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Phylogenetic relationships in *Brachyotum* and allies (Melastomataceae, Melastomateae): a reassessment of the limits of the genera

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In the past decade, several phylogenetic studies based on molecular data have been generated and changed our view on the evolutionary history and classification of Melastomataceae. Nonetheless, given the size of the family, some groups are still under-sampled and poorly understood, such as the clade formed by *Brachyotum* and allies in Melastomateae, including three genera, *Andesanthus*, *Brachyotum* and *Chaetogastra*. The principal objective of this work was to further test the relationships in this clade by increasing taxon and locus sampling and by including morphological character reconstructions. In this study, we included nuclear (nrITS, nrETS and *waxy*) and plastid sequences (*accD-psaI*, *psbK-psbL*, *trnS-trnG*) from 129 species and 29 genera of Melastomataceae, corresponding to *c*. 46.5% of the species belonging to the clade, and that were used to build phylogenetic hypotheses. We also estimated the evolution of 23 morphological characters through ancestral state reconstruction and the elevational ranges of the species. Our results recovered two major clades: (1) *Brachyotum*, with species traditionally recognized in *Brachyotum*, but also including a few species traditionally recognized in *Tibouchina*; and (2) *Chaetogastra*, with most species traditionally recognized in *Tibouchina,* mainly from Tibouchina sections *Pseudopterolepis*, *Diotanthera*, *Simplicicaules* and *Purpurella*. *Andesanthus* was placed as sister to *Brachyotum* and allies in previous phylogenetic analyses; however, in this study it has been recovered as sister to the clades formed by *Heterocentron* and allies, *Monochaetum* and allies, and *Brachyotum* and allies. Four morphological characters can be useful to distinguish genera and clades among *Brachyotum* and allies: habit; flower position; the angle formed by the petals in relation to the hypanthium; and stamen arrangement. We also find that species in the *Brachyotum* clade occur at higher elevations (1500–4700 m) than *Chaetogastra* spp. (sea level to *c*. 3200 m, but more common at lower elevations, *c*. 600 to 1800 m). Based on all this evidence we propose the maintenance of *Brachyotum* as a genus segregated from the recently reinstated *Chaetogastra*. This work is a contribution to the systematics of Melastomateae, with an improvement in the resolution of the trees in relation to previous phylogenetic analyses, indicating that subclades have a strong relationship with geographical distribution.

ADDITIONAL KEYWORDS: *Andesanthus* – *Chaetogastra* – character reconstruction – elevational reconstruction – molecular markers – rogue taxa – *Tibouchina*.

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INTRODUCTION

Melastomateae ["Melastomeae" *sensu* Renner (1993)] are the third most species-rich tribe of Melastomataceae (Michelangeli *et al.*, 2020). They have a pantropical distribution and include *c.* 870 species in 47 genera. Most of the diversity is concentrated in the Neotropical region, with *c.* 570 species in 30 genera (Renner, 1993; Michelangeli *et al.*, 2013). Molecular phylogenetic analyses of Neotropical Melastomateae have shown that the traditionally accepted genera (*sensu* Cogniaux, 1885, 1891) are not monophyletic (Michelangeli *et al.*, 2013; Guimarães *et al.*, 2019). This is the case for the polyphyletic *Tibouchina* Aubl. (*sensu* Cogniaux, 1885, 1891), with species recovered in three clades: (1) *Brachyotum* (DC.) Triana and allies; (2) *Pleroma* D.Don; and (3) *Tibouchina s.s.* (Michelangeli *et al.*, 2013; Guimarães *et al.*, 2019). Based on the results of Michelangeli *et al.* (2013), and anticipating a revised classification (Guimarães *et al.*, 2019), some species that would have been described in *Tibouchina* have already been described in *Chaetogastra* DC. (Meyer & Goldenberg, 2016) or *Pleroma* (Fraga & Guimaraes, 2014; Meyer & Goldenberg, 2014; Oliveira *et al.*, 2014; Guimarães & Da Silva, 2015; Freitas & Van Den Berg, 2016; Goldenberg & Kollmann, 2016; Meyer *et al.*, 2016; Rocha *et al.*, 2017; Meyer *et al.*, 2018). Moreover, some species have also been transferred to *Pleroma* (e.g. Meyer & Matos, 2017), including the genera *Itatiaia* Ule (Da Silva *et al.*, 2014) and *Microlepis* (DC.) Miq. (Romero & Versiane, 2014). However, it was only recently that Guimarães *et al.* (2019) proposed more comprehensive taxonomic rearrangements to adjust the classification of *Tibouchina*. Under this new classification, *Tibouchina* is restricted to a group of 30 species from *Tibouchina* section *Tibouchina* (as section *Eutibouchina* Cogniaux in Cogniaux, 1885, 1891) and *Tibouchina* section *Barbigerae* (Naudin) Cogn. *Pleroma* has been resurrected and it now contains 157 species; in addition to the species formerly included in *Microlepis* and *Itatiaia*, it also includes *Svitramia* Cham. and *Tibouchinopsis* Markgr. *Chaetogastra*, with 117 species, has also been resurrected, and a new genus *Andesanthus* P.J.F.Guim. & Michelang., with nine species has been described. *Brachyotum*, with 55 species, has been maintained. *Andesanthus*, *Brachyotum and Chaetogastra* comprise the "*Brachyotum* and allies" clade (Fig. 1; Michelangeli *et al.*, 2013; Guimarães *et al.*, 2019).

However, relationships among *Brachyotum* and allies are far from settled due to the lack of strong support for major groups in this clade and to the moderate taxon sampling in previous analyses [e.g. only *c.* 27% of the species in the clade were sampled in the previous phylogenetic analysis (Guimarães *et al.*, 2019)]. This clade contains *Andesanthus*, that includes species from *Tibouchina* section *Lepidotae* Cogn. (*sensu* Cogniaux, 1891; Todzia & Almeda, 1991), *Brachyotum* and species transferred to *Chaetogastra* from *Tibouchina* sections *Pseudopterolepis* (Triana) Cogn., *Diotanthera* (Triana) Cogn., *Simplicicaules* (Naudin) Cogn., *Octomeris* Cogn. and *Purpurella* (Naudin) Cogn. *Andesanthus* has a mostly Andean distribution, with species that occur in high-elevation forests in Venezuela, Colombia, Ecuador and Peru, and two species in montane forests of Costa Rica and Panama (Todzia & Almeda, 1991; Guimarães *et al.*, 2019). *Brachyotum* is restricted to the Andes, and its species are found in high-elevation forests, paramo or puna vegetation, from Colombia to Argentina (Wurdack, 1953; Michelangeli *et al.*, 2013). *Chaetogastra* has a wider distribution and habitat diversity; it is found from Mexico and the Antilles to Uruguay and Argentina, mostly in tropical forests, high-elevation forests, grasslands, and pine-oak forests, but with some species in savanna and Amazonian vegetation (Todzia, 1999; Peralta, 2002; Meyer & Goldenberg, 2016; Guimarães *et al.*, 2019).

The *Brachytoum* and allies clade is mostly composed of species with persistent sepals in fruit, and anthers that, at least in part, are yellow or cream. However, its morphological heterogeneity is evidenced by the differences between *Brachyotum* and species formerly in *Tibouchina*, and by the number of sections of *Tibouchina* (*sensu* Cogniaux, 1891) with species that have been recently transferred to *Chaetogastra* or *Andesanthus*. *Brachyotum* is readily differentiated by the campanulate flowers with imbricate petals [vs. patent in the other genera of Melastomateae (Cogniaux, 1891; Wurdack, 1953)]. Species of *T.* section *Purpurella* were recognized by the truncate apex of the anther (vs. attenuate in the others), whereas species of *T.* section *Simplicicaules* would have conspicuous bracts or bracteoles encircling the floral bud, and often an unbranched habit. In the other sections (*T.* sections *Diotanthera*, *Pseudopterolepis* and *Octomeris*) the flowers would have inconspicuous bracts or bracteoles and would be pedicellate. *Tibouchina* sections *Diotanthera*, *Pseudopterolepis* and *Octomeris* were distinguished by the number of floral parts: tetramerous in *T.* section *Pseudopterolepis*; pentamerous in *T.* section *Diotanthera*; and octamerous in *T.* section *Octomeris* (Cogniaux, 1891). Most of the species positioned in the sections of *Tibouchina* mentioned above are currently placed in *Chaetogastra* (Guimarães *et al.*, 2019). Species of *Tibouchina* section *Lepidotae* (now in *Andesanthus*), can be recognized by their lepidote indument, free bracts, persistent calyx lobes and glabrous stamens (Todzia & Almeda, 1991).

