some populations of *A. gardneri* found in patches of humid habitats known as "brejos de altitude" in northeastern Brazil, no species is native to the seasonal dry forests of central Brazil.

Thus, we hypothesize that the biogeographical history of Cyclanthaceae has been impacted by major climatic and geological events that shaped the modern distribution of Neotropical rainforests. These include: (i) the complex biotic exchanges between South and North America through the Panama Isthmus (multiple events between the Oligocene and Pliocene; Bacon & al., 2015); (ii) the isolation of the Tumbes-Chocó-Magdalena region as a consequence of the uplift of the Northern Andes (Miocene to Pleistocene; Gregory-Wodzicki, 2000); and (iii) the opening of the South American dry diagonal, which disconnected rainforests in the Amazon Basin and Atlantic Forests (Miocene to Pliocene; Simon & al., 2009). Testing this hypothesis may shed light on the history of other groups with a similar biogeographical distribution.

In this study, we assembled the first species-level molecular dataset for Cyclanthaceae, comprising a total of seven plastid and nuclear markers for 122 specimens representing 99 species, and all 12 genera in the family. We used this dataset to (i) infer species-level relationships in Cyclanthaceae, (ii) test the current classification of the family, which is based entirely on morphological data, (iii) generate a calibrated phylogeny of Cyclanthaceae, and (iv) perform ancestral range reconstructions to shed light on the biogeographical history of Neotropical rainforests.

■ MATERIALS AND METHODS

Taxon sampling for molecular analysis. — We sampled 122 Cyclanthaceae specimens representing 99 species (43% of the species diversity) and all 12 genera in the family (number of accessions and proportion of sampled species shown in parenthesis): 48 species (58, ca. 48%) in *Asplundia*, 4 species (4, 100%) in *Carludovica*, 2 species (2, 29%) in *Chorigyne*, 1 species (4, 50%) in *Cyclanthus*, 1 species (1, 100%) in *Dianthoveus*, 14 species (14, 24%) in *Dicranopygium*, 1 species (4, 100%) in *Evodianthus* Oerst., 3 species (7, 100%) in *Ludovia*, 1 species (1, 100%) in *Schultesiophytum* Harling, 21 species (22, 40%) in *Sphaeradenia*, 2 species (2, 50%) in *Stelestylis*, and 1 species (3, 100%) in *Thoracocarpus* Harling. We included the type species of most genera; these were sampled from their type localities whenever possible (Appendix 1). We also sampled 14 outgroup taxa from the Pandanales families Pandanaceae, Stemonaceae, and Velloziaceae.

DNA extraction, amplification and sequencing. — We extracted DNA from silica-dried leaf tissue or herbarium specimens using the DNeasy plant mini kit (QIAGEN, Valencia, California, U.S.A.), with modifications proposed by Alexander & al. (2007). Herbarium samples were extracted using a 24 h incubation period at 42°C, and resuspended in 50 μl elution buffer. We amplified a total of seven molecular markers: five from the plastid genome, the *matK* gene, *atpB-rbcL*, *psbA-trnH*, *trnL-trnF* and *trnQ-rps16* intergenic spacers, and two from the nuclear genome, the *phyC* coding portion and the second-largest subunit of *rpb2*. The utility of these loci for phylogenetic reconstruction in Pandanales was demonstrated in studies of the families Velloziaceae (Mello-Silva & al., 2011) and Pandanaceae (Buerki & al., 2012; Gallaher & al., 2014), showing good potential for phylogenetic reconstruction without, in the case of the nuclear genes, detectable paralog problems.

DNA amplification was performed using polymerase chain reaction (PCR), with parameters and amplification primers optimized for each locus based on previous studies: *atpB-rbcL* as in Manen & al. (1994); *matK* as in Ford & al. (2009); *phyC* as in Hertweck & al. (2015); *psbA-trnH* as in Shinozaki & al. (1986); *rpb2* as in Denton & al. (1998), Roncal & al. (2005) and Sass & Specht (2010); *trnL-trnF* as in Taberlet & al. (1991); and *trnQ-rps16* as in Shaw & al. (2007). Sequences were obtained through the Macrogen (New York, New York, U.S.A.) high-yield sequencing service, using the same primers as those employed for amplification. The software Geneious v.9.1.7 (Kearse & al., 2012) was used to generate contigs, to manually edit and remove low-quality sequences. We generated a total of 788 new sequences. For the outgroups, all sequences were retrieved from GenBank (Appendix 1). Sequence alignment (suppl. Appendix S1, S2) was performed using the MAFFT algorithm (Katoh & Standley, 2013) implemented on Geneious.

Phylogenetic inference. — We performed maximum likelihood (ML) and Bayesian inference (BI) analyses using RAxML v.8.2.12 (Stamatakis, 2014) and BEAST v.2.5.0 (Bouckaert & al., 2014), respectively, as implemented in the CIPRES portal (Miller & al., 2010). We partitioned data into two subsets, plastid (cpDNA) and nuclear (nrDNA), and performed tests to find optimal substitution models for each, using the corrected Akaike information criterion (AICc) in jModelTest 2 (Darriba & al., 2012); the best-fit model was GTR+Γ for both partitions. We used ML to first analyze the cpDNA and nrDNA partitions individually. We found no strongly supported conflicts across these two partitions (suppl. Figs. S1, S2) and used ML and BI to also analyze a concatenated plastid-nuclear matrix consisting of 8526 aligned positions (5695 cpDNA and 2831 nrDNA). In the ML analyses, we used the following RAxML parameters: GTRCAT (general time reversible under the CAT model) model for the bootstrapping phase, 25 distinct rate categories, and random starting tree. We assessed support using 1000 rapid bootstrap replicates. Parameters for the BI analysis are described in the next section. Clades are considered to have moderate support when ML bootstrap values (BS) are higher than 70 and high support when they are above 90 (Hillis & Bull, 1993) and BI posterior probabilities (PP) are higher than 0.95.

Molecular dating analysis. — We analyzed the concatenated matrix using BEAST v.2.5.0 (Bouckaert & al., 2014) to reconstruct a time-calibrated tree of Cyclanthaceae.

Trees and clocks were linked across nuclear and plastid genome partitions, whereas models of sequence evolution were unlinked. We used GTR as the substitution model for both partitions, and a lognormal relaxed clock model. The tree prior was set to a birth-death model, and Velloziaceae was set as the sister group of all other sampled taxa. The fossil *Cyclanthus messelensis* S.Y.Sm. & al. was placed at the crown node of Cyclanthaceae (= stem node of *Cyclanthus* as suggested by Iles & al., 2015), using the minimum fossil age of 47 Ma as the offset value and standard deviation = 1.25. The MCMC was run for 200 million generations, sampling trees every 1000 generations. The resulting files were analyzed using Tracer v. 1.7 (Rambaut & al., 2018) to confirm effective sample size (ESS) values above 200 for all parameters. A maximum clade credibility (MCC) tree was produced using TreeAnnotator v.2.5.0 (Rambaut & Drummond, 2015), discarding 10% of the trees as burn-in and setting the node height parameter as common ancestor height.

Historical biogeography analysis. — Age estimates obtained from the BEAST analyses were used to infer early diversification events in all major clades of Cyclanthaceae, and to reconstruct hypotheses of historical biogeography in the group. We used a chronogram that was pruned using the *drop.tip* function of the R package *ape* v-5 (Paradis & Schliep, 2019) to (i) retain a single specimen per species to avoid pseudo-replication, and (ii) remove most lineages outside Cyclanthaceae as being beyond the focus of this analysis, leaving only Pandanaceae species as outgroup taxa.

Coding of biogeographic areas was based on the current distribution of Cyclanthaceae and on the geography of the Neotropics. The tips of the pruned chronogram were scored for distribution in a presence-absence matrix representing six geographical areas. Scores were based on collection records and data from the literature. The geographical areas are: Continental Central America rainforests (southern Mexico to the Panama Isthmus), Lesser Antilles rainforests, Tumbes-Chocó-Magdalena rainforests, Amazon Basin rainforests and Atlantic Rainforest. A sixth area representing the Paleotropics was included to accommodate the distribution of the outgroup family Pandanaceae. Biogeographical scores were based on collection records and data from the literature. Although *Thoracocarpus bissectus* has been recorded in the Greater Antilles (Cuba), this area was not included because we were unable to corroborate its occurrence in this region. Species of uncertain identity (“aff.” or “sp.” in the phylogenetic tree) were included in the analysis and scored as present only for the area where the collection was made. Ancestral area reconstruction was performed using the R package BioGeoBEARS (Matzke, 2012) under a maximum likelihood implementation. The maximum range allowed was set to seven to encompass all geographic areas considered here, and six models were evaluated (DEC, DEC+J, DIVALIKE, DIVALIKE+J, BAYAREA, BAYAREA+J); we focused on results based on DEC+J, which was selected as the best-fit model under the AICc (see suppl. Table S1 for model comparisons and suppl. Table S2 with scored areas).

