



## Phylogenetic relationships and distribution of New World Melastomeae (Melastomataceae)

FABIÁN A. MICHELANGELI<sup>1\*</sup>, PAULO J. F. GUIMARAES<sup>2</sup>, DARIN S. PENNEYS<sup>3</sup>, FRANK ALMEDA<sup>3</sup> and RICARDO KRIEBEL<sup>1,4</sup>

<sup>1</sup>*The New York Botanical Garden, Bronx, NY 10458, USA*

<sup>2</sup>*Jardim Botânico de Rio de Janeiro, Rio de Janeiro, RJ Brazil*

<sup>3</sup>*The California Academy of Sciences, San Francisco, CA, USA*

<sup>4</sup>*The Graduate Center, City University of New York, New York, NY, USA*

*Received 1 December 2011; revised 17 June 2012; accepted for publication 24 July 2012*

In this study we present a phylogenetic analysis of Melastomeae, focusing on the Neotropical members of the tribe, a group of *c.* 70 species in 30 genera. In total, 236 species, including outgroups (Miconieae and Meranieae) and representatives of the Microlicieae and Rhexieae, were sequenced for the nuclear ribosomal internal transcribed spacer (nrITS), and the plastid spacers *accD-psaI* and *psbK-psbL*. Melastomeae are not resolved as monophyletic because a group of mostly herbs and small trees with mostly tetramerous flowers (*Acanthella*, *Aciotis*, *Acisanthera*, *Appendicularia*, *Comolia*, *Ernestia*, *Fritzschia*, *Marcetia*, *Macairea*, *Nepsera*, *Sandemania* and *Siphanthera*) is nested between Rhexieae and Microlicieae. The remaining New World Melastomeae are not resolved as monophyletic, because a group of Old World genera (*Osbeckia*, *Melastoma*, *Tristemma* and allied genera) are nested in the tribe. The large genus *Tibouchina* is not monophyletic because *Brachyotum*, *Bucquetia*, *Castratella*, *Centradenia*, *Chaetolepis*, *Heterocentron*, *Itatiaia*, *Microlepis*, *Monochaetum*, *Pilocosta*, *Svitramia*, and *Tibouchinopsis* are nested in it, even although all of these genera are recovered as monophyletic. Each major clade has remarkable habitat and geographical integrity. The clade formed by *Tibouchina* and allies appears to have arisen in savannas in lowland South America and later expanded to forest, campo and high Andean biomes. At least two groups have radiated in eastern Brazil, and two other groups in the Andes and mountains of Central America. Niche conservatism and colonization of adjacent environments seem to have driven speciation in Neotropical Melastomeae. © 2012 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2013, **171**, 38–60.

**ADDITIONAL KEYWORDS:** capsular fruit – Microlicieae – niche conservatism – Osbeckieae – Rhexieae – *Tibouchina*.

### INTRODUCTION

Phylogenetic analyses published over the last 10 years have shown that traditional tribal delimitations (e.g. Triana, 1871; Cogniaux, 1891; Renner, 1993) in Melastomataceae are unnatural and in need of revision (Clausing & Renner, 2001; Michelangeli *et al.*, 2004; Renner, 2004a; Amorim, Goldenberg & Michelangeli, 2009; Penneys *et al.*, 2010; Penneys & Judd, 2011). Most of these analyses also recovered a clade that groups the species with anthers with pedoconnectives and capsular fruits, corresponding to tribes Melastomeae, Microlicieae and Rhexieae.

However, generic and species sampling has been insufficient to fully assess the relationships among these tribes or to evaluate generic limits and relationships. This level of taxonomic confusion among Melastomeae, Rhexieae and Microlicieae is long-standing, as evidenced by the fact that every infrafamilial classification to date has differed on how these groups are related to each other and on the generic composition of each tribe (Candolle, 1828; Naudin, 1849–1853; Triana, 1871; Cogniaux, 1891; van Vliet, Koek-Noorman & Ter Welle, 1981; Renner, 1993). These differences have resulted from the relative importance that different authors have placed on calyx, stamen, ovary and seed morphology, biogeography and wood anatomy.

\*Corresponding author. E-mail: fabian@nybg.org

The lack of phylogenetic information for Melastomeae is unfortunate because, in Melastomataceae, a large amount of generic diversity (and therefore morphological diversity) is concentrated in the tribe. Melastomeae are pantropical, and include >870 species in 47 genera. The tribe is characterized by having stamens provided with a pedoconnective (poorly developed or reduced in some genera), appendages when they are present only ventral and paired, and capsular fruits that contain cochleate seeds with curved embryos. In Melastomeae, the majority of species are in South America (c. 570 species in 30 genera) (Renner, 1993), followed by Africa (c. 185 species) (Wickens, 1974; Jacques-Félix, 1994). Madagascar, India, Indonesia and Malaysia each have c. 50 species (Perrier de la Bâthie, 1934, 1951; Hansen, 1977; Hansen, 1992; Meyer, 2001; Renner *et al.*, 2001a) and the group extends, with four species each, into northern Australia (Whiffin, 1990) and Japan.

The 570 New World species are distributed among 30 genera that vary widely in size. *Tibouchina* Aubl. is the largest genus with 240 species, six others have 20–60 species and eight genera are monotypic. To date, <25% of the genera have been included in molecular analyses, and no genus has been represented by more than two species, thus making it impossible to evaluate the monophyly of currently recognized genera and phylogenetic relationships among them. The distribution patterns also make the New World Melastomeae a remarkable group. They range from Mexico, through the Antilles, south to Argentina, and from sea level to well above the tree line in the Andes and eastern Brazil. New World Melastomeae occupy a variety of forest and open vegetation types including lowland savannas, cerrados, campos rupestres, lowland and cloud forests, paramos and punas, and some species even grow in seasonally flooded habitats. In habit they vary from small annual herbs to medium-sized trees, although the majority of the species are shrubs or small trees. Such morphological and ecological diversity makes this group an ideal candidate in which to study morphological character evolution and a model system to track the establishment of different Neotropical vegetation types.

## MATERIAL AND METHODS

### TAXON SAMPLING

To study the phylogenetic relationships of taxa putatively assigned to Neotropical Melastomeae (*sensu* Renner, 1993), ingroup sampling in this analysis comprises 219 terminals (217 species) from 42 genera. Of these, 191 terminals from 32 genera correspond to

species found in the New World (25 genera out of 30 genera of Neotropical Melastomeae *sensu* Renner, 1993, plus seven genera from Rhexieae or of uncertain placement) and 28 species from ten genera from Asia, Australia and Africa (including Madagascar). Additionally, we included ten species from four genera of Microlicieae. We also included two species of *Cambessedesia* DC., a capsular-fruited Neotropical genus previously considered to be a member of Microlicieae, but that has been shown to fall outside that tribe (Fritsch *et al.*, 2004). Seven species of Miconieae (including the *Physeterostemon* R. Goldenb. & Amorim + *Eriocnema* Naudin clade) and Merianieae were used as outgroups; following previous family-wide analyses (Clausing & Renner, 2001; Renner, 2004a; Amorim *et al.*, 2009). Trees were rooted at the node that unites the latter two tribes.

### DNA EXTRACTION AND SEQUENCING

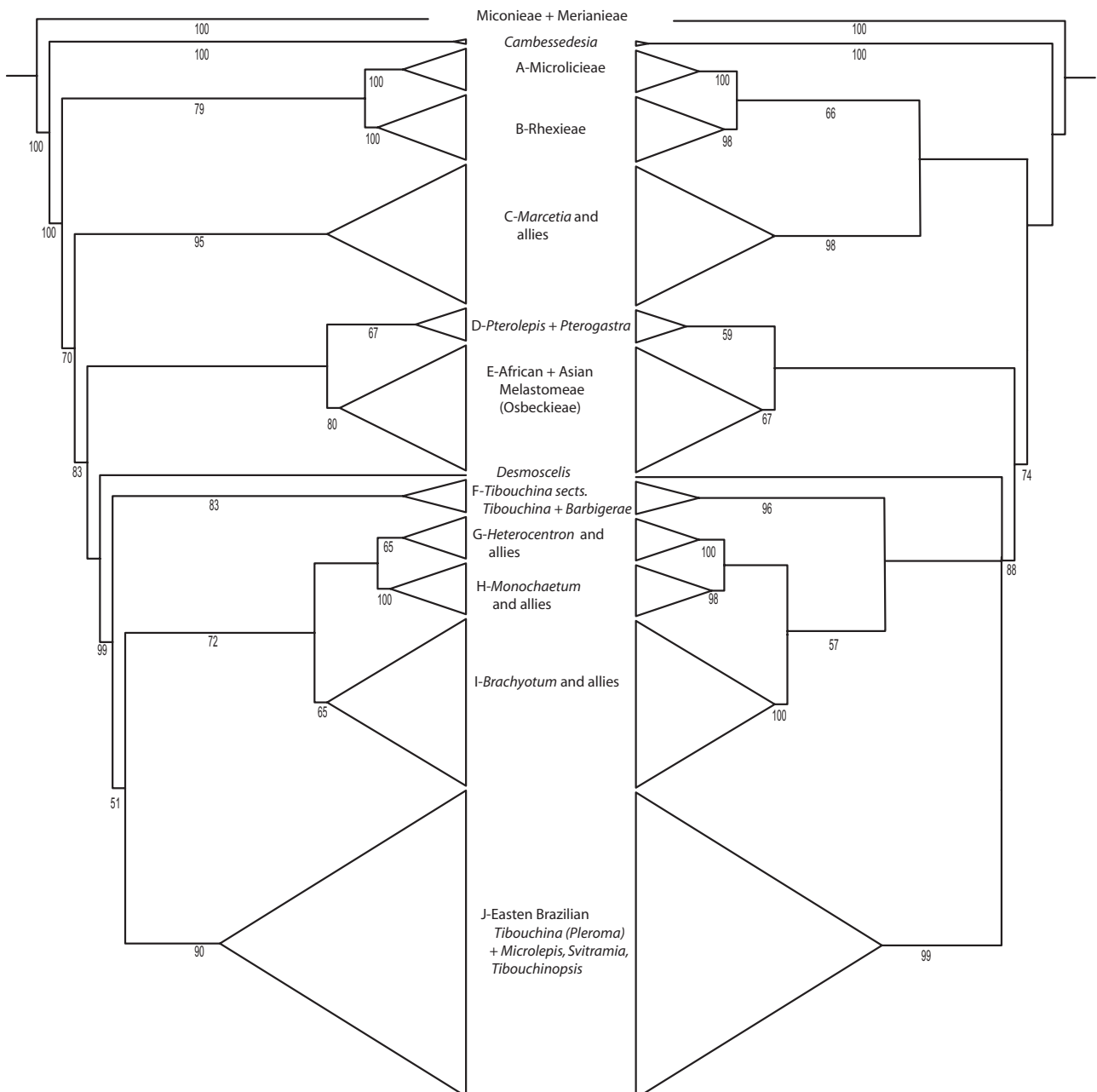
Total genomic DNA was isolated from silica-dried or herbarium material using the DNeasy plant mini kit from Qiagen and following the manufacturer's instructions. Some samples were isolated with modifications that have been shown to improve DNA quality and yield in Melastomataceae and/or with herbarium specimens, such as the addition of proteinase-K (30 µL per extraction to the lysis buffer) and/or β-mercaptoethanol (30 µL per extraction to the lysis buffer), with longer incubation periods at lower temperatures (6–24 h at 42 °C) (Martin *et al.*, 2008; Michelangeli *et al.*, 2008). In order to assess the phylogenetic relationships of Melastomeae, we sequenced one nuclear locus [the nuclear ribosomal internal transcribed spacer (nrITS) region] and two plastid spacers (*accD-psaI* and *psbK-psbL*). ITS has been used to elucidate phylogenetic relationships at the tribal and generic level in Melastomataceae (Michelangeli *et al.*, 2004, 2008; Ionta *et al.*, 2007; Goldenberg *et al.*, 2008) and we used the protocols outlined in those publications. The *psbK-psbL* spacer was amplified using primers designed by Kim-Joong Kim (Korea University, South Korea) and published by Reginato, Michelangeli & Goldenberg (2010), and the *accD-psaI* spacer was amplified using primers designed by Shaw *et al.* (2005). Protocols for amplifying the plastid markers were detailed in Reginato *et al.* (2010). Cycle sequencing was performed with the same forward and reverse primers used for amplification at the high-throughput sequencing service at the University of Washington (USA). Contigs were assembled with Sequencher 4.9 (GeneCodes Corp., Ann Arbor, MI, USA). Sequence alignment was performed with Clustal X (Thompson *et al.*, 1997) and manually adjusted in BioEdit (Hall, 2007).