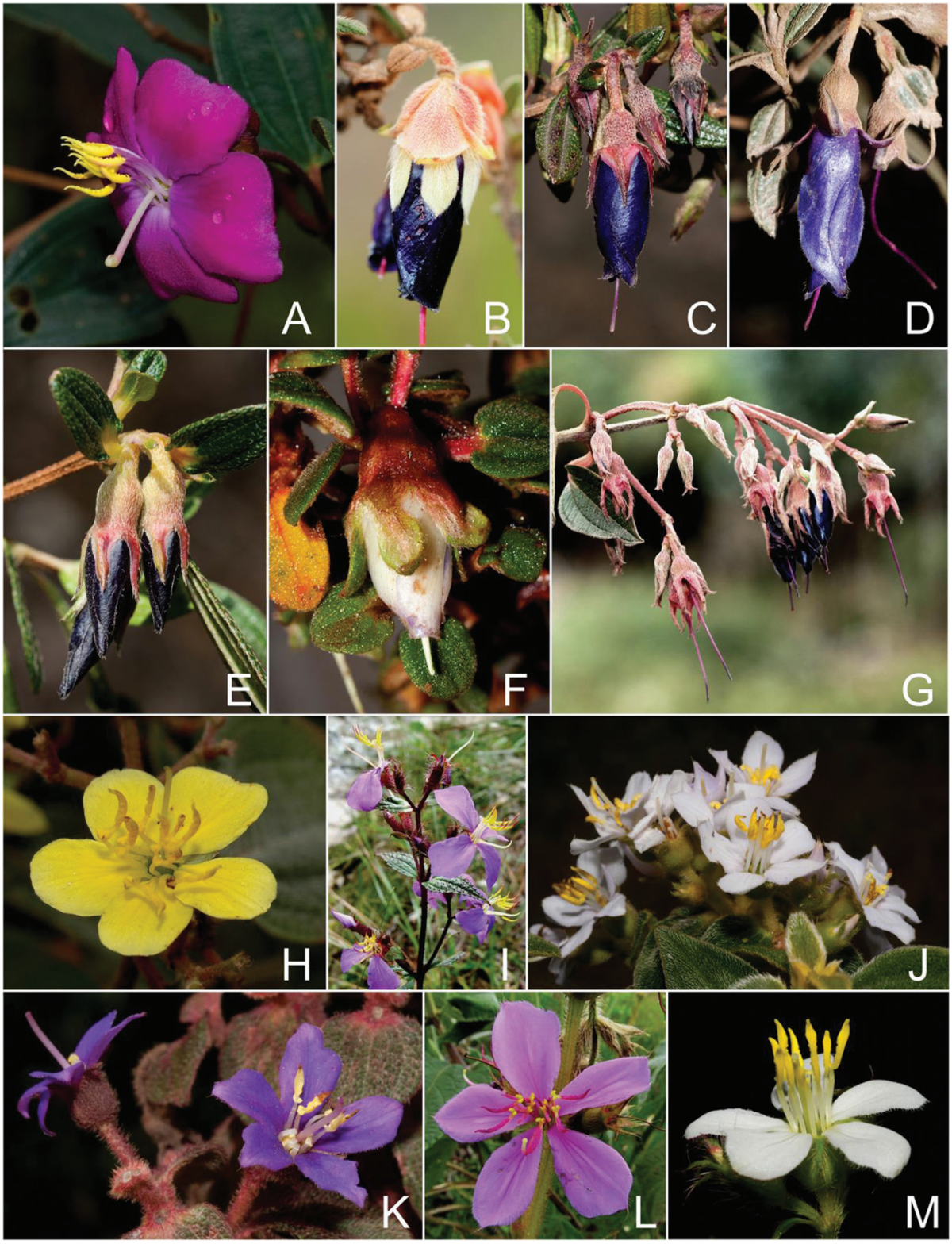

Figure 1. Species in the ingroup. A, *Andesanthus lepidotum.* B, *Brachyotum cogniauxii*. C, *Brachyotum grisebachii.* D, *Brachyotum huancavelicae*. E, *Brachyotum lutescens*. F, *Brachyotum parvifolium*. G, *Brachyotum quinquenervis*. H, *Chaetogastra citrina*. I, *Chaetogastra cristaensis*. J, *Chaetogastra decora.* K, *Chaetogastra dimorphophylla*. L, *Chaetogastra gracilis*. M, *Chaetogastra longifolia*. (A-H, J-K and M: Fabián Michelangeli; I and L: Fabrício Schmitz Meyer).

Although Guimarães *et al.* (2019) chose to recognize *Andesanthus*, *Brachyotum* and *Chaetogastra*, several issues remain to be resolved. First, the support for *Andesanthus* as part of the *Brachyotum* and allies clade remains weak. Second, the distinction between *Brachyotum* and *Chaetogastra* remains complicated because some Andean *Tibouchina* spp. (with floral morphology that is similar to *Chaetogastra* spp.) were positioned in the same subclade with *Brachyotum* spp., rendering *Chaetogastra* paraphyletic (Michelangeli *et al.*, 2013; Guimarães *et al.*, 2019). Moreover, only 49 out of the 181 species in the *Brachyotum* and allies clade have been sampled, and this study was based only on three molecular markers (Guimarães *et al.*, 2019). In this paper, we provide an improved phylogenetic hypothesis for the *Brachyotum* and allies clade based on a wider sampling, including more terminals and molecular markers. We also evaluate morphological characters that may help diagnose clades within the group, contributing to the recognition of natural taxonomic entities and improving the knowledge on the evolution of this clade.

MATERIAL AND METHODS

Taxon sampling

To study the phylogenetic relationships among *Brachyotum* and allies, we sampled 129 species from 25 genera of Melastomataceae (Supporting Information, Appendix S1). Sampling design was based on previous studies of Melastomateae, and the ingroup consisted of species of this tribe as indicated by Michelangeli *et al.* (2013); Guimarães *et al.* (2019). The ingroup consisted of species of Melastomateae. The number of species sampled by genus in relation to the total number of known species in *Tibouchina* and allies (see Guimarães *et al.*, 2019) is 5/9 for *Andesanthus*, 21/55 for *Brachyotum*, 1/4 for *Centradenia* G.Don, 62/117 for *Chaetogastra* (but with four species having two terminals each), 1/11 for *Chaetolepis* (DC.) Miq., 1/2 for *Desmoscelis* Naudin, 2/29 for *Heterocentron* Hook & Arn., 2/50 for *Monochaetum*, 1/5 for *Pilocosta* Almeda & Whiffin, 4/157 for *Pleroma* D.Don and 2/30 for *Tibouchina s.s.* [number of species according to Renner *et al.* (2007–); Guimarães *et al.* (2019)]. For the clade of lowland South American Melastomateae (see Michelangeli *et al.*, 2013: fig. 2, clade D) the number of species sampled by genus in relation to the total number of known species is 1/2 for *Pterogastra* Naudin, and 3/14 for *Pterolepis* [number of species according to Renner (1994a, b)]. For the clade of African Melastomateae (see Michelangeli *et al.*, 2013: fig. 2, clade E) it is 1/13 for *Heterotis* Benth. [number of species according to Renner *et al.* (2007–)]. Some species in the clade of *Chaetogastra* were sampled with more than one terminal because they have wide distributions, varietal subdivisions or confusing taxonomic delimitation (*sensu* Meyer, 2016). Not all varieties described for these species could be sampled, since not all of them were found and collected during fieldwork or recognized at variety level. For example, *Chaetogastra gracilis* (Bonpl.) DC. has been divided into 11 varieties (Cogniaux, 1885, 1891), but we included only two morphotypes that we considered distinct entities among these 11 names, despite not being formally segregated (Meyer, 2016).

This sampling represents an increment in the number of species sampled in the internal group (*Brachyotum* and allies) compared to the study of Guimaraes *et al.* (2019) with the addition of one *Andesanthus* sp., two *Brachyotum* spp. and 39 *Chaetogastra* spp. On the other hand, seven terminals from six taxa of *Brachyotum* and 11 terminals from nine taxa of *Chaetogastra* sampled in Guimarães *et al.* (2019) were not included in this study. These taxa were not included here because their sequences presented patterns that differed from most species of *Brachyotum* and allies on alignments and previous analyses [ML, with RAxML v.8 (Stamatakis, 2014)] and/or were resolved on long branches, possibly representing paralogous sequences. Other taxa were not included because they represented "rogue species" (see *Detecting rogue taxa*, below) or produced low quality sequences, affecting the quality of the final alignments.

The outgroup consisted of taxa from the tribes Marcetieae, Miconieae, Microlicieae and Rhexieae. In the Marcetieae, the sampling was based on two species of *Acisanthera* P.Browne, and one species each for *Aciotis* D.Don, *Ernestia* DC., *Macairea* DC. and *Marcetia* DC. In the Miconieae, it was based on one species of *Miconia* Ruiz & Pav. In the Microlicieae, it was based on one species of *Microlicia* D.Don, two of *Rhynchanthera* DC. and one of *Trembleya* DC. In the Rhexieae, it was based on one species of *Pachyloma* DC. and one of *Rhexia* L.

DNA extraction and molecular markers

DNA extraction, amplification and purification were done in two laboratories: Laboratório de Filogenia e Genética da Conservação de Plantas (Department of Botany, Universidade Federal do Paraná, Curitiba, Brazil) and the Cullman Program for Molecular Systematics (New York Botanical Garden, New York, USA). Sequencing reactions were performed at the University of Washington, USA (High Throughput Genomics Center) and Macrogen Inc. (Seoul, South Korea).

Total DNA was extracted from leaves of specimens collected in the field, stored in silica and then in a

regular freezer (-4 to -8 °C). Vouchers are deposited in BH, BHCB, CAS, COL, CUZ, FLAS, INB, MEXU, MO, NY, RB, UEC, UFB, UPCB, UPTC, US and USM herbaria [acronyms according to Thiers (2020-)]. Genomic DNA for each species was extracted either with 2× CTAB protocol (Doyle & Doyle, 1987) or using the DNeasy plant mini kit (Qiagen), following the modifications suggested by Alexander *et al.* (2007). Phylogenetic analyses were based on six molecular markers, including three nuclear sequences [nrITS (ribosomal internal transcribed spacer, including nrITS1 and nrITS2), nrETS (ribosomal external transcribed spacer) and *waxy* (a low-copy nuclear gene)] and three plastid intergeneric spacers (*accD-psaI*, *psbK-psbL*, *trnS-trnG*); for primers see Table 1. The markers nrITS, *accD-psaI* and *psbK-psbL* were chosen because there were sequences already available in GenBank for the internal and external groups from previous works (Michelangeli *et al.*, 2013; Rocha *et al.*, 2016; Guimarães *et al.*, 2019) or while waxy, nrETS and trnS-trnG have been shown to be informative for other genera in the family and *trnS-trnG* (Bécquer-Granados *et al.*, 2008; Reginato & Michelangeli, 2016a; Rocha *et al.*, 2016; Bochorny *et al.*, 2019).

Amplification, editing and alignment

DNA amplification was performed through PCR (polymerase chain reaction) reactions using kits from two brands. The first was the TopTaq Master Mix kit (Qiagen Biotechnology), with 20 µL final reaction volume, 1 µL total DNA sample, 6.6 µL purified water, 2 µL 10× dye, 0.2 µL of each primer (1 µM) and 10 µL TopTaq Master Mix. The second brand was the EconoTaq Plus Green kit, with 15 µL final volume, 0.7 µL total DNA sample, 7.5 µL EconoTaq Plus Green (Lucigen Technologies), 2 µL of each primer (1 µM), 0.75 µL spermidine and 2.05 µL ultra-pure water. DNA purification and sequencing reactions were performed at the University of Washington, USA (High Throughput Genomics Center) and Macrogen Inc. (Seoul, South Korea). The conditions of amplification (temperature and time) for the different markers used in this study are presented in Table 2.

