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Melastomataceae species. Melastomataceae. Melastomataceae family characteristics.

PDF Split View Article contents Figures & tables Video Audio Supplementary Data The Marcetia alliance, or valuate their phylogenetic relationships and generic boundaries, and investigate morphological characters as potential synapomorphis for edimiting clades or genera. We used nuclear (ITS, ETS) and plastid classification in the Marcetia alliance, evaluate their phylogenetic relationships and generic boundaries, and investigate morphological characters. Other genera with variable morphological characters, comola, Ernestia and Macairea, were returned they are potentially useful for the diagnosis of genera and infrageneric groups. This study represents a major step in understanding internal relationships and provides the basis for a revision of the genera characters as potentially useful for the diagnosis of genera and infrageneric groups. This study represents a major step in understanding internal relationships and provides the basis for a revision of the genera characters and portiodia characters are concentrated in the Neotropics. They are usually recolmost bloever, most species are concentrated in the Neotropics. They are usually recolmost bloever, most species are concentrated in the Neotropics. They are usually recolmolastic characters and period larcing the family is the have shown that Melastomaceae are monophyletic, as supported by morphological and molecular data (Clausing & Renner, 2001). However, many questions remain regarding the family is the family shown and relationships of trans. 2001; Denover, Based and transcers, 2008; Goldenberg et al., 2012; Michelangeli et al., 2012; Michelangeli et al., 2012; Michelangeli et al., 2003, and dithouted & Martins, 2001; Stone, 2006; Goldenberg et al., 2008; Anorim, Goldenberg & Michelangeli et al., 2013, Den and they selecand the this vested (Clausing & Renner, 2001). Michelangeli et al., 2013, Michelangeli et al., 2012; Michelangeli et al., 2013, Michelangeli et al., 2003, Michelangeli et

vascular bundles (Wilson, 1950; K. Sosa, P.J.F. Guimaraes & F.A. Michelangeli, unpubl. data). On the other hand, the Marcetia alliance was characterized by cochleate, oval or lacrimiform seeds with foveolate cells (except Siphanthera; Whiffin & Tomb, 1972; Almeda & Robinson, 2011), ovaries that are either glabrous or with scattered trichomes flowers often tetramerous, hypanthium glabrous or with glandular trichomes, and two to four ovary locules. In general, species of the Marcetia alliance are predominantly herbs or subshrubs, some annual, mainly distributed in Neotropical savannas. Brazil, with > 41% endemic species, is probably the major centre of diversity (Baumgratz et al., 2015). A similar distribution is also found in Microlicieae (Fritsch et al., 2004) and some clades of Melastomeae s.l. (Michelangeli et al., 2013). The Marcetia alliance putatively comprises c. 137 species); Aciotis D.Don. (13 species); Aciotis D.Don. (13 species); Aciotis D.Don. (13 species); Aciotis D.Don. (14 species); Aciotis D.Don. (15 species); Aciotis D.Don. (15 species); Aciotis D.Don. (16 species); Aciotis D.Don. (17 species); Aciotis D.Don. (18 species); Aciotis D.Don. (19 DC. (19 species); Ernestia DC. (16 species); Fritzschia Cham. (three species); Macairea DC. (22 species); Marcetia DC. (15 species); Sandemania Gleason (one species); Marcetia DC. (15 species); Sandemania Gleason (one species); Sandemania Gleas Comoliopsis Wurdack, Loricalepis Brade, Mallophyton Wurdack and Poteranthera Bong. could potentially be included in the Marcetia alliance. A, Nepsera aquatica. B, Appendicularia thymifolia. C, Ernestia glandulosa. D, Comolia microphylla. E, Comolia stenodon. F, Fritzschia erecta. G, Marcetia macrophylla. E, Comolia stenodon. F, Fritzschia erecta. G, Macairea radula. P, Acanthella sprucei. Photographs: A-C, Olivier Gaubert; P, Francisco Fajardo-Gutiérrez; D-O, M. J. Rocha. The Marcetia alliance (four terminals) and the Marcetia alliance (four terminals) in that study was insufficient to recognize these groups. Michelangeli et al (2013), with a broader sampling, confirmed the existence of this group, calling it the Marcetia alliance, and suggested that it could be segregated from Melastomeae. These results also hinted that some of the genera in the alliance by Michelangeli et al. (2013), many questions remain about the monophyly of the genera, their relationships and limits. Additionally, thorough evaluation of different morphological characters is needed to better define genera in the alliance and to produce a workable taxonomy. In view of these questions and the taxonomic problems found in some genera of the Marcetia alliance, the main objectives of this study were: (1) to test the monophyly of the genera with an increased sampling of taxa and molecular markers; (2) to assess the generic limits and infrageneric relationships; and (3) to investigate selected morphological characters as potential synapomorphies for delimiting clades or genera in the alliance. Material and methods Taxon sampling We sampled 107 taxa of 27 genera. Of these, 89 accepted species and 12 genera correspond to taxa putatively in the Marcetia alliance, representing 64% of the 137 species thought to belong to this group. The numbers of species sampled per genus were as follows: Acanthella (1/50% of the accepted species); Aciotis (8/61%); Acisanthera (12/85%); Appendicularia (1/100%); Comolia (17/89%); Ernestia (10/66%). Whenever possible, we tried to cover the greatest morphological variation and geographical distribution for each genus. Most samples were field collected and identified by M. J. Rocha, P. J. Guimarães, F. A. Michelangeli and other specialists in Melastomataceae. We included the type of which is C. berberifolia (Bonpl.) DC., known only from the type material. Nevertheless, this species is morphologically similar and possibly conspecific with C. villosa (Aubl.) Triana (Wurdack, 1973), which was sampled. As outgroups we included 13 representatives of core Melastomeae, Microlicieae and Rhexieae. Trees were rooted with Cambessedesia hilariana DC., following the results of Goldenberg et al. (2012), Michelangeli et al. (2013) and Michelangeli, Ulloa & Sosa (2014). DNA extraction and markers Total genomic DNA was extracted from silica-dried leaves collected in the field or from herbarium specimens. Samples were extracted using NucleoSpin 96 Plant II extraction kit (Macherey-Nagel), following the manufacturer's instructions or DNeasy plant mini kit (Qiagen), with the modifications suggested by Alexander et al. (2007). Phylogenetic analyses were based on five molecular markers: two nuclear (nrITS, nrETS) and three plastid intergenic spacers (accD-psaI, atpH-atpF, trnS-trnG). The ITS region consisted of the ribosomal gene. The ETS(atpH-atpF, trnS-trnG) and three plastid intergenic spacers (accD-psaI, atpH-atpF, trnS-trnG). consisted of a section of about 241 bp at the 3' end of the ribosomal external transcribed spacer (ETS) and 5' end of the 18S ribosomal gene. Primers used for amplification are listed in Table 1. The ITS region has been used in several studies to elucidate phylogenetic relationships of tribes and genera in Melastomataceae (Fritsch et al., 2004; Michelangeli et al., 2004, 2008, 2013; Ionta et al., 2007; Bécquer-Granados, 2008; Goldenberg et al., 2008; Reginato et al., 2010; Kriebel, Michelangeli & Kelly, 2015), whereas the ETS region is still little used in Melastomataceae, but has proved to be useful in understanding