## PYLOGENETIC ANALYSES

The separate nuclear and plastid data sets and the combined matrix were analysed using parsimony and maximum likelihood. The resulting topologies from the individual analyses were inspected by eye to discount the possibility of hard incongruence across data sets (i.e. support > 70% for placement of a taxon

in different clades or for relationships among major clades identified in Fig. 1).

Parsimony analyses were performed in Tree analysis using New Technology (TNT) (Goloboff, Farris & Nixon, 2008) after the indels were coded following the 'simple gap coding' procedure of Simmons & Ochoterena (2000) as implemented in 2xRead (Little, 2006). Tree searches were performed with 1000 random



**Figure 1.** Summary of phylogenetic analyses of Melastomeae based on the combined nuclear (nrITS; 1197 bp), and plastid (*accD-psaI*; 1570 bp, and *psbK-psbL*; 666 bp) data sets. Maximum likelihood analysis (left) with bootstrap support values below branches. Maximum parsimony analysis (right) with jackknife support values below branches.

addition sequences, holding five trees per replicate. The resulting most-parsimonious trees were then swapped to completion. Clade support was calculated using the parsimony jackknife with 1000 replicates. Each replicate was performed with 20 random addition sequences and holding three trees. The strict consensus of each replicate was saved. Data editing and examination of phylogenetic trees was performed with WinClada (Nixon, 1999–2002). To ensure that the entire tree space had been searched, we also conducted a search using the parsimony ratchet (Nixon, 1999) as implemented in WinClada (Nixon, 1999–2002) and spawned to NONA (Goloboff, 1993). Three sequential runs were performed, each of them with 300 iterations, holding five trees per iteration and sampling 10% of the characters. The resulting most-parsimonious trees obtained were then swapped to completion. Maximum likelihood analyses and bootstrap were performed with RAxML using default parameters (Stamatakis, 2006; Stamatakis, Hoover & Rougemont, 2008), run through the Cypress Science Gateway (<http://www.phylo.org/>; Miller, Pfeiffer & Schwartz, 2010).

Morphological characters discussed in the text were taken from a data set developed for a forthcoming detailed study of *Tibouchina* and allies (P. J. F. Guimaraes & F. A. Michelangeli, unpubl. data).

## RESULTS

Table 1 summarizes the number of taxa and the length and level of variation for the three loci included in this study. The Appendix contains all the voucher and GenBank accession information for the taxa included in this study. No strong topological incongruence was found for major clades when comparing the nuclear and plastid data.

Parsimony analyses resulted in > 100 000 trees (CI = 0.37, RI = 0.79). Fifty-one nodes collapsed in the strict consensus (not shown). Melastomeae *s.l.* (Renner, 1993) are not monophyletic in either the parsimony or maximum likelihood analyses (Fig. 1), as, in both cases, Microlicieae are nested in

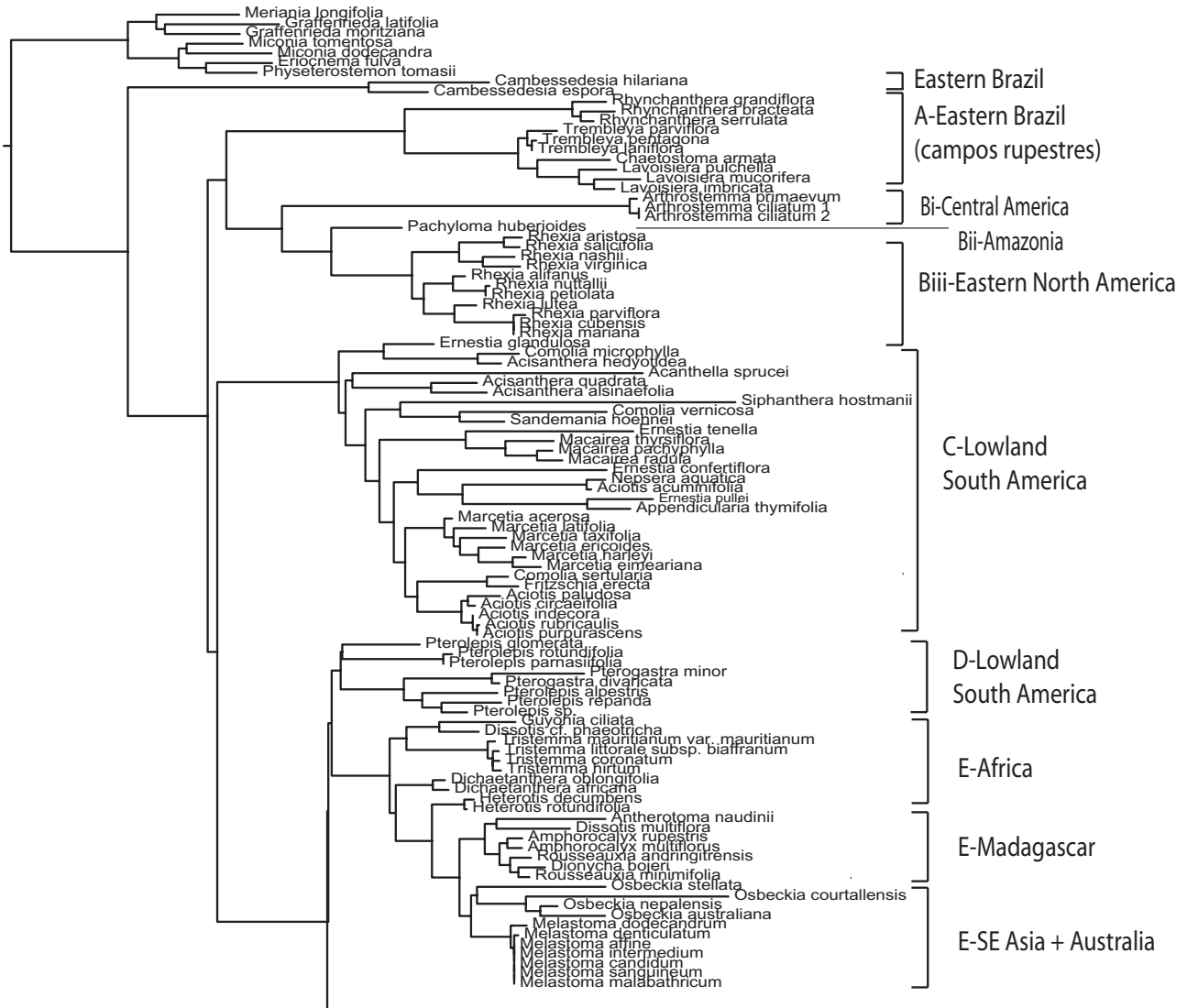
Melastomeae. *Cambessedesia* is resolved as sister to all other Melastomeae + Microlicieae and Rhexieae. In both likelihood and parsimony analyses there are four well-supported clades excluding *Cambessedesia*: (clade A) Microlicieae (*sensu* Fritsch *et al.*, 2004), (clade B) a clade composed of *Rhexia* L., *Arthrostemma* DC. and *Pachyloma* DC. (Rhexieae), (clade C) a clade composed of *Acanthella* Hook.f., *Aciotis* D. Don, *Acisanthera* P. Browne, *Appendicularia* DC., *Comolia* DC., *Ernestia* DC., *Fritzschia* Cham., *Marcetia* DC., *Macairea* DC., *Nepsera* Naudin, *Sandemania* Gleason and *Siphanthera* Pohl ex DC. (from hereon called *Marcetia* and allies) and (clades D–J) a clade of ‘core Melastomeae’. The clade of core Melastomeae is composed of the Neotropical genera *Brachyotum* (DC.) Triana, *Bucquetia* DC., *Castratella* Naudin, *Centradenia* G. Don, *Chaetolepis* (DC.) Miq., *Desmoscelis* Naudin, *Heterocentron* Hook. & Arn., *Itatiaia* Ule, *Microlepis* (DC.) Miq., *Monochaetum* (DC.) Naudin, *Pilocosta* Almeda & Whiffin, *Pterolepis* (DC.) Miq., *Pterogastra* Naudin, *Svitramia* Cham., *Tibouchina* Aubl. and *Tibouchinopsis* Markgr. Additionally, in the Neotropical Melastomeae are nested all the Old World members of the tribe sampled in this study [*Amphorocalyx* Baker, *Antherotoma* (Naudin) Hook.f., *Dichaetanthera* Endl., *Dionycha* Naudin, *Dissotis* Benth., *Guyonia* Naudin, *Heterotis* Benth., *Melastoma* L., *Osbeckia* L. and *Rousseauxia* DC.; i.e., Osbeckieae *p.p.*, *sensu* Cogniaux, 1891], forming a single clade (clade E).

Parsimony and likelihood analyses differ in the relationships among these main four clades, with *Marcetia* and allies (Figs 1–2, clade C) resolved as sister to Rhexieae + Microlicieae in the maximum parsimony (MP) analysis (Figs 1–2, clades A–B) and as sister to core Melastomeae in the maximum likelihood (ML) analysis (Figs 1–2, clades D–J). However, this relationship lacks support in the MP analysis and has only moderate support in the ML analysis. In core Melastomeae, there are three distinct clades: *Pterogastra* + *Pterolepis* (Figs 1–2, clade D), Old World Melastomeae (Figs 1–2, clade E) and New World *Tibouchina* and allied genera (Figs 1–2; clades

**Table 1.** Aligned length, indels and informative characters for the three loci sequenced

Loci	Taxa sampled	Aligned base pairs	Potentially informative	Indels	Potentially informative indels	Total potentially informative characters
nrITS	234	1197	518	378	175	693
<i>accD-psaI</i>	211	1570	458	298	144	602
<i>psbK-psbL</i>	212	666	251	179	89	340
Total	236	3433	1227	855	408	1635





To fig. 2B

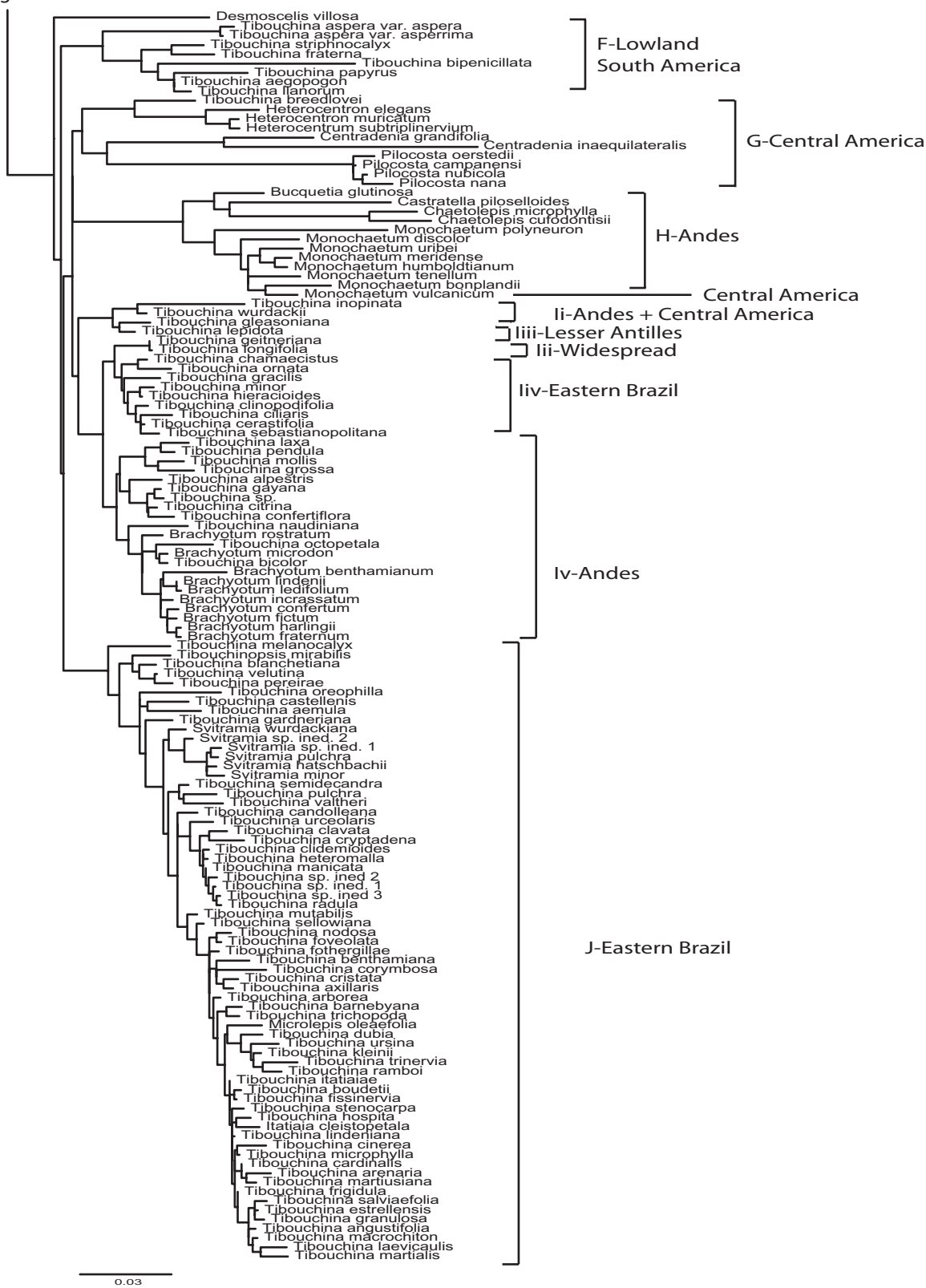
**Figure 2.** A, estimation of phylogenetic relationships in Melastomeae. Maximum likelihood analysis of combined nuclear (nrITS) and plastid (*accD-psaI*, *psbK-psbL*) data sets, with geographical distribution of each clade. See Figure 1 for support values of major clades. B, continuation of Figure 2A, estimation of phylogenetic relationships in Melastomeae. Maximum likelihood analysis of combined nuclear (nrITS) and plastid (*accD-psaI*, *psbK-psbL*) data sets, with geographical distribution of each clade. See Figure 1 for support values of major clades.