Consensus sequences were obtained through bidirectional readings in the Staden Package software (Staden *et al.*, 2003) or Sequencher 4.10.1 (GeneCodes Corp.), and added to the matrix for further alignment. Low quality sequences were discarded. Multiple alignments were generated in

Table 1. List of molecular markers and primers used in this study

Locus	Primer	Sequence (5'–3')	Reference
nrITS	ITS92	5' AAG GTT TCC GTA GGT GAA 3'	Desfeux *et al.* (1996)
nrITS	ITS75	5' TAT GCT TAA ACT CCA CGG G 3'	Desfeux *et al.* (1996)
nrITS	ITS5a	5' CCT TAT CAT TTA GAG GAA GGA G 3'	Stanford *et al.* (2000)
nrITS	ITS8	5' ATT GAT GGT TCG CGG GAT TCT GC 3'	Michelangeli *et al.* (2004)
nrITS	ITS3	5' GCA TCG ATG AAG AAC GCA GC 3'	White *et al.* (1990)
nrITS	ITS241r	5' CAG TGC CTC GTG GTG CGA CA 3'	Michelangeli *et al.* (2004)
nrETS	18S-R	5' AGA CAA GCA TAT GAC TAC TGG CAG G 3'	Nicholas & Michelangeli (in prep.)
nrETS	NY-1428	5' ACG TGT CGC GTC TAG CAG GCT 3'	Nicholas & Michelangeli (in prep.)
accD–psaI	accD-769F	5' GGA AGT TTG AGC TTT ATG CAA ATG G 3'	Shaw *et al.* (2005)
accD–psaI	accD-299	5' CGG GAA AGA AAC CTC TTT TAA C 3'	Burke & Michelangeli (in prep.)
accD–psaI	psaI-75R	5' AGA AGC CAT TGC AAT TGC CGG AAA 3'	Shaw *et al.* (2005)
psbK–psbL	psbK	5' TTA GCC TTT GTT TGG CAA G 3'	Reginato *et al.* (2010)
psbK–psbL	psbL	5' AGA GTT TGA GAG TAA GCA T 3'	Reginato *et al.* (2010)
trnS-trnG	17SE	5' ACG AAT TCA TGG TCC GGT GAA GTG TTC G 3'	Bécquer-Granados *et al.* (2008)
trnS-trnG	26SE	5' TAG AAT TCC CCG GTT CGC TCG CCG TTA C 3'	Bécquer-Granados *et al.* (2008)
waxy	waxyF1	5' GTG GTC TTG GGG ACG TGC TC 3'	Reginato & Michelangeli (2016b)
waxy	waxyF2	5' ACA CTT GCG TGG TCG TYC AG 3'	Reginato & Michelangeli (2016b)
waxy	waxyR	5' AGC AGT GTG CCA RTC GTT GG 3'	Reginato & Michelangeli (2016b)

Table 2. Programming temperature and amplification time for the markers used in the study

Locus	*accD–psaI*	*psbK–psbL*	*trnS-trnG*	nrITS	nrETS	*waxy*
Denaturation	94 °C for 45 s	94 °C for 45 s	94 °C for 30 s	94 °C for 30 s	94 °C for 30 s	94 °C for 30 s
Annealing	58 °C for 45 s	55 °C for 45 s	Gradient 50–58 °C for 60 s	50 °C for 45 s	58 °C for 45 s	58 °C for 60 s
Extension	72 °C for 60 s	71 °C for 60 s	71 °C for 60 s	71 °C for 60 s	71 °C for 60 s	71 °C for 60 s

the web server of the software MAFFT v.7 (Katoh & Standley, 2013), using the "G-INS-1" strategy, and also with later manual adjustments in Mega 5 (Tamura *et al.*, 2011). The identification of the sequences was checked through "Basic Local Alignment Search Tool" (Altschul *et al.*, 1990). The alignments were then analysed in MaxAlign (Gouveia-Oliveira *et al.*, 2007), through its web server to remove non-informative gaps.

Phylogenetic analyses

The models of nucleotide substitution were selected through jModeltest 2.1.7, with the models evaluated for all markers, according to all criteria (Dariba *et al.*, 2012). The matrices were concatenated through Sequence Matrix (Vaidya *et al.*, 2011). The matrices were analysed (individually and concatenate) using maximum likelihood (ML) and Bayesian inference (BI). ML trees were generated in RAxML 8, as implemented through the CIPRES portal (http://www.phylo.org; Miller *et al.*, 2010) with default parameters, with 1000 bootstrap replicates for support evaluation. BI trees were generated in Mr. Bayes v.3 (Ronquist & Huelsenbeck, 2003), through the CIPRES portal using mixed models and independent parameters. Two runs with four Markov chains each for 150 000 000 generations were performed, sampling every 1000 trees, temperature 0.2 and discarding 25% of the trees from the first runs. The command "sumt" in Mr. Bayes v.3 was used to summarize trees from several independent analyses. Markov chain parameter runs were evaluated through Tracer 1.7 (Rambaut *et al.*, 2018), and we considered that the run was satisfactory when ESS was > 200. Clades were considered well supported when bootstrap values were ≥ 70% (ML) and posterior probability ≥ 0.90 (BI).

Detecting rogue taxa

"Rogue taxa" are terminals the position of which varies considerably across trees in phylogenetic analyses, leading to low support in the consensus tree. The detection and removal of these terminals may help to obtain trees with higher support (Aberer *et al.*, 2013). Here, potential rogue taxa were identified with the RogueNaRok method (Aberer *et al.*, 2013). The input data were ML trees from the concatenated RAxML analysis (both the bootstrap and the best tree). The parameters were kept as default: threshold = majority-rule consensus; optimize = support; maximum dropset size = 1; algorithm = RogueNaRok. RogueNaRok calculates the RBIC (relative bipartition information criterion) index for all terminals, from which the ones with values > 0.5 were removed (Aberer *et al.*, 2013).

Morphology: character evolution

Twenty-three discrete morphological characters were chosen to be optimized on the phylogenetic tree for *Brachyotum* and allies, to estimate ancestral states and identify possible diagnostic characters for major clades (Supporting Information, Appendix S2). Of these, 13 characters were binary and ten were multistate. Characters were selected because: (1) they have been used to distinguish the tribes included in the sampling [e.g. the type of the fruit, seed form; see Fritsch *et al.* (2004); Michelangeli *et al.* (2004); Michelangeli *et al.* (2013); Rocha *et al.* (2016)]; (2) they have been used to distinguish genera in core Melastomateae [e.g. number of functional stamens, persistence of the sepals on the fruits; see Michelangeli *et al.* (2013)]; or (3) they have been indicated as important in the distinction of genera that were previously recognized in *Brachyotum* and allies [e.g. flower position, presence of nectaries on the stamens and type of indument on the hypanthium; see Cogniaux (1885, 1891); Wurdack (1953); Meyer & Goldenberg (2016)]. Character states were coded based on protologues, monographs, regional floras, herbarium specimens (BHCB, BR, EFC, ESA, FI, G, HAS, HBR, HUFU, IAC, IBGE, ICN, IRAI, K, M, MBM, NY, P, SP, SPF, SPSF, SPSF, UB, UEC, UFOP and UPCB, acronyms according to Thiers, 2020-) and direct field observations.

Discrete characters were mapped on the maximum clade credibility tree using stochastic character mapping (Huelsenbeck *et al.*, 2003). Three models of morphological character evolution ("ER", Equal Rates; "SYM", Symmetric; "ARD", All Rates Different) were evaluated with fitDiscrete from the R package geiger v.2.0.6 (Harmon *et al.*, 2008). The best model under the Akaike information criterion (AIC) was selected. Stochastic mapping was implemented in the R package phytools v.0.6 (Revell, 2012), based on 1000 stochastic maps. Maps were built and summarized with the functions "make.simmap" and "describe.simmap" (Revell, 2012). Taxa with missing or polymorphic data were treated as having the same probability for each possible state. Plots were generated with basic functions of the R package ape (Paradis *et al.*, 2004).

Elevation range reconstruction

The elevational range of each species was estimated based on data collection on specimens deposited in the herbaria BHCB, BR, EFC, ESA, FI, G, HAS, HBR,

HUFU, IAC, IBGE, ICN, IRAI, MBM, P, SP, SPF, SPSF, UB, UEC, UFOP and UPCB (acronyms according to Thiers, 2020-). These data were supplemented with information from protologues, taxonomic treatments (Cogniaux, 1885, 1891; Wurdack, 1953, 1962; James, 1956; Almeda & Whiffin, 1981; Souza, 1986; Renner, 1990, 1994a, b; Todzia & Almeda, 1991; Guimarães, 1997; Todzia, 1999; Peralta, 2002; Gómez, 2004, 2009; Meyer *et al.*, 2010; Jørgensen *et al.*, 2014; Almeda, 2009; Meyer, 2016; Rocha *et al.*, 2018) and online databases such as Tropicos (http://www.tropicos.org/), C.V.Starr Virtual Herbarium (http://sweetgum.nybg.org/science/vh/) and the Smithsonian National Museum of Natural History (https://collections.nmnh.si.edu/search/botany/), always based only on specimens determined by specialists. Reconstructions were based on the median value of the elevational amplitude for each species, or on a single value, when we had information from only one specimen (Supporting Information, Appendix S3). Ancestral character estimation of elevation was performed using the function "contMap" in the R package phytools v.0.6 (Revell, 2012), with default options. This function estimates the ancestral states in each node using maximum likelihood and then interpolates the states along the edges.