infrageneric relationships (Stone & Andreasen, 2010 Kriebel et al., 2015) and to be easily amplified. The accD-psaI, atpH-atpF and trnS-trnG plastid intergenic spacers have also been informative for Melastomataceae and have been employed in several studies (Reginato et al., 2010; Michelangeli et al., 2013). Table 1.List of molecular markers and primers used in this study Locus . Primer . Sequence (5'-3') . Reference . nrITS NY 183 CCTTATCATTTAGAGGAAGGAG Michelangeli et al. (2004) NY 887 ATTGATGGCTAGCAGG Kriebel et al. (2015) NY1428 ACGTGTCGCGTCTAGCAGGCT accD-psa1 NY826 AATYGTACCACGTAATCYTTTAAA Shaw et al. (2005) NY827 AGAAGCCATTGCAATTGCCAGGAAA atpH-atpF NY822 ACTCGCACACACTCCCTTTCC Reginato et al. (2010) NY 823 GCTTTTATGGAAGCCTTTACCAC Amplification, editing and alignment DNA amplification was performed by polymerase chain reaction (PCR) in a final volume of 15 µL with the following reaction components: 0.5-0.7 µL genomic DNA (c. 30 ng µL-1), 7.5 µL spermidine (4 mm) and 2.5 µL purified water. The PCR conditions were similar for all markers, with small adjustments in the annealing temperature and extension time, as follows: initial denaturation at 94 °C for 3 min; 40 cycles of denaturation at 94 °C for 45 s; annealing at 58 °C (ETS), 50 °C (ITS), 57 °C (accD-psaI) or 55 °C (trnS-trnG, atpH-atpF) for 45 s; extension at 72 °C for 1 min (except for trnS-trnG and atpH-atpF which was 1 min 30 s); and a final extension at 72 °C for 3 min for all markers. All reactions were performed in Eppendorf thermocyclers. Cycle sequencing service at the University of Washington, USA (High Throughput Genomics Center - htSEQ). Consensus sequences obtained for each marker from bidirectional reads were generated in Sequences of low quality were discarded. Sequences of low quality were discarded. Sequences (Simmons, 2004). The 5' and 3' ends of each matrix were trimmed and internal regions with ambiguous or problematic alignment were excluded. Individual gap positions were treated as missing data.DNA substitution models for Bayesian inference (BI) and maximum-likelihood (ML) analyses were selected for each marker using jModeltest v.2.1.3 (Darriba et al., 2012), using the fivemodel scheme with or without four discrete rate categories approximating a gamma distribution (+G) and including models with equal/unequal base frequencies (+F) and a proportion of invariable sites (+I). The likelihoods were calculated using an ML optimized base tree with NNI topology search using phyml (Guindon & Gascuel, 2003) and the models were evaluated using the corrected Akaike's information criterion (AICc). In total, 273 sequences were generated for this study, and another 96 were obtained from Michelangeli et al. (2013). Voucher information and GenBank accession numbers are listed in the Appendix 1. Phylogenetic analyses All data sets were analysed using maximum parsimony (MP), ML and BI. First, phylogenetic analyses were performed individually for each marker and the congruence between the topologies was visibly evaluated. The matrices for each marker and the congruence between the topologies was visibly evaluated. using Fitch parsimony as the optimality criterion (Fitch, 1971). Heuristic searches consisted of 10 000 replicates of random taxa addition, using the tree bisection-reconnection algorithm (TBR) and saving up to 15 MP trees per replicate. The strict consensus was then built from all the most-parsimonious trees obtained. All characters were treated as unordered and of equal weight. Internal support was evaluated by non-parametric bootstrapping (Felsenstein, 1985) with 10 000 replicates, random addition and TBR branch swapping, saving up to 15 trees per replicate. For bootstrap support levels, we considered bootstrap percentages (BPs) of 50-70% as weak, 71-85% as moderate and >85% as strong (Kress, Prince & Williams, 2002).ML analyses were performed with RAxML using default parameters (Stamatakis, 2006; Stamatakis, 2006; Stamatakis, 2006; Stamatakis, 2008) and run through the CIPRES Science Gateway (Miller, Pfeiffer & Schwartz, 2010). Bootstrap values were estimated on the ML tree also using RAxML based on 1000 searches run through the CIPRES Science Gateway (results not shown). Bayesian analyses were performed using MrBayes 3.1.2 run through the CIPRESS Science Gateway (Miller et al., 2010). Analyses were performed with mixed models and independent parameters. The analysis consisted of two independent runs, each with four Markov chains for ten million generations, sampling one tree every 1000 generations. To achieve convergence the temperature parameter for heating the chains was lowered to 0.05. Convergence between the chains with the generated graphical outputs. Convergence was achieved after 1 941 000 generations and the first 25% of the resulting trees were discarded as burn-in. The remaining trees were used to assess topology and posterior probabilities (PPs) in a majority-rule consensus. Because PPs in Bayesian analysis are not equivalent to BP, but are generally much higher (Erixon et al., 2003), we used criteria similar to a standard statistical test, considering groups with PP > 95% as strongly supported, PP 90-95% as moderately supported and PP < 90% as weakly supported and PP < 90% as weakly supported. Triana (1871), Naudin (1849) and Cogniaux (1885) and characters used in identification keys. The goal was to investigate the evolution of these characters within the clade and to identify putative synapomorphies that might distinguish well-supported groups in the Marcetia alliance. The characters were coded from herbarium collections (ALCB, BHCB, CEPEC, HUEFES, HUFU, INPA, IAN, MG, MIRR, NY, RB, SP, SPF, US) and/or obtained from descriptions and monographs (Renner, 2002; Seco, 2006; Kriebel, 2008; Almeda & Robinson, 2011; Michelangeli et al., 2013). The morphological matrix was edited using Xper2 v.2.0 (Ung et al., 2013). The morphological matrix was edited using Xper2 v.2.0 (Ung et al., 2014). al., 2010) and Mesquite v.2.74 (Maddison & Maddison, 2001). Characters were optimized using parsimony in Winclada 1.00.008 (Nixon, 1999). All characters were coded as non-additive. Both algorithms for optimization [ACCTRAN (accelerated transformation) and DELTRAN (delayed transformation)] were considered. The matrix with all characters and their respective characters and coding Twenty-four discrete characters from life cycle, perianth, androecium, gynoecium, fruit and seed were coded (Table S1). Other characters were not included in the analysis because it was difficult to establish primary homology hypotheses, they were shown to be continuous or would need field data to be coded, and therefore were not available for all species. Examples of these excluded characters include habitat, leaf and hypotheses, they were shown to be continuous or would need field data to be coded, and therefore were not available for all species. anther colour, inflorescence type, stamen size, shape of the stamen appendages, anther shape and seed testa. The following six characters were recovered as the most common numbers are four, five or six (Michelangeli, 2000). The Marcetia alliance is commonly tetramerous, although pentamerous, although pentamerous, and the number of ovary locules was used to establish the sections in Acisanthera (Triana, 1871) and Ernestia (Triana, 1871; Cogniaux, 1885). Although intraspecific variation in petal number was observed in other groups of Melastomataceae, we did not observe it in the species included in this study. Ovay pubescence: absent (0); glandular (1); eglandular (2). Cogniaux (1885) used this character, associated