F–J). *Pterogastra* + *Pterolepis* are resolved as sister to the Old World Melastomeae, and together these clades are sister to *Tibouchina* and allies.

In the *Tibouchina* and allies clade (Figs 1–2; clades F–J), *Desmoscelis* is resolved either as the first diverging branch, or as part of a basal polytomy. Above *Desmoscelis*, the large genus *Tibouchina* is not recovered as monophyletic, as several smaller genera are nested in it, although the majority of these genera are recovered as monophyletic. Within this clade there are five well-supported groups: F – *Tibouchina* sections *Tibouchina* and *Barbigeriae* (Naud.) Cogn.; G – *Hetero-*

*centron*, *Centradenia* and *Pilocosta* (with one species of *Tibouchina*); H – *Monochaetum*, *Bucquetia*, *Chaetolepis* and *Castratella*. I – *Brachyotum* and members of *Tibouchina* sections *Simplicicaulis* (Naudin) Cogn., *Pseudopterolepis* Cogn. and *Lepidotae* Cogn. and some members of sections *Diotanthera* (Triana) Cogn. and *Purpurella* (Naudin) Cogn.; and J – eastern Brazilian *Tibouchina*, i.e. *Tibouchina* sections *Pleroma* (D. Don) Cogn., *Diplostegia* (D. Don) Cogn., *Involucrales* Triana and the remainder of section *Diotanthera* and *Purpurella*, with the genera *Itatiaia*, *Microlepis*, *Svitramia* and *Tibouchinopsis* (Fig. 2B).

To fig. 2A



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Figure 2. Continued.

## DISCUSSION

New World Melastomeae, as currently defined (Renner, 1993), are not resolved as monophyletic, because *Rhexia*, tribe Microlicieae and Palaeotropical Melastomeae are nested in it. Although these results are incongruent with the traditional tribal classification of the family (Triana, 1871; Cogniaux, 1891) and more recent realignments (van Vliet *et al.*, 1981; Renner, 1993), four major clades that have been identified in previous molecular phylogenetic studies (Clausing & Renner, 2001; Renner, 2004a, b) are also recovered here, with a significantly increased sampling, i.e. *Marcetia* and allies, an expanded Rhexieae, Microlicieae and core Melastomeae. These four major clades are united by the presence of anthers with well-developed pedoconnectives (although these have been lost a number of times; see below) as previously shown in other molecular systematic studies (Clausing & Renner, 2001; Renner & Meyer, 2001; Renner, 2004a). Additionally, all of these groups except Microlicieae have cochleate seeds (with further modifications in some genera; see below).

## MICROLICIEAE

Results of this study are in agreement with Fritsch *et al.* (2004) regarding a reduced generic composition of Microlicieae, including only *Chaetostoma*, *Lavoisiera*, *Microlicia*, *Rhynchanthera*, *Stenodon* and *Trembleya* (Fig. 2A, clade A). Likewise, the former study removed *Cambessedesia*, *Eriocnema*, *Siphanthera* and *Castratella* from their 'core Microlicieae.' Microlicieae are supported by reniform, ellipsoid or elongate seeds with a foveolate or reticulate testa (Almeda & Martins, 2001; Fritsch *et al.*, 2004) and the absence of a staminal dorsal vascular bundle (Wilson, 1950; P. J. F. Guimaraes, K. Sosa, R. Kriebel & F. A. Michelangeli, unpublished data). Most species also have rostrate anthers with a ventrally oriented terminal pore, but rostrate anthers are also present in some *Acisanthera*, *Siphanthera* and *Tibouchina*. Additionally, if ventral connective appendages are present in the stamens, these are always vascularized, a trait otherwise only found in *Arthrostemma* (Wilson, 1950). This character probably evolved in the ancestor of Rhexieae + Microlicieae and was later lost in *Pachyloma* and *Rhexia*, which have reduced ventral staminal appendages. In most genera, the anthers are also unique in having long pedoconnectives with short thecae, a character combination not seen in other groups with pedoconnectives. *Chaetostoma*, however, has some species with long anthers and a greatly reduced pedoconnective (Koschnitzke & Martins, 1999, 2006; Fritsch *et al.*, 2004). Polysporangiate anthers have been reported in some species of *Microlicia*

and *Chaetostoma* (Baumgratz *et al.*, 1996; Almeda & Martins, 2001), and may be a synapomorphy for these two genera. For details on the systematics and biogeography of Microlicieae see Fritsch *et al.* (2004).

## RHEXIEAE

*Rhexia*, *Arthrostemma* and *Pachyloma* form a clade distinct from core Melastomeae (Fig. 2A, clade B). These genera of herbs and shrubs have tetramerous flowers and cochleate, costate seeds that are tuberculate or rugose. Unlike core Melastomeae, in which the tuberculae are composed of a single cell, in these genera the tuberculae are composed of several cells (Whiffin & Tomb, 1972; Renner & Meyer, 2001). In all three genera, the ovaries lack apical projections. Anthers in this clade are widely variable, but in all genera (but not all species) the anthers have dorsal connective appendages. In *Pachyloma* the anthers have a long dorsal appendage and two ventral appendages that are not vascularized, whereas *Arthrostemma* has two vascularized ventral appendages and a short or absent dorsal appendage (Gleason, 1929; Wilson, 1950). Both of these genera have well-developed pedoconnectives. In contrast, *Rhexia* lacks pedoconnectives and either has short dorsal appendages or lacks them altogether (Wilson, 1950; Kral & Bostick, 1969; Ionta *et al.*, 2007). Additionally, *Rhexia* can be distinguished by its constricted hypanthia (in Neotropical capsular-fruited genera, otherwise restricted to the small genus *Poteranthera* Bong.), ovary locules opposite the petals (they are alternating in most Melastomataceae where the number of petals is the same as the number of ovary locules) and unilocular anthers (Ionta *et al.*, 2007). In spite of the differences in anther morphology, Gleason (1929) postulated that *Pachyloma* was closely related to *Rhexia* (and *Monochaetum*, see below), based on the presence of stamens with dorsal appendages and their seed morphology, but he seems to have missed the connection with *Arthrostemma*.

## MARCETIA ALLIANCE

Most genera in the clade comprising *Marcetia* and allies [Fig. 2A, clade C; *Acanthella*, *Aciotis* (Fig. 3A), *Acisanthera*, *Appendicularia*, *Comolia*, *Ernestia*, *Fritschia*, *Marcetia* (Fig. 3B), *Macairea*, *Nepsera* (Fig. 3C), *Sandemania* and *Siphanthera*], were traditionally placed in Melastomeae based on anther and fruit morphology. Most of the species in this group are herbs or small shrubs, and the annual habit, although rare in the family, has appeared repeatedly in this group (Freire-Fierro, 2002; Almeda & Robinson, 2011; Kriebel, 2012). Additionally, some species of *Macairea*





**Figure 3.** See caption on next page.



**Figure 3.** Representatives of Neotropical Melastomeae. A, *Aciotis paludosa*. B, *Nepsera aquatica*. C, *Marcetia taxifolia*. D, *Pterogastra divaricata*. E, *Pterolepis* sp., notice intercalycine emergence (against petal). F, *Desmoscelis villosa*. G, *Tibouchina bipenicillata* (section *Barbigerae*). H, *Chaetolepis microphylla*. I, *Monochetum humboldtianum*. J, *Bucquetia glutinosa*. K, *Heterocetron elegans*. L, *Centradenia inaequilateralis*. M, *Brachyotum strigosum*. N, *Tibouchina gayana* (section *Diotanthera*, from the Andes). O, *Tibouchina clinopodifolia* (section *Purpurella* from eastern Brazil). P, *Tibouchina bicolor* (section *Diotanthera* from the Andes), longitudinal section, showing persistent calyx and ovary with apical appendages. Q, *Tibouchina lepidota* (section *Lepidotae*). R, *Tibouchina heteromalla* (section *Pleroma*). S, *Tibouchina stenocarpa* (section *Pleroma*), fruit with caducous calyx. (All pictures by F. A. Michelangeli.).

are trees up to 12 m tall (Renner, 1989). This clade is further characterized by tetramerous flowers (Fig. 3A–C) (although pentamerous flowers are present in *Acisanthera* and *Ernestia cordifolia* O.Berg ex Triana) and ovaries that are either glabrous or with glandular trichomes at the apex, but that lack appendages (see below). In *Marcetia*, *Aciotis*, *Fritzschia*, *Siphanthera* and *Nepsera*, the pedoconnectives are small or lacking and connective appendages are absent (Fig. 3A–C). All genera sampled in this clade have seeds that are cochleate, ovate or lacrimiform. With the exception of *Siphanthera*, all these genera also have seeds with foveolate testas (Whiffin & Tomb, 1972). In some cases, these features can be obscured by the presence of tubercles or secondary sculpturing, but the foveolate nature is evident at least near the raphe. All of these genera were classified by Whiffin & Tomb (1972) as having a microliticoid seed type, not the typical tibouchinoid type of other Melastomeae. The number of ovary locules can be equal to the number of petals (usually four), but several taxa have a reduced number of locules, a condition also common in Microlicieae, but not common in Palaeotropical Melastomeae or the *Tibouchina* and allies group. Lastly, all of these species, except *Acanthella sprucei* Hook.f and *Acisanthera hedyotoidea* (C.Presl) Triana, have a deletion of 381 bp in the *psbK-psbL* spacer.

Generic limits in some elements of the *Marcetia* alliance have been notoriously difficult, especially between *Comolia* and *Ernestia*. Sampling in this investigation is insufficient to resolve the problematic generic circumscriptions in this clade, but results suggest (Fig. 2A) that *Macairea* and *Marcetia* are monophyletic. Almeda & Robinson (2011) demonstrated the monophyly of *Siphanthera* using morphological data; Almeda & Martins (2001) had previously removed it from Microlicieae on the basis of seed morphology, and that result is confirmed here. *Aciotis* might be rendered monophyletic with some small adjustments. *Poteranthera* and *Mallophyton* were not sampled in this study, but, based on the presence of tetramerous flowers, ovary apex without a corona or hairs and seed morphology, they are likely to belong to the *Marcetia* alliance (Wurdack, 1964; Kriebel, 2012). *Loricalepis* Brade, a monotypic genus of small

shrubs with tetramerous flowers and white petals from northern Brazil (Brade, 1958), may also be in this clade.

