AN ANALYSIS OF THE SECTIONAL CLASSIFICATION OF *ANTHURIUM* (ARACEAE): COMPARING INFRAGENERIC GROUPINGS AND THEIR DIAGNOSTIC MORPHOLOGY WITH A MOLECULAR PHYLOGENY OF THE GENUS[1]

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Abstract

This study presents an evaluation of the currently accepted sectional classification of the genus *Anthurium* Schott (Araceae) in light of a recently published molecular phylogeny for the group. In general, disagreements between these two occur because many diagnostic morphological characters used in the sectional classification turned out to be highly homoplasious within *Anthurium*, with multiple independent gains or losses of seemingly similar morphologies in distantly related clades. A new sectional classification of *Anthurium* that more accurately represents species relationships and the evolutionary history of the genus is much needed, and here we propose the first steps toward it. Results from this study suggest that out of the 18 sections and two series recognized in *Anthurium*, only seven of these groups are monophyletic (i.e., sections *Andiphilum* (Schott) Croat, *Calomystrium* (Schott) Engl., *Dactylophyllium* (Schott) Engl., *Leptanthurium* (Schott) Engl., *Polyphyllium* Engl., *Tetraspermium* (Schott) Engl., and the newly recognized section *Multinervia* (Croat) Carlsen & Croat, previously a series within section *Pachyneurium* (Schott) Engl.). All other sections are either not monophyletic or their monophyly could not be accurately tested. A complete revision of the sectional classification of *Anthurium* will require a more comprehensive taxon sampling and a better supported molecular phylogeny.

Key words: *Anthurium*, Araceae, lectotypification, monophyly tests, Neotropics, sectional classification.

Anthurium Schott is a monophyletic (Carlsen, 2011; Carlsen & Croat, 2013) and strictly Neotropical genus of Araceae ranging from southern Mexico into Central America and the West Indies, to southern Brazil, northern Argentina, and Paraguay. It includes approximately 950 largely well-differentiated species (Mayo et al., 1997; Govaerts & Frodin, 2002; Govaerts et al., 2015; eMonocot Team CATE Araceae, 2015; Boyce & Croat, 2018), with many more still being discovered (Boyce & Croat, 2018). *Anthurium* is placed in the subfamily Pothoideae, one of the earliest divergent lineages in Araceae, and is sister to the Old World genus *Pothos* L. (ca. 58 species; Boyce & Croat, 2018) from Southeast Asia, Australasia, and Madagascar (French et al., 1995; Barabé et al., 2002; Rothwell et al., 2004; Tam et al., 2004; Cabrera et al., 2008; Carlsen, 2011; Cusimano et al., 2011, 2012; Nauheimer et al., 2012; Carlsen & Croat, 2013; Chartier et al., 2013; Henríquez et al., 2014). *Anthurium* species are distinguished by their terrestrial, rupicolous, epiphytic, or climbing habit, sympodial growth, spirally arranged leaves, petioles variously shaped in cross-section but never completely flattened, a geniculum at the apex of the petiole, reticulate minor venation, collective veins along the leaf margins, uniform spadix with open spathe, 4-merous bisexual flowers with tepals, and seeds with copious endosperm (Grayum, 1990; Mayo et al., 1997).

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Throughout the years, taxonomists have proposed several groupings within *Anthurium* in attempts to partition the extraordinary morphological diversity of this genus. The first infrageneric classification of *Anthurium* was that of Schott (1860) in which he grouped the 183 known species of *Anthurium* into 28 "greges" (Table 1). This arrangement was largely based on a combination of vegetative and floral characters, such as leaf venation, leaf shape, spathe color and length, and internode length. In the most recent revision of the genus (Engler, 1905), the 486 then-known species of *Anthurium* were divided into 18 sections (Table 1), again mainly using leaf shape characters as well as number of seeds and spadix form. Although most of Schott's and Engler's sections do seem to contain a core of related species, placement of the remaining species included in them seems subjective. The currently accepted sectional classification of *Anthurium* recognizes 18 sections and two series, in a slightly modified version of Engler's system (Croat & Sheffer, 1983; with amendments by Croat, 1991; Croat et al., 2005; Croat & Carlsen, 2013; Croat & Hormell, 2017) (Table 1). In general, these sections were characterized by a combination of characters, mainly differences in leaf shape, vernation, punctation, and venation; habit; roots; cataphylls; and number or appearance of seeds. Only a few groups of species share a distinctive feature not found elsewhere in the genus (e.g., cataphylls persisting intact along the entire length of the stem, and not decomposing, in section *Calomystrium* (Schott) Engl.) and are apparently "natural" (Croat & Sheffer, 1983). Most groups have a more complicated combination of diagnostic characters and quite frequently appear to have overlapping limits. Moreover, it is unclear if groups recognized in these classifications truly reflect putative species relationships or if the diagnostic characteristics of such sections were simply used to facilitate group recognition, the groups serving to partition an otherwise unwieldy genus.

Phylogenetic relationships within *Anthurium* remained poorly understood and its classification untested until recently. The latest molecular phylogeny of the genus (Carlsen & Croat, 2013) is based on maximum parsimony, maximum likelihood, and Bayesian analysis of combined cpDNA and nDNA sequence data from 102 *Anthurium* species representing all but one of the recognized sections and series (Croat & Sheffer, 1983; Croat, 1991; Croat et al., 2005; Croat & Carlsen, 2013; Croat & Hormell, 2017). Within *Anthurium*, the analyses recovered 18 well-supported major clades with a combination of bootstrap values (both for parsimony and likelihood) higher than 70% and posterior probabilities greater than 0.9 (Carlsen & Croat, 2013). However, only a few of these clades appear to be congruent with the sectional groupings in the genus, and several infrageneric taxa seem to be non-monophyletic. Recently, efforts to accurately represent the newly proposed evolutionary relationships among *Anthurium* species have started by redefining some sectional groups to match the molecular phylogeny, for example, section *Dactylophyllium* (Schott) Engl., emend. Croat & Carlsen (Croat & Carlsen, 2013) and section *Andiphilum* (Schott) Croat (Croat & Hormell, 2017). Although deeper relationships among clades were largely unresolved in Carlsen and Croat (2013), that does not preclude the recognition of several monophyletic species groups within *Anthurium*.

It is evident that the currently accepted sectional classification of *Anthurium* and the morphological characters on which it was based (Table 1) need to be reevaluated against the new molecular phylogenetic framework of Carlsen and Croat (2013). Therefore, the main goal of this study is to use topology tests to evaluate support for the monophyly of *Anthurium* sections or series by statistically comparing the best scoring trees (in parsimony and likelihood analyses) with alternative phylogenetic hypotheses that constrain each recognized grouping to be monophyletic. In addition, morphological features used to characterize sections are reconstructed along the phylogeny to determine their usefulness in separating groups within *Anthurium*.