RESULTS

Phylogenetic analyses

Our matrix includes 588 sequences, from which we generated 356: 80 for *trnS-trnG*, 65 for *accD-psaI*, 64 for *waxy*, 59 for *psbK-psbL*, 46 for nrITS and 42 for nrETS. The other 229 sequences were obtained from previous phylogenetic analyses: 63 for nrITS, 62 for *psbK-psbL*, 52 for *accD-psaI*, 43 for nrETS and nine for *trnS-trnG*. The most incomplete partition was for the *waxy* locus (63 taxa with missing sequences) followed by nrETS (41), *trnS-trnG* (38), nrITS (20), *accD-psaI* (11) and *psbK-psbL* (7; Supporting Information, Appendix S1). The common markers between this and previous (Guimarães *et al.*, 2019) phylogenetic analyses are *accD psaI*, *psbK psbL* and nrITS. Based only on the internal group, 41 new sequences were made available for the *accD psaI* region, 41 sequences for *psbK psbL* region and 31 for nrITS.

The concatenated matrix with all markers contained 6312 characters, and for *accD-psaI* 739 characters were potentially informative, 466 for *psbK-psbL*, 993 for *trnS-trnG*, 483 for nrETS, 590 for nrITS and 298 for *waxy*. The selected models for the BI analyses were GTR+G for the partitions with *accD-psaI*, *psbK-psbL*, *trnS-trnG* and nrITS, GTR+I+G for nrETS, and K80+G for *waxy*. The BI majority-rule consensus tree with combined nuclear (*waxy*, nrETS, nrITS) and plastid sequences (*accD-psaI*, *psbK-psbL*, *trnS-trnG*) presented the highest support values for clades and subclades within the ingroup (Figs 2, 3). The same clades of the combined dataset were recovered in the nuclear gene tree, although with a backbone with low support values (Supporting Information, Figs S2, S3).

Six terminals of *Brachyotum* [*Brachyotum coronatum* (Triana) Wurdack, *Brachyotum intermedium* Wurdack, *Brachyotum intermedium* Wurdack (specimen 2), *Brachyotum radula* Triana, *Brachyotum rostratum* (Naudin) Triana, *Brachyotum rostratum* (specimen2)] and three terminals of *Chaetogastra* [*Chaetogastra congestiflora* (Todzia) P.J.F.Guim. & Michelang., *Chaetogastra cordeiroi* F.S.Mey. & R.Goldenb. and *Chaetogastra* sp.11; Supporting Information, Fig. S1] had a RBIC index > 0.5 and were detected as "rogue taxa" and removed from the final analysis; after their removal, support values increased for several internal nodes in the ingroup (Supporting Information, Fig. S1).

The BI majority-rule consensus tree with combined nuclear (*waxy*, nrETS, nrITS) and plastid sequences (*accD-psaI*, *psbK-psbL*, *trnS-trnG*) had the highest support values for clades and subclades in the ingroup (Figs 2, 3). Most clades were recovered in the nuclear gene tree, although with a backbone with low support values (Supporting Information, Figs S2, S3). The only exception being the relationships between the Rhexieae, Microlicieae and Marcetieae. *Brachyotum* and allies were recovered as monophyletic with high support (BP = 100%, PP = 1). *Andesanthus* was recovered in core Melastomateae, as sister to *Centradenia* and allies+*Heterocentron* and allies+*Monochaetum* and allies+*Brachyotum* and allies (BP = 78%, PP = 1; Figs 2, 3). The sister group of *Brachyotum* and allies is a clade composed of *Centradenia* and allies+*Heterocentron* and allies+*Monochaetum* and allies, albeit with moderate to low support (clade A, BP = 44%, PP = 0.81; Figs 2, 3).

Brachyotum (*sensu* Cogniaux, 1891; Wurdack, 1953) formed a well-supported clade (subclades B+C; BP = 90%, PP = 1; Figs 2, 3), along with few species that were previously recognized in *Tibouchina* sections *Diotanthera* and *Octomeris* [some were recently transferred to *Chaetogastra* by Guimarães *et al.* (2019)]: *Chaetogastra decora* (Gleason) P.J.F.Guim. & Michelang. (≡*Tibouchina decora* Gleason), *Chaetogastra dimorphophylla* (Gleason) P.J.F.Guim. & Michelang. (≡*Tibouchina dimorphophylla* Gleason), *Chaetogastra pleromoides* (Naudin) P.J.F.Guim. & Michelang. [=*Tibouchina pleromoides* (Naudin) Macbr.], *Chaetogastra pulcherrima* (Gleason) P.J.F.Guim. & Michelang. (≡*Tibouchina pulcherrima* Gleason), *Tibouchina bicolor* (Naudin) Cogn., *Tibouchina calycina* Cogn. and *Tibouchina octopetala* Cogn. ex Britton. The *Brachyotum* spp. from subclades B and C are from the Andes, ranging from Bolivia to Colombia. Subclade B includes the type species of *Brachyotum*, *Brachyotum quinquenerve* (Ruiz & Pav.)

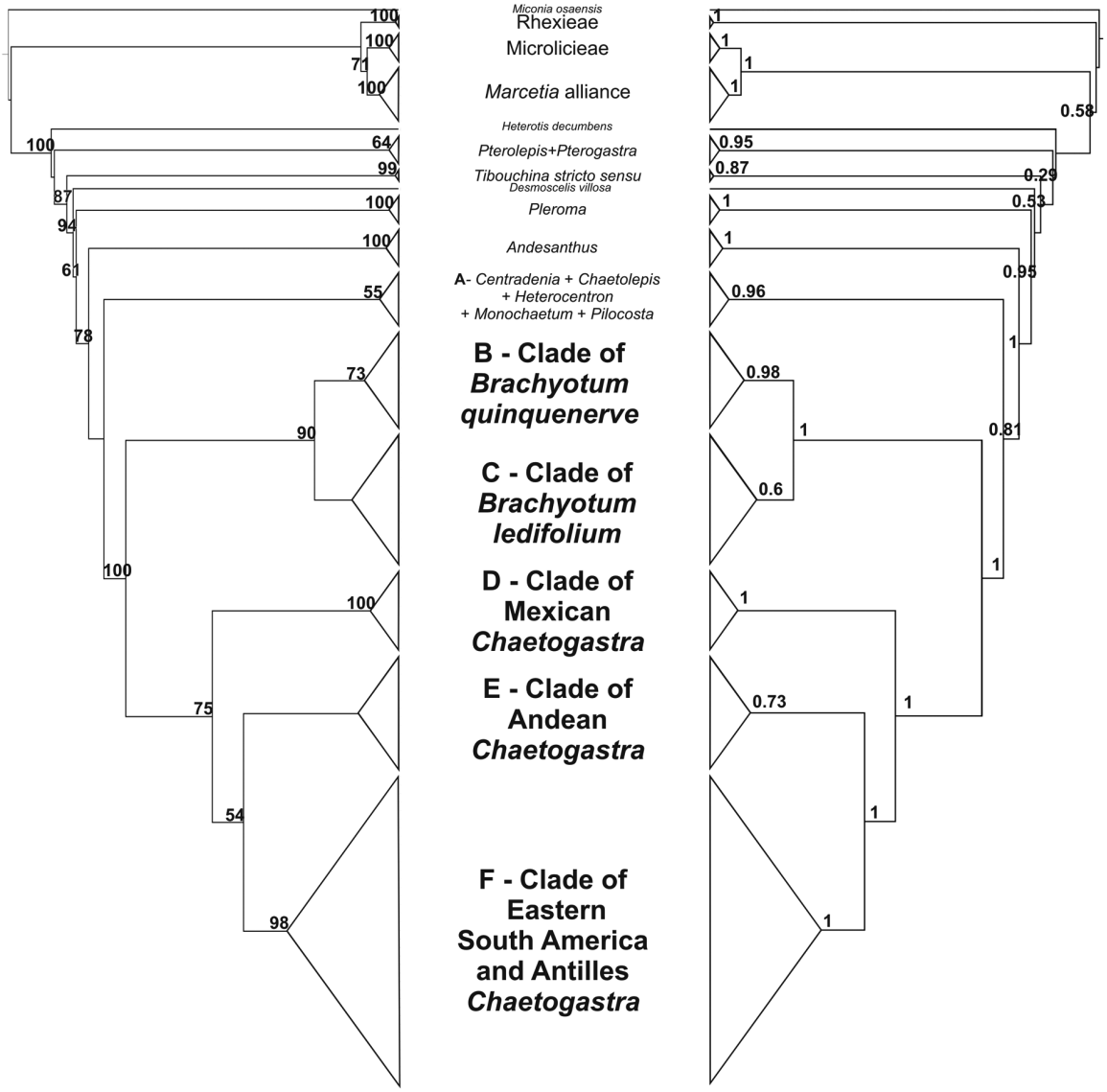

Figure 2. Summary of phylogenetic analyses of *Brachyotum* and allies based on the combined nuclear (*waxy*+nrITS+nrETS), and plastid (*accd-psaI+psbK-psbL+trnS-trnG*) data sets. ML analysis (left) with bootstrap support values on the branches and BI (right) with posterior probability values on the branches.

Triana, and also other species traditionally positioned in this genus (BP = 73%, PP = 0.98). The subclade C, named *Brachyotum ledifolium* (Desr.) Triana, also has species traditionally positioned in *Brachyotum*, but it also included species of *Chaetogastra* and *Tibouchina* (BP = 41%, PP = 0.6). Both subclades B and C showed internal nodes with support ranging from low to high (PP = 0.24–1.00; Fig. 3).