#### CORE MELASTOMEAE

The largest group in number of genera and species is what we have designated core Melastomeae (Fig. 2B, clades D–J). Putative morphological synapomorphies for this pantropical clade include cochleate seeds with tubercles or papillae composed of a single cell (tibouchinoid seeds *sensu* Whiffin & Tomb, 1972), a crown of hairs or appendages on the ovary apex (Fig. 3P) and the presence of staminal pedoconnectives with bifurcated dorsal vascular bundles (Wilson, 1950; P. J. F. Guimaraes, K. Sosa, R. Kriebel & F. A. Michelangeli, unpubl. data).

*Pterogastra* and *Pterolepis* form a strongly supported clade sharing several plesiomorphic characters, but there are no clear synapomorphies for this group (Fig. 2A, clade D). Both genera have tetra- and pentamerous species, herbaceous to suffruticose habit, dimorphic stamens with developed pedoconnectives and short, bilobed ventral appendages (Fig. 3D–E) (Renner, 1994a, b). They also have emergences or trichomes in the calyx sinuses, but these differ between them. In *Pterolepis* the intercalycine emergences are stellate–penicillate (Fig. 3E), whereas they are slender and simple in *Pterogastra*. Intercalycine emergences are also present in some *Chaetolepis*, *Tibouchina* and Palaeotropical Melastomeae (see below). *Pterogastra* has prominently ribbed or winged hypanthia, but this homoplasious character is also present in *Schwackaea* Cogn. and *Pilocosta* Ameda & Whiffin (see below) (Renner, 1994b). Unlike *Pterogastra*, the latter two genera have the same number of wings as sepals (instead of double). In *Schwackaea* the hypanthium is terete and in *Pilocosta* it is quadrangular. Although the hypanthia in *Pterolepis* are not winged, they can be slightly angular, especially in fruit. Some Palaeotropical Melastomeae also have intercalycine emergences, and these are similar to those found in *Pterolepis*. However, this character cannot be used as diagnostic of the Palaeotropical clade, because it is absent in some genera (i.e. *Guyonia*, *Dichaetanthera* and *Tristemma*).

Additionally, some Palaeotropical Melastomeae have persistent fleshy placentas, and some species even have berries (mostly in *Melastoma*) (Clausing, Meyer & Renner, 2000; Clausing & Renner, 2001).

Although *Tibouchina* is not resolved as monophyletic, the groups in this large clade (Fig. 2B, clades F–J) are each well characterized by stamen and hypanthium morphology, and biogeography (see below). This large assemblage of Neotropical genera is well supported by molecular analyses, but morphological synapomorphies are not readily evident. *Desmoscelis* (Fig. 3F), the first diverging group of *Tibouchina* and allies, is a genus of two species from lowland savannas. It is characterized by its erect, herbaceous habit, pentamerous flowers, long simple (eglandular or glandular) trichomes and dimorphic anthers with long, paired ventral connective appendages. The larger anthers are slender and subulate, whereas the smaller ones are short, truncate and with a broad pore. These characters are plesiomorphic in core Melastomeae or autapomorphic for *Desmoscelis*.

The species of *Tibouchina* sections *Tibouchina* and *Barbigerae* (Fig. 2B, clade F) have pink to purple anthers without glandular trichomes (Fig. 3G). In section *Barbigerae* the union between the filament and the connective has simple, long trichomes. The hypanthium in section *Tibouchina* has tufts of simple hairs in the calyx sinuses, but whether or not these structures are homologous to the intercalycine emergences of *Pterolepis* and Palaeotropical Melastomeae is hard to assess without a detailed study of these structures and better resolution in that section of the estimated phylogeny.

*Heterocentron*, *Pilocosta* and *Centradenia* (Fig. 2B, clade G) are herbs or small shrubs (sprawling in the case of *Pilocosta* and a few species of *Heterocentron*) with tetramerous flowers and tetralocular ovaries (Fig. 3 K–L). Species in this clade have stamens that are almost always dimorphic with well-developed pedoconnectives and ventral appendages that are usually bilobed in the larger series (Whiffin, 1972; Almeda, 1977, 1993; Almeda & Whiffin, 1980). Each of these genera are resolved as monophyletic (Fig. 2B, clade G), and characters of hypanthium shape and leaf and anther morphology support the recognition of each of them as separate. *Tibouchina breedlovei* Wurdack, a rarely collected species from southern Mexico, is also placed in this clade. This species also has tetramerous flowers and anthers that closely resemble those of *Heterocentron*. In the original description, Wurdack (1967) suggested that *T. breedlovei* could be placed near or in *Heterocentron*. Most *Heterocentron* spp. have penninerved venation (Whiffin, 1972), a character otherwise rare in the family, and all species of *Centradenia* have asymmetrical leaves, also rare in the family (Almeda,

1977). *Schwackaea*, a monotypic genus ranging from Mexico to north-western Colombia, shares all these features (Renner, 1994b), and recent DNA data confirm this placement (D. S. Penneys, F. Almeda, P. W. Fritsch & F. A. Michelangeli, unpubl. data).

The group formed by *Monochaetum*, *Chaetolepis*, *Castratella* and *Bucquetia* (Fig. 2H), like the *Heterocentron* group, share tetramerous flowers with tetralocular ovaries. *Chaetolepis*, *Castratella* and *Bucquetia* have isomorphic, linear anthers without pedoconnectives or well-developed appendages (Fig. 3H–J). *Monochaetum*, however, has well-developed dorsal appendages, at least in the largest set of stamens (Fig. 3I). Some *Monochaetum* spp. have one whorl of stamens reduced to staminodia, or even lack them, and the species in the genus exhibit a high degree of variation in the size of the pedoconnective. In most Melastomataceae with stamen dimorphism, the larger series of stamens is usually opposite the calyx, with the reduced series opposite the petals, but in *Monochaetum* this situation is reversed (Almeda, 1978). *Bucquetia* and *Castratella* had been placed in Microlicieae (Cogniaux, 1891), but seed morphology clearly excluded them from this group (Whiffin & Tomb, 1972; Fritsch *et al.*, 2004).

*Brachyotum* is characterized by pendant flowers with copious nectar, in which the dark purple or yellow to greenish petals are pseudocampanulate (Fig. 3 M). The pedoconnective is highly reduced in this group, and the entire genus is pollinated by birds, mostly hummingbirds (Wurdack, 1953; Vogel, 1958; Stiles, Ayala & Giron, 1992), although bat pollination may also be possible. At least one *Tibouchina* sp. in this clade [*T. grossa* (L.f.) Cogn.] also produces nectar, and it is visited by bats (Vogel, 1958, 1997) and hummingbirds (K. Schumman, pers. comm. cited in von Helversen & Winter, 2003). However *T. grossa* lacks pendant flowers with closed petals that have traditionally defined *Brachyotum*, and has a base chromosome number of  $x = 10$  instead of  $x = 9$  (Solt & Wurdack, 1980). *Brachyotum* is nested among representatives of *Tibouchina* that generally have yellow or white anthers, and many of them also have reduced pedoconnectives (Fig. 3N–Q). In this *Brachyotum* clade, those species with tetramerous flowers (*Tibouchina* section *Pseudopterolespis*) are resolved as a unit, as are the species with lepidote scales on the hypanthium, free bracteoles and glabrous stamens (*Tibouchina* section *Lepidotae*; Fig. 3Q) (Todzia & Almeda, 1991). This clade also contains the majority of the species of *Tibouchina* section *Diotanthera*, characterized by attenuate anthers and persistent calyx lobes (Fig. 3P) (Cogniaux, 1891; Todzia, 1999). Several species in section *Diotanthera* also have bicoloured petals (Fig. 3N). Based on anther and calyx morphology, we expect several Mexican and Central

American species that were not sampled in this study (Todzia, 1999) to fall within this clade.

The *Pleroma* group (Fig. 2B, clade J) is characterized by species with a calyx that is caducous in fruit (Fig. 3S) (Guimaraes & Martins, 1997). Most species in this group have well-developed pedoconnectives, purple, pink or white anthers, and if the anther connectives have trichomes these are glandular (Fig. 3R) (Cogniaux, 1891; Guimaraes & Martins, 1997). Most species are pentamerous, but some *Tibouchina* with small flowers are tetramerous. The *Pleroma* clade also includes four genera that have been maintained separate from *Tibouchina* (*Itatiaia*, *Microlepis*, *Svitramia* and *Tibouchinopsis*); these genera have persistent calyces (Triana, 1871; Ule, 1908; Brade & Markgraf, 1961; Romero & Martins, 2003), a character difference that may be responsible for all of these groups not being recognized as part of *Tibouchina*. Additionally, *Svitramia* has reduced anthers that lack pedoconnectives and have highly reduced or absent ventral appendages (Romero & Martins, 2003).

#### TRIBAL AND GENERIC TAXONOMY

This study contains more than 14 times the number of species of Melastomeae and three times the number of genera included in any previous published molecular study of Melastomataceae. Many of the generic groupings shown here are consistent with those studies, but, as a result of increased generic and specific sampling, a clearer picture of the evolution of the capsular taxa with pedoconnectives in Melastomataceae is starting to emerge, with some new groups clearly identified (i.e. *Marcetia* and allies, the affinities of *Monochaetum* with other high Andean taxa, the composition of Rhexieae, etc.). Additionally, this study represents the first insight into the relationships in the large and complex genus *Tibouchina* and between *Tibouchina* and other Neotropical Melastomeae. However, the level of sampling of some groups (particularly *Ernestia*, *Comolia* and Central American and Mexican representatives of *Tibouchina*) and the level of resolution and support along the spine of the tree stills makes it premature to propose any overhaul of the taxonomy. For example, whether *Marcetia* and allies, or the *Pterogastra* clade, deserve tribal recognition will depend on the final resolution of the relationships between this latter group and Palaeotropical Melastomeae, or the relationships between the Rhexieae and *Marcetia* clades. Similarly, *Tibouchina* could be recognized as a much expanded genus (but, as noted above, there are no clear morphological synapomorphies for this clade) or all the other genera maintained and *Tibouchina* divided into smaller and diagnosable units. The

*Tibouchina* and allies clade is already the subject of a more detailed study that includes additional species, markers and a morphological matrix (P. J. F. Guimaraes, K. Sosa, R. Kriebel & F. A. Michelangeli, unpubl. data), and these open questions will be addressed in forthcoming publications.

The fact that many groupings at the generic or sectional level are recovered here as monophyletic, or nearly so, is evidence that characters traditionally used in Melastomeae taxonomy, such as androecium morphology, merosity, seed morphology, calyx persistence and hypanthium indument (Naudin, 1849–1853; Triana, 1871; Cogniaux, 1885, 1891; Whiffin & Tomb, 1972; Wurdack, 1986), are good predictors of phylogenetic relationships. The presence/absence of a corona on the ovary apex (core Melastomeae vs. Microlicieae + Rhexieae + *Marcetia* alliance), and the difference between ventral staminal appendages with or without vascular bundles (Microlicieae + *Arthrostemma* vs. *Marcetia* alliance and core Melastomeae) have not traditionally been used for taxonomic purposes and are shown here as a taxonomically important characters. *Tibouchina*, as currently defined, is not resolved as a monophyletic group, mostly because it is defined by characters that are plesiomorphic in core Melastomeae: pentamerous flowers with anthers with developed pedoconnectives and shortly bilobed ventral anther appendages.

#### HABITAT AND DISTRIBUTION

As shown for other groups of Melastomataceae (Fritsch *et al.*, 2004; Renner, 2004a; Penneys & Judd, 2005; Michelangeli *et al.*, 2008), even if the generic or tribal classification does not closely match phylogenetic results, there is a close correspondence between most clades recovered and the geographical distribution or type of environment in which the plants live (Fig. 2).

Although a minority of outlying taxa are native to areas north of South America, most species of the *Marcetia* and allies clade are distributed in central and north-eastern South America. Most are found in open habitats, in either successional or ruderal environments, savannas, campo rupestres and the Guayana highlands. Some, mostly widespread, species reach the Antilles and the Andes.

Microlicieae are almost exclusively found in eastern and central Brazil in campos rupestres. A few *Rhynchanthera* spp. are found farther to the north and south-west and in wetter environments, and one *Microlicia* sp. is found in the Guayana Highlands. The geographical distribution of this group has already been examined in detail by Fritsch *et al.* (2004) and Simon *et al.* (2009).