with other reproductive structures, to delimit genera in Melastomeae and to characterize the sections of Ernestia section Ernestia section Ernestia section Ernestia section Pseudoernestia Cogn. comprises species with pentamerous flowers and a glabrous, trilocular ovary, whereas Ernestia section Pseudoernestia Cogn. sections of Acisanthera proposed by Triana (1871), except for Acisanthera tetraptera (Cogn.) Gleason which has glandular pubescence on the ovary, Triana (1871) except for Acisanthera tetraptera (Cogn.) Gleason which has glandular pubescence on the ovary, Triana (1871) except for Acisanthera tetraptera (Cogn.) Gleason which has glandular pubescence on the ovary apex. Ovary locule number: 2 (0); 3 (1); 4 (2); 5 (3). Since the 1800s this character has been used in taxonomic studies of Melastomataceae. Based on the number of locules in the ovary, Triana (1871) proposed two sections in Comolia. Comolia section Comolia section Dicrananthera, A. section Dicranattica, A. section Dicranatt section Dichaetandra (Naudin) Triana has tetramerous flowers and a tetralocular ovary and A. section Noterophila (Mart.) Triana has pentamerous flowers and a bilocular ovary. Filament/anther angle at anthesis: straight or lightly curved (0); curved or arched (1). State 0 includes species with an angle > 90° between the anther base and filament whereas in species scored as 1 the angle between the pedoconnective and filament is \leq 90°. In most species coded as 0 the style is surrounded by the stamens; when the anther is curved or arched the filament tends to bend to one side of the flower, opposite the style. Pedoconnective in antesepalous stamens: absent (0); present (1). Stamens of Melastomataceae vary widely and therefore provide many morphological characters, including shape, colour and size and the presence or absence of associated structures, among others. The pedoconnective is the extension of the connective is the extension of the connective between the thecae base and filament insertion. This character was scored as present when the prolongation is visible, regardless of size. In the Marcetia alliance this structure can have different modifications, such as appendages, or can sometimes be dorsally thickened and basally enlarged below the thecae. Although the stamens provide many other characters, it is difficult to compare them among different taxa and to establish hypotheses of homology. Anther fertility: both cycles fertile (0); only the antesepalous cycle fertile (1). Most species of Melastomataceae are diplostemonous and both cycles of stamens are fertile, but in some cases the number of fertile stamens of fertile (1). Siphanthera: S. section Eumeisneria (DC.) Triana was characterized by having eight stamens, four of them reduced, whereas S. section Siphanthera genliseoides (Hoehne) Wurdack and many Siphanthera spp., only the antesepalous cycle is fertile (character 11, state 0). The antepetalous cycle, if sterile, may be completely absent or staminodial. Results Phylogenetic analyses The aligned matrix with all regions consisted of 5264 characters, 1502 (28%) of which were potentially information from the parsimony analyses is shown in Table 2. The models selected for the BI and ML analyses were GTR + I + G for both nuclear markers produced better resolved trees, probably because of the higher polymorphism between the sequences and the greater number of informative characters. However, lower CI and RI values for the nuclear markers indicate a greater proportion of homoplasy. Table 2.Dataset and statistical results from phylogenetic analyses . nrITS . accD-psaI . atpH-atpF . trnS-trnG . Nuclear . Plastid . Total . Taxa 90 92 77 53 66 102 85 107 Aligned characters 1110 730 1218 933 1249 1840 3400 5264 Potentially informative sites 382 (34%) 490 (67%) 233 (19%) 141 (15%) 256 (20%) 872 (47%) 630 (18%) 1561 (29%) Length of most-parsimonious trees 1657 2467 605 354 755 4258 1786 6109 Number of trees retained 38 820 40 097 78 615 1931 145 995 64 740 57 090 54 616 Consistency index 0.52 0.46 0.76 0.81 0.74 0.47 0.74 0.47 0.74 0.47 0.74 0.54 Retention index 0.78 0.79 0.88 0.85 0.77 0.83 0.78 In all analyses, the Marcetia alliance was recovered as monophyletic with high support (PP = 1.00, BP = 100%) (Fig. 2). The same major clades are present in the combined datasets of the BI, MP and ML analyses and the topology is completely congruent, considering the clades with PP \geq 0.95 and BP \geq 85%. Open in new tabDownload slideThe majority-rule consensus tree from a Bayesian analysis of the combined nuclear (ETS, ITS) and plastid (accD-psaI, trnS-trnG, atpH-atpF) DNA sequences. Numbers above and below the nodes are posterior probabilities and bootstrap percentages from the Bayesian and parsimony analyses, respectively (only for clades with BS ≥ 60%). Well-supported clades from the BI and parsimony analyses of individual and combined matrices. The main difference was the position of the possible first-branching lineage of the Marcetia alliance. In the BI analysis the Comolia montana Gleason clade was resolved as sister to the rest of the group, whereas in the MP and ML analyses the Comolia s.s. + Ernestia s.s. clade was sister to the rest of the group, whereas in the MP and ML analysis the Comolia montana Gleason clade was sister to the rest of the group. However, in all three cases support for these sister clades was low (PP = 0.53, BP = 61%), indicating that relationships at the base of the Marcetia alliance clade are not well supported. We have chosen the BI analyses for presentation and all further comments on relationships and characters. The majority-rule consensus trees from a Bayesian analyses of the combined nuclear (ETS, ITS) and plastid (accD-psaI, trnS-trnG, atpH-atpF) data sets are shown in Figs. S1 and S2, respectively. Aciotis, Fritzschia, Marcetia and Siphanthera, as currently defined, were recovered as monophyletic and were recovered as monophyletic and had strong support in all analyses. Additionally, Acisanthera could easily become monophyletic and were recovered in four and three unrelated clades, respectively. Macairea is resolved as paraphyletic due to Ernestia s.s. being nested in it. In the Bayesian analysis the Comolia montana clade (clade B: PP = 0.99; BP = 95%) is resolved as sister to Comolia s.s. (clade C: PP = 1.00; BP = 87%), A. tetraptera was recovered as the first divergent branch (PP = 0.99; BP = 87%), Sister to a clade with three consistent groups, as follows. The A. hedyotidea (C.Presl.) Triana subclade (PP = 0.99; BP = 87%), Sister to a clade with three consistent groups, as follows. The A. hedyotidea (C.Presl.) Triana subclade (PP = 0.99; BP = 87%), Sister to a clade with three consistent groups, as follows. The A. hedyotidea (C.Presl.) Triana subclade (PP = 0.99; BP = 87%), Sister to a clade with three consistent groups, as follows. The A. hedyotidea (C.Presl.) Triana subclade (PP = 0.99; BP = 87%), Sister to a clade with three consistent groups, as follows. The A. hedyotidea (C.Presl.) Triana subclade (PP = 0.99; BP = 87%), Sister to a clade with three consistent groups, as follows. The A. hedyotidea (C.Presl.) Triana subclade (PP = 0.99; BP = 87%), Sister to a clade with three consistent groups, as follows. The A. hedyotidea (PP = 0.99; BP = 87%), Sister to a clade with three consistent groups, as follows. The A. hedyotidea (PP = 0.99; BP = 87%), Sister to a clade with three consistent groups, as follows. The A. hedyotidea (PP = 0.99; BP = 87%), Sister to a clade with three consistent groups. The A. hedyotidea (PP = 0.99; BP = 87%), Sister to a