Most species traditionally recognized in *Tibouchina* sections *Pseudopterolepis*, *Diotanthera* and *Simplicicaules* and some species from *Tibouchina* section *Purpurella* (clades D+E+F) were also positioned in a well-supported clade in BI (BP = 75%, PP = 1; Figs 2, 3). This clade is named *Chaetogastra* here and includes three groups: (1) clade D has species from Mexico and Central America (BP = 100%, PP = 1); (2) clade E is Andean, with species ranging from Colombia to Argentina, and is the only one with low support values in *Chaetogastra* (BP = 49%, PP = 0.73); and (3) clade F has species predominantly from Brazil and Antilles, and a few widely distributed species. The type species of *Chaetogastra*, *Chaetogastra longifolia* (Vahl.) DC. was recovered in clade F (BP = 98%, PP = 1). Clade D, with the Mexican *Chaetogastra* is sister to clades E (Andean *Chaetogastra*)+F (Eastern South America and Antilles *Chaetogastra*). Clades D and E have several internal

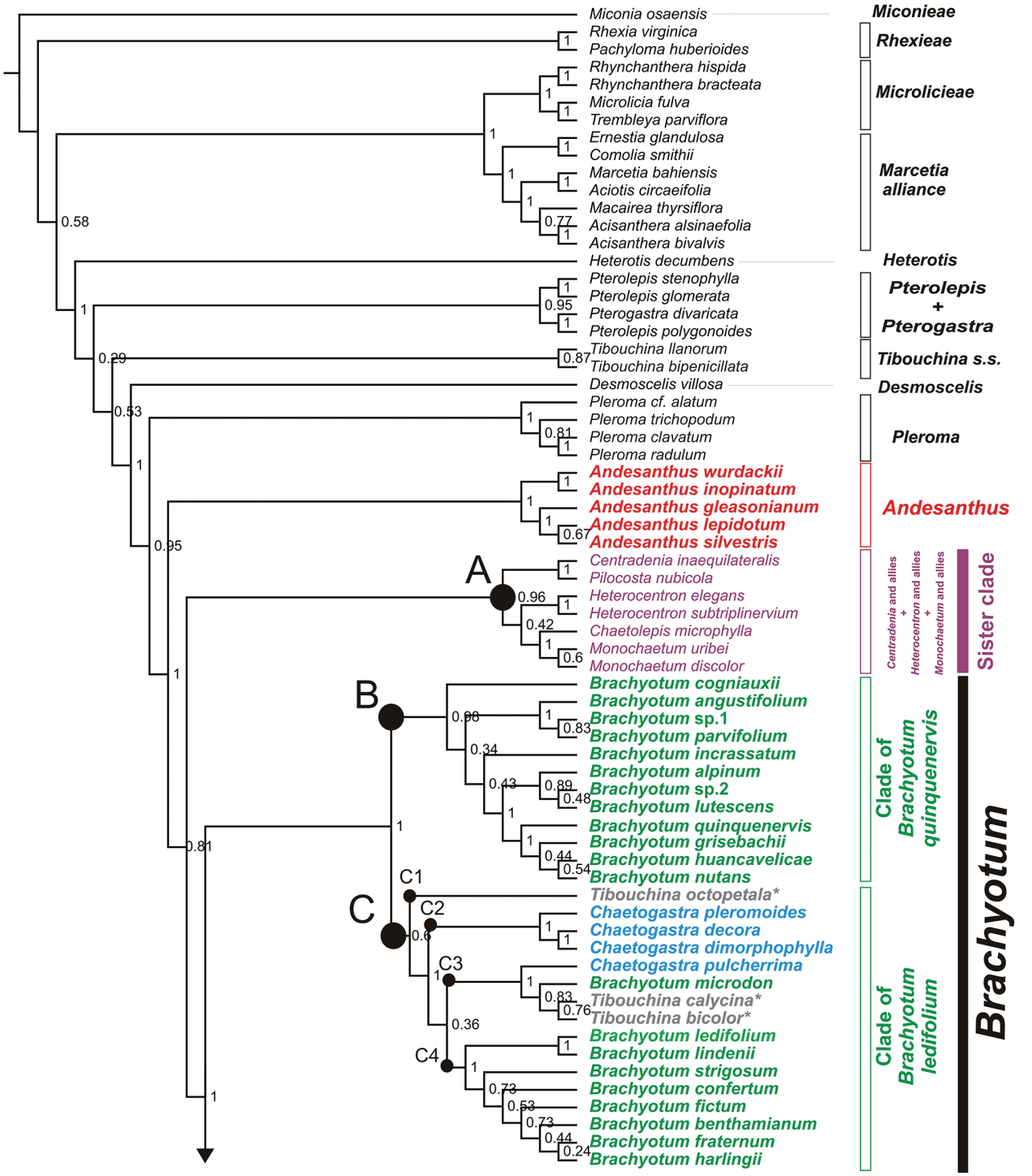

Figure 3. Consensus tree obtained from a Bayesian analysis of the combined nuclear (*waxy*+nrETS+nrITS) and plastid (*accd-psal*+*psbK-psbL*+*trnS-trnG*) data sets. Posterior probabilities are indicated at nodes. Terminals marked in red are *Andesanthus* species, in purple are species from the clades of *Heterocentron* and allies, and *Monochaetum* and allies, in green are *Brachyotum* species, in blue are *Chaetogastra* species, and in grey are species kept as *Tibouchina incertae sedis* in Guimarães *et al.* (2019). Arrows point to species with incongruent positioning. A-F represent the sister group and subclades inside Brachyotum and allies.

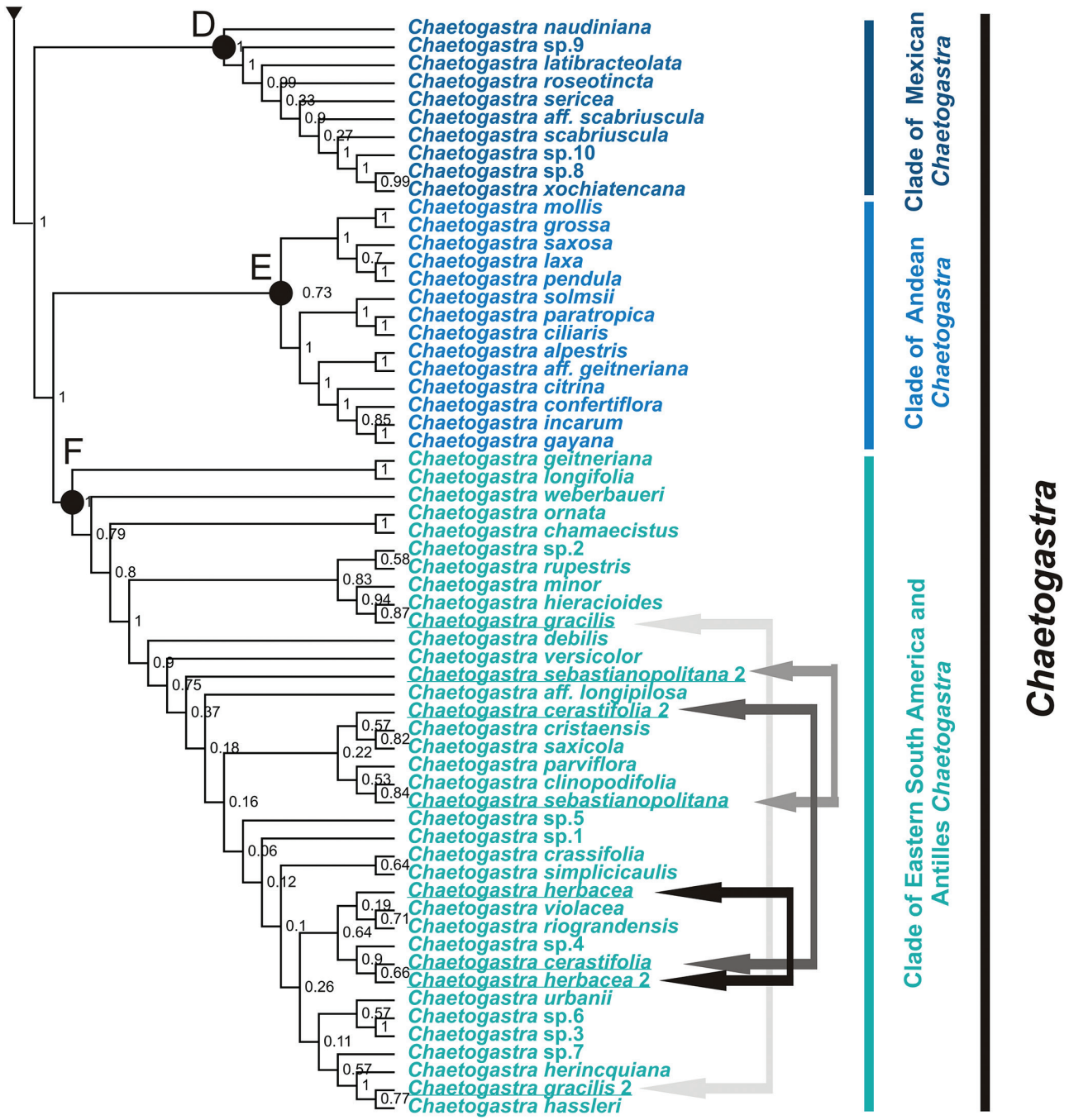

Figure 3. Continued.

nodes with high support values (PP = 0.9–1), whereas F has several internal nodes with low support (PP = 0.1–0.82; Fig. 3).

Character evolution

Four characters were useful for the recognition (or distinction) of the genera in the clade of *Brachyotum* and allies: habit, flower position, the angle formed by the petals in relation to the hypanthium and the arrangement of the stamens (Fig. 4); those characters were already used for the recognition of these genera in classic taxonomic treatments (Cogniaux, 1885, 1891; Wurdack, 1953). However, we did not find characters that could be used to recognize any of the subclades. Regarding habit, *Brachyotum* spp. are usually shrubs, whereas *Chaetogastra* spp. are mostly subshrubs. The flowers