The *Rhexia* clade as a whole deviates from this pattern of geographical integrity, but each genus is



geographically restricted. *Pachyloma*, a genus of four species, is restricted to north-western Amazonia, whereas *Arthrostemma*, also with four species, is found along the Andes, from Bolivia to Venezuela and northern Brazil, and in Central America, Mexico and the Antilles. This widespread distribution of *Arthrostemma* is attributable only to one species, *A. ciliatum* Pav. ex D. Don, which is a tetraploid ( $N = 30$ ), probably derived from *A. primaevum* Almeda, a diploid species ( $N = 15$ ) restricted to southern Mexico (Almeda & Chuang, 1992; Almeda, 1994). *Rhexia* is the only genus of Melastomataceae found in subtropical and temperate North America, with most species being distributed from Texas to Nova Scotia. One widespread species is also found in Cuba, Hispaniola and Puerto Rico (Kral & Bostick, 1969; Liogier, 2000; Ionta *et al.*, 2007). Even although these species are found in three different regions, all three genera are found in poorly drained, usually acidic soils. Fossil seeds from the early to mid-Miocene that have been collected throughout Eurasia (Dorofeev, 1960, 1963, 1988; Collinson & Pinggen, 1992; Dyjor *et al.*, 1992; Mai, 2000) closely match those of this clade with a cochleate shape and multicellular tubercles (Renner, Clausing & Meyer, 2001b; Renner & Meyer, 2001). This is especially relevant considering that these fossils have been used as calibration points in molecular dating and biogeographical studies (Renner *et al.*, 2001b; Renner & Meyer, 2001; Morley & Dick, 2003; Fritsch *et al.*, 2004; Renner, 2004a, b), and the fossil is found well outside the modern distribution of these three extant genera.

*Pterolepis* (with 14 species) and *Pterogastra* (with two species) grow almost exclusively in different types of grasslands in the Neotropics. Most species of *Pterolepis* are endemic to cerrado vegetation in central and eastern Brazil, with one widespread species reaching into the Caribbean and a second into Central America and Southern Mexico (Renner, 1994a). One *Pterogastra* sp. is only found in savannas in south-west Venezuela and Colombia, and a second is widespread on the eastern slopes of the Andes from sea level to 2600 m (Renner, 1994b).

The Palaeotropical Melastomeae clade includes species of open and forested areas. Sampling in this group is far from adequate to answer biogeographical questions with a high level of certainty, but, based on morphology, it is almost certain that all Palaeotropical Melastomeae do indeed fall into this group. This preliminary sampling shows that Madagascan and Asian lineages are derived from within Africa, and not from the Neotropics.

In the group formed by *Tibouchina* and allied genera, *Desmoscelis* and *Tibouchina* sections *Tibouchina* and *Barbigerae* are also found in open habitats in the savannas and the lower portion of the

Andean slopes of South America. *Heterocentron*, *Centradenia* and *Pilocosta* are mostly found on the edges of mid-elevation and cloud forest from north-western Colombia to Mexico (with one *Pilocosta* sp. extending into Ecuador), constituting a predominantly Mexican/Central American clade. The other group with tetramerous species, *Monochaetum* and allies, is mostly distributed at high elevation in paramos and cloud forests. *Castratella* and *Bucquetia* are restricted to paramos in western Venezuela and eastern Colombia. *Chaetolepis* is mostly found in South American paramos, with one species endemic to the highest elevations in Costa Rica and one species in the Guayana highlands. *Chaetolepis gentianoides* (Naudin) Jacq.-Fél., a species restricted to the sandstone highlands of western Africa, renders *Chaetolepis* the only genus in Melastomatoideae disjunct between the Neotropics and Paleotropics. Unfortunately, material of this species was not available for sequencing during the course of this study. A morphological cladistic analysis (Grimm, 2009) found that this species grouped with New World *Chaetolepis*, but most of the anther morphology in this group is highly reduced, and, because of the presence of intercalycine projections at the apex of the hypanthium, a placement in the Old World Melastomeae cannot be discounted. *Monochaetum* is the most species-rich genus in the clade with c. 30 species distributed in South America and 20 in Mexico and Central America. Most Central American species are found in cloud forests in Costa Rica and Panama, and a second, smaller group in the mountains of southern Mexico. Most South American species are found in the paramos and cloud forests of Venezuela and Colombia, with a few species extending as far south as central Peru and one widespread species in the Guayana Highlands (Almeda, 1978, 2009; Alvear, 2010).

All *Brachyotum* spp. are found at high elevations in the Andes from Colombia to Argentina (but not in Chile), either in paramo or puna vegetation, or in the surrounding cloud forests (Wurdack, 1953). The majority of the members of *Tibouchina* in this clade (*Tibouchina* sections *Diotanthera* and *Lepidotae*) are also found at high elevations in the Andes and mountains of southern Central America. A small group of species in this clade [see clade with *T. clinopodifolia* (DC.) Cogn.] is found in the forests of the Mata Atlantica, which may provide evidence of a dispersal event from the Andes to Eastern Brazil. This connection between the Andes and high elevation floras in eastern Brazil has been reported for other plant groups (e.g. Berry *et al.*, 2004; Perret, Chautems & Spichiger, 2006; Struwe *et al.*, 2009; Vasco, 2011). A connection through favourable habitats in southern Brazil during cool periods, rather than long distance dispersal, seems to be the most likely explanation for

this pattern (Safford, 2007). The distribution pattern of species in the *T. clinopodifolia* clade would also favour this hypothesis. One species, *T. longifolia* (Vahl) Baill., is widespread from Mexico and the Antilles to Bolivia, and a close relative *T. geitneriana* (Schltdl) Cogn. is also widely distributed, but usually found at slightly higher elevations.

*Tibouchina* sections *Pleroma*, *Diplostegia*, *Involucrales* and the remainder of sections *Diotanthera* and *Purpurella*, along with the genera *Itatiaia*, *Microlepis*, *Svitramia* and *Tibouchinopsis* are all found in eastern Brazil, mostly in Mata Atlantica vegetation, but some also grow on the exposed summits of rocky outcrops and campos rupestres, cerrados and coastal vegetation.

#### NICHE CONSERVATISM AND HABITAT SHIFTS

The strong geographical structuring found in the pedoconnective clade of Melastomataceae can be attributed to phylogenetic niche conservatism (Harvey & Pagel, 1991; Wiens, 2004; Donoghue, 2008), coupled with limited colonization of new environments and/or dispersal and with *in situ* speciation (Pennington, Richardson & Lavin, 2006; Pennington, Lavin & Oliveira, 2009; Schrire *et al.*, 2009; Pennington *et al.*, 2010). Not only are many groups restricted to the same geographical area, but the vast majority of the species are found in open habitats, regardless of soil, temperature or elevation. Thus, even in cases of habitat shift or colonization of new environments (e.g. with the uplift of the Andes or the appearance of the cerrado and Mata Atlantica biomes), this has occurred through habitats that share some characteristics that have allowed the incoming group to be successful. These types of habitat shifts to similar, but not identical environments have been shown to occur at higher phylogenetic levels and broader biome types for several plant groups (see review by Crisp *et al.*, 2009, and references therein).

Phylogenetic niche conservatism has also been invoked to explain the presence of closely related groups in disjunct areas with similar environmental conditions (Donoghue, 2008). Several plant groups in the high Andes seem to follow this pattern, but in many cases they have originated in temperate environments outside South America (von Hagen & Kadereit, 2001, 2003; Bell & Donoghue, 2005; Hughes & Eastwood, 2006; Fritsch *et al.*, 2008). A lowland, tropical origin for Andean groups, as shown here for some members of the pedoconnective clade of Melastomataceae, can also be inferred in tribe Miconieae (Michelangeli *et al.*, 2008), and recently has been shown for other groups of angiosperms (Antonelli *et al.*, 2009; Jabaily & Sytsma, 2011; Luebert, Hilger

& Weigend, 2011; Simon *et al.*, 2011). In the pedoconnective clade, this situation is seen in *Monochaetum* (found at high elevations in the northern Andes and mountains of Central America), *Chaetolepis* (paramos or northern South America, mountains in Costa Rica and summits of tepuis in the Guayana shield), and representatives of *Tibouchina* from the southern Andes and high elevations of the Mata Atlantica (see Fig. 2b clades Iiv and Iv).

When viewed as a whole, the pedoconnective clade is found in a wide variety of environments from sea level to 4000 m, in both tropical and subtropical climates (with some species of *Rhexia* and *Melastoma* extending through temperate climates). This distribution of taxa across such different environments may at first contradict our claim of phylogenetic niche conservatism in the group. However, it is important to note that habitat distribution is phylogenetically clustered, and the widespread distribution of our study group is only attributable to the broad phylogenetic scope of the study. Moreover, if we look at any two taxa in the same or closely related clades and with extremely different habitats (e.g. lowland savannas vs. mid-elevation cloud forests of Mata Atlantica in clade J), we can see how other closely related taxa of the second group are found in intermediate environments (i.e. open habitats at high elevations). Thus, the widespread Neotropical distribution of the pedoconnective clade could have been accomplished through successive colonization of neighbouring or similar environments (as described by Crisp *et al.*, 2009) and by 'niche crawling' from one environment to another, and the ultimate result would be a broad distribution. Unfortunately, the current level of phylogenetic resolution between clades F–J, and, in some of these clades, is insufficient to test this hypothesis. A more resolved phylogenetic tree will also help address questions about multiple colonizations of Central America (clades G and Ii and some members of clade H), the Andes (clades H and Iv) or the cerrado biome (Microlicieae and some members of clades C, D and J).

In summary, the pedoconnective clade of Melastomataceae appears to have radiated and speciated mostly through open habitats, with wind dispersal of seeds produced in capsular fruits playing an important role. Competition for pollinators (mostly bees), and pollen economy (through heteranthery), may have driven the evolution and diversification of stamen morphology in this group (Gross, 1993; Larson & Barrett, 1999; Luo & Zhang, 2005; Vallejo-Marin *et al.*, 2010). These hypotheses were already advanced by Renner & Meyer (2001) and would be in agreement with the predictions of the niche conservatism hypothesis and colonization of similar or

adjacent environments and are supported here with increased taxon and character sampling.

#### ACKNOWLEDGEMENTS

We thank wish to thank M. Alford, J. F. Baumgratz, I. Capote, R. Goldenberg, W. Judd, L. Kelly, L. Kollman, A. Lobao, C. V. Martin, H. Mendoza, R. Naczi, M. Nee, K. Redden, A. K dos Santos, K. Steiner and K. Wurdack for providing leaf and/or herbarium material. Antoine Nicolas provided invaluable help in the laboratory. This research was supported by a grant from CAPES, Brazil to P.J.F.G. (Scholarship Process Number BEX 2128/09-8). Partial support was also provided by the Cullman Program for Molecular Systematics and the structural botany laboratory at The New York Botanical Garden and grant DEB- 0818399 from NSF to F.A.M. R.K. was supported by the Oliver Hazard Perry Graduate Fellowship at The New York Botanical Garden and D.S.P. was partially supported by the John J. Rose Postdoctoral Fellowship at the California Academy of Sciences. Susanne Renner, an anonymous reviewer and Toby Pennington provided valuable comments that greatly improved this article.

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## APPENDIX

List of species, voucher information, provenance and GenBank accession data included in this study [nuclear ribosomal internal transcribed spacer (nrITS), *accD-psaI*, *psbK-psbL*]. Voucher information only provided for species newly sequenced for this study; all others taken from GenBank. Additional vouchers may be deposited at other herbaria (acronyms following Thiers, 2012).