Materials and Methods

MOLECULAR PHYLOGENETIC FRAMEWORK

This study is based on an analysis of combined DNA sequence data from Carlsen and Croat (2013), which included four gene loci, the chloroplast *trnG* intron (Shaw et al., 2005), and *trnH-psbA* (Hamilton, 1999) and *trnC-ycf6* (Shaw et al., 2005) intergenic spacers, and the nuclear first intron of the chalcone synthase (*CHS*) gene (Carlsen & Croat, 2013). A total of 102 *Anthurium* species were included in all analyses, comprising at least one and up to 13 representatives of each of the 18 sections and two series proposed by previous authors (Croat & Sheffer, 1983; Croat, 1991; Croat et al., 2005; Croat & Carlsen, 2013; Croat & Hormell, 2017), except for the monotypic section *Gymnopodium* Engl. endemic to Cuba (Table 1). Details of taxon sampling, GenBank accession numbers, laboratory protocols, data alignment, outgroup selection, and phylogenetic analyses were discussed by Carlsen and Croat (2013).

Unconstrained tree topologies were obtained from the analyses of combined cpDNA-nDNA dataset under maximum parsimony and maximum likelihood by Carlsen and Croat (2013). The unconstrained parsimony topologies used in this study encompass all of the most parsimonious trees obtained from parsimony ratchet analyses (Nixon, 1999; Sikes & Lewis, 2001) by Carlsen and Croat (2013). The unconstrained likelihood topology (fig. 2 of Carlsen & Croat, 2013) is the best scoring maximum likelihood tree from analyses performed

Table 1. A comparison of the sectional classification systems in *Anthurium* Schott to date. Species diversity and main diagnostic features are included only for each of the previously recognized groups before this study (in bold italics). The circumscriptions of groups vary somewhat among authors. Groups confirmed as monophyletic in this study are noted with an asterisk (*), and an updated set of diagnostic features is given for them. Authorship for names not previously listed are according to the author column, unless otherwise noted.

Schott (1860)	Engler (1879, 1898, 1905)	Croat & Sheffer (1983)	Accepted sections/ series (before this study)	No. of species (estimated)	Main morphological characters
Andiphilum	p.p. Calomystrium p.p. Pachyneurium		***Andiphilum***[1]*	25	petioles D-shaped, leaves ovate-cordate, berries orange with pasty mesocarp, seeds large, greenish white
Belolonchium	Belolonchium	Belolonchium	***Belolonchium***	220	cataphyll fibers dense, blades cordate, thick, spathe hooded, spadix pendent, plants growing at high elevations
Calomystrium	Calomystrium	Calomystrium	***Calomystrium****	184	cataphylls persisting intact, blades cordate with pale lineations and dark (not glandular) punctations, spathe and spadix thick, colorful
Cardiolonchium	Cardiolonchium	Cardiolonchium	***Cardiolonchium***	175	internodes short, blades velvety, drying greenish often with pale venation, petiole ribbed
	Chamaerepium	Chamaerepium	***Chamaerepium***	1	habit repent, spadix short, ellipsoid
Dactylophyllium	Schizoplacium series Dactylophyllium	Dactylophyllium	***Dactylophyllium***[2]*	24	leaves palmately divided with 3 or more segments free to the base or united at the base
Oxycarpium	Oxycarpium	Oxycarpium	***Decurrentia***[3] p.p. Pachyneurium	45	internodes short, leaf blades elongated, epunctate, peduncle ridged
	Digitinervium	Digitinervium	***Digitinervium***	41	blades glandular-punctate, parallel primary lateral veins numerous, collective veins 2 or more pairs
	Gymnopodium	Gymnopodium	***Gymnopodium***	1	stems scandent, blades cordate, berries up to 4 seeds

Table 1. Continued.

Schott (1860)	Engler (1879, 1898, 1905)	Croat & Sheffer (1983)	Accepted sections/ series (before this study)	No. of species (estimated)	Main morphological characters
Leptanthurium	Leptanthurium	Leptanthurium	***Leptanthurium****	1	roots with velamen, leaves long and slender, primary lateral veins weakly differentiated, spadix pendent, long and thin, flowers relatively large, few per spiral, berries reddish
Pachyneurium	Pachyneurium	Pachyneurium	***Pachyneurium* series *Multinervia***[4]*	16	leaf vernation involute, habit "bird's nest," blades oblong to elliptic, drying green to yellow-green, primary lateral veins numerous, conspicuous, closely spaced
Pachyneurium	Pachyneurium	Pachyneurium	***Pachyneurium* series *Pachyneurium***[4]	120	leaf vernation involute, habit "bird's nest," primary lateral veins thick, collective vein sometimes absent
	Polyneurium	Polyneurium	***Polyneurium***	149	blades thin with many close primary lateral veins
	Polyphyllium	Polyphyllium	***Polyphyllium****	2	adventitious roots along internodes, stems wiry, 1-ribbed cataphylls absent, seeds black
Porphyrochitonium	Porphyrochitonium	Porphyrochitonium	***Porphyrochitonium***	215	internodes short, roots dense, cataphylls fibrous persistent, blades glandular-punctate
Semaeophyllium	Semaeophyllium	Semaeophyllium	***Semaeophyllium***	23	leaves deeply 3-lobed
Tetraspermium	Tetraspermium	Tetraspermium	***Tetraspermium****	35	stems scandent, thin, internodes long, blades glandular-punctate, seeds 4 per berry

Table 1. Continued.

Schott (1860)	Engler (1879, 1898, 1905)	Croat & Sheffer (1983)	Accepted sections/ series (before this study)	No. of species (estimated)	Main morphological characters
	Urospadix	Urospadix	***Urospadix***	96	primary veins close, numerous, internodes short
Xialophyllium	Xialophyllium	Xialophyllium	***Xialophyllium***	108	internodes long, blades thin, longer than broad
Schizoplacium	Schizoplacium series Euschizoplacium	Schizoplacium	= Dactylophyllium[2]		
Episeiostenium	Episeiostenium	Episeiostenium[5]			
Acamptophyllium	= Urospadix				
Amphineurium	p.p. Calomystrium p.p. Polyneurium				
Chondrophyllium	p.p. Pachyneurium p.p. Urospadix				
Cosmetophyton	p.p. Cardiolonchium				
Dorylonchium	p.p. Belolonchium				
Erythropodium	= Urospadix				
Eucardium	= Pachyneurium				
Macrophyllium	p.p. Pachyneurium				
Neurolysium	= Cardiolonchium				
Oophyllium	= Urospadix				
Parabasium	= Urospadix				
Platylonchium	= Urospadix				
Pleonophlebium	p.p. Cardiolonchium p.p. Belolonchium				
Sobaronium	p.p. Calomystrium p.p. Belolonchium p.p. Pachyneurium				

[1] Section *Andiphilum* was recently resurrected to include all species belonging to Clade 16 in Figure 1 (Croat & Hormell, 2017).