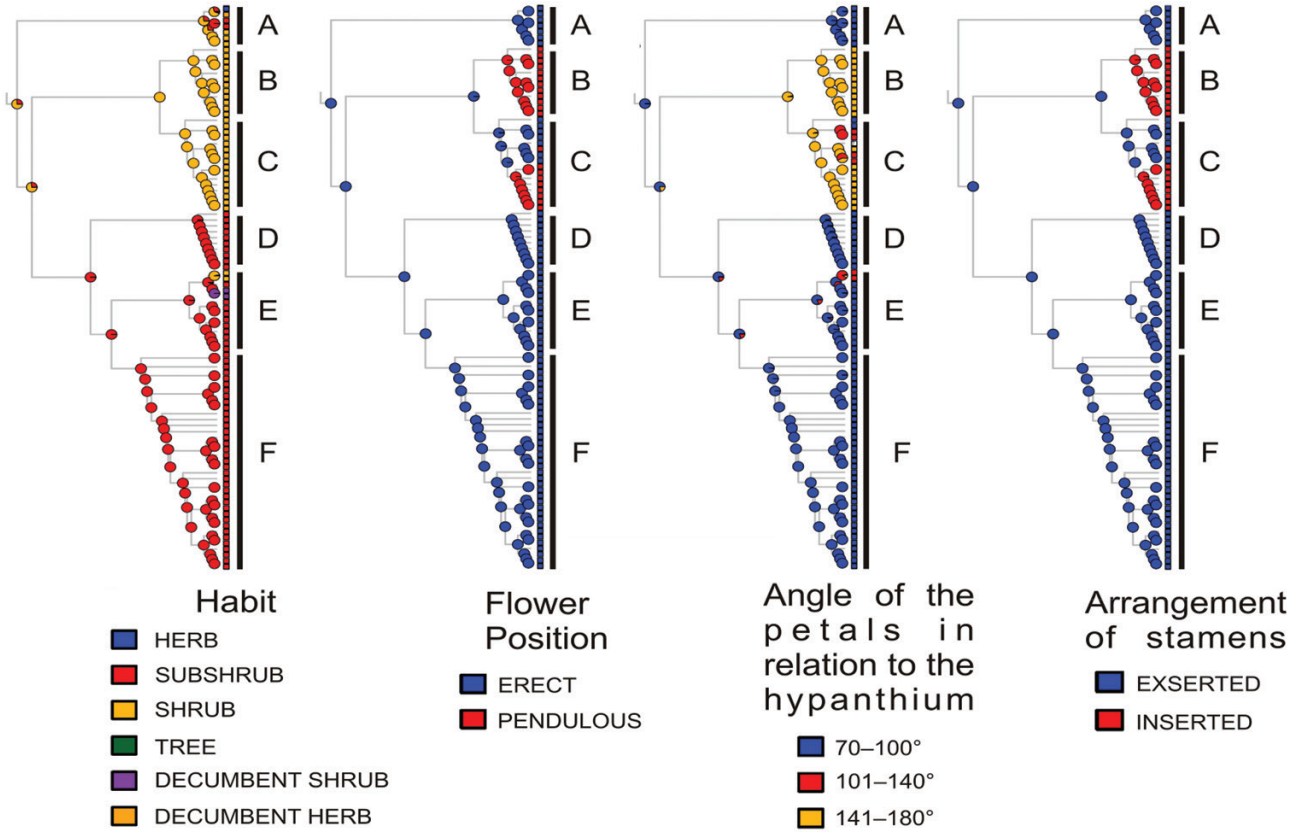

Figure 4. Reconstruction of informative morphological characters to the recognition of the genera in *Brachyotum* and allies, respectively: habit, flower position, angle of the petals in relation to the hypanthium, and arrangement of stamens.

are mostly pendulous, with erect petals (these angling 141–180° in relation to the hypanthium) in *Brachyotum* (with a few exceptions), whereas in *Chaetogastra* the flowers are always erect, with patent petals (these angling 70–100° in relation to the hypanthium). Only *Chaetogastra grossa* (L.f.) P.J.F.Guim. & Michelang. and *Chaetogastra mollis* (Bonpl.) DC. (clade E, Fig. 4) have petals that form a 101–140° angle in relation to the hypanthium. The stamens were mostly inserted in *Brachyotum* (with a few exceptions), and always exserted in *Chaetogastra*.

Elevational range reconstruction

There are differences in elevation range patterns for the species positioned in the *Brachyotum* clade (subclade B+C) and *Chaetogastra* (subclades D+E+F; Fig. 5). The species in the *Brachyotum* clade occur at high elevations on the eastern slope of the Andes, from 1500 to 4700 m. The species in the *Chaetogastra* clade occur from sea level to *c*. 3200 m, but they are more common at lower elevations. Although some *Chaetogastra* spp. may occur at > 2000 m (Supporting Information, Appendix S3), most species occur from 600 to 1800 m (Fig. 5).

DISCUSSION

Phylogenetic relationships among *Brachyotum* and allies

Our phylogenetic results show some differences from previous studies on this group (Michelangeli *et al.*, 2013; Guimarães *et al.*, 2019), notably, the position of *Andesanthus* within Melastomateae, the resolution in *Chaetogastra* and the resolution and support between *Chaetogastra* and *Brachyotum*. *Andesanthus*, which was previously recovered inside the *Brachyotum* and allies clade (Michelangeli *et al.*, 2013; Guimarães *et al.*, 2019), was recovered here as sister to a larger clade composed of *Centradenia* and allies+*Heterocentron* and allies+*Monochaetum* and allies+*Brachyotum* and allies. Our results from a broader ingroup sampling also allowed the recognition of a geographical structure for the clades in *Chaetogastra*: Mexican *Chaetogastra* (clade D); Andean *Chaetogastra* (clade E) and Eastern South America and Antilles *Chaetogastra* (clade F;

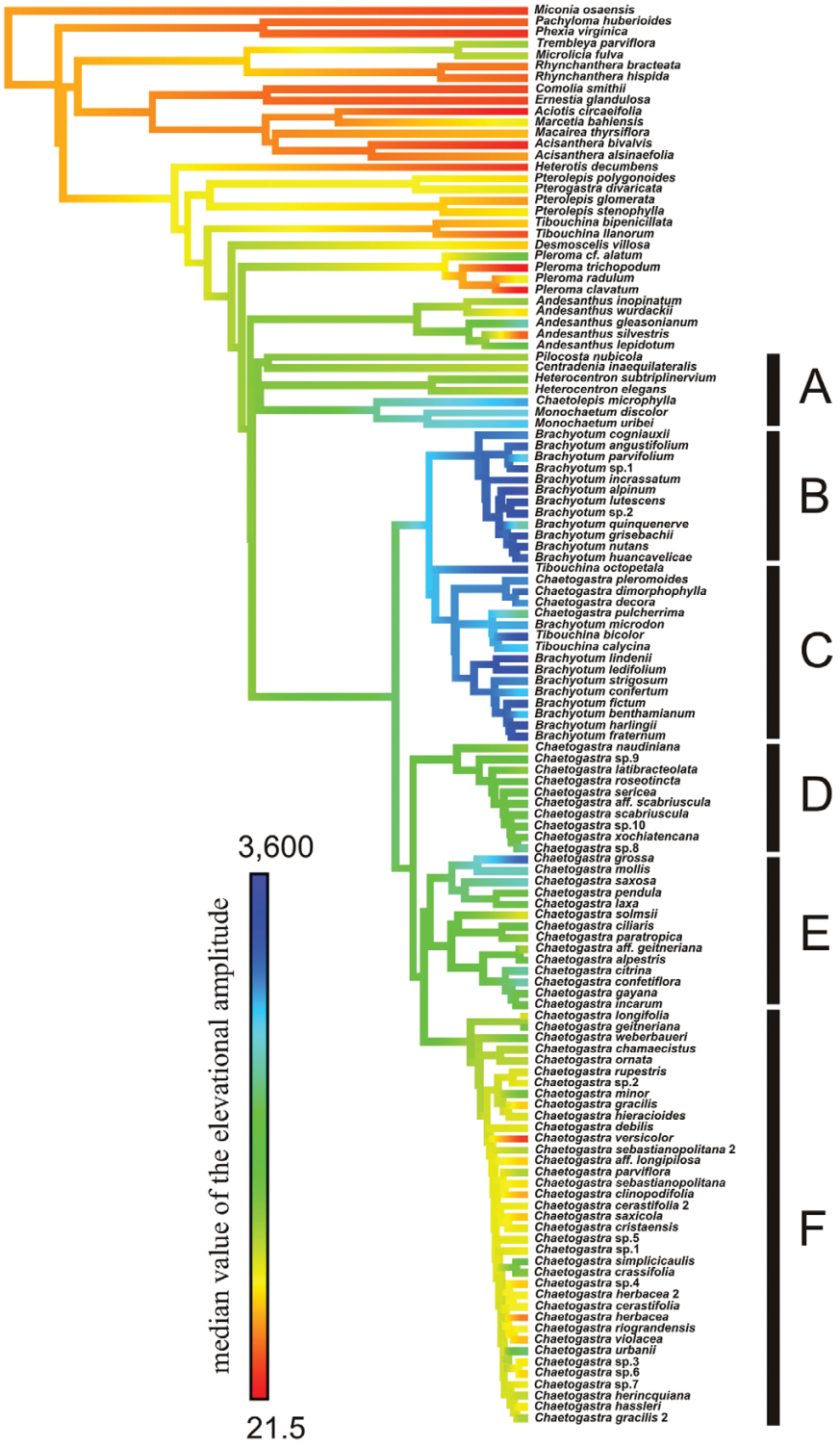

Figure 5. Elevation range reconstruction to *Brachyotum* and allies. Subclades (A-F) shown with black bars.

Figs 2, 3). Additionally, our estimates of ancestral states for selected morphological characters demonstrated that some characters may be useful for distinguishing *Brachyotum* and *Chaetogastra*.

Clade A, with *Centradenia* and allies, *Heterocentron* and allies and *Monochaetum* and allies, remains the sister group of *Brachyotum* and allies as previously suggested (Michelangeli *et al.*, 2013), although with

weak support in ML (BP = 44, PP = 0.81). The sampling for this clade is smaller than that of Guimarães *et al.* (2019), but with additional markers. The phylogenetic relationships of major clades obtained in our analyses are discussed in the next paragraphs.