Species	Collector, number (herbarium)	Provenance	nrITS	<i>accD-psaI</i>	<i>psbK-psbL</i>
<i>Acanthella sprucei</i> Hook.f.	Diaz, W., 4538 (NY)	Brazil	JQ730036	JQ730247	JQ730456
<i>Aciotis acuminifolia</i> (Mart. ex DC.) Triana	Martin, C. V., 487 (NY)	French Guiana	JQ730037	JQ730248	JQ730457
<i>Aciotis circaeifolia</i> (Bonpl.) Triana	Caddah, M.K., 621 (NY)	Brazil	JQ730038	JQ730249	JQ730458
<i>Aciotis indecora</i> (Bonpl.) Triana	Martin, C. V., 411 (NY)	French Guiana	JQ730039	JQ730250	JQ730459
<i>Aciotis paludosa</i> (Mart. ex DC.) Triana	Guimarães, P., 317 (RB)	Brazil	JQ730040	JQ730251	JQ730460
<i>Aciotis purpurascens</i> (Aubl.) Triana	Martin, C. V., 422 (NY)	French Guiana	JQ730041	JQ730252	JQ730461
<i>Aciotis rubricaulis</i> (Mart. ex DC.) Triana	Goldenberg, R., 850 (NY)	Brazil	JQ730042	JQ730253	JQ730462
<i>Acisanthera alsinaefolia</i> (DC.) Triana	Goldenberg, R., 826 (NY)	Brazil	JQ730043	JQ730254	JQ730463
<i>Acisanthera hedyotidea</i> (C.Presl.) Triana	Wurdack, K. J., 4145 (NY)	Guyana	JQ730044	JQ730255	JQ730464
<i>Acisanthera quadrata</i> Pers.	Michelangeli, F. A., 826 (BH)	Venezuela	JQ730045	JQ730256	JQ730465
<i>Amphorocalyx multiflorus</i> Baker	Almeda, F., 8669 (CAS)	Madagascar	JQ730046	JQ730257	JQ730466
<i>Amphorocalyx rupestris</i> H.Perrier	Almeda, F., 8723 (CAS)	Madagascar	JQ730047	JQ730258	JQ730467
<i>Antherotoma naudinii</i> Hook.f.	Almeda, F., 8624 (CAS)	Madagascar	JQ730048	JQ730259	–
<i>Appendicularia thymifolia</i> (Bonpl.) Triana	Martin, C. V., 441 (NY)	French Guiana	JQ730049	JQ730260	JQ730468
<i>Arthrostemma ciliatum</i> 1 Pav. ex D.Don			DQ985619	–	–
<i>Arthrostemma ciliatum</i> 2 Pav. ex D.Don			AY460429	–	–
<i>Arthrostemma primaevum</i> Almeda	Penneys, D. S., 1429 (FLAS)	Mexico	JQ730050	JQ730261	JQ730469
<i>Brachyotum benthamianum</i> Triana	Alford, M., 3083 (BH)	Ecuador	JQ730051	JQ730262	JQ730470
<i>Brachyotum confertum</i> (Bonpl.) Triana	Penneys, D. S., 1603 (FLAS)	Ecuador	JQ730052	JQ730263	JQ730471
<i>Brachyotum fictum</i> Wurdack	Penneys, D. S., 1594 (FLAS)	Ecuador	JQ730053	JQ730264	JQ730472
<i>Brachyotum fraternum</i> Wurdack	Penneys, D. S., 1604 (FLAS)	Ecuador	JQ730054	JQ730265	JQ730473
<i>Brachyotum harlingii</i> Wurdack	Penneys, D. S., 1593 (FLAS)	Ecuador	JQ730055	JQ730266	JQ730474
<i>Brachyotum incrassatum</i> E.Cotton	Clark, J. L., 8896 (NY)	Ecuador	JQ730056	JQ730267	JQ730475
<i>Brachyotum ledifolium</i> (Desr.) Triana	Penneys, D. S., 1554 (FLAS)	Ecuador	JQ730057	JQ730268	JQ730476
<i>Brachyotum lindenii</i> Cogn.	Penneys, D. S., 1555 (FLAS)	Ecuador	JQ730058	JQ730269	JQ730477
<i>Brachyotum microdon</i> (Naudin) Triana	Nee, M., 55327 (NY)	Bolivia	JQ730059	JQ730270	JQ730478
<i>Brachyotum rostratum</i> (Naudin) Triana	Penneys, D. S., 1586 (FLAS)	Ecuador	JQ730060	JQ730271	JQ730479
<i>Bucquetia glutinosa</i> (L.f.) DC.	Alvear, M., 1398 (CAS)	Colombia	JQ730061	JQ730272	JQ730480
<i>Cambessedesia espora</i> (A.St.Hil. ex Bonpl.) DC.	Guimarães, P., 397 (RB)	Brazil	JQ730062	JQ730273	JQ730481
<i>Cambessedesia hilariana</i> (A.St.Hil. ex Bonpl.) DC.	Guimarães, P., 405 (RB)	Brazil	JQ730063	JQ730274	JQ730482
<i>Castratella pilosoides</i> (Bonpl.) Naudin	Gonzalez, F., 3830 (COL)	Colombia	JQ730064	JQ730275	JQ730483
<i>Centradenia grandifolia</i> (Schltdl.) Endl. ex Walp.	Penneys, D. S., 1544 (FLAS)	Costa Rica	JQ730065	JQ730276	–
<i>Centradenia inaequilateralis</i> (Schltdl. & Cham.) G.Don	Michelangeli, F. A., 838-a (NY)	Costa Rica	JQ730066	JQ730277	JQ730484
<i>Chaetolepis cufodontisii</i> Standl.	Michelangeli, F. A., 1160 (NY)	Costa Rica	JQ730067	JQ730278	JQ730485
<i>Chaetolepis microphylla</i> (Bonpl.) Miq.	Michelangeli, F. A., 1268 (NY)	Brazil	JQ730068	JQ730279	JQ730486
<i>Chaetostoma armatum</i> (Spreng.) Cogn.	Guimarães, P., 396 (RB)	Brazil	JQ730069	JQ730280	JQ730487

APPENDIX *Continued*

Species	Collector, number (herbarium)	Provenance	nrITS	<i>accd-psaI</i>	<i>psbK-psbL</i>
<i>Comolia microphylla</i> Benth.	Redden, K. M., 1454 (NY)	Guyana	JQ730070	JQ730281	JQ730488
<i>Comolia sertularia</i> (DC.) Triana	Almeda, F., 7724 (CAS)	Brazil	JQ730071	JQ730282	JQ730489
<i>Comolia vernicosa</i> (Benth.) Triana	Wurdack, K. J., 4181 (NY)	Guyana	JQ730072	JQ730283	JQ730490
<i>Desmocelis villosa</i> (Aubl.) Naudin	Michelangeli, F. A., 827 (BH)	Venezuela	JQ730073	JQ730284	JQ730491
<i>Dichaetanthera africana</i> Jacq.-Fél.	Smith, S., 1885 (US)	Gabon	JQ730074	JQ730285	JQ730492
<i>Dichaetanthera oblongifolia</i> Baker	Almeda, F., 7926a (CAS)	Madagascar	JQ730075	JQ730286	JQ730493
<i>Dionycha bojeri</i> Naudin	Almeda, F., 8626 (CAS)	Madagascar	JQ730076	JQ730287	JQ730494
<i>Dissotis</i> cf. <i>phaeotricha</i> Harv.	Steiner, K., 3561 (NBG)	Madagascar	JQ730078	JQ730289	JQ730496
<i>Dissotis multiflora</i> (Sm.) Triana	Smith, S., 1886 (US)	Gabon	JQ730077	JQ730288	JQ730495
<i>Eriocnema fulva</i> Naudin	Almeda, F., 8414 (CAS)	Brazil	EF418811	JQ730291	JQ730497
<i>Ernestia confertiflora</i> Wurdack	Penneys, D. S., 1913 (FLAS)	French Guiana	JQ730079	JQ730292	JQ730498
<i>Ernestia glandulosa</i> Gleason	Martin, C. V., 471 (NY)	French Guiana	JQ730080	JQ730293	JQ730499
<i>Ernestia pullei</i> Gleason	Martin, C. V., 460 (NY)	French Guiana	JQ730081	JQ730294	JQ730500
<i>Ernestia tenella</i> (Bonpl.) DC.	Michelangeli, F. A., 386 (BH)	Venezuela	JQ730082	JQ730295	JQ730501
<i>Fritzchia erecta</i> Cham.	Guimarães, P., 406 (RB)	Brazil	JQ730083	JQ730296	JQ730502
<i>Graffenrieda latifolia</i> (Naudin) Triana	Michelangeli, F. A., 794 (BH)	Venezuela	AY460450	JQ730297	JQ730503
<i>Graffenrieda moritziana</i> Triana	Michelangeli, F. A., 832 (BH)	Venezuela	AY460451	JQ730298	JQ730504
<i>Guyonia ciliata</i> Hook.f.	Mambo, P., 248 (NY)	Cameroon	JQ730084	–	JQ730505
<i>Heterocentron elegans</i> (Schltdl.) Kuntze	Cultivated NY, (NY)	USA*	JQ730085	JQ730299	JQ730506
<i>Heterocentron muricatum</i> Gleason	Penneys, D. S., 1949 (FLAS)	USA*	JQ730086	JQ730300	JQ730507
<i>Heterocentron subtriplinerium</i> (Link & Otto) A.Braun & C.D.Bouché	Penneys, D. S., 1430 (FLAS)	Mexico	JQ730087	JQ730301	JQ730508
<i>Heterotis decumbens</i> (P.Beauv.) Trian	Smith, S., 1705 (US)	Gabon	JQ730088	JQ730302	JQ730509
<i>Heterotis rotundifolia</i> (Sm.) Jacq.-Fél.	Penneys, D. S., 1304 (FLAS)	Dominica*	JQ730089	JQ730290	–
<i>Itatiaia cleistopetala</i> Ule	Baumgratz, J. F. A., 1138b (R)	Brazil	JQ730090	JQ730303	JQ730510
<i>Lavoisiera imbricata</i> (Thunb.) DC.	Goldenberg, R., 820 (NY)	Brazil	JQ730091	JQ730304	JQ730511
<i>Lavoisiera mucrifera</i> Mart. ex Schrank ex DC.	Guimarães, P., 345 (RB)	Brazil	JQ730092	JQ730305	JQ730512
<i>Lavoisiera pulchella</i> Cham.	Goldenberg, R., 814 (NY)	Brazil	JQ730093	JQ730306	JQ730513
<i>Macairea pachyphylla</i> Benth.	Redden, K. M., 3869 (NY)	Guyana	JQ730094	–	–
<i>Macairea radula</i> (Bonpl.) DC.	Lima, J., 715 (UPCB)	Brazil	JQ730095	JQ730307	JQ730514
<i>Macairea thyrsoflora</i> DC.	Wurdack, K. J., 4153 (NY)	Guyana	JQ730096	JQ730308	JQ730515
<i>Marcetia acerosa</i> DC.	Santos, A. K. A., 681 (UFB)	Brazil	JQ730097	–	JQ730516
<i>Marcetia eimeriana</i> A.B.Martins & E.M.Woodgyer	Santos, A. K. A., 832 (UFB)	Brazil	JQ730098	JQ730309	JQ730517
<i>Marcetia ericoides</i> Cogn.	Santos, A. K. A., 532 (UFB)	Brazil	JQ730099	JQ730310	JQ730518
<i>Marcetia harleyii</i> Wurdack	Santos, A. K. A., 558 (UFB)	Brazil	JQ730100	–	JQ730519
<i>Marcetia latifolia</i> Naudin	Santos, A. K. A., 366 (UFB)	Brazil	JQ730101	–	JQ730520
<i>Marcetia taxifolia</i> (A.St.Hil.) DC.	Michelangeli, F. A., 680 (BH)	Venezuela	JQ730102	JQ730311	JQ730521
<i>Melastoma affine</i> D.Don			GQ265878	–	–
<i>Melastoma candidum</i> D.Don	Chen, C. H., 6443 (TAIE)	Taiwan	JQ730103	JQ730312	JQ730522
<i>Melastoma denticulatum</i> Labill.	Simmons, M. P., 1842 (BH)	New Caledonia	JQ730104	JQ730313	JQ730523
<i>Melastoma dodecandrum</i> Desr.			GQ265883	–	–
<i>Melastoma intermedium</i> Dunn			GQ265879	–	–
<i>Melastoma malabathricum</i> L.	Penneys, D. S., 1998 (CAS)	China	JQ730105	JQ730314	JQ730524
<i>Melastoma sanguineum</i> Sims	Penneys, D. S., 2000 (CAS)	China	JQ730106	JQ730315	JQ730525
<i>Meriania longifolia</i> (Naudin) Cogn.	Michelangeli, F. A., 610 (BH)	Venezuela	AY460454	JQ730316	JQ730526
<i>Miconia dodecandra</i> (Desr.) Cogn.	Judd, W. S., 8093 (FLAS)	Dominican Republic	AY460506	JQ730317	JQ730527
<i>Miconia tomentosa</i> (Rich.) D.Don ex DC.	Michelangeli, F. A., 1344 (NY)	Brazil	EF418905	JQ730318	JQ730528
<i>Microlepis oleaefolia</i> (DC.) Triana	Goldenberg, R., 1036 (NY)	Brazil	JQ730107	JQ730319	JQ730529
<i>Monochaetum bonplandii</i> (Kunth.) Naudin	Michelangeli, F. A., 1239 (NY)	Venezuela	JQ730108	JQ730320	JQ730530