■ RESULTS

Phylogenetic inference. — Analyses of the plastid, nuclear, and concatenated plastid-nuclear datasets resulted in congruent relationships across ML frameworks for most well-supported relationships (i.e., BS > 90%; Fig. 4 and suppl. Figs. S1, S2). The concatenated matrix yielded generally stronger ML BS values, likely reflecting a higher overall number of informative sites than its individual plastid and nuclear components, so we focused our discussions on this data matrix. Both the BI and ML analyses of the concatenated data produced highly consistent topologies and support values (Fig. 4 shows the ML topology; the BI topology can be found in suppl. Fig. S3). Most genera in the family were recovered as monophyletic with high support in both the BI (PP ≥ 0.98) and ML (BS ≥ 93%) analyses. The sole exception was *Asplundia*, which was weakly supported as a clade in the ML analysis (BS = 55%). *Cyclanthus*, the only genus in subfamily Cyclanthoideae, was strongly supported as the sister group of the remaining Cyclanthaceae (PP = 1, BS = 100%). Within Carludovicoideae, both analyses recover an *Asplundia*-*Dicranopygium* clade with moderate to strong support (PP = 0.99, BS = 79). The position of *Schultesiophytum* differs between analyses, as either sister to the *Asplundia*-*Dicranopygium* clade in the BI analysis with high support (PP = 0.99) or unsupported in the ML analysis (BS = 21) as sister to a clade including all Carludovicoideae, except *Asplundia* and *Dicranopygium*. The monophyly of the *Sphaeradenia* group and relationships among its constituent genera (*Ludovia* (*Sphaeradenia* (*Chorigyne*, *Stelestylis*))) were recovered with high support in both analyses (PP = 1 and BS = 86 for the crown node; PP = 1 and BS = 100 for the remaining relationships). *Carludovica*, *Thoracocarpus*, *Dianthoveus* and *Evodianthus* are found as the successive sister groups of the *Sphaeradenia* group in the ML analysis, but there is weak support for the relationships among these four genera. In the BI phylogenetic tree, *Carludovica* was recovered with high support (PP = 1, Fig. 4, suppl. Fig. S3) as sister to the remaining members of the subfamily Carludovicoideae, and *Evodianthus*, *Dianthoveus*, and *Thoracocarpus* form a strongly supported clade with the *Sphaeradenia* group (PP = 1).

Molecular dating analysis. — Age estimates point to a late Cretaceous-Early Paleocene origin for Cyclanthaceae (stem node = 62.83 Ma, 95% HPD = 50.45–79.27 Ma; Table 1, Fig. 5). The first split in the family, between Cyclanthoideae and Carludovicoideae (= Cyclanthaceae crown node), occurred in the early Eocene (50.61 Ma, 95% HPD = 47.02–58.97 Ma; Table 1, Fig. 5). The subfamily Carludovicoideae has an estimated late Eocene-early Oligocene origin (crown node = 35.94 Ma, 95% HPD = 25.01–46.46 Ma; Table 1, Fig. 5), with early diversification of most genera dated from the late Oligocene or early Miocene (ca. 25 to 20 Ma). Within Carludovicoideae, the oldest genus is *Asplundia* (crown age of 25.04 Ma, 95% HPD: 16.66–33.69 Ma), and the youngest is *Stelestylis* (crown age of 2.48 Ma, 95% HPD: 0.46–5.15 Ma). We did not infer the crown age of Cyclanthoideae

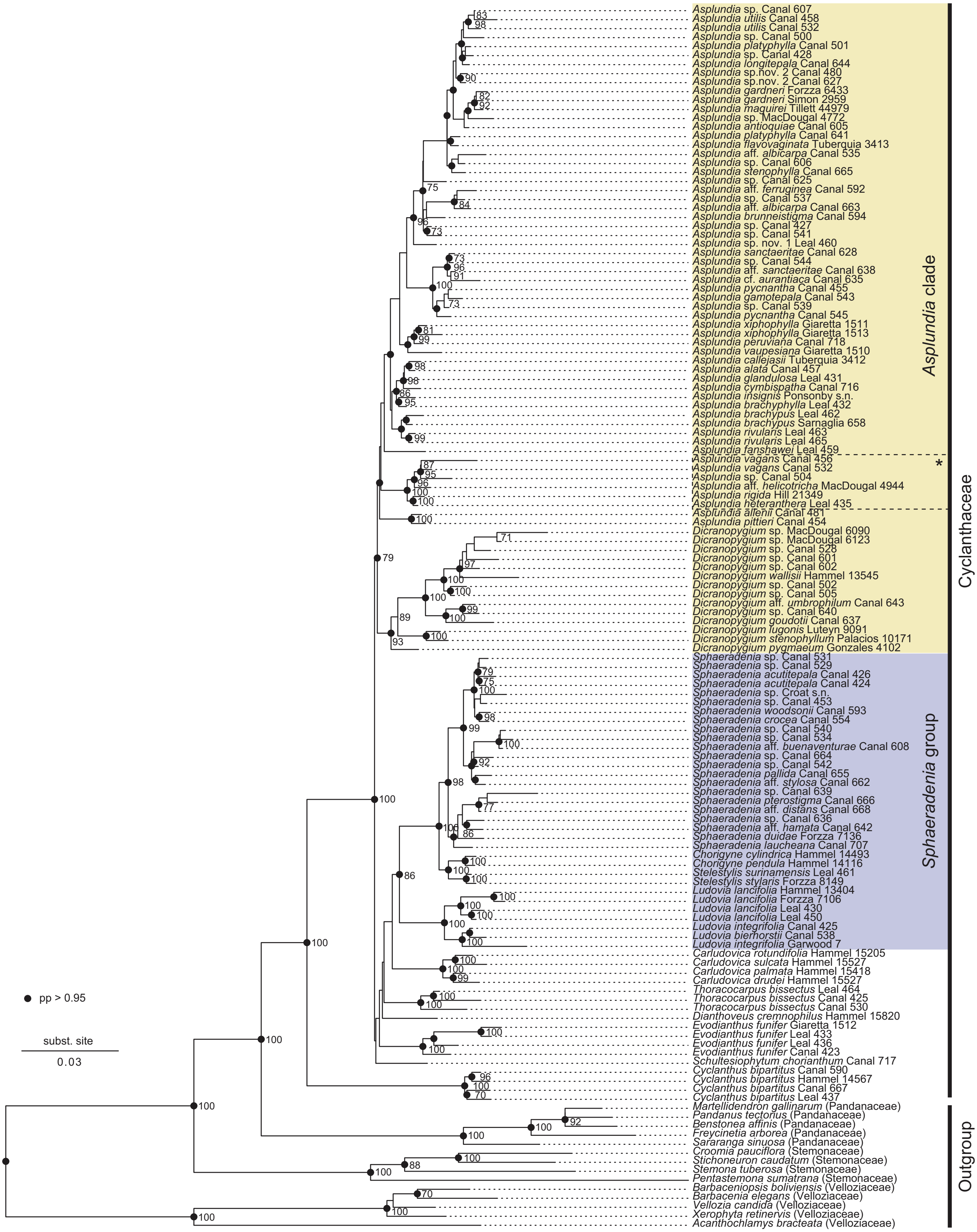

Fig. 4. Maximum likelihood (ML) tree of a concatenated matrix of two nuclear (*phyC*, *rpb2*) and five plastid (*atpB-rbcL*, *psbA-trnH*, *trnL-trnF*, *trnQ-rps16*, *matK*) markers for Cyclanthaceae. An asterisk highlights representatives of *Asplundia* subg. *Choanopsis*. Numbers on the phylogram show BS values for branches with BS > 50. Black dots indicate branches supported by posterior probability (PP) ≥ 0.95 in the Bayesian inference analysis using the same matrix (BI tree available in suppl. Fig. S3).

as we only sampled one of the two species that comprise this subfamily.

Ancestral area reconstruction. — Our range reconstructions inferred a broad distribution for the common ancestor of Cyclanthaceae and Pandanaceae that includes the Paleotropics ("A") and the Tumbes-Chocó-Magdalena rainforests ("D") in northwestern South America (Fig. 6). The most recent common ancestor of all Cyclanthaceae appears to have been distributed in the Central America ("B"), Tumbes-Chocó-Magdalena rainforests ("D") and the Amazon Basin ("E"). Range expansions between the Tumbes-Chocó-Magdalena rainforests and Central America rainforests ("BD") were frequently reconstructed between the mid (15 Ma) and late Miocene (6 Ma). The widespread distribution of the most recent common ancestor of Carludovicoideae (excluding *Carludovica*) across the Amazon Basin and Tumbes-Chocó-Magdalena suggests that a vicariance event separated the early diversification of the two main clades of the subfamily in each of these two areas. More recent migrations back and forth between the Amazon Basin and Tumbes-Chocó-Magdalena, mostly by *Asplundia* and *Dicranopygium*, were usually dated to the Miocene (23–6 Ma). Two distribution shifts between the Amazon Basin ("E") and the Atlantic Rainforest ("F") were observed within *Asplundia*, one dated to the late Miocene (10 Ma) and another to the period from the Pliocene onwards (last 6 Ma). The two migration events of Cyclanthaceae to the Lesser Antilles (C) within *Asplundia* occurred relatively recently in the late Miocene-early Pliocene boundary (6 Ma).

■ DISCUSSION

Systematics of Cyclanthaceae. — Cyclanthaceae comprises two well-delimited subfamilies, Cyclanthoideae and Carludovicoideae (both PP = 1 and BS = 100%), corroborating recent studies (e.g., Soto Gomez & al., 2020) and the current infrafamiliar classification of the family (Fig. 3). We also confirm the monophyly of all 12 currently recognized genera within Cyclanthaceae. This includes 10 of the 11 genera by Harling (1958), and all 12 genera that were previously treated in a morphology-based phylogenetic study (Eriksson, 1994).