[2] Section *Dactylophyllium* was recently redefined to include all species belonging to Clade 3 in Figure 1 (Croat & Carlsen, 2013).

[3] The name section *Oxycarpium* (Schott) Engl. was synonymized with section *Pachyneurium* due to the transfer of the type species, *Anthurium oxycarpium* Poeppig & Endl., to that section by Croat (1991), and a new sectional name, section *Decurrentia*, was proposed to accommodate the remaining species in section *Oxycarpium* (Croat et al., 2005).

[4] Both series within section *Pachyneurium* were newly proposed by Croat (1991).

[5] Section *Episeiostenium* (Schott) Engl. was mentioned in Croat and Sheffer's classification system but specifically not discussed or further recognized because it was "the least likely to be a valid [section]" (Croat & Sheffer, 1983: 105).

using RAxML v. 7.2.7 (Stamatakis, 2006; Stamatakis et al., 2008) by Carlsen and Croat (2013).

HYPOTHESIS TESTING

Fifteen constrained trees were constructed in MacClade v. 4.08 OS X (Maddison & Maddison, 2000), each corresponding to one of the accepted sections or series of *Anthurium* (Table 1) being monophyletic, except for the unsampled section *Gymnopodium*, the monotypic sections *Chamaerepium* (Schott) Engl. and *Leptanthurium* (Schott) Engl., which clearly could not be tested for monophyly, and sections *Andiphilum* (Croat & Hormell, 2017) and *Dactylophyllium* (Croat & Carlsen, 2013), which were recently amended to be monophyletic based on the molecular phylogeny (Table 2). The Templeton test (Templeton, 1983) was used for hypothesis testing under maximum parsimony. Individual constrained trees were loaded in PAUP* version 4.0b10 (Swofford, 2002) and evaluated under parsimony in order to obtain the constrained tree length using heuristic search, 10 random-addition sequence replicates, tree bisection and reconnection (TBR) branch swapping, and MULTREES=yes. Tree length differences between each constrained tree and the unconstrained parsimony topologies were compared statistically using the Templeton test as implemented in PAUP*. If the constrained parsimony tree was significantly longer ($P_{TT} \leq 0.05$)

Table 2. Hypothesis testing of topological differences among parsimony and likelihood phylogenetic hypothesis using the Templeton and Shimodaira-Hasegawa tests. Constraint trees test the monophyly of the previously recognized sections of *Anthurium* Schott (Araceae) from Table 1. P_{TT} is the P value for the Templeton test. P_{SH} is the P value for the Shimodaira-Hasegawa test. Statistically worse trees as compared to the best tree are marked with an asterisk (*) and P values < 0.05. Monotypic sections *Leptanthurium*, *Chamaerepium*, and *Gymnopodium* (not sampled) were not tested; neither were sections *Andiphilum* and *Dactylophyllium* (see methodology for more information).

		Templeton test		Shimodaira-Hasegawa test		
Phylogenetic hypothesis of monophyletic section		Most parsimonious trees from parsimony ratchet analysis (tree length: 903)		Maximum likelihood tree (–ln likelihood: 9705.96007)		
Sections	No. spp. sampled	Constrained tree length	P_{TT} value	Likelihood difference from best tree	P_{SH} value	Overall result
Belolonchium	6	967	< 0.0001*	341.56097	0*	non-monophyletic
Calomystrium	8	903	1	0.08781	1	monophyletic
Cardiolonchium	7	929	0.0002*	147.9498	0.001*	non-monophyletic
Decurrentia	5	974	< 0.0001*	380.25238	0*	non-monophyletic
Digitinervium	4	970	0.0497*	130.84055	0.049*	non-monophyletic
Pachyneurium	13	926	0.0002*	125.11551	0.003*	non-monophyletic
series *Multinervia*	4	903	1	5.59836	0.992	monophyletic
series *Pachyneurium*	9	925	0.0012*	111.50427	0.006*	non-monophyletic
Polyneurium	5	917	0.0164*	82.13048	0.004*	non-monophyletic
Polyphyllium	2	904	0.8405	6.33472	0.913	monophyletic
Porphyrochitonium	7	919	0.0136*	108.48379	0.046*	non-monophyletic
Semaeophyllium	3	921	0.001*	87.30137	0.004*	non-monophyletic
Tetraspermium	5	911	0.0881	47.53016	0.421	monophyletic
Urospadix	10	919	0.026*	81.26785	0.146	inconclusive
Xialophyllium	2	904	0.8273	17.08595	0.889	monophyletic

than the unconstrained parsimony topologies, then the monophyly of the section was rejected. The Shimodaira-Hasegawa test (Shimodaira & Hasegawa, 1999; Goldman et al., 2000) was used for topology testing under maximum likelihood settings. The most likely topology under the constraint was inferred using RAxML and the GTRGAMMA model of evolution. Both the unconstrained likelihood topology and the most likely topologies inferred under the constraints for each section or series of *Anthurium* were used as inputs in PAUP*, and a Shimodaira-Hasegawa test was performed using 1000 bootstrap replicates and the resampling estimated log likelihoods (RELL) option. As before, if the constrained likelihood tree was significantly less likely ($P_{SH} \leq 0.05$) than the unconstrained likelihood topology, then the monophyly of the section was rejected.

MORPHOLOGICAL CHARACTERS

Twenty-two morphological characters used to identify sections or series within *Anthurium* were scored for all species in the dataset (Supplementary Appendix S1) and their evolution was reconstructed along the unconstrained likelihood topology under parsimony criterion in MacClade (Supplementary Appendix S2). They represent all the characters used to identify groups in the sectional classification of *Anthurium* (Table 1). These characters include 20 vegetative characters (six related to stem morphology and 14 to leaf characteristics) and two reproductive characters (one flowering and one fruiting character). Scoring of morphological characters was based on a combination of species descriptions available in the literature (Croat, 1983, 1986; Croat & Rodríguez, 1995; Croat & Mora, 2004; Croat & Acebey, 2005; Croat et al., 2005; Coelho et al., 2009) and study of herbarium specimens and living collections (*Anthurium* LUCID key; Croat, unpublished data). A number of the characters are quantitative and the limits of the states recognized are arbitrary. Every character was traced individually on the phylogeny without resolving equivocal tracings. For every character, the number of steps, consistency index (CI), and retention index (RI) were also calculated (Farris, 1989) (Table 3).