clade with three consistent groups. The A. hedyotidea (PP = 0.99; PP = 0.990.99; BP = 97%) is constituted by members of Acisanthera section Dicrananthera. The A. bivalvis (Aubl.) Cogn. subclade (PP = 1.00; BP = 75%) is represented by the type species and other species allied to Acisanthera section Acisanthera. Sandemania and Comolia vernicosa (Benth.) Triana form a strongly supported group (clade E: PP = 1.00; BP = 100%), termed Sandemania and allies, that is sister (PP = 0.99; BP = 79%) to a strongly supported Group (clade E: PP = 1.00; BP = 100%). In the Bayesian analysis Clade E+F is sister to the remaining clades G-K (PP = 0.95), whereas in the parsimony analysis this relationship is unresolved. Macairea and some Ernestia s.s. (PP = 1.00; BP (Benth.) Wurdack and M. multinervia Benth. are successively recovered as sisters to Ernestia s.s. Clade H (Nepsera and allies) (PP = 0.98; BP = 85%) is composed of two major subclades with intermingled genera. The monotypic genus Nepsera is sister to (PP = 0.92; BP = 92%) the Ernestia pullei Gleason + Appendicularia thymifolia (Bonpl.) DC. subclade (PP = 1.00; BP = 100%). The other subclade is formed by Acanthella and the Ernestia maguirei Wurdack subclade (PP = 0.79; BP < 50%). Marcetia was recovered as monophyletic with strong support in all analyses (clade I: PP = 1.00; BP = 99%). Although the relationships of this clade to other genera is not strongly supported in all analyses, our results suggest that Marcetia is related to the Fritzschia and Comolia section Tricentrum clade (clade J: PP = 1.00; BP = 100%) is composed of two geographically related subgroups: the weakly supported and/or paraphyletic Comolia section Tricentrum clade and Comolia section Tricentrum clade (clade J: PP = 1.00; BP = 100%) is composed of two geographically related subgroups: the weakly supported and/or paraphyletic Comolia section Tricentrum clade (clade J: PP = 1.00; BP sertularia (DC.) Triana subclade, but which is morphological inference Six morphological inference Six morphological characters (clade K: PP = 1.00; BP = 95%), which is strongly supported in all analyses. Lastly, Aciotis (clade K: PP = 1.00; BP = 95%), which is strongly supported in all analyses. traditionally used in taxonomy of the genera of the Marcetia alliance were reconstructed onto the combined phylogenetic tree (Fig. 3). Although most of them revealed some degree of homoplasy, when combined they can be useful in diagnosing some of the clades recovered in the molecular analyses. In the optimization of floral merosity, the presence of pentamerous flowers was informative for characterizing the Acisanthera bivalvis and Acisanthera s.s. subclades, except for Comolia ayangannae which is tetramerous, and this may be why Wurdack (1964) described it in Comolia. The number of ovary locules was highly homoplastic. However, in association with floral merosity it was useful to circumscribe the Acisanthera bivalvis (pentamerous; bilocular) and Acisanthera s.s. subclades (pentamerous; trilocular). Although Macairea and Ernestia have not been adequately sampled, our analyses showed that ovary pubescence is an important character to diagnose the Ernestia s.s. subclade, which is the only clade of Ernestia with trichomes on the ovary. Most species of the alliance have arched or curved anthers; however, straight anthers are common in the monophyletic Aciotis, Marcetia and Siphanthera. Almost all genera have well-developed pedoconnectives on the anther. Lastly, in only one species of the Acisanthera bivalvis subclade and most Siphanthera spp. the antesepalous stamens are fertile. Open in new tabDownload slideReconstruction of morphological characters onto a 50% majority-rule Bayesian tree showing the evolution of: A, floral merosity; B, ovary pubescence; C, ovary locule number; D, filament/anther angle at anthesis; E, pedoconnective in antesepalous stamens; and F, anther fertility. CI, consistency index; RI, retention index. Discussion Phylogenetic relationships in the Marcetia alliance was characterized by the tetramerous flowers, number of ovary locules equal to the number of petals (tetralocular) or reduced to two or three locules, absence of crown hairs on the ovary apex, and the seeds cochleate, ovate or lacrimiform (Michelangeli et al., 2013). Furthermore, in the Marcetia alliance the pubescence of the ovary is glandular, whereas in most of members of Melastomeae s.s. it is eglandular. A recent study suggested the presence of three layers in the outer integument of the ovule as a possible synapomorphy for the Marcetia alliance (Caetano, 2014). In this study, with a more comprehensive sampling, we tested for the first time the monophyly of all genera of the Marcetia alliance and their boundaries and relationships. Among the genera with more than two species, Aciotis, Fritzschia, Siphanthera and Macairea were shown geographically structured. Few of the morphological characters analysed constituted strict synapomorphies; nonetheless, it is possible to circumscribe most clades morphologically with a specific combination of features. With the aim of supporting and informing a future generic revision of groups in the Marcetia alliance, we discuss and characterize each of the clades recovered in our phylogenetic analyses in the following paragraphs. Comolia montana clade This lineage includes two species endemic to tepuis in the Guayana highlands. Gleason (1939a; 1952) recognized and distinguished C. coriacea Gleason and C. montana from other Comolia spp. mainly by the coriaceous leaves with ciliate trichomes. Additionally, the leaves are thick, with visible stomatal crypts, a hypanthium with indument in the torus region and almost pyramidal seeds that are larger than in other Comoliopsis was not sampled in this study, but based on morphology of the leaves, anthers, seeds and geographical distribution it may belong in this clade. However, this needs to be further evaluated because C. montana and C. coriacea have flowers that are tetramerous, the ovary has glandular trichomes and it is (tri-) tetramerous (Wurdack, 1984). If indeed Comoliopsis forms part of this clade, then these Comolia spp. may be combined into Comoliopsis. Ernestia section Pseudoernestia clade This clade is composed of E. cordifolia in Ernestia section Pseudoernestia Cogn. Later, Krasser (1893) elevated this section to generic rank, whereas Wurdack, Renner & Morley (1993) synonymized it in Ernestia. These two species differ from other Ernestia spp. by their glabrous, trilocular ovary, almost rounded calyx tube with narrowly oblong lobes and tuberculate dorso-basal connective with ventral, simple aristae, but differ from each other in the inflorescence and floral merosity. Commonly, E cordifolia has a terminal inflorescence with pentamerous flowers and E. glandulosa an axillary inflorescence and tetramerous flowers. A relationship between these species was suggested by Gleason (1925), based on their trilocular ovary. Despite the differences between these species was suggested by Gleason (1925), based on their trilocular ovary. Ernestia s.s. clade and should be segregated as a resurrected Pseudoernestia Krasser. Comolia s.s. clade includes almost all species of Comolia s. which is tetralocular and occurs in restinga vegetation in northern Brazil, all other species in this clade are found in lowland savannas of northern Brazil, all other species in this clade indeed represents Comolia s.s. Comolia berberifolia is known only from the type collection. However, it is clear that C. berberifolia is part of the same species complex as C. villosa (Wurdack, 1973, cited as a group of small segregated species. Acisanthera s.l. clade Acisanthera was included in previous molecular phylogenetic analyses (Fritsch et al., 2004; Michelangeli et al., 2013), but the limited sampling so far has been insufficient to understand relationships in this morphologically complex group. Kriebel (2008) performed a morphological phylogenetic analysis for this genus, suggesting that Acisanthera was not monophyletic because Acisanthera tetraptera was more closely related to Siphanthera, based on the rostrate anther apex and bilobed ovary apex. However, in our study, A. tetraptera was more closely related to Siphanthera, based on the rostrate anther apex and bilobed ovary apex. inflorescences, the capitate cymes subtended by foliaceous bracts, anthers with a rostrate apex, glandular style, tetralocular ovary with glandular style, tetra These species resemble A. tetraptera in the tetramerous flowers and bilocular ovary, but differ in the morphology of leaves, stamens and seeds: the leaves are fleshy, the thecae are small with broad pores and the connective is prolonged into two upturned, subulate-aristate appendages. Additionally, the seed surface is not covered with tubercles. The A. bivalvis subclade is composed of six species of annual herbs, commonly found in swampy areas. It is easily diagnosed by the commonly inflated stems, sessile leaves that can be heterophyllous, pentamerous flowers and bilocular ovary. Lastly, the Acisanthera s.s. subclade is the only group in the Marcetia alliance with pentamerous flowers and trilocular ovaries. Seco (2006) suggested that Acisanthera and Comolia could be related based on their seed morphology, ovary locules and stamens. Also, only the Acisanthera s.s. clade has anthers that are similar to Comolia s.s., but the floral merosity and the number of ovary locules are different. Acisanthera s.l. could become monophyletic with the inclusion of Comolia ayangannae in Acisanthera. Although the morphological relationship of C. ayangannae with this clade is not obvious, this possibility should be studied further, as in the original description of this species, Wurdack (1964) compared its stamens to Acisanthera could easily become (1964) compared its stamens to Acisanthera could easily become monophyletic with the inclusion of C. ayangannae, perhaps it is more appropriate to recognize each of the four clades as separate genera because they are morphologically heterogeneous and difficult to characterized, whereas Acisanthera and Noterophila were previously treated as genera by Presl (1832) and Martius (1831), respectively. Additionally, the four groups of Acisanthera are also ecologically distinct. Sandemania and allies clade Sandemania has long been a nomenclaturally and taxonomically confusing entity. Its sole species was first described in Leandra Raddi (Miconieae) by Cogniaux (1909), using an illegitimate name, and later based on a different type in Comolia (Tibouchineae. However, Wurdack (1970) later realized that Comolia hoehnei Cogn. and Sandemania lilacina were indeed the same species and made the appropriate transfer. Renner (1987) reviewed this genus and argued that it was closely related to Macairea, Comolia and Tibouchina Aubl. However, the phylogenetic studies of Michelangeli et al. (2013) revealed that Sandemania is not related to Tibouchina and does not belong in Melastomeae s.s. Our results confirmed that the sole species in the genus, S. hoehnei (Cogn.) Wurdack, belongs to the Marcetia alliance and is related to Comolia vernicosa. These two species share some characters, such as tetramerous flowers, a glabrous ovary, and rostrate and corrugated anthers. Also, both occur in open savannas from the Amazon Basin. Despite these similarities, we agree with Renner (1987) that S. hoehnei cannot be accommodated in any other genus, because of its unique combination of characters: paniculate inflorescence with many small flowers, stamens with ventrally bilobed pedoconnectives at filament insertion, corrugated anthers, glabrous ovary and seeds with a shallowly tuberculate surface. Likewise, C. vernicosa was first described in Leiostegia Benth. (Bentham, 1840) and later synonymized in Comolia by Triana (1871). However, it is easily distinguished from all the groups of Comolia and from S. hoehnei by its glabrous, uninerved leaves with a revolute margin, fasciculate and axillary flowers, and tetralocular ovary. Siphanthera was long assigned to Microlicieae in traditional morphological studies by Naudin (1849), Triana (1871), Cogniaux (1883, 1891) and Krasser (1893), probably based on its staminal ventral appendages and seeds (Almeda & Robinson, 2011). Later, Renner (1993) transferred the genus to a broadly circumscribed Melastomeae and this was corroborated by morphological and molecular analyses (Almeda & Martins, 2001; Clausing & Renner, 2001; Fritsch et al., 2013). The monophyly of Siphanthera was previously recovered in morphological analyses (Almeda & Robinson, 2011) and is corroborated in this study. The ellipsoid to lacrimiform seed withera was previously recovered in morphological analyses (Almeda & Robinson, 2011) and is corroborated in this study. elongated cells can be considered an autapomorphy for Siphanthera. Beyond the unique seed morphology, Siphanthera is also characterized by the herbaceous habit (annual or perennials), usually < 100 cm tall, mostly four fertile stamens, sometimes with one to four staminodes, anthera is also characterized by the herbaceous habit (annual or perennials), usually < 100 cm tall, mostly four fertile stamens, sometimes with one to four staminodes, anthera is also characterized by the herbaceous habit (annual or perennials), usually < 100 cm tall, mostly four fertile stamens, sometimes with one to four staminodes, anthera is also characterized by the herbaceous habit (annual or perennials), usually < 100 cm tall, mostly four fertile stamens, sometimes with one to four staminodes, anthera is also characterized by the herbaceous habit (annual or perennials), usually < 100 cm tall, mostly four fertile stamens, sometimes with one to four staminodes, anthera is also characterized by the herbaceous habit (annual or perennials), usually < 100 cm tall, mostly four fertile stamens, sometimes with one to four staminodes, anthera is also characterized by the herbaceous habit (annual or perennials), usually < 100 cm tall, mostly four fertile stamens, sometimes with one to four staminodes, anthera is also characterized by the herbaceous habit (annual or perennials), usually < 100 cm tall, mostly four fertile stamens, sometimes with one to four staminodes, and the herbaceous habit (annual or perennials), usually < 100 cm tall, mostly four fertile stamens, sometimes with one to four staminodes, anthera is also characterized by the herbaceous habit (annual or perennials), usually < 100 cm tall, mostly four fertile stamens, sometimes with one to four staminodes, and the herbaceous habit (annual or perennials), usually < 100 cm tall, mostly four fertile stamens, sometimes with one to four staminodes, and the herbaceous habit (annual or perennials), usually < 100 cm tall, mostly four fertile stamens, sometimes with one to four stamens, so connective dorsally thickened, rarely prolonged below the thecae, modified into well-developed ventral appendages and style occasionally related to Acisanthera tetraptera. However, Almeda & Robinson (2011) suggested that the similarity of the anther between the two taxa could be due to convergence or parallelism, as it occurs between the seeds of Siphanthera and