Subfamily Cyclanthoideae. — Cyclanthoideae is characterized by elaborately folded lamina (Wilder, 1981a), one short main costa, lateral costae that originate from the apex of the main costa and reach the apex of the leaf segments, pistillate and staminate flowers in alternate whorls where individual flowers are indistinguishable, and numerous carpels and placentae. The presence of laticifers (Wilder & Harris, 1982), lysigenous aerenchyma (Wilder, 1985), pollination by Scarabaeideae (Beach, 1982; Moore & Jameson, 2013) and unique floral odor chemical profile (Schultz & al., 1999) are also probable characters shared by Cyclanthoideae. The subfamily comprises a single genus, *Cyclanthus*, and two species (Hammel, 1986, 2003; Hammel & Wilder, 1989; Correa & al., 2004): the polymorphic *Cyclanthus bipartitus* and *Cyclanthus indivisus* R.E.Schult.

Subfamily Carludovicoideae. — Carludovicoideae is characterized by leaves having plicate prefoliation (Wilder, 1976), lateral costae usually absent (but when present never reaching the leaf segment apex), pistillate flowers surrounded by groups of four staminate flowers, staminate flowers with sterile lobes, long filiform staminodes, four carpels with one or four placentae (Harling, 1958; Harling & al., 1998), and pollination by curculionid weevils (Gottsberger, 1991).

The ML, BI, and time-calibrated analyses show slightly different relationships among the genera due to low support of some nodes. Plastid phylogenomic analyses by Soto Gomez & al. (2020) also showed less strong support for clades within

Table 1. Age estimates (in Ma) for stem and crown nodes of major lineages in Cyclanthaceae.

Clade	Stem node (credible interval)	Crown node (credible interval)
Cyclanthaceae (a)	62.83 (50.45–79.27)	50.61 (47.02–58.97)
Cyclanthoideae	50.61 (47.02–58.97)	NA (only one species sampled)
Carludovicoideae (b)	50.61 (47.02–58.97)	35.94 (25.01–46.46)
Asplundia (c)	27.75 (18.92–36.68)	25.04 (16.66–33.69)
Dicranopygium (d)	27.75 (18.92–36.68)	23.54 (15.64–31.51)
Schultesiophytum	29.61 (20.31–38.98)	NA (monotypic)
Sphaeradenia group (e)	26.61 (18.28–35.06)	23.25 (15.90–31.29)
Thoracocarpus (f)	26.61 (18.28–35.06)	12.90 (5.55–21.07)
Dianthoveus	28.28 (18.97–36.30)	NA (monotypic)
Evodianthus (g)	29.04 (20.09–38.33)	15.73 (8.23–23.82)
Carludovica (h)	35.94 (25.01–46.46)	12.77 (5.91–20.74)
Chorigyne	10.01 (4.55–16.11)	3.20 (0.69–6.46)
Stelestylis	10.01 (4.55–16.11)	2.48 (0.46–5.15)

Letters in parenthesis after clade names indicate crown nodes in Fig. 5. Ages represent median estimates; credible intervals (95% highest posterior density, HPD) are shown in parenthesis.

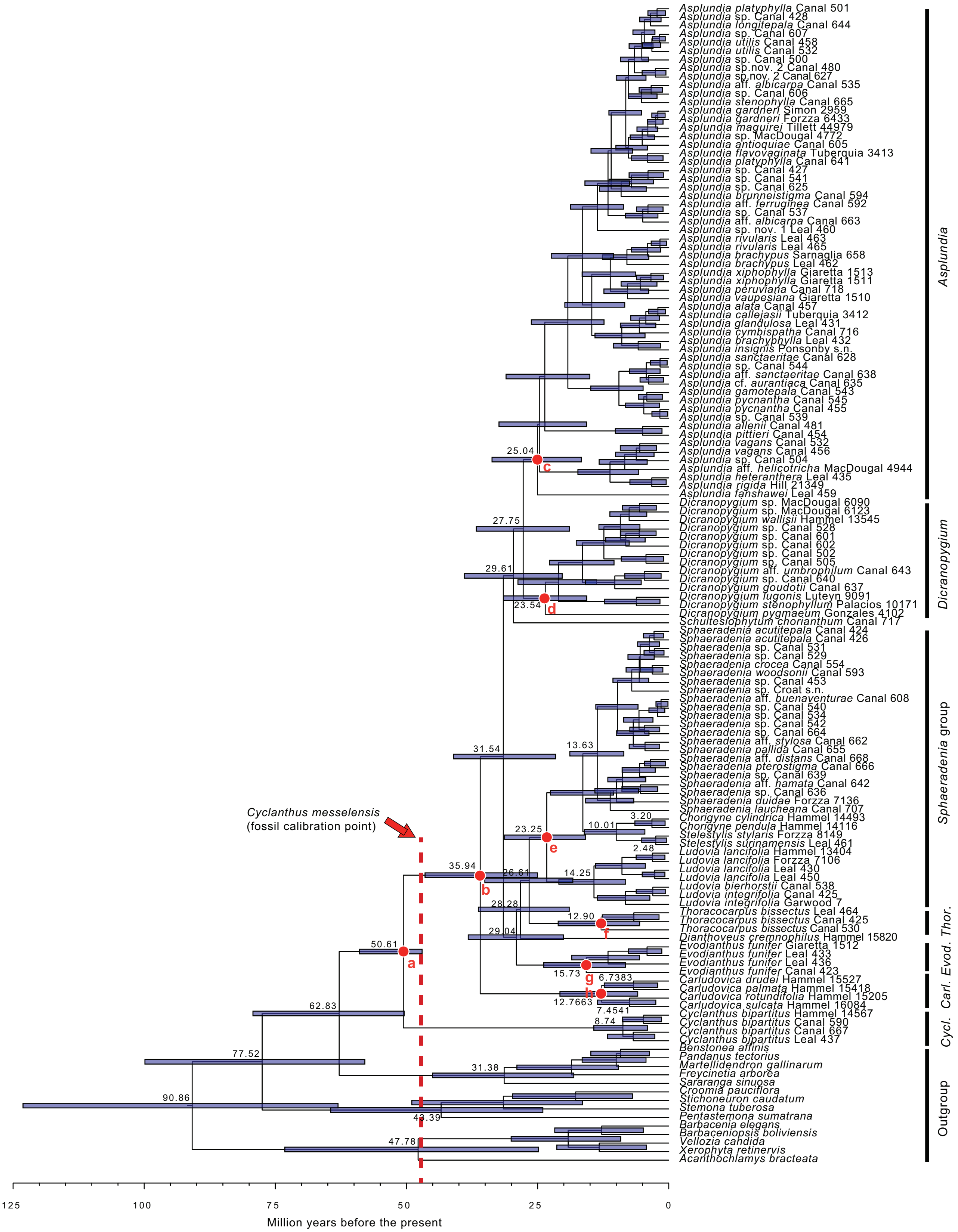

Fig. 5. Time-calibrated phylogeny of Cyclanthaceae based on a concatenated matrix of two nuclear (*phyC*, *rpb2*) and five plastid (*atpB-rbcL*, *psbA-trnH*, *trnL-trnF*, *trnQ-rps16*, *matK*) markers, inferred using BEAST 2. Blue bars represent credible intervals expressed as 95% HPD values. Red letters indicate crown nodes of groups shown in Table 1. Arrow indicates fossil calibration point at the crown node of the family. For tree showing posterior probabilities, see suppl. Fig. S3.