Results

The most parsimonious unconstrained trees used in the Templeton tests were 903 steps long (CI = 0.734, RI = 0.819), whereas alternative topologies that constrained each section or series within *Anthurium* as

Table 3. Parsimony reconstruction of morphological characters associated with the sectional classification of *Anthurium* Schott (in Table 1). Characters and their states are divided as per original descriptions of each section. Consistency and retention indices according to Farris (1989).

No.	Character	Character states	No. of steps	Consistency index (CI)	Retention index (RI)
1	Habit	caespitose (0), scandent (1), repent (2), "bird's nest" (3)	23	0.13	0.39
2	Stem thickness	thick $>$ 1 cm (0), thin $<$ 1 cm (1)	4	0.25	0.63
3	Root position	in nodes (0), along internodes (1)	1	1	1
4	Internode length	short $<$ 3 cm (0), long $>$ 3 cm (1)	14	0.07	0.35
5	One-ribbed cataphyll presence	present (0), absent (1)	1	1	1
6	Cataphyll texture	persistent fibers (0), persistent intact (1), deciduous (2), not applicable (3)	23	0.13	0.33
7	Petiole length (compared to lamina length)	shorter (0), shorter-equal (1), equal-longer (3), longer (4)	21	0.14	0.22
8	Petiole shape	not ribbed (0), ribbed (1)	8	0.13	0
9	Leaf vernation	supervolute (0), involute (1)	2	0.5	0.92
10	Leaf shape 1, lobes	entire (0), lobed to three or more lobes (1)	6	0.17	0.67
11	Leaf shape 2, overall shape	lanceolate-elliptic (0), linear (1), cordate (2), trilobed (3), palmate (4)	35	0.11	0.5
12	Leaf texture 1, velvety	not velvety (0), subvelvety (1), velvety (2)	17	0.12	0.06
13	Leaf texture 2, thickness	thin (0), medium-thin (1), medium (2), medium-thick (3), thick (4)	32	0.09	0.24
14	Palmate leaf shape 1, segments per leaf	not applicable (0), 3 segments (1), $>$ 3 segments (2)	7	0.29	0.64
15	Palmate leaf shape 2, union of segments	not applicable (0), segments united at base (1), segments free at base (2)	8	0.25	0.57
16	Punctation presence	no (0), yes (1)	2	0.5	0.94
17	Punctation position	not applicable (0), abaxial surface only (1), both surfaces (2)	8	0.25	0.65
18	Venation, collective veins	zero (0), one (1), two (2)	5	0.4	0.4
19	Venation, primaries same as interprimaries	no (0), yes (1)	10	0.1	0.59
20	Venation, primary lateral veins	few-sparse $<$ 5 (0), medium-sparse 5 to 10 (1), numerous-close $>$ 10 (2)	27	0.07	0.54
21	Spadix length	short 0–5 cm (0), short-medium 5–10 cm (1), medium-long 10–15 cm (2), long $>$ 15 cm (3)	48	0.06	0.36
22	Seed number per locule	one (0), two (1), up to three (2)	2	1	1

monophyletic ranged between 903 and 974 steps in length (Table 2). The topologies represented by the unconstrained parsimony trees closely matched the maximum likelihood and Bayesian consensus trees of Carlsen and Croat (2013) except for some minor rearrangements on deeper-node relationships along the largely unresolved backbone of the trees. The unconstrained likelihood topology used in hypothesis testing (Carlsen & Croat, 2013) has a –ln likelihood of 9705.96007 (Table 2) and the difference in likelihood scores between unconstrained and constrained topologies ranged from almost zero to +380.25238 (Table 2).

Results of the Templeton tests comparing the parsimony unconstrained trees and alternative constrained topologies showed that 10 of the 15 (67%) sections/series of *Anthurium* included in the analyses are not monophyletic ($P_{TT} < 0.05$) (Table 2). The Shimodaira-Hasegawa tests among unconstrained and alternative constrained likelihood topologies also suggested that the majority of the sections/series of *Anthurium*, nine out of 15 (60%), are not monophyletic ($P_{SH} < 0.05$) (Table 2). The only discrepancy among parsimony-based and likelihood-based results of hypothesis testing was for section *Urospadix* Engl., for which monophyly could not be rejected by the Shimodaira-Hasegawa test ($P_{SH} = 0.146$) but could be rejected when the Templeton test was used ($P_{TT} = 0.026$) (Table 2).

Reconstructions of character evolution for each of the 22 morphological characters examined here showed widespread patterns of homoplasy, and therefore most characters did not track the molecular phylogeny well (Table 3; Supplementary Appendix S2). The CI and RI for each character were in general very low, averaging 0.26 for CI and 0.50 for RI for all characters studied (Table 3). Three quarters of the characters showed high levels of homoplasy, with CI as low as 0.06 (character 21, spadix length) to 0.29 (character 14, palmate leaf, number of lobes per leaf). The RI are also significantly low for many characters analyzed (50% of the total), with values ranging from 0 (character 8, petiole shape) to 0.54 (character 20, venation, number of primary lateral veins), indicating that most morphological characters used in the sectional classification of *Anthurium* are both incongruent with the molecular phylogeny and not good synapomorphies for the clades recovered (Table 3).

Reconstructions of only five of the 22 characters analyzed show very high (i.e., character 3, root position; 5, presence of 1-ribbed cataphyll; and 22, number of seeds per locule) or moderate (i.e., character 9, leaf vernation; and 16, punctation presence) congruence with the clades recovered in the molecular phylogeny. These five characters are the least homoplasious of those analyzed (i.e., have high CI and RI values), but they comprise only ca. 23% of the characters currently used to separate groups in the sectional classification of *Anthurium* (Table 3; Supplementary Appendix S2).

DISCUSSION

MORPHOLOGY AND ITS USEFULNESS IN *ANTHURIUM* SECTIONAL CLASSIFICATION

In general, reconstructions of the 22 morphological characters (Table 3; Supplementary Appendix S2) used to recognize sections and series within *Anthurium* showed high levels of homoplasy, and for the most part, do not correspond well with the strongly supported clades recovered in the molecular phylogeny of the genus (Carlsen & Croat, 2013). Not surprisingly, many sections and series based on these characters were identified as non-monophyletic according to topological hypothesis testing performed here (Table 2).