Microlicieae. In our study, Siphanthera is phylogenetically related to the Sandemania and allies clade. However, the two species in this clade are differentiated from Siphanthera mainly by the stamens, in which both cycles are fertile, the anthers are larger and the pedoconnective is clearly prolonged below the thecae. Also, the leaves are completely coriaceous, and they are mostly shrubs up to 2 m tall. Macairea is characterized by the presence of a dorso-basal connective anther appendage and glandular trichomes in the vegetative and reproductive structures. In our analysis, Macairea was not resolved as monophyletic because Ernestia s.s. is resolved in Macairea spp. were sampled, from a total of 22, making it difficult to infer internal relationships, the characters used by Cogniaux (1891), Gleason (1934) and Renner (1989) as diagnostic are clearly not appropriate for recognizing the genus or its sections, because they also occur in unrelated genera. Macairea was divided by Renner (1989) into two groups based on trichome types. Even though our sampling does not allow a clear test of these groups, some trends are apparent. Macairea thyrsiflora DC. treated in 'group A' by Renner (1989) was recovered with M. pachyphylla Benth. and M. radula (Bonpl.) DC. from 'group B', indicating that hair type alone is not an informative character for recognizing species groups in this genus. The Macairea s.s. subclade is phylogenetically well resolved and supported by staminal filaments with short-stalked glands, a prolonged and dorso-basally expanded connective, without well-developed appendages, and a glandular style and ovary. On the other hand, M. lasiophylla has a set of characters that are not clearly related to any other genera, including straight anthers with the connective briefly prolonged and modified into two bilobed appendages and a glabrous filament and style, besides other differences in vegetative structure and habit. In general, the flowers of M. multinervia are similar to those of the Macairea s.s. subclade, except for the presence of glands on the filament and style. Also, its leaves are thinner, basally cordate and seven- to nine-nerved; differing from all other Macairea spp. (Renner, 1989). Wurdack (1966) argued that the pubescence and floral features of M. lasiophylla indicate that it represents a reduced evolutionary offshoot related to M. multinervia, with stamens really quite conformable to other species in the genus. Renner (1989) suggested that the ventral appendages of M. lasiophylla could be similar to those of Acisanthera and Ernestia s.s. subclade is constituted by the species of Ernestia s.s. subclade is weak, this group is morphologically well characterized by tetramerous flowers and a tetralocular ovary with a glandular-setose apex (Cogniaux, 1885). Also, this is the only clade of Ernestia where the large stamens have aristate and bifurcated ventral appendages and a dorsal spur at the median part of the antesepalous pedoconnective. Nepsera and allies clade This strongly supported clade includes two easily recognized monotypic genera: Nepsera and Appendicularia. It also includes the only species sampled of Acanthella, a genus composed of two species, and some Ernestia spp. Nepsera aquatica (Aubl.) Naudin is a herb or small shrub, commonly found in swampy areas and it differs from Appendicularia by its paniculate lax inflorescences, terminal and nearly isomorphic stamens with a briefly prolonged connective and bilobed ventral appendages. In the Appendicularia + Ernestia pullei subclade the inflorescences are paniculate and terminal, but not lax and slender as in Nepsera. Also, the hypanthium is clearly eight-ridged, tubulose-campanulate and terminal appendages. with semicircular calyx lobes and the connective is prolonged with ventral appendages basally enlarged with long terminal aristae. Acanthella shares some features with members of this tribe, they are differentiated by seed morphology. All genera of Marianeae have elongate, wingless or narrowly winged seeds, whereas in Acanthella they are large, broad and strongly winged (Gleason, 1952). Renner (1993) transferred Acanthella to Melastomeae and more recently it was recovered in the Marcetia alliance (Michelangeli et al., 2013). Our results did not determine accurately the relationships of Acanthella sprucei Benth. & Hook.f. However, this genus is supported by morphological synapomorphies including yellow to orange petals and winged seeds. Although the Ernestia maguirei subclade is phylogenetically well supported, this clade consists of three morphologically distinct species. ventral appendages with two terminal aristae. In E. maguirei, the stamens are not enlarged at the base, the aristae are smaller and the appendages are dorsally auriculate, similar to those of E. rubra but different from E. confertiflora. In addition, E. maguirei has a glandular style and tetralocular, glabrous ovary. Morphologically, this subclade is particularly difficult to characterize due to the absence of synapomorphies or even a set of exclusive morphological characterization of the E. maguirei subclade, as well as resolving generic relationships. Currently, this is the most complex clade in the Marcetia alliance, with great diversity of habit, inflorescence, stamen and seed morphology, and the one most in need of further studies. Marcetia is well supported and the genus was previously recovered as monophyletic by Santos (2009) using nrITS sequence data. Accordingly, its floral morphology is quite homogeneous, despite being the largest genus in the alliance. Putative morphological synapomorphies for Marcetia include usually isomorphic, straight anthesis and a connective without appendages, not prolonged and thickened at the base of the thecae. Aciotis, Comolia, Fritzschia and Nepsera were traditionally associated with Marcetia in molecular and/or morphological studies (Martins, 1989; Santos, 2009; Almeda & Robinson, 2011; Michelangeli et al., 2013). In our analysis, Marcetia is resoved as sister to the clade formed by Fritzschia and Comolia section Tricentrum clade + Aciotis. In terms of morphological relationships, Aciotis lacks? a pedoconnective and appendages or they are occasionally poorly developed, as in Marcetia, but the connective of Aciotis spp. are different from Marcetia. In Comolia, species of Comolia section Tricentrum (the Comolia spp. in clade J) are those phylogenetically more closely related to Marcetia. In terms of distribution, Fritzschia and Marcetia occur predominantly in the campos rupestres (rocky fields) vegetation of the Espinhaço, whereas the Fritzschia + Comolia section Tricentrum clade is found in the southern part. This group of Comolia is distinguished from Marcetia mainly by the well-developed pedoconnective, modified at the filament insertion, into conspicuous lobes or auricules, as in F. erecta Cham., or have well-developed pedoconnective and ventral appendages. Also, Fritzschia has anthers that are purple/dark pink, whereas in Marcetia they are always yellow. Lastly, the phylogenetically distantly related genus Nepsera has a shortly developed pedoconnective, ventral appendages and a unique inflorescence pattern. Fritzschia and Comolia section Tricentrum clade This clade is strongly supported by molecular data and recognized mainly by its stems and leaves with glandular trichomes, and tetralocular ovary. Additionally, this clade is mostly endemic to the Espinhaço Range in Minas Gerais state, except for Comolia spp recovered here were treated in Comolia section Tricentrum by Cogniaux (1885). Comolia section