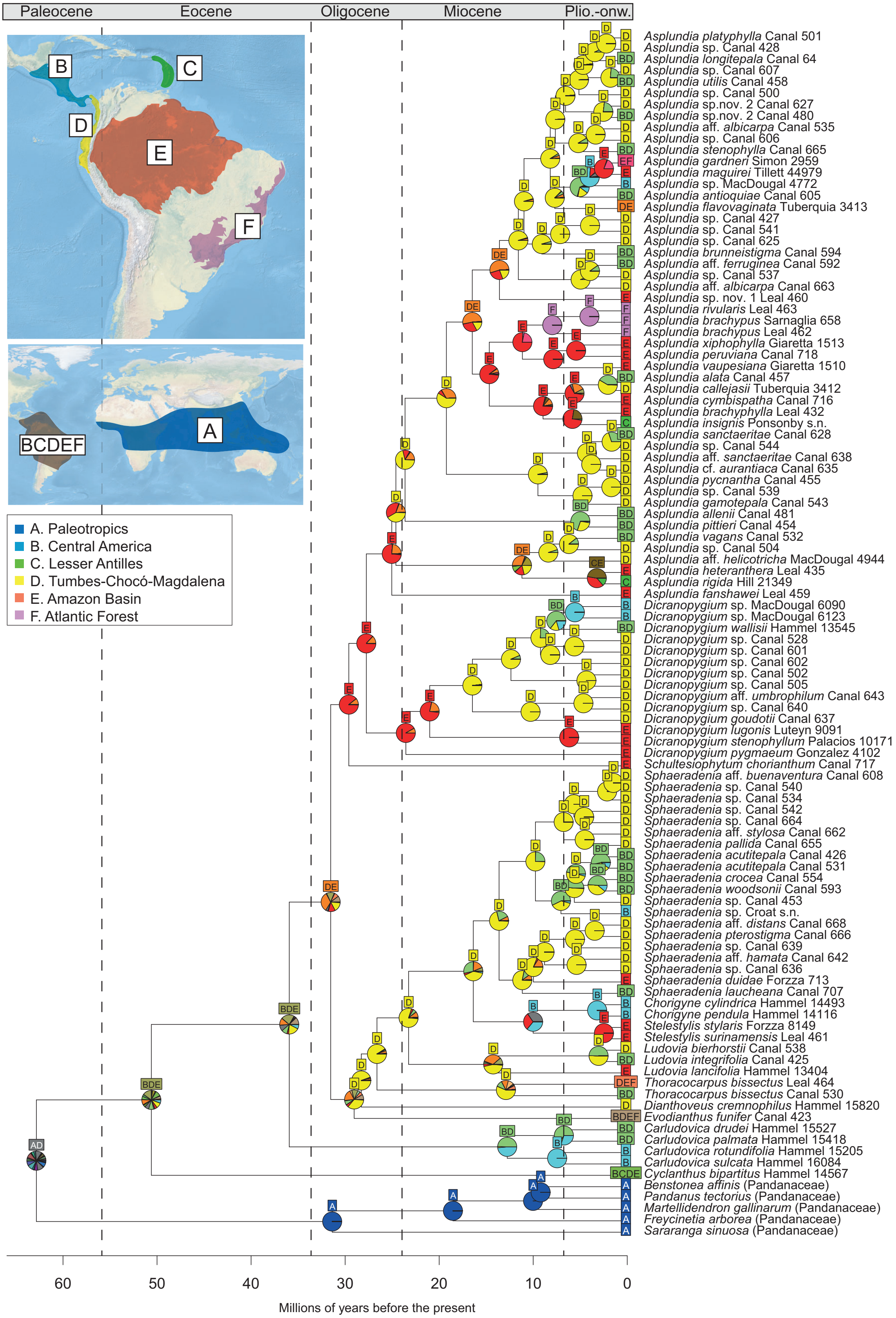

Fig. 6. Historical biogeography of Cyclanthaceae reconstructed using the model DEC+J (483.3 AICc) in BioGeoBEARS over the time-calibrated phylogeny presented in Fig. 5. Tip scoring and model comparisons are available in suppl. Tables S1 and S2.

this subfamily than a matrix comprising both plastid and mitochondrial genomes. However, at least two clades were consistently recovered by our analyses and the latter study: (i) the *Sphaeradenia* group, comprising *Sphaeradenia*, *Stelestylis*, *Chorigyne*, and *Ludovia*, and (ii) a clade comprising *Asplundia* and *Dicranopygium*. The *Sphaeradenia* group was proposed by Harling (1958) without a formal status. This group was subsequently recovered as monophyletic in morphology-based cladistic analyses (Hammel & Wilder, 1989; Eriksson, 1994), with the same topology as the sequence-based analyses here and in Soto Gomez & al. (2020). All three species of *Ludovia* were sampled in this study. The only accession of *Ludovia bierhorstii* G.J.Wilder was placed among samples of *L. integrifolia* (Woodson) Harling. These species have somewhat overlapping circumscriptions (Wilder, 1978) with highly variable leaves (Wilder, 1981b), and likely represent a single species.

Eriksson (1995, 2007) recognized 52 species of *Sphaeradenia* and proposed six informal morphological groups within the genus. Our sampling of ca. 40% of the species, many of them unidentified, did not cover all morphological groups, so we opted to not discuss their relationships here. The clade *Chorigyne-Stelestylis* was also recovered by Eriksson (1994). *Chorigyne* is the most recently described genus in Cyclanthaceae, two of its species being segregated from *Sphaeradenia*, and the remaining five described as new at the same time (Eriksson, 1989). We were unable to sample the type species of *Chorigyne*, *Stelestylis*, and *Sphaeradenia*, but due to their morphological similarity and close relationships inferred using molecular data here, we do not discard lumping them in future studies. Species within these three genera are strikingly similar and the genera themselves can only be differentiated by the number and position of the placenta in ovaries of dissected flowers. While the monophyly of the clade containing *Chorigyne*, *Stelestylis*, and *Sphaeradenia* was supported by both the concatenated plastid-nuclear matrix and plastid trees, this clade was not recovered in analyses using nuclear data only. Further studies on this group are therefore necessary before any taxonomic change can be formally proposed.

The *Asplundia-Dicranopygium* clade was highly supported by our analyses and those of Soto Gomez & al. (2020) but had not been recovered in previous morphology-based studies (Harling, 1958; Hammel & Wilder, 1989; Eriksson, 1994). It represents the most species-rich lineage within the family, encompassing ca. 154 species. *Asplundia*, the largest genus with ca. 100 species (Govaerts & Eriksson, 2020), is divided into two subgenera: *A*. subg. *Asplundia* characterized by asymmetrical staminate flowers and leaf blades usually with three costae, and *A*. subg. *Choanopsis* (marked with asterisk in Fig. 4) characterized by symmetrical staminate flowers and leaf blades with one costa (Harling, 1958). We recovered *A*. subg. *Choanopsis* as nested within a paraphyletic *A*. subg. *Asplundia*. We inferred a highly supported clade comprising *A. allenii* Hammel and *A. pittieri* (Woodson) Harling as the sister group to all remaining species in the genus, but the low support for the deepest splits in *Asplundia* preclude conclusions about the status of *A*. subg. *Asplundia* sensu Harling (1958), although *A*. subg. *Choanopsis* is well supported across all our analyses.

The general topology of the *Asplundia-Dicranopygium* clade contradicts previous morphology-based systematic studies in the family (Harling, 1958; Hammel & Wilder, 1989; Eriksson, 1994). The morphological similarities between *Asplundia* subg. *Choanopsis* and the monotypic *Thoracocarpus* led previous phylogenetic analyses to suggest that *Asplundia* could be nonmonophyletic, with *A*. subg. *Choanopsis* as a possible sister to *Thoracocarpus* (Eriksson, 1994). Indeed, the two lineages are remarkably similar in their profusely branched climbing habit, funnel-shaped receptacle with evenly distributed perianth lobes, and unicostate leaves. However, our results show that *Thoracocarpus* and *Asplundia* are only distantly related and confirm the monophyly of the latter.

Dicranopygium has the most complex formal subdivision within the family (Harling, 1958). The ca. 50 recognized species in the genus (Govaerts & Eriksson, 2020) are classified in four subgenera, differentiated mainly by structures of the staminate flower: *D*. subg. *Dicranopygium* (45 species), *D*. subg. *Uribanthus* Harling (1 species), *D*. subg. *Gleasonianthus* Harling (4 species), and *D*. subg. *Tomlinsonianthus* G.J.Wilder (1 species). Possibly due to the lack of proper collections and systematic studies, identification of *Dicranopygium* species is challenging and only 6 of the 14 species included in our study could be identified. Of those, one belongs to *D*. subg. *Gleasonianthus* (*D. pygmaeum* (Gleason) Harling) and the other five belong to *D*. subg. *Dicranopygium* (*D. goudotii* Harling, *D. lugonis* Harling, *D. stenophyllum* Harling, *D*. aff. *umbrophilum* Hammel, *D. wallisii* Harling), which accommodates most of the genus diversity. Our inference supports the monophyly of these subgenera, as the species belonging to them are placed in well-supported clades (PP > 0.95, BS > 90%) that are sister to each other. Also, given the species-richness of *D*. subg. *Dicranopygium*, there is a high probability that currently unidentified species also belong to this subgenus. Further studies are necessary to improve our understanding of the infrageneric classification of *Dicranopygium*.

The monospecific genera *Evodianthus*, *Dianthoveus*, and *Thoracocarpus* are recovered as a strongly supported clade in the mitochondrial and combined organellar phylogenomic analyses by Soto Gomez & al. (2020). However, our ML analysis retrieved these genera as one degree below *Carludovica* and the *Sphaeradenia* group, a relationship that was not observed either in the time-calibrated analyses (Figs. 5, 6), nor in the BI analysis (suppl. Fig. S3) or in the partitioned analyses (suppl. Figs. S1, S2).

The positions of *Carludovica* and *Schultesiophytum* are unstable across analyses here and in the previous studies based on morphological data. In the latter, the monospecific genus *Schultesiophytum* had an uncertain placement (Harling, 1958), or was recovered as either sister to the clade (*Carludovica* (*Dianthoveus*, *Evodianthus*) (Hammel & Wilder, 1989) or to the remaining genera in Carludovicoideae (Eriksson, 1994). For *Carludovica*, Harling (1958) hypothesized that the genus is sister to *Asplundia* and *Thoracocarpus*, while

Hammel & Wilder (1989) and Eriksson (1994) recovered *Carludovica* as sister to an *Evodianthus*-*Dianthoveus* clade. Based on mitochondrial and combined organellar data, Soto Gomez & al. (2020) found a strongly supported *Carludovica*-*Schultesiophytum* clade, which is sister to the remaining genera in Carludovicoideae. From the infrageneric point of view, the highly supported relationships ((*Carludovica drudei* Mast., *C. palmata*) (*C. rotundifolia* Schaedtler, *C. sulcata* Hammel)) in our study differ from that of Franz (2004), who recovered *C. palmata* as sister to the remaining species of the genus in an analysis based on morphological data.