Vegetative characters

The most homoplasious morphological characters in *Anthurium* are related to leaf characteristics, such as petiole length and shape, and leaf texture, including thickness and velvety appearance (Table 3; Supplementary Appendix S2). They have not been used on their own to distinguish groups within *Anthurium*, but instead in combination with other homoplasious leaf characters (Table 1). For example, thin blades (character 13) with many close primary lateral veins (character 20) (Table 3) are two leaf characters that have been used to distinguish species in section *Polyneurium* Engl. (Table 1), a group for which monophyly was rejected ($P_{SH} = 0.004$, $P_{TT} = 0.0164$) (Table 2). Twelve of the 14 leaf-related characters ranked the most homoplasious among all characters studied (Table 3). Cusimano et al. (2011) also found that leaf characters used in the intrafamilial classification of Araceae as a whole were highly homoplasious. Only two leaf characters, leaf vernation (character 9; RI = 0.92) and the presence of punctations on the leaf blade (character 16; RI = 0.94) (Table 3), can be used to support monophyletic groups in *Anthurium*.

Homoplasious characters might imply repetitive adaptive shifts, but in most cases, it is very difficult to interpret the ecological significance of the morphologies being analyzed. Madison (1978) suggested that shape and venation of leaves were the most useful taxonomic characters for species identification in *Anthurium* but that they had no, or at least not a convincing, evolutionary or biological meaning. For instance, the strongly trilobed leaves found in section *Semaeophyllium* (Schott) Engl. (e.g., as in *A. trilobum* Hort. ex André) are unique to this group. However, intermediates between trilobed and cordate leaves are well known in species belonging to section *Belolonchium* (Schott) Engl. (e.g., *A. draconopterum* Sodiro and *A. effusilobum* Croat), as well as in *Semaeophyllium* itself (e.g., *A. sagittaria* Linden ex Schott, *A. signatum* K. Koch & L. Mathieu, and *A. subsignatum* Schott). Such cases may therefore imply that trilobed leaves are more likely to be a special case of plasticity of cordate leaf morphology rather than actually adaptive. Alternatively, some leaf morphologies may relate more to local ecological characteristics than to the evolutionary history of the genus. For example, the velvety appearance of leaves in *Anthurium* comes from convexly curved outer anticlinal epidermal cell walls, which have been postulated as an ecological adaptation to low-light environments (Vogelmann, 1993), as in *A. warocqueanum* T. Moore (Bone et al., 1985), to high moisture conditions (Brodersen & Vogelmann, 2007), or to both (Bone et al., 1985). This morphology has evolved at least nine times independently in *Anthurium* (Supplementary Appendix S2), probably associated with repetitive incursions into medium- to high-elevation cloud forests by several unrelated species. In general, leaf characteristics emphasized by taxonomists are both difficult to interpret ecologically and certainly do not correlate with the evolutionary history of the genus *Anthurium* as represented by the molecular phylogeny of Carlsen and Croat (2013).

Stem characteristics used to delimit sections in *Anthurium* are a combination of homoplasious and highly conserved characters. Root position along nodes or internodes (character 3) and presence or absence of 1-ribbed cataphylls (character 5) ranked the best in terms of synapomorphies (Table 3). Adventitious roots arising along the internodes and the absence of 1-ribbed cataphylls are characteristics of section *Polyphyllium*

Engl. (Table 1), a strongly supported clade ($P_{SH} = 0.913$, $P_{TT} = 0.8405$) (Table 2) that forms the earliest divergent lineage within *Anthurium* (Clade A, Fig. 1). The four other stem characters used in the sectional classification are homoplasious, but some unique character states might serve as synapomorphies. For example, the presence of cataphylls persisting intact along the stem (character 6) (Table 3; Supplementary Appendix S2) distinguishes very clearly species in section *Calomystrium* (Clade 13, Fig. 1), a strongly supported clade ($P_{SH} = P_{TT} = 1$) (Table 2), whereas the other two character states (i.e., cataphylls persisting as fibers or deciduous) are highly homoplasious in the phylogeny (Supplementary Appendix S2).

On the other hand, two highly correlated stem characters, habit and internode length, are very homoplasious along the molecular phylogeny and cannot be used to uniquely characterize any clades in *Anthurium*. The combination of bird's nest habit (character 1) and short internodes less than 3 cm long (character 4) (Table 3; Supplementary Appendix S2) have been used to distinguish section *Pachyneurium* (Schott) Engl. (Table 1), a group for which monophyly was rejected ($P_{SH} = 0.003$, $P_{TT} = 0.0002$) (Table 2). This general morphology has evolved at least four and up to seven times in *Anthurium* (Supplementary Appendix S2) probably as the result of repeated adoptions of the epiphytic habit or incursions into seasonally dry environments. The bird's nest habit could help cope with periods of dryness by accumulation of organic matter and water in the basket formed by the leaf bases (Benzing, 1987).

Reproductive characters

Historically, reproductive characteristics have been used to distinguish species of *Anthurium* but not to unite them into groups. The only flowering character used to distinguish groups in the sectional classification of the genus (Table 1), the spadix length (character 21), ranked among the most homoplasious in this study (Table 3; Supplementary Appendix S2). Madison (1978) suggested that evolution in *Anthurium* might have comprised two adaptive radiations, one of them related to the diversification of pollination syndromes, with species producing sweet-spicy fragrances being pollinated by bees and species with rotten fruitlike aroma pollinated by flies. He also argued that pollination syndromes have a loose correlation with spadix color, purple in fly-pollinated species and white-yellow in bee-pollinated ones, but that this character had been employed in classification only to a very limited extent. He thought that in general, characters used in *Anthurium* classification reflected these biological adaptations only indirectly, if at all (Madison, 1978). Unfortunately, too little is known about the reproductive biology of *Anthurium* and detailed pollination studies in the genus are scarce (see Díaz Jiménez et al., 2019, in this issue).

One fruit character, two seeds per locule (character 22) (Table 3), has been used to distinguish section *Tetraspermium* (Schott) Engl. (Croat & Sheffer, 1983) (Clade 5, Fig. 1). This section is monophyletic, but the character might not be a very good synapomorphy given the fact that two or more ovules per locule are also found in members of the closely related section *Porphyrochitonium* (Schott) Engl. Exploration of other fruit and infructescence characteristics disregarded in the sectional classification may yield other characters useful for recognition of clades within *Anthurium*. For example, Madison (1978) proposed that color differences in berries could be a good taxonomic character but that not enough was known about its correlation with dispersal mechanisms. Croat (1991) explored some species groupings within section *Pachyneurium* based on berry color and found that most South American species tend to have purple fruits, whereas orange-red berries were more common among Central American species. However, he did not explicitly recognize the value of such color differences in terms of evolutionary relationships among species groups.