Although the objective of this study was to test the monophyly of the genera in the *Brachyotum* and allies clade, our sampling across Melastomateae was broad enough to include other members of the large pedoconnective clade (see Michelangeli *et al.*, 2013; Guimarães *et al.*, 2019), and consequently we can make some general comments about them. A large clade composed of *Centradenia* and allies+*Heterocentron* and allies+*Monochaetum* and allies (clade A) was recovered as sister to a reduced *Brachyotum* and allies clade, as *Andesanthus* is now recovered as sister to this entire group. Plants from the clades of *Centradenia* and allies+*Heterocentron* and allies+*Monochaetum* and allies share (1) the subshrubby or shrubby habit, (2) vegetative and reproductive parts of the plants covered with trichomes, (3) erect flowers, (4) flowers with four or five petals, (5) hypanthium with a circular cross-section (except for *Pilocosta nubicola* Almeda, with a quadrangular section like all members of this genus), (6) petals positioned at 70–100º angle in relation to the hypanthium, (7) petals glabrous on the abaxial surface (except for *C. grossa*, with petals that are pilose on the abaxial surface), (8) twice as many stamens as petals, (9) exserted stamens, (10) the antesepalous stamens longer than the antepetalous stamens (except for *Monochaetum*, with the antepetalous stamens longer than the antesepalous), (11) glabrous filaments, (12) connectives with appendages, (13) appendages ventral (except for *Monochaetum*, with dorsal appendages), (14) appendages glabrous, (15) anthers with attenuate apex in most species, (16) glabrous style [except for *C. mollis*, *Chaetogastra paratropica* (Griseb.) P.J.F.Guim. & Michelang. and *Chaetogastra violacea* (Cogniaux) P.J.F.Guim. & Michelang., with pilose styles], (17) ovary with the apex covered with trichomes, (18) ovary with four locules (only in subclades B and F), (19) capsular fruits, (20) fruits with persistent sepals and (21) cochleate seeds (Supporting Information, Fig. S4).

The species in the *Centradenia* and allies and *Heterocentron* and allies clades occur mainly in tropical forests in Mexico and Central America, whereas those of *Monochaetum* and allies occur mainly at high elevations in tropical forests in the Andes, Mexico and Central America (Almeda, 1977, 1993; Michelangeli *et al.*, 2013; Alvear & Almeda, 2019). The distribution patterns in both subclades overlap that for *Brachyotum* and allies, in apparent agreement with the close relationship between these clades. As for the elevation, species in clades of *Centradenia* and allies and *Heterocentron* and allies occur between 200 and 2499 m, similar to most *Chaetogastra* spp.; species in the *Monochaetum* and allies clade occur between 1800 and 4250 m (Alvear & Almeda, 2019), which in turn is similar to most *Brachyotum* spp.

Brachyotum clade

The genus *Brachyotum* was proposed by Triana (1867) based on a section of *Arthrostemma* Pav. ex D.Don. In the original treatment for *Brachyotum*, most species in the genus were transferred from *Chaetogastra* section *Dicentrae* Naudin and *C.* section *Adesmia* Naudin (both sections with 19 spp.) and from *Rhexia* (10 spp). In the following revisions of the genus, Triana (1873) recognized 24 species, and Cogniaux (1891) recognized 32 species, divided in two sections. In the last revision of *Brachyotum*, Wurdack (1953) recognized 44 species and designated *B. quinquenerve* as the lectotype of the genus. After that, more species were described by Wurdack (1965, 1967, 1974, 1977, 1988) or by other specialists (Cotton, 2000, 2008; Ulloa, 2007); 55 species are presently recognized in the genus (Renner *et al.*, 2007–; Guimarães *et al.*, 2019).

Most species in the clade have pendant, nectar-producing flowers, with an imbricate corolla forming a long and narrow tube, erect petals in relation to the hypanthium, and isomorphic stamens, inserted inside the corolla tube pendant flowers. Seven species that were traditionally placed in *Tibouchina* but have been recovered in *Brachyotum* in our analysis [and also by Michelangeli *et al.* (2013) and Guimarães *et al.* (2019)], although with differences in the sampling and markers] differ from the pattern described above (i.e. erect, with the petals forming a 70–100º angle in relation to the hypanthium and exserted stamens). These species were usually placed in *Tibouchina* section *Diotanthera* (characterized by flowers with five petals); but some of them have flowers with 8 petals, which in turn is a feature usually associated with *Tibouchina* section *Octomeris* (Cogniaux, 1891). As discussed below, these changes in flower morphology may be associated with changes in pollinators, a pattern that is common in other groups of angiosperms (Thomson *et al.*, 2000; Perret *et al.*, 2007; Cronk & Ojeda, 2008; Thomson & Wilson, 2008) and even in Melastomataceae, from buzz-pollinated to vertebrate-pollinated.

As for the distribution, the species in subclade B (including *B. quinquenerve*) occur on the eastern slopes of the Andes, from Carchi (Ecuador) to Inquisivi (Bolivia), but with the highest richness in northern Peru. The species in subclade C (with *B. ledifolium*) also occur on the eastern slope of the Andes, but with two distinct distribution patterns: (1) subclades C1, C2 and C3 have species previously recognized in *Tibouchina* [except for *Brachyotum microdon* (Naudin) Triana] occuring from Huánuco (Peru) to Jujuy (Argentina) (southern pattern); (2) subclade C4 has species

previously recognized in *Brachyotum*, occurring from Boyacá (Colombia) to Zamora-Chinchipe (Ecuador), near the border with Peru (northern pattern). These patterns still need a more detailed investigation through specific biogeographic methods and an increased sampling.

The infrageneric classification of *Brachyotum* by Cogniaux (1891) followed mostly Naudin (1850) was based on the number and colour of petals, and the morphology of the stamens, more precisely, on the anther apex, and connective size and appendages. This division proved to be artificial, since subclade B has species traditionally placed in *Brachyotum* sections *Adesmia* (*Brachyotum alpinum* Cogn.) and *Dicentrae* (*Brachyotum naudinii* Triana, *B. quinquenerve* and *Brachyotum grisebachii* Cogn.) and other species that have not been assigned to any section, either because they were described recently or because their morphology does not allow a clear placement in one of Cogniaux's sections. The same pattern is repeated in subclade C, with species from *Brachyotum* sections *Adesmia* (*B. ledifolium*) and *Dicentrae* [*Brachyotum benthamianum* Triana, *Brachyotum lindenii* Cogn., *B. microdon* and *Brachyotum strigosum* (L.f.) Triana] and some species not assigned to any section. Wurdack (1953) had already disregarded the use of these sections in *Brachyotum* due to the difficulty in positioning species; the same author suggested that the species could be clustered according to the size of the anther pores but did not propose any formal infrageneric classification. Although this character could be useful, it has been seldom reported. This could be a promising field of study, but the information on pore size is not available in the taxonomic treatments (Wurdack, 1953); specific studies will be required to gather this information and reconstruct it into more complete phylogenetic trees.

Chaetogastra clade

Chaetogastra was described with three sections and 30 species, of which some are currently positioned in *Andesanthus*, *Brachyotum*, *Desmoscelis*, *Meriania* Sw., *Pleroma*, *Pterogastra*, *Pterolepis* and *Rhexia* (De Candolle, 1828). Several subsequent authors kept generic limits similar to the original concept (De Candolle, 1828), with differences in the placement of some taxa (Martius, 1829; Chamisso, 1834; Neumann, 1847; Naudin, 1850; Schlechtendal, 1854; Planchon, 1854–1855. Grisebach, 1864, 1866; Triana, 1873). *Chaetogastra* was proposed as a synonym under *Tibouchina* by Cogniaux (1885, 1891), and this circumscription was accepted in subsequent works until quite recently (Todzia, 1999; Gómez, 2004, 2009; Meyer *et al.*, 2009). The genus was resurrected after recent phylogenetic analyses (Michelangeli *et al.*, 2013; see Meyer & Goldenberg, 2016; Guimarães *et al.*, 2019), although with a different and narrower circumscription than originally proposed by De Candolle (1828). Under its current circumscription, *Chaetogastra* is the second largest genera of Melastomateae, with 117 species (Guimarães *et al.*, 2019).

Despite the absence of a consistent morphological synapomophy (i.e. a character with no homoplasy), *Chaetogastra* can be recognized by a set of characters. Most species are subshrubs, with erect, small flowers (1.9–4.8 cm diameter), usually smaller than the flowers in other clades inside *Tibouchina s.l.* (Cogniaux 1885, 1891), and patent petals. The stamens have glabrous filaments and either short or long connectives that always have ventral, bilobed appendages (yellow in most species); the anthers may be white, cream, yellow, lilac, purple or yellow with pink, red, lilac or purple spots, and may have a truncate to attenuate apex. The ovary is covered with trichomes or ending in a crown with trichomes on its apex, and the style is glabrous in most species. The fruits have persistent sepals, and the seeds are cochleate with a tuberculate surface (Meyer & Goldenberg, 2016). Most species in the genus are probably buzz-pollinated by bees (Franco *et al.*, 2011); however, *C. grossa*, in which the stamens produce nectar, is pollinated by birds or bats (Stein & Tobe, 1989; Varassin *et al.*, 2008). This species differs from most species in the genus also by the shrubby habit (vs. subshrubby in *Chaetogastra*), red petals that form a 101–140° angle in relation to the hypanthium (vs. predominantly dark lilac to purple, seldom white or yellow petals, positioned at a 70–100° angle in relation to the hypanthium); the petals also have a sparse to dense indument on the abaxial surface (vs. glabrous). *Chaetogastra mollis* also differs from the general pattern in *Chaetogastra* due to the shrubby habit, petals that form a 101–140° angle in relation to the hypanthium, and the style covered with trichomes. Probably due these characters, *C. mollis* was indicated as the possible ancestor of *Brachyotum* by Wurdack (1953).

Chaetogastra spp. are found from Mexico to Uruguay. Subclade D includes species from Mexico, Central America and an important endemism centre in Guerrero, Mexico (Todzia, 1999; Gómez, 2004, 2009). Subclade E is probably the richest in the genus, but it is still poorly sampled; it includes Andean species, most of them occurring in Bolivia and Peru with several species boundary and hybridization issues yet to be resolved. Species in clade F occur predominantly in eastern South America, with a high level of species richness and endemism in Brazil, mostly in the Atlantic Forest (clade F, Michelangeli *et al.*, 2013; Meyer, 2016; Meyer & Goldenberg, 2016). In this same subclade there are also some species endemic to the

Antilles. As an exception to the general pattern in the genus, i.e. narrowly distributed and endemic to near-endemic species, *C. gracilis* and *C. longifolia* have broad distributions, ranging from Mexico to Brazil and overlap their distributions with other species in subclades D and E. Four species in clade F are represented by two terminals, each of which are not positioned in the same subclades (*Chaetogastra cerastifolia* (Naudin) P.J.F.Guim. & Michelang and *C. cerastifolia* 2, *C. gracilis* and *C. gracilis*2, *Chaetogastra herbacea* DC.) P.J.F.Guim. & Michelang and *C. herbacea*2, *Chaetogastra sebastianopolitana* (Raddi) P.J.F.Guim. & Michelang and *C. sebastianopolitana*2; Fig. 3). These species were all divided into varieties by Cogniaux (1885, 1891); however, these were disregarded by Guimarães *et al.* (2019). The revisionary work for Brazilian species in this group [(Meyer, 2016) not published] recognizes some of these varieties as segregated entities, and on the basis of their position in the phylogenetic tree it is possible that they indeed represent distinctive taxa.