Early diversification of Cyclanthaceae. — The origin of Cyclanthaceae in the late Cretaceous or early Eocene inferred here is consistent with previous chronograms that sampled several Cyclanthaceae species in the phylogenetic context of the order Pandanales (Gallaher & al., 2014; Soto Gomez & al., 2020). The crown node age recovered in the study of Gallaher & al. (2014) (45 Ma vs. 50 Ma), which focused on Pandanaceae, is slightly older that the one obtained here, but still within their credible interval (95% HPD = 45–72 Ma). The similar age estimates are due to the use of the same fossil *Cyclanthus* as calibration point (Iles & al., 2015). Interestingly, this fossil was found in Europe, an area outside the current distribution of the family. Given that the only age constraint in this study was placed on the crown node of Cyclanthaceae, we acknowledge that age estimates for outgroups are not completely in accordance with previous studies in the order Pandanales (see also Soto Gomez & al., 2020). While Gallaher & al. (2014) found a late Cretaceous-early Eocene origin of Pandanaceae, our analysis returned a more recent origin of 31.87 Ma. Likewise, Alcantara & al. (2018) found older estimates for the crown node of Velloziaceae than our analysis (75 Ma vs. 48 Ma). Age estimates within the Cyclanthaceae are similar to those recovered by Soto Gomez & al. (2020), which shows an early Eocene diversification of the family and a late Oligocene to early Miocene diversification of most genera.

Biogeographical events of Cyclanthaceae. — The ancestral range estimation recovered an “AD” range, a widespread distribution across the Tumbes-Chocó-Magdalena and Paleotropical rainforests, for the most recent common ancestor of Cyclanthaceae and Pandanaceae during the late Cretaceous-early Paleocene. Today, this distribution makes little sense since it represents a disjunct distribution between two very distant areas. A possible explanation for the “AD” range is an ancient vicariance event and extinction involving areas where neither Cyclanthaceae nor Pandanaceae occur today. The climate was much warmer during the Cretaceous, and tropical and subtropical forests extended up to higher latitudes (Mannion & al., 2014). We argue that the past climatic conditions and the discovery of *Cyclanthus* fossil remains in Europe (Smith & al., 2008) can be interpreted as evidence for a boreotropical route of migration between the Paleotropics and the Neotropics, followed by vicariance events when global temperatures dropped (see also Davis & al., 2002, 2004). If it is possible to score enough morphological characters from the fossil *Cyclanthus* to correctly place it as a terminal taxon in the Cyclanthaceae phylogeny (as in Wood & al., 2013), future analyses could test this biogeographical hypothesis.

The ancestral area of Cyclanthaceae is reconstructed as Central America (area “B”) and northern South America rainforests, including the Tumbes-Chocó-Magdalena region (“D”) and the Amazon Basin (“E”), in the late Eocene at 50 Ma. According to one of the models explored by Bacon & al. (2016), it is possible that the first shift of migration between North and South America occurred around 40 Ma. This migration route did not necessarily require transoceanic long dispersal due to the Antillean Land Bridge (GAARlandia), an Eocene land bridge between North and South America (see also Dick & Pennington, 2019). If the boreotropical route is considered, then Cyclanthaceae may have invaded South America during the first wave of migrations between North and South America, and long before the final closure of the Panama Isthmus (at around 5 Ma; Keigwin, 1978). The group would have then diversified in South America and only recolonized Central America from the late Miocene onwards (i.e., the last 10 Ma), when most of the “BD” ranges are recovered in our analysis.

The early diversification of the major clades of Cyclanthaceae during the Oligocene in the Tumbes-Chocó-Magdalena rainforest (“D”) and Amazon Basin (“E”) precedes the uplift of the northern portion of the Andes around 15 Ma (Gregory-Wodzicki, 2000; Hoorn & al., 2010), so there were no strong dispersal barriers between these areas at that time. Later on, this connection was severed, and the two subsequent lineages are either restricted to the Tumbes-Chocó-Magdalena (“D”) or to the Amazon Basin (“E”). It is possible that the formation of the Pebas system, a swamp-like environment in the western Amazon (23–10 Ma, Hoorn & al., 2010), coupled with the earlier phases of the Northern Andes uplift (Gregory-Wodzicki, 2000), led to the vicariance of Cyclanthaceae lineages that were more widely distributed in northern South America around that time. The Tumbes-Chocó-Magdalena rainforests may have acted as an older-than-expected refugium for surviving lineages (Gentry, 1982), possibly explaining the high frequency of species-poor genera that emerge from old nodes in the phylogeny (e.g., *Dianthoveus*; depauperons sensu Donoghue & Sanderson, 2015) in that region. This scenario contradicts recent findings for Orchidaceae, for which an Andean origin precedes radiations in the Chocó rainforests that are more recent (i.e., Pleistocene, or the last 2.6 Ma) (Pérez-Escobar & al., 2019). Further evidence from fossil record (as in Jaramillo & al., 2006) or from comparative analysis of multiple clades (as in Vasconcelos & al., 2020) is necessary to provide support for one or the other scenario.

The Chocó-refugium hypothesis may not apply to the *Asplundia*-*Dicranopygium* clade, where migration events back and forth the Amazon Basin are observed from the early Miocene transition (around 20 Ma) to the Pliocene (around 5 Ma). These multiple area shifts indicate that the uplift of the Northern Andes (Gregory-Wodzicki, 2000; Hoorn & al., 2010) did not impose a strong barrier for the dispersal of this lineage. Similar shifts are observed in *Ludovia* and in the *Sphaeradenia* group, though they are generally older and less frequent than in the *Asplundia-Dicranopygium* clade. Shifts between the western and eastern sides of the Andes may be linked to diversifications patterns in these areas (see also Luebert & Weigend, 2014) and may help to explain why the *Asplundia-Dicranopygium* clade is the most species-rich lineage in Cyclanthaceae. *Asplundia* is also the genus with the highest number of shifts between Amazon Basin ("E") and Atlantic Rainforest ("F"). The initial split between these two areas in the mid-Miocene makes sense considering the age estimates for the establishment of the dry diagonal (Simon & al., 2009). However, more recent splits between these two areas are also observed in several other Cyclanthaceae genera, including several species that occur in both areas (see examples in the Introduction). These may indicate either that the dry diagonal is not a strong migration barrier for these species or provide evidence for the existence of rainforest corridors that have connected Amazon and Atlantic Rainforest in the recent past (Ledo & Colli, 2017). These two possibilities are not mutually exclusive and probably both contributed to the observed patterns of disjunction in Cyclanthaceae and other lineages (e.g., Sobral-Souza & al., 2015).

■ CONCLUSIONS

Our broad sampling of Cyclanthaceae allowed us to elucidate phylogenetic relationships among major lineages and to compare these results to previously published genus-level phylogenies (Hammel & Wilder, 1989; Eriksson, 1994; Soto Gomez & al., 2020). It is worth noticing that all 12 genera previously circumscribed solely based on morphology were recovered as monophyletic, well-delimited groups. This highlights a strong congruence between morphological and molecular data at the genus-level in Cyclanthaceae. Even though all genera were recovered as monophyletic, further studies are necessary to improve infrageneric delimitations in the large *Asplundia*, *Dicranopygium*, and *Sphaeradenia* group genera, where the current sampling does not include all infrageneric groups. The species-level phylogeny for Cyclanthaceae presented here is also likely to be a useful framework for future evolutionary studies in the family, as demonstrated by our analysis of historical biogeography. This analysis, combined with the distribution of fossil *Cyclanthus*, indicates a possible boreotropical route for the colonization of the Neotropics by the most recent common ancestor of Cyclanthaceae. It also emphasizes the importance of northern South American rainforests and particularly of the Tumbes-Chocó-Magdalena region as important areas for the early diversification of the family.

■ AUTHOR CONTRIBUTIONS

ESL, RCF & RMS conceived the idea and designed the research; ESL & FAM conducted experiments; ESL & TNCV conducted data analyses; ESL, DT & RCF collected samples; ESL, TNCV, DT, MSG, FAM, RCF & RMS prepared the manuscript. — ESL, https://orcid.org/0000-0002-2180-8362; TNCV, https://orcid.org/0000-0001-9991-7924; DT, https://orcid.org/0000-0001-7846-0099; MSG, https://orcid.org/0000-0003-1812-7416; FAM, https://orcid.org/0000-0001-7348-143X; RCF, https://orcid.org/0000-0002-7035-9313; RMS, https://orcid.org/0000-0002-5895-489X

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Appendix 1. Voucher information and GenBank accession numbers for taxa used in the present study.

Species, geographic origin, voucher information (collector and number, and herbarium of deposition), and GenBank accession numbers for *atpB-rbcL*, *matK*, *phyC*, *psbA-trnH*, *rpb2*, *trnL-trnF*, *trnQ-rps16*. Newly generated sequences are indicated by an asterisk (*) and lacking sequences by a dash (–). Previously published sequences are indicated by a superscript: 1 = Mello-Silva & al. (2011); 2 = Hertweck & al. (2015); 3 = Buerki & al. (2012); 4 = Gallaher & al. (2014); 5 = Li & al. (2008); 6 = Callmander & al. (2003); 7 = Li & al. (2012); 8 = Lam & al. (2016); 9 = Hsu & al. (2013); 10 = Chen & al. (2010); 11 = Vongsak & al. (2008); 12 = Hilu & al. (2003); † = Unpublished sequence.