Fruit and seed characteristics have been recently used to distinguish species in the newly resurrected section *Andiphilum* (Croat & Hormell, 2017), characterized by having orange berries with pasty mesocarp and large greenish-white seeds. In addition, species in section *Polyphyllium* are notable for having black seeds (Croat & Baker, 1978), although seed color has not been explicitly used as a diagnostic sectional character for the group. Both of these sections are strongly supported as monophyletic in this study and clearly characterized by unique fruit/seed morphologies, therefore showcasing the value of these previously overlooked characters.

MONOPHYLY TESTS OF SECTIONAL GROUPINGS

It is now clear that the sectional classification of *Anthurium* (Table 1; Croat & Sheffer, 1983; Croat, 1991; Croat et al., 2005; Croat & Carlsen, 2013; Croat & Hormell, 2017) is in need of a thorough revision. Therefore, we here concentrate on understanding the fate of the accepted sections and series of *Anthurium* in the light of evolutionary relationships proposed in the molecular phylogeny of Carlsen and Croat (2013), focusing on exploring their monophyly (Table 2) and providing updated descriptions, as well as lectotypifications and authorship corrections when necessary.

Monophyletic sections

Only seven groups, out of the 20 sections and series included in the sectional classification of *Anthurium*, form strongly supported clades according to the molecular phylogeny of Carlsen and Croat (2013). These are presented here (Fig. 1).

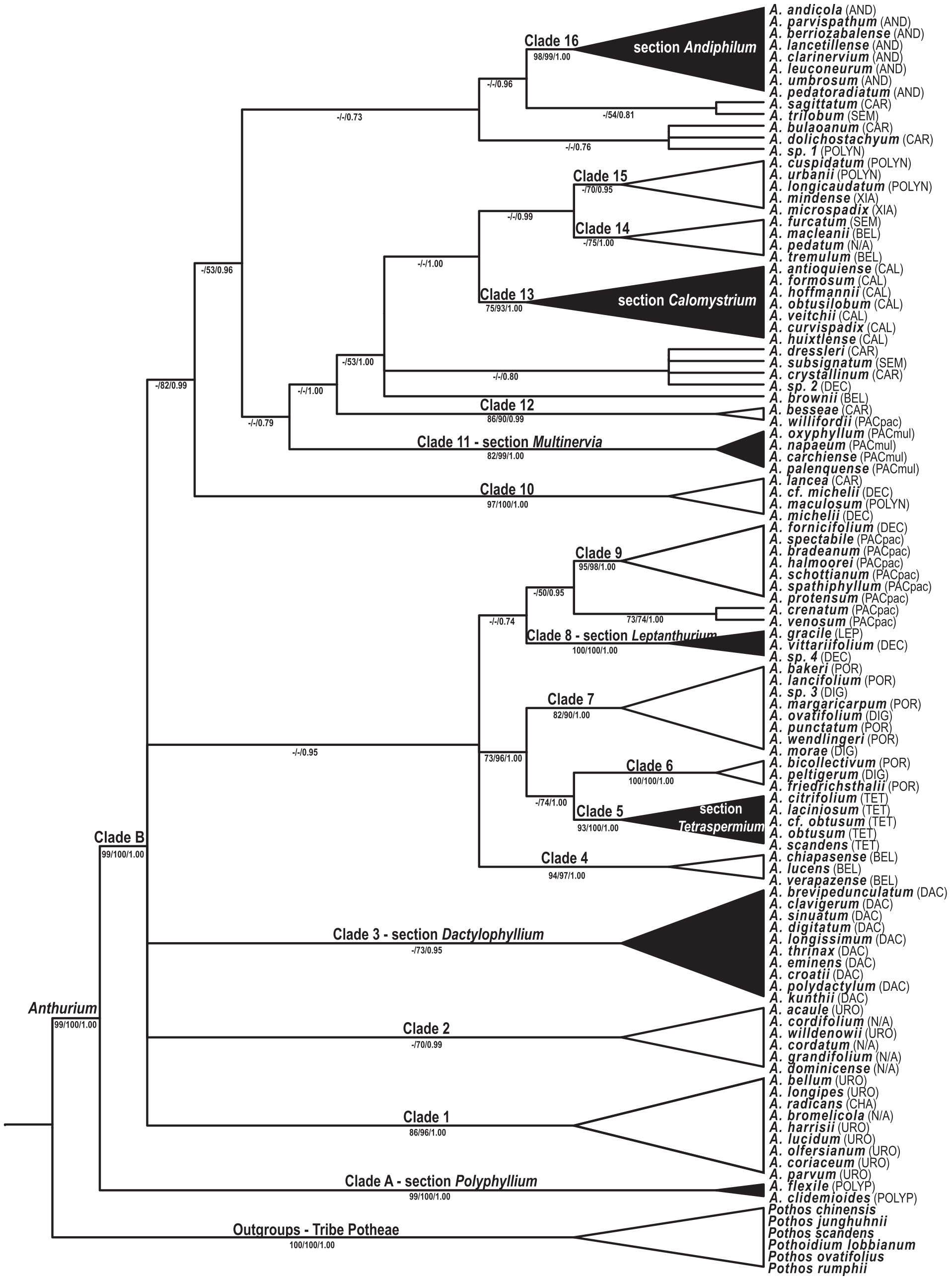

Figure 1. A schematic phylogeny of the genus *Anthurium* Schott (Araceae) showing well-supported major clades. Clades are shown as black triangles when in agreement with the sectional classification. The topology is based on the Bayesian consensus tree from the analysis of combined chloroplast and nuclear DNA dataset from Carlsen and Croat (2013), with maximum parsimony bootstrap values, maximum likelihood bootstrap values, and Bayesian posterior probabilities shown below branches in that order. Bootstrap values $< 50\%$ are labeled with a dash (-). Sectional associations are shown in parentheses after the species name, except for species with unknown sectional affinities ("N/A"). Sectional names and the two series are abbreviated as follows: *Andiphilum*, AND; *Belolonchium*, BEL; *Calomystrium*, CAL; *Cardiolonchium*, CAR; *Chamaerepium*, CHA; *Dactylophyllium*, DAC; *Decurrentia*, DEC; *Digitinervium*, DIG; *Leptanthurium*, LEP; *Pachyneurium* ser. *Multinervia*, PACmul; *Pachyneurium* ser. *Pachyneurium*, PACpac; *Polyneurium*, POLYN; *Polyphyllium*, POLYP; *Porphyrochitonium*, POR; *Semaeophyllium*, SEM; *Tetraspermium*, TET; *Urospadix*, URO; *Xialophyllium*, XIA.