APPENDIX *Continued*

Species	Collector, number (herbarium)	Provenance	nrITS	<i>accd-psaI</i>	<i>psbK-psbL</i>
<i>Monochaetum discolor</i> H. Karst. ex Triana	Capote I., 811 (NY)	Venezuela	JQ730109	JQ730321	JQ730531
<i>Monochaetum humboldtianum</i> (Kunth & Boché) Kunth ex Walp.	Michelangeli, F. A., 796 (BH)	Venezuela	JQ730110	JQ730322	JQ730532
<i>Monochaetum meridense</i> (Klotzsch ex H.Karst.) Naudin	Capote I., 862 (NY)	Venezuela	JQ730111	JQ730323	JQ730533
<i>Monochaetum polyneuron</i> Triana	Michelangeli, F. A., 1267 (NY)	Venezuela	JQ730112	JQ730324	JQ730534
<i>Monochaetum tenellum</i> Naudin			AY460432	–	–
<i>Monochaetum uribe</i> Wurdack	Mendoza, H., 17593 (FMB)	Colombia	JQ730113	JQ730325	JQ730535
<i>Monochaetum volcanicum</i> Cogn.	Michelangeli, F. A., 718 (BH)	Costa Rica	JQ730114	JQ730326	JQ730536
<i>Nepsera aquatica</i> (Aubl.) Naudin	Struwe, L., 1158 (NY)	Puerto Rico	JQ730115	JQ730327	JQ730537
<i>Osbeckia australiana</i> Naudin	Brennan, K. G., 7008 (NY)	Australia	JQ730116	JQ730328	JQ730538
<i>Osbeckia courtalensis</i> Gamble	Klackenberg, 376 (NY)	India	JQ730117	–	–
<i>Osbeckia nepalensis</i> Hook.	Penneys, D. S., 1986 (CAS)	China	JQ730118	JQ730329	JQ730539
<i>Osbeckia stellata</i> Buch.-Ham. ex Ker Gawl.	Penneys, D. S., 1969 (CAS)	China	JQ730119	JQ730330	JQ730540
<i>Pachyloma huberioides</i> (Naudin) Triana	Caddah, M.K., 558 (NY)	Brazil	JQ730120	JQ730331	JQ730541
<i>Physeterostemon tomasii</i> Amorim, Michelangeli & Goldenb.	Amorim, A., 5054 (NY)	Brazil	JQ730121	JQ730332	JQ730542
<i>Pilocosta campanensis</i> (Almeda & Whiffin) Almeda	Penneys, D. S., 1647 (FLAS)	Panama	JQ730122	JQ730333	JQ730543
<i>Pilocosta nana</i> (Standl.) Almeda & Whiffin	Moran, R. C., 6928 (NY)	Costa Rica	JQ730123	JQ730334	JQ730544
<i>Pilocosta nubicola</i> Almeda	Penneys, D. S., 1775 (FLAS)	Costa Rica	JQ730124	JQ730335	JQ730545
<i>Pilocosta oerstedii</i> (Triana) Almeda & Whiffin	Kriebel, R., 5412 (NY)	Costa Rica	JQ730125	JQ730336	JQ730546
<i>Pterogastra divaricata</i> (Bonpl.) Naudin	Michelangeli, F. A., 540 (BH)	Venezuela	JQ730126	JQ730337	JQ730547
<i>Pterogastra minor</i> Naudin	Romero, G. A., 1682 (CAS)	Brazil	JQ730127	JQ730338	JQ730548
<i>Pterolepis</i> sp.	Nee, M., 55383 (NY)	Bolivia	JQ730133	JQ730344	JQ730554
<i>Pterolepis alpestris</i> (DC.) Triana	Almeda, F., 8469 (CAS)	Brazil	JQ730128	JQ730339	JQ730549
<i>Pterolepis glomerata</i> (Rottb.) Miq.	Martin, C. V., 419 (NY)	French Guiana	JQ730129	JQ730340	JQ730550
<i>Pterolepis parnasiifolia</i> (DC.) Triana	Almeda, F., 8306 (CAS)	Brazil	JQ730130	JQ730341	JQ730551
<i>Pterolepis repanda</i> (DC.) Triana	Almeda, F., 7731 (CAS)	Brazil	JQ730131	JQ730342	JQ730552
<i>Pterolepis rotundifolia</i> Wurdack	Almeda, F., 8290 (CAS)	Brazil	JQ730132	JQ730343	JQ730553
<i>Rhexia alifanus</i> Walter			DQ985623	–	–
<i>Rhexia aristosa</i> Britton	Naczi, R. F. C., 12065 (NY)	USA	JQ730134	JQ730345	JQ730555
<i>Rhexia cubensis</i> Griseb.			DQ985627	–	–
<i>Rhexia lutea</i> Walter			DQ985628	–	–
<i>Rhexia mariana</i> L.	Longbottom, W. D., 11730 (NY)	USA	JQ730135	–	JQ730556
<i>Rhexia nashii</i> Small			DQ985662	–	–
<i>Rhexia nutallii</i> C.W.James			DQ985634	–	–
<i>Rhexia parviflora</i> Chapm.			DQ985636	–	–
<i>Rhexia petiolata</i> Walter			DQ985637	–	–
<i>Rhexia salicifolia</i> Kral & Bostick			DQ985639	–	–
<i>Rhexia virginica</i> L.	Michelangeli, F. A., 1448 (NY)	USA	JQ730136	JQ730346	JQ730557
<i>Rhynchanthera bracteata</i> Triana	Zenteno, F., 8801 (NY)	Bolivia	JQ730137	JQ730347	JQ730558
<i>Rhynchanthera grandiflora</i> (Aubl.) DC.	Michelangeli, F. A., 541 (BH)	Venezuela	JQ730138	JQ730348	JQ730559
<i>Rhynchanthera serrulata</i> (Rich.) DC.	Michelangeli, F. A., 828 (BH)	Venezuela	AY460435	JQ730349	JQ730560
<i>Rousseauxia andringitrensis</i> (H.Perrier) Jacq.-Fél.	Almeda, F., 9390 (CAS)	Madagascar	JQ730139	JQ730350	JQ730561
<i>Rousseauxia minimifolia</i> (Jum. & H.Perrier) Jacq.-Fél.	Almeda, F., 8704 (CAS)	Madagascar	JQ730140	JQ730351	JQ730562



APPENDIX *Continued*

Species	Collector, number (herbarium)	Provenance	nrITS	<i>accd-psaI</i>	<i>psbK-psbL</i>
<i>Sandermania hoehnei</i> (Cogn.) Wurdack	Goldenberg, R., 1007 (NY)	Brazil	JQ730141	JQ730352	JQ730563
<i>Siphanthera hostmanii</i> Cogn.	Wurdack, K. J., 4142 (NY)	Guyana	JQ730142	JQ730353	JQ730564
<i>Svitramia hatschbachii</i> Wurdack	Guimarães, P., 391 (RB)	Brazil	JQ730143	JQ730354	JQ730565
<i>Svitramia minor</i> R.Romero & A.B.Martins	Guimarães, P., 390 (RB)	Brazil	JQ730144	JQ730355	JQ730566
<i>Svitramia pulchra</i> Cham.	Guimarães, P., 388 (RB)	Brazil	JQ730145	JQ730356	JQ730567
<i>Svitramia</i> sp. ined. 1	Guimarães, P., 402 (RB)	Brazil	JQ730146	JQ730357	JQ730568
<i>Svitramia</i> sp. ined. 2	Guimarães, P., 400 (RB)	Brazil	JQ730147	JQ730358	JQ730569
<i>Svitramia wurdackiana</i> R.Romero & A.B.Martins	Guimarães, P., 395 (RB)	Brazil	JQ730148	JQ730359	JQ730570
<i>Tibouchina aegopogon</i> (Naud.) Cogn.	Almeda, F., 9523 (CAS)	Brazil	–	–	JQ730571
<i>Tibouchina aemula</i> (Triana) Cogn.	Guimarães, P., 313 (RB)	Brazil	JQ730149	JQ730360	JQ730572
<i>Tibouchina alpestris</i> Cogn.	Nee, M., 55379 (NY)	Bolivia	JQ730150	JQ730361	JQ730573
<i>Tibouchina angustifolia</i> (Naudin) Cogn.	Almeda, F., 9568 (CAS)	Brazil	JQ730151	JQ730362	JQ730574
<i>Tibouchina arborea</i> (Gardn.) Cogn.	Guimarães, P., 324 (RB)	Brazil	JQ730152	JQ730363	JQ730575
<i>Tibouchina arenaria</i> Cogn.	Guimarães, P., 352 (RB)	Brazil	JQ730153	JQ730364	JQ730576
<i>Tibouchina aspera</i> Aubl.	Martin, C. V., 409 (NY)	French Guiana	JQ730154	JQ730365	JQ730577
<i>Tibouchina aspera</i> var <i>asperima</i> Cogn.	Martin, C. V., 423 (NY)	French Guiana	JQ730155	JQ730366	JQ730578
<i>Tibouchina axillaris</i> Cogn.	Guimarães, P., 338 (RB)	Brazil	JQ730156	JQ730367	JQ730579
<i>Tibouchina barnebyana</i> Wurdack	Almeda, F., 8262 (CAS)	Brazil	JQ730157	JQ730368	–
<i>Tibouchina benthamiana</i> (Gardn.) Cogn.	Almeda, F., 9759 (CAS)	Brazil	JQ730158	JQ730369	JQ730580
<i>Tibouchina bicolor</i> (Naudin) Cogn.	Nee, M., 55307 (NY)	Bolivia	JQ730159	JQ730370	JQ730581
<i>Tibouchina bipenicillata</i> (Naudin) Cogn.	Michelangelo, F. A., 735 (BH)	Venezuela	JQ730160	JQ730371	JQ730582
<i>Tibouchina blanchetiana</i> Cogn.	Santos, A. K. A., 332 (UFB)	Brazil	JQ730161	JQ730372	–
<i>Tibouchina boudetii</i> P.J.F.Guim. & Goldenb.	Kollman & Goldenberg, 8563 (NY)	Brazil	JQ730162	JQ730373	JQ730583
<i>Tibouchina breedlovei</i> Wurdack	Kelly, L., 1361 (CAS)	Mexico	JQ730163	JQ730374	JQ730584
<i>Tibouchina candolleana</i> (DC.) Cogn.	Lima, J., 711 (UPCB)	Brazil	JQ730164	JQ730375	JQ730585
<i>Tibouchina cardinalis</i> (Bonpl.) Cogn.	Guimarães, P., 407 (RB)	Brazil	JQ730165	JQ730376	JQ730586
<i>Tibouchina castellensis</i> Brade	Goldenberg, R., 1071 (NY)	Brazil	JQ730166	JQ730377	JQ730587
<i>Tibouchina cerastifolia</i> (Naudin) Cogn.	Varassin, I. G., 96 (UPCB)	Brazil	JQ730167	–	JQ730588
<i>Tibouchina chamaecistus</i> (Naudin) Cogn.	Penneys, D. S., 1276 (FLAS)	Martinique	JQ730168	JQ730378	JQ730589
<i>Tibouchina ciliaris</i> (Vent.) Cogn.	Kriebel, R., 5461 (NY)	Costa Rica	JQ730169	–	JQ730590
<i>Tibouchina cinerea</i> Cogn.	Almeda, F., 9843 (CAS)	Brazil	JQ730170	JQ730379	JQ730591
<i>Tibouchina citrina</i> (Naudin) Cogn.	Nee, M., 55308 (NY)	Bolivia	JQ730171	JQ730380	JQ730592
<i>Tibouchina clavata</i> (Pers.) Wurdack	Santos, A. K. A., 696 (UFB)	Brazil	JQ730172	JQ730381	JQ730593
<i>Tibouchina clidemiodes</i> (O.Berg ex Triana) Cogn.	Goldenberg, R., 1439 (NY)	Brazil	JQ730173	JQ730382	–
<i>Tibouchina clinopodifolia</i> (DC.) Cogn.	Goldenberg, R., 774 (NY)	Brazil	JQ730174	JQ730383	JQ730594
<i>Tibouchina confertiflora</i> (Naudin) Cogn.	Nee, M., 55377 (NY)	Bolivia	JQ730175	JQ730384	JQ730595
<i>Tibouchina corymbosa</i> (Raddi) Cogn.	Guimarães, P., 327 (RB)	Brazil	JQ730176	JQ730385	JQ730596
<i>Tibouchina cristata</i> Brade	Baumgratz, J. F. A., 819 (R)	Brazil	JQ730177	JQ730386	JQ730597
<i>Tibouchina cryptadena</i> Gleason	Michelangelo, F. A., 708 (BH)	Venezuela	JQ730178	JQ730387	JQ730598
<i>Tibouchina dubia</i> (Cham.) Cogn.	Varassin, I. G., 101 (UPCB)	Brazil	JQ730179	JQ730388	JQ730599
<i>Tibouchina estrellensis</i> (Raddi) Cogn.	Guimarães, P., 340 (RB)	Brazil	JQ730180	JQ730389	JQ730600
<i>Tibouchina fissinervia</i> DC.	Guimarães, P., 351 (RB)	Brazil	JQ730181	JQ730390	JQ730601
<i>Tibouchina fothergillae</i> (Schrank & Mart. ex DC.) Cogn.	Guimarães, P., 314 (RB)	Brazil	JQ730182	JQ730391	JQ730602
<i>Tibouchina foveolata</i> Cogn.	Guimarães, P., 350 (RB)	Brazil	JQ730183	JQ730392	JQ730603