OUTGROUP: ***Acanthochlamys bracteata*** P.C.Kao, China, *Chase 842* (K), JN016989[1], KP083039[2], –, JN017041[1], –, JN016885[1]; –; ***Barbaceniopsis boliviensis*** (Baker) L.B.Sm., Bolivia, *Mello-Silva 2107* (SPF), JN016996[1], –, –, JN017048[1], –, JN016892[1], –; ***Benstonea affinis*** (Kurz) Callm. & Buerki, Malaysia, *Gallaher 265* (BISH), –, JX286801[3], KJ681806[4], –, –, JX286957[3], JX287150[3]; ***Croomia pauciflora*** Torr. ex Torr. & A.Gray, Florida, U.S.A., *Gholson 10360* (FLAS), EU075377[5], KP083061[2], –, –, –, DQ831506[5], JX287063[3]; ***Freycinetia arborea*** Gaudich., New Caledonia, *Gallaher 195* (BISH), –, JX286815[3], KJ681799[4], –, –, KJ681511[4], JX287164[3]; ***Martellidendron gallinarum*** (Callm.) Callm., Madagascar, *Callmander M114* (NEU), AY337625[6], JX286738[3], –, –, –, AY337669[6], JX287087[3]; ***Pandanus tectorius*** Parkinson, O‘ahu, Hawai‘i (cultivated), origin unknown, *Gallaher 288* (BISH), –, JX286775[3], KJ681789[4], JN407018[7], –, JX286937[3], JX287123[3]; ***Pentastemona sumatrana*** Steenis, Leiden Botanical Garden (cultivated), Acc. No.: 910375, –, KU127303[8], –, –, –, –, –; ***Sararanga sinuosa*** Hemsl., Botanical Garden, Lawai, Hawaii (cultivated), origin New Guinea, AY337638[6], JX286874[3], KJ681807[4], –, –, AY337682[6], JX287223[3]; ***Stemona tuberosa*** Lour., Nantou, Taiwan, *Hsu 401* (TCB), JQ733661[9], GQ434036[10], –, GQ434873[10], –, FJ19446[†], –; ***Stichoneuron caudatum*** Ridl., Malaysia, *Bygrave 50* (K), –, JX286712[3], –, AB373199[11], –, –, JX287061[3]; ***Vellozia candida*** J.C.Mikan, Rio de Janeiro, Brazil, *Mello-Silva 2877* (SPF), JN017017[1], –, –, JN017069[1], –, JN016913[1], –; ***Xerophyta elegans*** Baker, origin unknown, *Chase 253* (NUC), JN017009[1], AY491664[12], –, JN017061[1], –, JN016905[1], JX287059[3]; ***Xerophyta retinervis*** Baker, South Africa, *GR 14* (K), JN017040[1], KU127267[8], –, JN017092[1], –, JN016936[1], JX287264[3]. — **INGROUP:** ***Asplundia alata*** Harling, Chocó, Colombia, *Canal 457* (JBB), OM479324*, OM478648*, OM479226*, OM479012*, OM479129*, OM478770*, OM478890*; ***Asplundia*** aff. ***albicarpa*** Hammel, Chocó, Colombia, *Canal 535* (JBB), OM479334*, OM478659*, OM479234*, OM479023*, –, OM478781*, OM478901*; Nariño, Colombia, *Canal 663* (JBB), OM479313*, OM478636*, OM479215*, OM479000*, –, OM478758*, OM478878*; ***Asplundia allenii*** Hammel, Chocó, Colombia, *Canal 481* (JBB), OM479355*, OM478680*, –, OM479044*, OM479155*, OM478801*, OM478922*; ***Asplundia antioquiae*** Harling, Chocó, Colombia, *Canal 605* (JBB), OM479318*, OM478642*, OM479221*, OM479006*, OM479126*, OM478764*, OM478884*; ***Asplundia*** cf. ***aurantiaca*** Harling, Nariño, Colombia, *Canal 635* (JBB), OM479385*, OM478716*, OM479279*, OM479080*, –, OM478836*, OM478958*; ***Asplundia brachyphylla*** Harling, French Guiana, *Leal 432* (SPF), –, OM478639*, OM479218*, OM479003*, OM479123*, OM478761*, OM478881*; ***Asplundia brachypus*** Harling, São Paulo, Brazil, *Leal 462* (SPF), OM479317*, OM478641*, OM479125*, OM479005*, OM479125*, OM478763*, OM478883*; Espírito Santo, Brazil, *Sarnaglia 658* (RB), OM479380*, OM478710*, –, OM479074*, –, OM478831*, OM478952*; ***Asplundia brunneistigma*** Hammel, Chocó, Colombia, *Canal 594* (JBB), OM479322*, OM478646*, OM479225*, OM479010*, –, OM478768*, OM478888*; ***Asplundia callejasii*** Tuberq. & E.S.Leal, Antioquia, Colombia, *Tuberquia 3412* (HUA), OM479350*, OM478675*, OM479246*, OM479039*, OM479151*, OM478797*, OM478917*; ***Asplundia cymbispatha*** Harling, Amazonas, Colombia, *Canal 716* (JBB), OM479367*, OM478697*, OM479263*, OM479061*, OM479167*, OM478818*, OM478939*; ***Asplundia fanshawei*** Harling,

Appendix 1. Continued.