Anthurium sect. **Andiphilum** (Schott) Croat, Aroideana 40(1): 118. 2017. *Anthurium* grex *Andiphilum* Schott, Prodr. Syst. Aroid. 508–509. 1860. TYPE: *Anthurium andicola* Liebm., Vidensk. Meddel. Naturhist. Foren. Kjøbenhavn 1849(1–2): 22–23. 1849 (lectotype, designated by Croat & Hormell [2017: 118]).

Section *Andiphilum* (Clade 16, Fig. 1) was recently resurrected by Croat and Hormell (2017) after it was found to be a distinct clade, comprising eight representative species, in the molecular phylogeny; therefore, it was not included in the monophyly tests. Under its current circumscription, this section includes up to 25 mostly northern Central American species characterized (Table 1) by having D-shaped petioles, more or less ovate-cordate leaf blades, orange berries with a pasty mesocarp, and large greenish white seeds. Some discrepancies regarding the original publication date and spelling in Croat and Hormell (2017) are here clarified in the taxonomic section above.

Anthurium sect. **Calomystrium** (Schott) Engl., Bot. Jahrb. Syst. 25: 419–420. 1898. *Anthurium* grex *Calomystrium* Schott, Prodr. Syst. Aroid. 496–497. 1860. TYPE: *Anthurium nymphaeifolium* K. Koch & C. D. Bouché, Index Sem. (Berlin) 1853(App.): 6. 1853 (lectotype, designated here).

The eight species (of 184 total) sampled to represent section *Calomystrium* in the molecular analysis form a highly supported monophyletic group (Clade 13, Fig. 1) in all analyses ($P_{SH} = P_{TT} = 1$) (Table 2). Monophyly of this section is supported not only by molecular characters but also by the presence of intact persisting cataphylls along the entire length of the stem (character 6). Traditionally, this section has also been recognized by cordate blades (character 11) but this is a highly homoplasious character (Table 3; Supplementary Appendix S2). Other good but not consistent characters to distinguish this section include the presence of short pale lineations on the upper blade surface and dark punctations (not glandular punctations) on the lower surface (Table 1; Croat et al., 2013). According to both Engler (1905) and Croat and Sheffer (1983), section *Calomystrium* is one of the most “natural” and recognizable groupings within *Anthurium*. Species in this section also have distinctive inflorescences (Croat & Sheffer, 1983; Croat et al., 2013), with erect and broad spathes, and rather thick, glossy tepals that are often variously pastel colored. However, Croat and Sheffer (1983) emphasized the presence of intact cataphylls in distinguishing the section more than any unique reproductive characters, arguing that inflorescences in this section are distinctive but more difficult to describe.

Anthurium sect. **Dactylophyllium** (Schott) Engl., emend. Croat & Carlsen, PhytoKeys 23: 51–52. 2013. *Anthurium* grex *Dactylophyllium* Schott, Prodr. Syst. Aroid. 542–543. 1860. TYPE: *Anthurium kunthii* Poepp., Nov. Gen. Sp. Pl. 3: 84–85. 1845 (lectotype, designated by Croat & Carlsen [2013: 51]).

Anthurium grex *Schizoplacium* Schott, Prodr. Syst. Aroid. 538. 1860. *Anthurium* sect. *Schizoplacium* (Schott) Engl., Monogr. Phan. 2: 192. 1879. TYPE: *Anthurium palmatum* (L.) Schott, Wiener Z. Kunst 1829(3): 828. 1829 (lectotype, designated by Croat & Carlsen [2013: 51]).

Croat and Carlsen (2013) redefined the limits of section *Dactylophyllium* in light of the new molecular phylogeny (Clade 3, Fig. 1), thus this section was not included in the monophyly tests. Species in this section represent a very distinct morphological group with palmately divided leaves (Table 1). The leaves are characterized by having either leaf segments (i.e., leaflets) that are free to the base (i.e., palmatisect leaves) or leaf segments (i.e., lobes) that are united at the base (i.e., palmatifid leaves). However, seemingly similar morphologies have evolved independently at least two more times in the genus (Supplementary Appendix S2). Recently, pollen studies have suggested that species in section *Dactylophyllium* are also characterized by having large pollen grains (ca. 20–21 μm diam.) in comparison with the smaller pollen size found in all other *Anthurium* species sampled to date (ca. 10–15 μm diam.) (Carlsen, unpublished data).

Anthurium sect. **Leptanthurium** (Schott) Engl., Monogr. Phan. 2: 117. 1879. *Anthurium* grex *Leptanthurium* Schott, Prodr. Syst. Aroid. 447. 1860. TYPE: *Anthurium gracile* (Rudge) Schott, Wiener Z. Kunst 1829: 828. 1829 [≡ *Pothos gracilis* Rudge, Pl. Guiane 23, t. 32. 1805] (lectotype, designated here).

According to Croat et al. (2006), section *Leptanthurium* contained only two species, *Anthurium gracile* and *A. barrieri* Croat, Scherber. & G. Ferry. In this study, we sampled only the former species; therefore, the group could not be included in monophyly tests. However, it was found that *A. gracile* occurs in a strongly supported clade (Clade 8, Fig. 1) with at least two other species, *A. vittariifolium* Engl. and the undescribed *Anthurium* sp. 4 (both previously assigned to section *Decurrentia* Croat). Section *Leptanthurium* is a well-distinguished morphological group, comprising species with rather long and slender (“strappy”) leaves; pendent, thin and long spadices that bear few (up to three per spiral) and relatively large flowers (Schott, 1860; Engler, 1905; Carlsen & Croat, 2013); white roots (due to the presence of velamen) (Croat & Sheffer, 1983); weakly differentiated primary lateral veins; and reddish berries (Table 1; Croat et al., 2006). Formerly, Croat and Sheffer (1983: 97) emphasized that section *Leptanthurium* was "nevertheless unique and apparently quite natural."

Anthurium sect. **Multinervia** (Croat) Carlsen & Croat, stat. nov. *Anthurium* ser. *Multinervia* Croat, Ann. Missouri Bot. Gard. 78: 573. 1991. TYPE: *Anthurium napaeum* Engl., Bot. Jahrb. Syst. 25: 407. 1898.