Tricentrum, is actually more closely related to Sandemania (see above). Comolia section Tricentrum, is actually more closely related to Sandemania (see above). small tuberculate ventral appendages and dorsal appendages, except for F. erecta, in which the pedoconnective is absent or shortly developed with small auriculate appendages. In addition, these species have a prostrate and decumbent habitat, leaf lamina with translucent glands and hypanthium and ovary with secretory structures. Martins (1989) suggested that Fritzschia is morphologically related to Marcetia, differing by the presence of glands in the leaves and by becoming black when dried. However, these genera also differ in stamen features: in Fritzschia they are similar to those of the Comolia section Tricentrum, except in F. erecta. As the species of Comolia section Tricentrum are paraphyletic, share several morphological characters and geographical distribution with Fritzschia, and clade J has strong support in all phylogenetic analyses, the best option to circumscribe a monophyletic genus would be to include everything in this clade in Fritzschia. Aciotis clade Aciotis is morphologically easily recognized by the presence of tetramerous flowers, < 1.5 cm long, absence of tetramerous flowers, < in flooded areas or in waterlogged soils, in open and forested areas. Some studies have suggested that Aciotis has affinities with Nepsera (Clausing & Renner, 2001; Fritsch et al., 2004; Kriebel, 2008) and/or Marcetia (Almeda & Robinson, 2011). However, in our analysis Aciotis is moderately to strongly supported as sister to the Fritzschia and Comolia section Tricentrum clade. In the Marcetia alliance, Aciotis and Nepsera are the only genera that occur mainly in moist areas in forest edges. According to Freire-Fierro (2002), it is possible to recognize two main groups with some intermediate species, as suggested by Freire-Fierro (2002). The first group, which includes Aciotis annua (Mart. ex DC.) Triana, As filiform sclereids, biparous to double biparous to double biparous cymose inflorescences and dry capsular fruits. The second group includes A. circaeifolia (Bonpl.) Triana, A. indecora (Bonpl.) Triana, A. purpurascens (Aubl.) Triana and A. rubricaulis (Mart. ex DC.) Triana and A. acuminifolia (Mart. ex DC.) taxonomy of the Marcetia alliance were reconstructed in light of the molecular phylogenetic analysis, emphasizing their evolution inside the alliance (Fig. 3). Levels of homoplasy for each character were measured by CI and RI (Fig. 3). Levels of homoplasy for each character were measured by CI and RI (Fig. 3). combined were useful for the diagnosis of clades and genera. Floral merosity (Fig. 3A) Pentamerous flowers are the plesiomorphic for the Marcetia alliance. This state is widely distributed in almost all genera, but it is not an uncontested synapomorphy as the character is optimized to have two reversals to pentamerous flowers, once in Acisanthera s.l. and once in Ernestia section Pseudoernestia. There was also a secondary shift to tetramerous flowers are diagnostic for the Acisanthera bivalvis subclade and the Acisanthera s.s. subclade, except for Comolia ayangannae. Ovary pubescence (Fig. 3B) A glabrous ovary is the ancestral state in the Marcetia alliance and that the plesiomorphic state was retained in almost all branches of the Sandular ovary in a few members of the Marcetia alliance. the alliance arose probably by convergence. Although glandular ovaries have evolved independently in four different lineages, this character state proved to be useful to recognize the Ernestia s.s. subclade, which is the only clade of Ernestia with a glandular ovary. Also, in Acisanthera s.l., the glandular ovary is an autapomorphy for A. tetraptera Ovary locule number (Fig. 3C) The number of ovary locules is reduced to two to four in the Marcetia alliance from five in the outgroups. This character has played an important role in the circumscription of genera and sections in the Marcetia alliance, but it is highly homoplastic with multiple character state transitions inferred by our reconstructions. In the Marcetia alliance and related tribes such as Microlicieae and Rhexieae, the number of ovary locules is commonly equal to or smaller than the number of petals, except in Melatomeae s.s. which has a pentalocular ovary and tetra- or pentamerous flowers (Michelangeli et al., 2013). Although homoplastic, the ancestral state (two locules) was retained in the Comolia montana clade, Acisanthera tetraptera, the Acisanthera bivalvis subclade, the Acisanthera bivalvis subclade, the Acisanthera and, by reversal, in Aciotis. Although the same number of ovary locules evolved independently in unrelated groups, this character is more conserved in monophyletic genera and can be potentially useful as diagnostic when associated with other characters. Filament/anther angle at anthesis (Fig. 3D) Straight anthers are uncommon in capsular-fruited Melastomataceae, which are usually characterized by the strongly curved anthers. Cogn., which is one of the most distinctive members of Microlicieae (Fritsch et al., 2004). The reconstruction of this character in the group. However, straight anthers evolved, independently, at least four or five times in unrelated clades of the group. Despite the high level of homoplasy, this character can be useful to characterize some clades of non-monophyletic genera. In Comolia, for example, only the C. montana clade has slightly straight anthers, whereas the other clades retained the ancestral state. The monophyletic Siphanthera, Marcetia and Aciotis (clades F, I and K, respectively) also have straight anthers. In these genera the pedoconnective is absent or, when present, it is not articulated at the filament insertion. Pedoconnective was treated by Clausing & Renner (2001) as a possible synapomorphy for an expanded concept of Melastomeae, Microlicieae and Rhexieae In the Marcetia alliance the pedoconnective varies widely; it may be well developed or reduced. The reconstruction analysis showed that this structure was lost in a few members of the Marcetia had pedoconnectives and that it was lost in more derived lineages of Marcetia, except in M. candolleana A.K.A.Santos & A.B.Martins and M. grandiflora Markgr., where it is present and probably represents a reversal. Marcetia is mainly characterized by a connective that is not prolonged, but is thickened at the base of the thecae. In future research, the evolution of the androecium should be investigated using morphometric tools to characterize this variation. In Aciotis, Nepsera and Siphanthera, the pedoconnective is poorly developed and briefly prolonged below the thecae. Anther fertility (Fig. 3F) Most genera of Melastomataceae are diplostemonous, having two cycles of stamens. The plesiomorphic state in the Marcetia alliance is for both cycles to be fertile and this character state was conserved in most genera. A single fertile cycle is an important character to characterize Siphanthera, in which only two species (S. cowanii Wurdack and S. paludosa Cogn.) have diplostemonous flowers. The remaining species can have an antepetalous cycle with one to four staminodia, or it may be absent altogether. According to Almeda & Robinson (2011), the loss of fertile stamens among the species of Siphanthera does not seem to have any consistent evolutionary pattern. Heteranthery has occurred to varying degrees in all major clades of the alliance. Our analyses also did not recover any apparent pattern and we agree with Almeda & Robinson (2011) that knowledge about the pollinator spectrum for