French Guiana, *Leal 459* (SPF), OM479391*, OM478722*, OM479284*, OM479086*, OM479186*, OM478842*, OM478964*; ***Asplundia*** aff. ***ferruginea*** Hammel, Chocó, Colombia, *Canal 592* (JBB), OM479314*, OM478637*, OM479216*, OM479001*, –, OM478759*, OM478879*; ***Asplundia flavovaginata*** Harling, Antioquia, Colombia, *Tuberquia 3413* (HUA), –, OM478726*, OM479287*, OM479090*, OM479188*, OM478846*, OM478968*; ***Asplundia gamotepala*** Harling, Chocó, Colombia, *Canal 543* (JBB), OM479386*, OM478717*, OM479280*, OM479081*, OM479183*, OM478837*, OM478959*; ***Asplundia gardneri*** Harling, Bahia, Brazil, *Forzza 6433* (RB), OM479354*, OM478679*, OM479249*, OM479043*, OM479154*, –, OM478921*; Maranhão, Brazil, *Simon 2959* (CEN), OM479394*, OM478727*, OM479288*, OM479091*, OM479189*, OM478847*, OM478969*; ***Asplundia glandulosa*** Harling, French Guiana, *Leal 431* (SPF), –, OM478692*, –, OM479056*, –, OM478813*, OM478934*; ***Asplundia*** aff. ***helicotricha*** Harling, Missouri Botanical Garden (cultivated), origin Pichincha, Ecuador, *MacDougal 4944* (MO, live collection Acc. No.: 1993-1666), OM479406*, OM478740*, OM479298*, OM479104*, OM479199*, OM478860*, OM478982*; ***Asplundia heteranthera*** Harling, French Guiana, *Leal 435* (SPF), –, OM478693*, OM479259*, OM479057*, OM479163*, OM478814*, OM478935*; ***Asplundia insignis*** (Duchass. ex Griseb.) Harling, Royal Botanical Garden, Kew (cultivated), origin Martinique, *Ponsonby s.n.* (K, barcode/ID 49409.000), –, OM478655*, OM478655*, OM479019*, OM479134*, OM478777*, JX287183[3]; ***Asplundia longitepala*** Harling, Nariño, Colombia, *Canal 644* (JBB), OM479327*, OM478651*, OM479229*, OM479015*, OM479132*, OM478773*, OM478893*; ***Asplundia maguirei*** Harling, Venezuela, *Tillett 44979* (NY), OM479395*, OM478728*, –, OM479092*, –, OM478848*, OM478970*; ***Asplundia peruviana*** Harling, Amazonas, Colombia, *Canal 718* (JBB), OM479393*, OM478724*, OM479286*, OM479088*, OM479187*, OM478844*, OM478966*; ***Asplundia pittieri*** (Woodson) Harling, Chocó, Colombia, *Canal 454* (JBB), OM479332*, OM478657*, OM479232*, OM479021*, OM479136*, OM478779*, OM478899*; ***Asplundia platyphylla*** Harling, Chocó, Colombia, *Canal 501* (JBB), OM479321*, OM478645*, OM479224*, OM479009*, OM479128*, OM478767*, OM478887*; Nariño, Colombia, *Canal 641* (JBB), OM479320*, OM478644*, OM479223*, OM479008*, OM479127*, OM478766*, OM478886*; ***Asplundia pycnantha*** Harling, Chocó, Colombia, *Canal 455* (JBB), OM479387*, OM478718*, OM479281*, OM479082*, OM479184*, OM478838*, OM478960*; Chocó, Colombia, *Canal 545* (JBB), OM479388*, OM478719*, OM479282*, OM479083*, –, OM478839*, OM478961*; ***Asplundia rigida*** (Aubl.) Harling, Dominica, *Hill 21349* (NY), OM479329*, OM478653*, –, OM479017*, –, OM478775*, OM478895*; ***Asplundia rivularis*** (Lindm.) Harling, São Paulo, Brazil, *Leal 463* (SPF), OM479364*, OM478694*, OM479260*, OM479058*, OM479164*, OM478815*, OM478936*; São Paulo, Brazil, *Leal 465* (SPF), OM479365*, OM478695*, OM479261*, OM479059*, OM479165*, OM478816*, OM478937*; ***Asplundia sanctae-ritae*** Galeano & R.Bernal, Chocó, Colombia, *Canal 628* (JBB), OM479409*, OM478743*, OM479300*, OM479107*, OM479201*, OM478863*, OM478985*; ***Asplundia*** aff. ***sanctae-ritae*** Galeano & R.Bernal, Nariño, Colombia, *Canal 638* (JBB), OM479384*, OM478715*, OM479278*, OM479079*, OM479182*, OM478835*, OM478957*; ***Asplundia stenophylla*** (Standl.) Harling, Nariño, Colombia, *Canal 665* (JBB), OM479397*, OM478730*, OM479290*, OM479094*, –, OM478850*, OM478972*; ***Asplundia utilis*** (Oerst.) Harling, Chocó, Colombia, *Canal 458* (JBB), OM479336*, OM478661*, OM479236*, OM479025*, OM479139*, OM478783*, OM478903*; Chocó, Colombia, *Canal 532* (JBB), OM479328*, OM478652*, OM479230*, OM479016*, OM479133*, OM478774*, OM478894*; ***Asplundia vagans*** Harling, Chocó, Colombia, *Canal 456* (JBB), OM479405*, OM478739*, OM479297*, OM479103*, OM479198*, OM478859*, OM478981*; Chocó, Colombia, *Canal 533* (JBB), –, OM478713*, OM479276*, OM479077*, OM479180*, OM478833*, OM478955*; ***Asplundia vaupesiana*** Harling, Amazonas, Brazil, *Giaretta 1510* (SPF), OM479392*, OM478723*, OM479285*, OM479087*, –, OM478843*, OM478965*; ***Asplundia xiphophylla*** Harling, Amazonas, Brazil, *Giaretta 1511* (SPF), –, OM478725*, –, OM479089*, –, OM478845*, OM478967*; Amazonas, Brazil, *Giaretta 1513* (SPF), OM479414*, OM478748*, OM479304*, OM479112*, OM479205*, OM478868*, OM478990*; ***Asplundia*** **sp. nov. 1**, French Guiana, *Leal 460* (SPF), OM479335*, OM478660*, OM479235*, OM479024*, OM479138*, OM478782*, OM478902*; ***Asplundia*** **sp. nov. 2**, Chocó, Colombia, *Canal 480* (JBB), OM479353*, OM478678*, OM479248*, OM479042*, OM479153*, OM478800*, OM478920*; Chocó, Colombia, *Canal 627* (JBB), OM479331*, OM478656*, OM479231*, OM479020*, OM479135*, OM478778*, OM478898*; ***Asplundia*** **indet. 1**, Missouri Botanical Garden (cultivated), origin Napo, Ecuador, *MacDougal 4772* (MO, live collection Acc. No.: 1993-0615), OM479316*, OM478640*, OM479219*, OM479004*, OM479124*, OM478762*, OM478882*; ***Asplundia*** **indet. 2,** Chocó, Colombia, *Canal 427* (JBB), OM479315*, OM478638*, OM479217*, OM479002*, OM479122*, OM478760*, OM478880*; ***Asplundia*** **indet. 3**, Chocó, Colombia, *Canal 428* (JBB), OM479339*, OM478664*, OM479239*, OM479028*, OM479142*, OM478786*, OM478906*; ***Asplundia*** **indet. 4**, Chocó, Colombia, *Canal 500* (JBB), OM479340*, OM478665*, OM479240*, OM479029*, OM479143*, OM478787*, OM478907*; ***Asplundia*** **indet. 5**, Chocó, Colombia, *Canal 504* (JBB), OM479382*, OM478712*, OM479275*, OM479076*, OM479179*, –, OM478954*; ***Asplundia*** **indet. 6**, Chocó, Colombia, *Canal 537* (JBB), OM479347*, OM478672*, OM479244*, OM479036*, OM479149*, OM478794*, OM478914*; ***Asplundia*** **indet. 7**, Chocó, Colombia, *Canal 539* (JBB), OM479389*, OM478720*, –, OM479084*, –, OM478840*, OM478962*; ***Asplundia*** **indet. 8**, Chocó, Colombia, *Canal 541* (JBB), OM479351*, OM478676*, OM479247*, OM479040*, OM479152*, OM478798*, OM478918*; ***Asplundia*** **indet. 9**, Chocó, Colombia, *Canal 544* (JBB), OM479410*, OM478744*, OM479301*, OM479108*, –, OM478864*, OM478986*; ***Asplundia*** **indet. 10**, Chocó, Colombia, *Canal 606* (JBB), OM479371*, OM478701*, OM479267*, OM479065*, OM479170*, OM478822*, OM478943*; ***Asplundia*** **indet. 11**, Chocó, Colombia, *Canal 607* (JBB), OM479319*, OM478643*, OM479222*, OM479007*, –, OM478765*, OM478885*; ***Asplundia*** **indet. 12**, Chocó, Colombia (CH), *Canal 625* (JBB), OM479341*, OM478666*, OM479241*, OM479030*, –, OM478788*, OM478908*; ***Carludovica drudei*** Mast., Missouri Botanical Garden (cultivated), origin Tabasco, Mexico, *Hammel 15527* (MO, live collection Acc. No.: 1989-1189), OM479337*, OM478662*, OM479237*, OM479026*, OM479140*, OM478784*, OM478904*; ***Carludovica palmata*** Ruiz & Pav., Missouri Botanical Garden (cultivated), origin Antioquia, Colombia, *Hammel 15418* (MO, live collection Acc. No.: 1990-3372), OM479374*, OM478704*, OM479270*, OM479068*, OM479173*, OM478825*, OM478946*; ***Carludovica rotundifolia*** Schaedtler, Missouri Botanical Garden (cultivated), origin Puntarenas, Costa Rica, *Hammel 15205* (MO, live collection Acc. No.: 1989-1191), OM479343*, OM478668*, OM479243*, OM479032*, OM479145*, OM478790*, OM478910*; ***Carludovica sulcata*** Hammel, Missouri Botanical Garden (cultivated), origin Heredia, Costa Rica, *Hammel 16084* (MO, live collection Acc. No.: 1995-1914), OM479338*, OM478663*, OM479238*, OM479027*, OM479141*, OM478785*, OM478905*; ***Chorigyne cylindrica*** R.Erikss., Missouri Botanical Garden (cultivated), origin Colón, Panama, *Hammel 14493* (MO, live collection Acc. No.: 1989-1186), OM479352*, OM478677*, –, OM479041*, –, OM478799*, OM478919*; ***Chorigyne pendula*** (Hammel) R.Erikss., Missouri Botanical Garden (cultivated), origin Heredia, Costa Rica, *Hammel 14116* (MO, live collection Acc. No.: 1995-1915), –, OM478690*, KP083119[2], OM479054*, OM479257*, OM478811*, OM478932*; ***Cyclanthus bipartitus*** Poit. ex A.Rich., Chocó, Colombia, *Canal 590* (JBB), OM479398*, OM478731*, OM479291*, OM479095*, OM479190*, OM478851*, OM478973*; Nariño, Colombia, *Canal 667* (JBB), OM479400*, OM478733*, –, OM479097*, OM479192*, OM478853*, OM478975*; Missouri Botanical Garden (cultivated), origin Colón, Panama, *Hammel 14567* (MO, live collection Acc. No.: 1989-1176), OM479401*, OM478734*, OM479293*, OM479098*, OM479193*, OM478854*, OM478976*; French Guiana, *Leal 437* (SPF), OM479399*, OM478732*, OM479292*, OM479096*, OM479191*, OM478852*, OM478974*; ***Dianthoveus cremnophilus*** Hammel & G.J.Wilder, Missouri Botanical Garden (cultivated), origin Pichincha, Ecuador, *Hammel 15820* (MO, live collection Acc. No.: 1990-1888), OM479422*, OM478756*, OM479311*, OM479120*, OM479213*, OM478876*, OM478998*; ***Dicranopygium goudotii*** Harling, Nariño, Colombia, *Canal 637* (JBB), OM479421*, OM478755*, –, OM479119*, OM479212*, OM478875*, OM478997*; ***Dicranopygium lugonis*** Harling, Sucumbios, Ecuador, *Luteyn 9091* (NY), OM479330*, OM478654*, –, OM479018*, –, OM478776*, OM478896*; ***Dicranopygium pygmaeum*** (Gleason) Harling, French Guiana, *Gonzalez 4102* (CAY, SPF), OM479408*, OM478742*, OM479299*, OM479106*, OM479200*, OM478862*, OM478984*; ***Dicranopygium stenophyllum*** Harling, Ecuador, *Palacios 10171* (NY), OM479381*, OM478711*, –, OM479075*, –, OM478832*, OM478953*; ***Dicranopygium*** aff. ***umbrophilum*** Hammel, Nariño, Colombia, *Canal 643* (JBB), OM479419*, OM478753*, OM479309*, OM479117*, OM479210*, OM478873*, OM478995*; ***Dicranopygium wallisii*** (Regel) Harling, Missouri Botanical Garden (cultivated), origin Panamá, Panama, *Hammel 13545* (MO, live collection Acc. No.: 1991-0006), OM479372*, OM478702*, OM479268*, OM479066*, OM479171*, OM478823*, OM478944*; ***Dicranopygium*** **indet. 1**, Missouri Botanical Garden (cultivated), origin Heredia, Costa Rica, *MacDougal 6123* (MO, live collection Acc. No.: 2002-0938), –, OM478684*, OM479253*, OM479048*, OM479158*, OM478805*, OM478926*; ***Dicranopygium*** **indet. 2**, Missouri Botanical Garden (cultivated), origin Heredia, Costa Rica, *MacDougal 6090* (MO, live collection Acc. No.: 2002-0926), –, OM478683*, OM479252*,

Appendix 1. Continued.