De Candolle (1828) recognized three sections in *Chaetogastra*, *Chaetogastra* sections *Monocentra* DC., *Diotanthera* Triana and *Bractearia* DC., based on the shape of the sepals, shape, number and arrangement of connective appendages and the colour of the petals. This classification is artificial, and several species listed in these sections actually belong to other genera, as mentioned above. The species groups in *Chaetogastra* seem to be strongly correlated with geographical distributions, a pattern that has been also found in other groups of Melastomataceae, such as the Bertolonieae *s.l.* (Bacci *et al.*, 2019) and the Miconieae (Michelangeli *et al.*, 2004, 2008; Reginato & Michelangeli, 2016a).

Morphological evolution

Four characters showed exclusive or almost exclusive states for the subclade of *Brachyotum*; when combined they can be considered diagnostic for the recognition of *Brachyotum*, but with a few exceptions (Fig. 4). The absence of morphological synapomorphies for some of the clades was also observed in other genera or clades studied in Melastomataceae (Michelangeli *et al.*, 2013; Rocha *et al.*, 2016; Veranso-Libalah *et al.*, 2017).

Habit

Plant habit is easy to assess for most species and thus is a valuable source of information. Species of Melastomateae can be herbaceous, subshrubs, shrubs or trees (or rarely herbs or decumbent shrubs). Subshrubs are dwarf shrubs with below-ground organs, woody stems only at the base of the plants, and annual aerial stems. Shrubs are usually larger plants with woody stems, and a greater investment in above-ground organs than subshrubs (Götmak *et al.*, 2016; Giroldo *et al.*, 2017). The plesiomorphic state in *Brachyotum* and allies seems to be shrubs, which was changed into subshrubs in *Chaetogastra*, although retained in the clade of *Brachyotum* and in the clade with *C. grossa*+*C. mollis* (Fig. 4, habit). Some studies demonstrate that the evolution of some shrub lineages to subshrubs may occur as an *in situ* adaptation to high-elevation climate conditions, as in different groups that occur on the Andean páramo (Sklenář *et al.*, 2011), but this needs further investigation. This apparently also occurred in other clades in core Melastomateae, such as *Heterocentron* and allies and *Monochaetum* and allies.

Only *Chaetogastra laxa* (Desr.) P.J.F.Guim. & Michelang. and *Chaetogastra pendula* (Cogn.) P.J.F.Guim. & Michelang. are decumbent shrubs, and they appear as sister species in the phylogenetic tree (subclade E, Fig. 3), demonstrating that the type of habit is related to phylogenetic relationships.

Flower position

Species of core Melastomateae have predominantly erect flowers pollinated by bees, a pattern that is also predominant across the family (Buchmann, 1983). The plesiomorphic state for flower position in *Brachyotum* and allies is erect, and this state changed into pendulous in the clade of *Brachyotum*, but was retained in some species (*Chaetogastra decora*, *C. dimorphophylla*, *C. pleromoides*, *C. pulcherrima*, *T. bicolor*, *T. calycina* and *T. octopetala*). The floral morphology is largely resulting from adaptation processes related to pollinators (Sprengel, 1793; Darwin, 1862; Fenster *et al.*, 2004; Reynolds *et al.*, 2009; Muchhala *et al.*, 2010). Pollination syndromes describe recurring adaptation to selection imposed by distinct pollinators; changes on them are important events along the evolution of lineages in Melastomataceae (Varassin *et al.*, 2008; Dellinger *et al.*, 2018, 2019). These events are generally reflected in the evolution of floral traces [as flower position, anther shape, style shape, petal colour, presence of nectaries etc. (Dellinger *et al.*, 2019)]. The floral traces in *Brachyotum* differ from the predominant pattern in the clade, and seem to be correlated to changes in pollinators, mostly favouring hummingbirds.

The angle of the petals in relation to the hypanthium and arrangement of the stamens

Species in core Melastomateae have flowers predominantly with patent petals (these angling 70–100° in relation to the hypanthium), a pattern that is also predominant among other Melastomataceae.

The same state is plesiomorphic for *Brachyotum* and allies, with a change to erect petals in *Brachyotum* (these angling 141–180º in relation to the hypanthium), but was retained in some species (*Chaetogastra decora*, *C. dimorphophylla*, *C. pleromoides*, *C. pulcherrima*, *T. bicolor*, *T. calycina* and *T. octopetala*). Most species in core Melastomateae have exserted stamens, and this is the plesiomorphic state in *Brachyotum* and allies. However, there was a change to inserted stamens in the clade of *Brachyotum*, with a later reversion in some species (the same species cited above). These characters seem to be correlated with flower position and are also clearly associated with a specialization for pollination by hummingbirds in *Brachyotum* (Stein & Tobe, 1989; Varassin *et al.*, 2008). In flowers with patent petals and exserted stamens, the resource offered for the pollinators is pollen, which can only be accessed by bees through vibratory movements (Buchmann, 1983). In the process of pollination by bees, which must occur in most *Chaetogastra* spp., it seems more likely that the involvement of the stamens by the corolla (for protection of the stamens) is not necessary; on the other hand, they must be exposed to allow the bees to grasp and to vibrate them. In the case of flowers with erect petals and inserted stamens, the pollinator reward is the nectar that is produced in the stamens; we suspect that this resource could be more easily accessed by other visitors (not pollinators) if not protected by the enclosing corolla.

Other characters

The basic chromosome number has been shown to be useful for the recognition of *Brachyotum* ($n = 10$) and for *Chaetogastra* ($n = 9$) (Meyer *et al.*, 2018). The predominant evolutionary pattern in *Chaetogastra* is stasis at the diploid level with interspecific polyploidy. For *Brachyotum*, it seems that there is stasis at the diploid level derived from a dysploid (Meyer *et al.*, 2018). Although there are only 45 species in the group with chromosome counts, these differences are strong evidence for the recognition of two distinct genera.

Heteranthery is prevalent among the species in the *Chaetogastra s.s.* clade. This may be related to specialization for pollination by bees with one whorl of stamens primarily having an attraction or reward function and the other set the reproductive function (see Renner, 1989; Luo *et al.*, 2008; Franco *et al.*, 2011; Ferreira & Araújo, 2016; Velloso *et al.*, 2018), in contrast to the pollination by hummingbirds in *Brachyotum*, in which the cycles of stamens have lower dimorphism [see descriptions by Wurdack (1953)].

Other characters such as the size and shape of the style and size of the anther pore also seem to be associated with specialization for mode of pollination (and associated with the other floral characters mentioned above). In *Chaetogastra*, most species have narrow anther pores that restrict the access to the pollen only for bees that vibrate the anthers; they also have a short to medium style (always smaller than in *Brachyotum* spp.), with a recurved apex, more suitable to visits by bees. On the other hand, most species in the *Brachyotum* clade have a rather elongated style with an erect apex that extends beyond the limits of the corolla, allowing it to touch the head of the hummingbird, and the anther pore is larger, which facilitates pollen release in visits by birds, even without vibration as performed by bees.

CONCLUSION

In summary, we present a more comprehensive phylogenetic hypothesis for the *Brachyotum* and allies clade, based on a wider taxonomic sampling [*c.* 46.5% of the species supposedly attributed vs. *c.* 27% in the previous phylogenetic analysis, see Guimarães *et al.* (2019)] and more molecular markers. We also present a reconstruction of 23 discrete morphological characters, and an elevational reconstruction shedding light on the morphological evolution in these lineages and providing diagnostic characters for the taxa. Taking this into account, we provide evidence to support the maintenance of *Brachyotum* as a genus segregated from *Chaetogastra*.

Brachyotum and allies form the largest clade in Melastomateae, with *c.* 172 species and deserve further sampling effort. For a better evaluation of the limits, both genera need taxonomic revisionary studies. In addition to phylogenetic analysis, studies on chromosome number variation, pollination, evolution of floral characters and historical biogeography are promising avenues for a better understanding of both the phylogenetic relationships and macroevolution in this clade.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Voucher information and GenBank accession numbers for the taxa used in this study.
Appendix S2. Morphological characters and character states scored in this study as primary homology hypotheses.
Appendix S3. Elevational values for species on the phylogeny.
Figure S1. Consensus trees obtained from ML analysis of the combined nuclear (*waxy*+nrETS+nrITS) and plastid (*accD-psaI+psbK-psbL+trnS-trnG*) data sets. A, tree generated before removal of the rogue species. B, tree generated after removal of the rogue species. Green markings indicate support value improvement. Names highlighted in red are rogue species.
Figure S2. Consensus tree obtained from a Bayesian analysis of the nuclear data sets (*waxy*+nrETS+nrITS). Terminals marked in red are *Andesanthus* species, in green are *Brachyotum* species, in blue are *Chaetogasta* species, and in grey are species kept as *Tibouchina incertae sedis* in Guimarães *et al.* (2019). Terminals marked in blue are *Chaetogastra* species (*sensu* Guimarães *et al.*, 2019).
Figure S3. Consensus tree obtained from a Bayesian analysis of the plastid data sets (*accd-psaI+psbK-psbL+trnS-trnG*). Terminals marked in red are *Andesanthus* species, in blue are *Chaetogasta* species (*sensu* Guimarães *et al.*, 2019). Terminals marked in in green are *Brachyotum* species, in blue are *Chaetogasta* species, and in grey are species kept as *Tibouchina incertae sedis* in Guimarães *et al.* (2019).
Figure S4. Reconstruction of 23 discrete morphological characters to *Brachyotum* and allies.