each species may help in understanding the forces that are driving these losses. Other characterization of clades were also investigated, but were not included in the results because it was difficult to code them and establish homology hypotheses or they were continuous. Nevertheless, some are useful for characterization of genera or groups of species. The stamens of the Marcetia alliance, for example, although highly variable, can be used to recognize some genera by the shape of the ventral connective appendages. In Ernestia s.s., the stamens of the Marcetia alliance, for example, although highly variable, can be used to recognize some genera by the shape of the ventral connective appendages. have a long pedoconnective and two aristate ventral appendages. This type of appendages, with developed long caudate projections, is common only in Ernestia and related groups, such as Appendicularia. In most other genera, the ventral appendages tend to be bilobed or bituberculate, with broad variation in size between genera Conclusions and perspectives This study represents a major step towards understanding generic relationships in the Marcetia alliance. Sampling was significantly expanded data set, we confirmed the monophyly of the Marcetia alliance and the genera Aciotis, Fritzschia, Marcetia and Siphanthera. The paraphyletic Comolia, Ernestia and Macairea have been traditionally diagnosed on the basis of a few, broadly distributed, homoplastic characters, and should be re-circumscribed based on well-supported clades and diagnostic morphological characters. A potential difficulty for taxonomic re-circumscriptions in Melastomataceae is the lack of synapomorphies or even of a set of morphological characters treated as diagnostic in the past appear to have evolved independently, a problem also seen in Miconieae (Michelangeli et al., 2004; Goldenberg et al., 2008; Kriebel et al., 2013). Due to this pervasive presence of homoplasy, character combinations could be more useful to diagnose well-supported clades associated with distributional and ecological data. This approach will be essential to understand and characterize different groups. In our study, we found few uncontested synapomorphies for larger clades, in which the species tend to occur in the same environment and, hence, biogeographical region. With these criteria in mind, our results suggest that several taxonomic realignments are necessary in the Marcetia alliance. However, additional sampling of taxa and markers could potentially improve resolution and enable a more meaningful interpretation of the morphological and biogeographical patterns for the recovered clades. For example, Ernestia and Comolia should be segregated into two or more genera. Generic recircumscriptions are also necessary for Macairea and Acisanthera. All four clades of Comolia are morphologically well characterized or geographically structured and our results support the recircumscription of this genus based on the recognition of monophyletic units. As currently understood, Macairea is paraphyletic. However, more taxa and probably also markers are needed to clarify relationships in this genus and with Ernestia. Another approach with potential to be investigated in the Marcetia alliance is the evolution of morphological characters, such as androecium and seeds. Understanding the evolution of these structures may provide some clues to the colonization of disjunct habitats such as the campos rupestres of the Espinhaço Range, cerrado of central Brazil, Amazonian savannas, restingas of northern and north-eastern Brazil and the Guayana highlands by the genera of this alliance.Lastly, three genera that may potentially be part of the Marcetia alliance remain unsampled: Comoliopsis, Loricalepis and Perhaps even closely related to Comolia montana (see above). Loricalepis is a poorly collected genus from northern Brazil characterized by tetramerous flowers and anthers without appendages or pedoconnectives, which would suggest a relationship with the Marcetia alliance (Brade, 1938; Pereira, 1959). Moreover, its leaves are similar to some Macairea spp. However, the seeds of Loricalepis are typically 'tibouchinoid' and the apex of the ovary is public second (Brade, 1938; Pereira, 1959). 1938; Pereira, 1959; Whiffin & Tomb, 1972), characters typically associated with core Melastomeae (Michelangeli et al., 2013). Poteranthera is a genus of uncertain affinities, with three species of tiny, tetramerous herbs from savannas of Brazil and Venezuela that at times has been suggested to be near Acisanthera or Siphanthera (Kriebel, 2012). Acknowledgements We thank the curators and staff of ALCB, BHCB, CEPEC, HUEFES, HUFU, INPA, IAN, MG, MIRR, RB, SP, SPF, NY and US for specimen loans or assistance during visits and the Brazilian conservation bodies ICMBio and IEF Minas Gerais for scientific collection permits. Financial support was provided by Fundação de Amparo a Pesquisa do Estado de Minas Gerais - FAPEMIG (PPM-00226-12), Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - CAPES (PNADB/UFMG-922/2010), Conselho Nacional Science Foundation - NSF (DEB-1343612 and DEB-1140409). This research was supported by scholarships from CAPES, FAPEMIG and CNPq (Pq-2). The first author thanks K. Sosa and M. Sewell for their assistance in the laboratory of the Cullman Program for Molecular Systematics at NYBG and Olivier Gaubert and F. Fajardo-Gutiérrez for the photographs. References , , , . Recovery of plant DNA using a reciprocating saw and silica-based columns. : -. , . New combinations and new names in some Brazilian Microlicieae (Melastomataceae), with notes on the delimitation of Lavoisiera, Microlicia, and Trembleya. : -. , . A new species of embriologia na sistemática e na elucidação da apomixia em Melastomataceae Juss. : Universidade Estadual de Campinas. . Melastomataceae peruvianae. 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KU500949 Ernestia tenella (Bonpl.) D.C. Michelangeli, F. A., 386 (BH) Venezuela JQ730082 KU501027 JQ730295 - KU500957 Fritzschia erecta Cham. Guimaräes, P., 406 (RB) Brazil JQ730083 KF462849 JQ730296 - Fritzschia anisostemon Cham. Mota, N., 2694 (BHCB) Brazil KU501070 KU501017 KU500914 KU50117 V KU500957 Macairee andrus (Bonph.) Vnc Tiana Simth, S., 1705 (US) Brazil JQ730098 KF46285 JQ730302 - KU500957 Macairee andrus Guimaräes, P., 406 (RB) Brazil JY750091 Macairee lasophylla (Benth.) Wurdack Rocha, M. J. R., 376 (BHCB) Brazil KU501035 KU501135 KU500135 KU501135 KU500135 Macairee andrus Guimaräes, P., 406 (RB) Brazil JY730095 KF46285 (VT) Statis KU501135 KU501145 KU501135 KU501145 KU501135 KU501145 KU501135 KU501145 KU501135 KU501145 KU501135 KU501145 KU501145 KU500966 Marcetia andelas Ak. A., 558 (UFB) Brazil JQ730092 - - - Marcetia tariolia Nadundi Sanda Sanda K. A. A., 558 (UFB) Brazil JQ730092 - - - Marcetia tariolia Nadundi Sanda Sanda K. A. A., 558 (UFB) Brazil JQ730092 - - - Marcetia tariolia Nadundi Sanda Sanda K. K. A., 558 (UFB) Brazil KU501095 Marcetia viscida WU501035 KU501144 KU500966 Marcetia viscida Wu50145 KU500966 Marcetia viscida Wu501145 KU500966 Marcetia viscida KU501195 KU501145 KU500968 Marcetia viscida KU501135 KU501198 KU501148 KU5009797 Marcetia viscida WU501035 KU501148 KU500193 KU501148 KU500193 KU501148 KU500959 Marcetia viscida WU50133 KU501148 KU500959 Marcetia viscida WU50133 KU501148 KU500193 KU501148 KU500193 KU501148 KU500193 KU501148 KU500959 Marcetia viscida WU50148 KU50193 KU501148 KU500193 KU501148 KU500959 Marcetia viscida WU500133 KU501148 KU500193 KU501148 KU50019

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