OM479047*, –, OM478804*, OM478925*; ***Dicranopygium*** **indet. 3**, Chocó, Colombia, *Canal 502* (JBB), OM479418*, OM478752*, OM479308*, OM479116*, OM479209*, OM478872*, OM478994*; ***Dicranopygium*** **indet. 4**, Chocó, Colombia, *Canal 505* (JBB), OM479396*, OM478729*, OM479289*, OM479093*, –, OM478849*, OM478971*; ***Dicranopygium*** **indet. 5**, Chocó, Colombia, *Canal 528* (JBB), OM479383*, OM478714*, OM479277*, OM479078*, OM479181*, OM478834*, OM478956*; ***Dicranopygium*** **indet. 6**, Chocó, Colombia, *Canal 601* (JBB), OM479379*, OM478709*, OM479274*, OM479073*, OM479178*, OM478830*, OM478951*; ***Dicranopygium*** **indet. 7**, Chocó, Colombia, *Canal 602* (JBB), OM479378*, OM478708*, OM479273*, OM479072*, OM479177*, OM478829*, OM478950*; ***Dicranopygium*** **indet. 8**, Chocó, Colombia, *Canal 640* (JBB), OM479420*, OM478754*, OM479310*, OM479118*, OM479211*, OM478874*, OM478996*; ***Evodianthus funifer*** (Poit.) Lindm., Amazonas, Brazil, *Giaretta 1512* (SPF), OM479376*, OM478706*, –, OM479070*, OM479175*, OM478827*, OM478948*; Chocó, Colombia, *Canal 423* (JBB), OM479325*, OM478649*, OM479227*, OM479013*, OM479130*, OM478771*, OM478891*; French Guiana, *Leal 433* (SPF), OM479375*, OM478705*, OM479271*, OM479069*, OM479174*, OM478826*, OM478947*; French Guiana, *Leal 436* (SPF), OM479377*, OM478707*, OM479272*, OM479071*, OM479176*, OM478828*, OM478949*; ***Ludovia bierhorstii*** G.J.Wilder, Chocó, Colombia, *Canal 538* (JBB), OM479323*, OM478647*, –, OM479011*, –, OM478769*, OM478889*; ***Ludovia integrifolia*** (Woodson) Harling, Chocó, Colombia, *Canal 425* (JBB), OM479333*, OM478658*, OM479233*, OM479022*, OM479137*, OM478780*, OM478900*; Missouri Botanical Garden (cultivated), origin unknown, *Garwood 7* (MO, live collection Acc. No.: 1989-6313), OM479342*, OM478667*, OM479242*, OM479031*, OM479144*, OM478789*, OM478909*; ***Ludovia lancifolia*** Brongn., Roraima, Brazil, *Forzza 7106* (RB), OM479346*, OM478671*, –, OM479035*, OM479148*, OM478793*, OM478913*; French Guiana, *Leal 430* (SPF), OM479411*, OM478745*, –, OM479109*, OM479202*, OM478865*, OM478987*; French Guiana, *Leal 450* (SPF), OM479344*, OM478669*, –, OM479033*, OM479146*, OM478791*, OM478911*; Missouri Botanical Garden (cultivated), origin Colón, Panama, *Hammel 13404* (MO, live collection Acc. No.: 1983-1702), OM479345*, OM478670*, –, OM479034*, OM479147*, OM478792*, OM478912*; ***Schultesiophytum chorianthum*** Harling, Amazonas, Colombia, *Canal 717* (JBB), OM479412*, OM478746*, OM479302*, OM479110*, OM479203*, OM478866*, OM478988*; ***Sphaeradenia acutitepala*** Harling, Chocó, Colombia, *Canal 424* (JBB), OM479326*, OM478650*, OM479228*, OM479014*, OM479131*, OM478772*, OM478892*; Chocó, Colombia, *Canal 426* (JBB), OM479423*, OM478757*, OM479312*, OM479121*, OM479214*, OM478877*, OM478999*; ***Sphaeradenia*** aff. ***buenaventurae*** Harling, Chocó, Colombia, *Canal 608* (JBB), OM479359*, OM478686*, –, OM479050*, –, OM478807*, OM478928*; ***Sphaeradenia crocea*** Harling, Chocó, Colombia, *Canal 554* (JBB), OM479415*, OM478749*, OM479305*, OM479113*, OM479206*, OM478869*, OM478991*; ***Sphaeradenia*** aff. ***distans*** R.Erikss., Nariño, Colombia, *Canal 668* (JBB), OM479369*, OM478699*, OM479265*, OM479063*, –, OM478820*, OM478941*; ***Sphaeradenia duidae*** Harling, Amazonas, Brazil, *Forzza 7136* (RB), OM479368*, OM478698*, OM479264*, OM479062*, OM479168*, OM478819*, OM478940*; ***Sphaeradenia*** aff. ***hamata*** Harling, Nariño, Colombia, *Canal 642* (JBB), OM479417*, OM478751*, OM479307*, OM479115*, OM479208*, OM478871*, OM478993*; ***Sphaeradenia laucheana*** (Sander ex Mast.) Harling, Cundinamarca, Colombia, *Canal 707* (JBB), OM479370*, OM478700*, OM479266*, OM479064*, OM479169*, OM478821*, OM478942*; ***Sphaeradenia pallida*** R.Erikss., Nariño, Colombia, *Canal 655* (JBB), OM479390*, OM478721*, OM479283*, OM479085*, OM479185*, OM478841*, OM478963*; ***Sphaeradenia pterostigma*** Harling, Nariño, Colombia, *Canal 666* (JBB), OM479403*, OM478736*, OM479294*, OM479100*, OM479195*, OM478856*, OM478978*; ***Sphaeradenia*** aff. ***stylosa*** Harling, Nariño, Colombia, *Canal 662* (JBB), OM479362*, OM478689*, OM479256*, OM479053*, OM479161*, OM478810*, OM478931*; ***Sphaeradenia woodsonii*** Harling, Chocó, Colombia, *Canal 593* (JBB), OM479373*, OM478703*, OM479269*, OM479067*, OM479172*, OM478824*, OM478945*; ***Sphaeradenia*** **indet. 1**, Missouri Botanical Garden (cultivated), origin unknown, *Croat s.n.* (MO, live collection Acc. No.: 1982-0503), OM479358*, OM478685*, –, OM479049*, –, OM478806*, OM478927*; ***Sphaeradenia*** **indet. 2**, Chocó, Colombia, *Canal 453* (JBB), OM479360*, OM478687*, OM479254*, OM479051*, OM479159*, OM478808*, OM478929*; ***Sphaeradenia*** **indet. 3**, Chocó, Colombia, *Canal 529* (JBB), OM479357*, OM478682*, OM479251*, OM479046*, OM479157*, OM478803*, OM478924*; ***Sphaeradenia*** **indet. 4**, Chocó, Colombia, *Canal 531* (JBB), OM479416*, OM478750*, OM479306*, OM479114*, OM479207*, OM478870*, OM478992*; ***Sphaeradenia*** **indet. 5**, Chocó, Colombia, *Canal 534* (JBB), OM479356*, OM478681*, OM479250*, OM479045*, OM479156*, OM478802*, OM478923*; ***Sphaeradenia*** **indet. 6**, Chocó, Colombia, *Canal 540* (JBB), OM479348*, OM478673*, –, OM479037*, –, OM478795*, OM478915*; ***Sphaeradenia*** **indet. 7**, Chocó, Colombia, *Canal 542* (JBB), OM479361*, OM478688*, OM479255*, OM479052*, OM479160*, OM478809*, OM478930*; ***Sphaeradenia*** **indet. 8**, Nariño, Colombia, *Canal 636* (JBB), OM479404*, OM478738*, OM479296*, OM479102*, OM479197*, OM478858*, OM478980*; ***Sphaeradenia*** **indet. 9**, Nariño, Colombia, *Canal 639* (JBB), –, OM478737*, OM479295*, OM479101*, OM479196*, OM478857*, OM478979*; ***Sphaeradenia*** **indet. 10**, Nariño, Colombia, *Canal 664* (JBB), OM479349*, OM478674*, OM479245*, OM479038*, OM479150*, OM478796*, OM478916*; ***Stelestylis stylaris*** (Gleason) Harling, Roraima, Brazil, *Forzza 8149* (RB), OM479407*, OM478741*, –, OM479105*, –, OM478861*, OM478983*; ***Stelestylis surinamensis*** Harling, French Guiana, *Leal 461* (SPF), OM479363*, OM478691*, OM479258*, OM479055*, OM479162*, OM478812*, OM478933*; ***Thoracocarpus bissectus*** (Vell.) Harling, São Paulo, Brazil, *Leal 464* (SPF), OM479413*, OM478747*, OM479303*, OM479111*, OM479204*, OM478867*, OM478989*; Chocó, Colombia, *Canal 530* (JBB), OM479402*, OM478735*, –, OM479099*, OM479194*, OM478855*, OM478977*; French Guiana, *Leal 441* (SPF), OM479366*, OM478696*, OM479262*, OM479060*, OM479166*, OM478817*, OM478938*.