The molecular analysis included four of the 16 species in this group and showed that they form a clade (Clade 11, Fig. 1) for which monophyly cannot be rejected ($P_{SH} = 0.992$, $P_{TT} = 1$) (Table 2) in any of the analyses. This group of species is clearly differentiated from the rest of section *Pachyneurium* (i.e., Clades 9 and 12, Fig. 1), to which they previously belonged; therefore, *Multinervia* is here elevated to sectional status. Croat (1991) recognized species in his series *Multinervia* as having involute leaf vernation, same as in section *Pachyneurium* (character 9); blades usually oblong-elliptic to oblong-oblanceolate or elliptic, rarely oblanceolate (character 11), frequently drying green to yellow-green, and with numerous and closely spaced primary lateral veins (character 20); fruits mostly orange, sometimes purple; and plants mostly endemic to Ecuador, Colombia, and Bolivia. Most of these characters are highly homoplasious (Table 3; Supplementary Appendix S2), so further morphological studies are needed to identify unique synapomorphies in this clade.

Anthurium sect. **Polyphyllium** Engl., Monogr. Phan. 2: 105. 1879. TYPE: *Anthurium flexile* Schott subsp. *muelleri* (J. F. Macbr.) Croat & R. A. Baker, Selbyana 2(2/3): 236. 1978 [≡ *Anthurium muelleri* J. F. Macbr., Candollea 5: 348. 1934, replacement name for *Anthurium mexicanum* Engl., Monogr. Phan. 2: 105. 1879, non Anthurium mexicanum Liebm.] (lectotype, designated here).

This small section of two species is well distinguished morphologically and molecularly from the rest of *Anthurium* (Clade A, Fig. 1). It was represented by two species in the molecular phylogeny, and its monophyly ($P_{SH} = 0.913$, $P_{TT} = 0.8405$) (Table 2) was supported in all analyses. The section is characterized (Table 1) by having slender, wiry stems (character 2) with adventitious roots along the entire internode (character 3) and lacking 1-ribbed cataphylls (character 5) (sheathing petioles protect the new growth instead of cataphylls). These characters are synapomorphic within *Anthurium* (Table 3; Supplementary Appendix S2). In addition, both these species have shiny black or dark brown seeds (Croat & Baker, 1978). Nevertheless, seed characters, although unique in the genus, have not been used to recognize the section, perhaps due to the difficulty of finding fruiting specimens in the field. All previous authors (Engler, 1905; Croat & Baker, 1978; Croat & Sheffer, 1983) have considered this section to be a "very natural" one. *Anthurium mexicanum* Engl. was the only species included in this section by Engler (1879) when it was first described; but this species name is illegitimate and was later replaced by *A. muelleri* based on the same type specimen (*F. J. Mueller 993*, collected in Mexico, Veracruz, Orizaba, in 1853). The latter is now considered a subspecies of *A. flexile*, and it was here chosen as the lectotype for the section.

Anthurium sect. **Tetraspermium** (Schott) Engl., Monogr. Phan. 2: 106. 1879. *Anthurium* grex *Tetraspermium* Schott, Prodr. Syst. Aroid. 436–437. 1860. TYPE: *Anthurium scandens* (Aubl.) Engl., Fl. Bras. 3(2): 78. 1878 [≡ *Dracontium scandens* Aubl., Hist. Pl. Guiane 2: 836. 1775] (lectotype, designated here).

This section of 35 species, represented in the molecular analysis by five species, is a monophyletic ($P_{SH} = 0.421$, $P_{TT} = 0.0881$) (Table 2) and strongly supported group (Clade 5, Fig. 1). All previous authors (Schott, 1860; Engler, 1905; Croat & Sheffer, 1983) agreed that *Tetraspermium* is a distinct section in *Anthurium* characterized (Table 1) by glandular punctations on the leaves (character 16) and fruits with two seeds per locule (character 22). However, these characters might not be good synapomorphies for this section given the fact that they are also found in members of the closely related sections *Digitinervium* Sodiro and *Porphyrochitonium* (Fig. 1), and that the limits of both these latter groups are being challenged in our analyses (Table 2). Species in section *Tetraspermium* also have scandent habit (character 1) and thin stems (character 2) with long internodes (character 4). More detailed studies in the group will be needed to reveal better morphological synapomorphies that could be used to distinguish this section.

Non-monophyletic sections

Topology tests for monophyly strongly rejected in all analyses the following nine groupings of *Anthurium*: sections *Belolonchium*, *Cardiolonchium* (Schott) Engl., *Decurrentia*, *Digitinervium*, *Pachyneurium*, *Polyneurium*, *Porphyrochitonium*, and *Semaeophyllium*, as well as series *Pachyneurium* (Schott) Croat (Table 2).

Two other sections show inconclusive results in the monophyly tests. Based on its accepted circumscription (Engler, 1905; Croat & Sheffer, 1983), section *Urospadix* was represented by 10 species (out of 96 total) in the molecular phylogeny (Clades 1 and 2, Fig. 1), and it is the only group with contradictory results in topology tests ($P_{SH} = 0.146$, $P_{TT} = 0.026$) (Table 2). *Anthurium* sect. *Xialophyllium* (Schott) Engl. is a species-rich (ca. 108 species) and variable section that was represented in the molecular phylogeny by only two species, which fall together in Clade 15 (Fig. 1) along with other seemingly unrelated taxa. So far, based on this very limited sampling, section *Xialophyllium* is deemed monophyletic (P_{SH} = 0.889, P_{TT} = 0.8273) (Table 2), but we argue that the morphological variation in this section is so striking that these results might not hold true after a more exhaustive species sampling in future molecular studies.

Section *Chamaerepium* could not be included as a constraint in the analyses because of its monotypic nature. Nonetheless, based on the position of *Anthurium radicans* K. Koch & Haage in the phylogeny (Clade 1, Fig. 1), separation of this species in its own section should not be maintained. We refrain from doing this taxonomic change here until the circumscription and statistical support for the closely related Clades 1 and 2 are improved in other studies.

The current delimitation of all the sections mentioned above is problematic, but the poor resolution along the backbone of the molecular phylogeny implies that although the monophyly of all these groups has been challenged, increased sampling (both in terms of number of taxa and gene regions) will be required in future phylogenetic analyses to determine the correct placement of all species presently assigned to these sections, and to corroborate these results. More detailed morphological analyses, with special emphasis on reproductive characters, will also be needed to uncover better synapomorphies for clades in *Anthurium*.

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