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Species	Collector, number (herbarium)	Provenance	nrITS	<i>accd-psaI</i>	<i>psbK-psbL</i>
<i>Tibouchina fraterna</i> N.E.Br.	Michelangeli, F. A., 512 (BH)	Venezuela	JQ730184	JQ730393	JQ730604
<i>Tibouchina frigidula</i> (DC.) Cogn.	Guimarães, P., 394 (RB)	Brazil	JQ730185	JQ730394	JQ730605
<i>Tibouchina gardneriana</i> (Triana) Cogn.	Guimarães, P., 305 (RB)	Brazil	JQ730186	JQ730395	JQ730606
<i>Tibouchina gayana</i> (Naudin) Cogn.	Nee, M., 55380 (NY)	Bolivia	JQ730187	JQ730396	JQ730607
<i>Tibouchina geitneriana</i> (Schltdl.) Cogn.	Capote I., 852 (NY)	Venezuela	JQ730188	JQ730397	JQ730608
<i>Tibouchina gleasoniana</i> Wurdack	Jaramillo, J., 7985 (NY)	Colombia	JQ730189	–	JQ730609
<i>Tibouchina gracilis</i> (Bonpl.) Cogn.	Guimarães, P., 336 (RB)	Brazil	JQ730190	JQ730398	JQ730610
<i>Tibouchina granulosa</i> (Desr.) Cogn.	Guimarães, P., 378 (RB)	Brazil	JQ730191	JQ730399	JQ730611
<i>Tibouchina grossa</i> (L.f.) Cogn.	Zabala, J. C., 1 (NY)	Colombia	JQ730192	JQ730400	JQ730612
<i>Tibouchina heteromalla</i> (D.Don) Cogn.	Guimarães, P., 339 (RB)	Brazil	JQ730193	JQ730401	JQ730613
<i>Tibouchina hieracioides</i> (DC.) Cogn.	Almeda, F., 8380 (CAS)	Brazil	JQ730194	JQ730402	JQ730614
<i>Tibouchina hospita</i> (DC.) Cogn.	Baumgratz, J. F. A., 1008 (R)	Brazil	JQ730195	JQ730403	JQ730615
<i>Tibouchina inopinata</i> Wurdack	Kriebel, R., 5342 (NY)	Costa Rica	JQ730196	JQ730404	JQ730616
<i>Tibouchina itatiaiae</i> Cogn.	Guimarães, P., 310 (RB)	Brazil	JQ730197	JQ730405	JQ730617
<i>Tibouchina kleinii</i> Wurdack	Almeda, F., 9868 (CAS)	Brazil	JQ730198	JQ730406	JQ730618
<i>Tibouchina laevicaulis</i> Wurdack	Guimarães, P., 412 (RB)	Brazil	JQ730199	JQ730407	JQ730619
<i>Tibouchina laxa</i> (Desr.) Cogn.	Harling, G., 23570 (NY)	Ecuador	JQ730200	JQ730408	JQ730620
<i>Tibouchina lepidota</i> (Bonpl.) Baill.	Morales, M. E., sn (UPTC)	Colombia	JQ730201	JQ730409	JQ730621
<i>Tibouchina lindeniana</i> Cogn.	Michelangeli, F. A., 1269 (NY)	Brazil	JQ730202	JQ730410	JQ730622
<i>Tibouchina llanorum</i> Wurdack	Michelangeli, F. A., 736 (BH)	Venezuela	JQ730203	JQ730411	JQ730623
<i>Tibouchina longifolia</i> (Vahl) Baill.	Michelangeli, F. A., 816 (BH)	Venezuela	JQ730204	JQ730412	JQ730624
<i>Tibouchina macrochiton</i> (Mart. ex DC.) Cogn.	Guimarães, P., 320 (RB)	Brazil	JQ730205	JQ730413	JQ730625
<i>Tibouchina manicata</i> Cogn.	Guimarães, P., 328 (RB)	Brazil	JQ730206	JQ730414	JQ730626
<i>Tibouchina martialis</i> (Cham.) Cogn.	Goldenberg, R., 821 (NY)	Brazil	JQ730207	JQ730415	JQ730627
<i>Tibouchina martiusiana</i> (DC.) Cogn.	Guimarães, P., 335 (RB)	Brazil	JQ730208	JQ730416	JQ730628
<i>Tibouchina melanocalyx</i> R. Romero, P. J. F. Guimaraes & Leoni	Guimarães, P., 341 (RB)	Brazil	JQ730209	JQ730417	JQ730629
<i>Tibouchina microphylla</i> Cogn. ex Schwacke	Guimarães, P., 344 (RB)	Brazil	JQ730210	JQ730418	JQ730630
<i>Tibouchina minor</i> Cogn.	Guimarães, P., 393 (RB)	Brazil	JQ730211	JQ730419	JQ730631
<i>Tibouchina mollis</i> (Bonpl.) Cogn.	Penneys, D. S., 1895 (FLAS)	Ecuador	JQ730212	JQ730420	JQ730632
<i>Tibouchina mutabilis</i> Cogn.	Lobão, A., 1450 (RB)	Brazil	JQ730213	JQ730421	JQ730633
<i>Tibouchina naudiniana</i> (Decne) Cogn.	CULTIVATED NY, (NY)	USA*	JQ730214	JQ730422	JQ730634
<i>Tibouchina nodosa</i> Wurdack	Santos, A. K. A., 1049 (UFB)	Brazil	JQ730215	JQ730423	JQ730635
<i>Tibouchina octopetala</i> Cogn.	Salomon, J. C., 14934 (CAS)	Brazil	JQ730216	JQ730424	JQ730636
<i>Tibouchina oreophilla</i> Wurdack	Santos, A. K. A., 829 (UFB)	Brazil	JQ730217	JQ730425	JQ730637
<i>Tibouchina ornata</i> (Sw.) Baill.	Penneys, D. S., 1298 (FLAS)	Dominica	JQ730218	JQ730426	JQ730638
<i>Tibouchina papyrus</i> (Pohl) Toledo	Guimarães, P., 380 (RB)	Brazil	JQ730219	JQ730427	JQ730639
<i>Tibouchina pendula</i> Cogn.	Penneys, D. S., 1893 (FLAS)	Ecuador	JQ730220	JQ730428	JQ730640
<i>Tibouchina pereirae</i> Brade & Markgr.	Santos, A. K. A., 302 (UFB)	Brazil	JQ730221	JQ730429	JQ730641
<i>Tibouchina pulchra</i> (Cham.) Cogn.	Baumgratz, J. F. A., 1068 (R)	Brazil	JQ730222	JQ730430	JQ730642
<i>Tibouchina radula</i> Markgr.	Goldenberg, R., 1281 (NY)	Brazil	JQ730223	JQ730431	JQ730643
<i>Tibouchina ramboi</i> Brade	Almeda, F., 9889 (CAS)	Brazil	JQ730224	JQ730432	JQ730644
<i>Tibouchina salviaefolia</i> Cogn.	Guimarães, P., 322 (RB)	Brazil	JQ730225	JQ730433	JQ730645
<i>Tibouchina sebastianopolitana</i> (Raddi) Cogn.	Guimarães, P., 330 (RB)	Brazil	JQ730226	JQ730434	JQ730646
<i>Tibouchina sellowiana</i> Cogn.	Guimarães, P., 331 (RB)	Brazil	JQ730227	JQ730435	JQ730647
<i>Tibouchina semidecandra</i> (Schrank & Mart. ex DC.) Cogn.	Goldenberg, R., 765 (NY)	Brazil	JQ730228	JQ730436	JQ730648
<i>Tibouchina sp.</i>	Nee, M., 55287 (RB)	Brazil	JQ730230	JQ730438	JQ730650
<i>Tibouchina sp. ined. 1</i>	Goldenberg, R., 1143 (NY)	Brazil	JQ730231	JQ730439	JQ730651
<i>Tibouchina sp. ined. 2</i>	Goldenberg, R., 1150 (NY)	Brazil	JQ730232	JQ730440	JQ730652

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Species	Collector, number (herbarium)	Provenance	nrITS	<i>accd-psaI</i>	<i>psbK-psbL</i>
<i>Tibouchina sp. ined.</i> 3	Guimarães, P., 377 (NY)	Bolivia	JQ730229	JQ730437	JQ730649
<i>Tibouchina stenocarpa</i> (DC.) Cogn.	Nee, M., 55386 (NY)	Bolivia	JQ730233	JQ730441	JQ730653
<i>Tibouchina striphnocalyx</i> (DC.) Pittier	Michelangeli, F. A., 379 (BH)	Venezuela	JQ730234	JQ730442	JQ730654
<i>Tibouchina trichopoda</i> (DC.) Baill.	Lobão, A, 1437 (RB)	Brazil	JQ730235	JQ730443	JQ730655
<i>Tibouchina trinervia</i> Cogn.	Almeda, F., 9682 (CAS)	Brazil	–	JQ730444	JQ730656
<i>Tibouchina urceolaris</i> (DC.) Cogn.	Guimarães, P., 321 (RB)	Brazil	JQ730236	JQ730445	JQ730657
<i>Tibouchina ursina</i> (Cham.) Cogn.	Almeda, F., 9859 (CAS)	Brazil	JQ730237	JQ730446	JQ730658
<i>Tibouchina valtheri</i> Cogn.	Almeda, F., 8443 (CAS)	Brazil	JQ730238	JQ730447	JQ730659
<i>Tibouchina velutina</i> (Naudin) Cogn.	Santos, A. K. A., 349 (UFB)	Brazil	JQ730239	JQ730448	JQ730660
<i>Tibouchina wurdackii</i> Almeda & Todzia	Penneys, D. S., 1749 (FLAS)	Panama	JQ730240	JQ730449	JQ730661
<i>Tibouchinopsis mirabilis</i> Brade & Markgr.	Santos, A. K. A., 338 (UFB)	Brazil	JQ730241	JQ730450	JQ730662
<i>Trembleya laniflora</i> Cogn.			AY553744	–	–
<i>Trembleya parviflora</i> Cogn.	Goldenberg, R., 824 (NY)	Brazil	JQ730242	JQ730451	JQ730663
<i>Trembleya pentagona</i> Naudin			AY553745	–	–
<i>Tristemma coronatum</i> Benth.	Schmidt, H. H., 3386 (CAS)	Ghana	JQ730243	JQ730452	JQ730664
<i>Tristemma hirtum</i> P. Beauv.	Smith, S., 1879 (US)	Gabon	JQ730244	JQ730453	JQ730665
<i>Tristemma littorale</i> Benth.	Smith, S., 1725 (US)	Gabon	JQ730245	JQ730454	JQ730666
<i>Tristemma mauritianum</i> J. F. Gmel.	Almeda, F., 8021 (CAS)	Madagascar	JQ730246	JQ730455	JQ730667

\*Collected in cultivation outside native range.

–, locus not sequenced.