

## Reproductive biology and species geographical distribution in the Melastomataceae: a survey based on New World taxa

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• **Background and Aims** Apomictic plants are less dependent on pollinator services and able to occupy more diverse habitats than sexual species. However, such assumptions are based on temperate species, and comparable evaluation for species-rich Neotropical taxa is lacking. In this context, the Melastomataceae is a predominantly Neotropical angiosperm family with many apomictic species, which is common in the Campos Rupestres, endemism-rich vegetation on rocky outcrops in central Brazil. In this study, the breeding system of some Campo Rupestre Melastomataceae was evaluated, and breeding system studies for New World species were surveyed to test the hypothesis that apomixis is associated with wide distributions, whilst sexual species have more restricted areas.

• **Methods** The breeding systems of 20 Campo Rupestre Melastomataceae were studied using hand pollinations and pollen-tube growth analysis. In addition, breeding system information was compiled for 124 New World species of Melastomataceae with either wide (>1000 km) or restricted distributions.

• **Key Results** Most (80%) of the Campo Rupestre species studied were self-compatible. Self-incompatibility in *Microlicia viminalis* was associated with pollen-tube arrest in the style, as described for other Melastomataceae, but most self-incompatible species analysed showed pollen-tube growth to the ovary irrespective of pollination treatment. Apomictic species showed lower pollen viability and were less frequent among the Campo Rupestre plants. Among the New World species compiled, 43 were apomictic and 77 sexual (24 self-incompatible and 53 self-compatible). Most apomictic (86%) and self-incompatible species (71%) presented wide distributions, whilst restricted distributions predominate only among the self-compatible ones (53%).

• **Conclusions** Self-compatibility and dependence on biotic pollination were characteristic of Campo Rupestre and narrowly distributed New World Melastomataceae species, whilst apomictics are widely distributed. This is, to a certain extent, similar to the geographical parthenogenesis pattern of temperate apomictics.

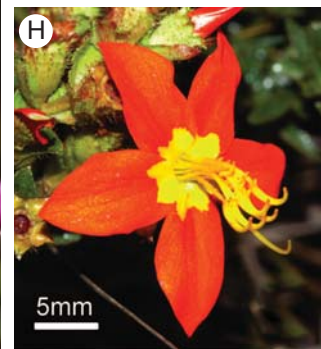
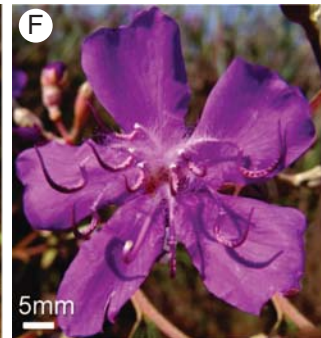
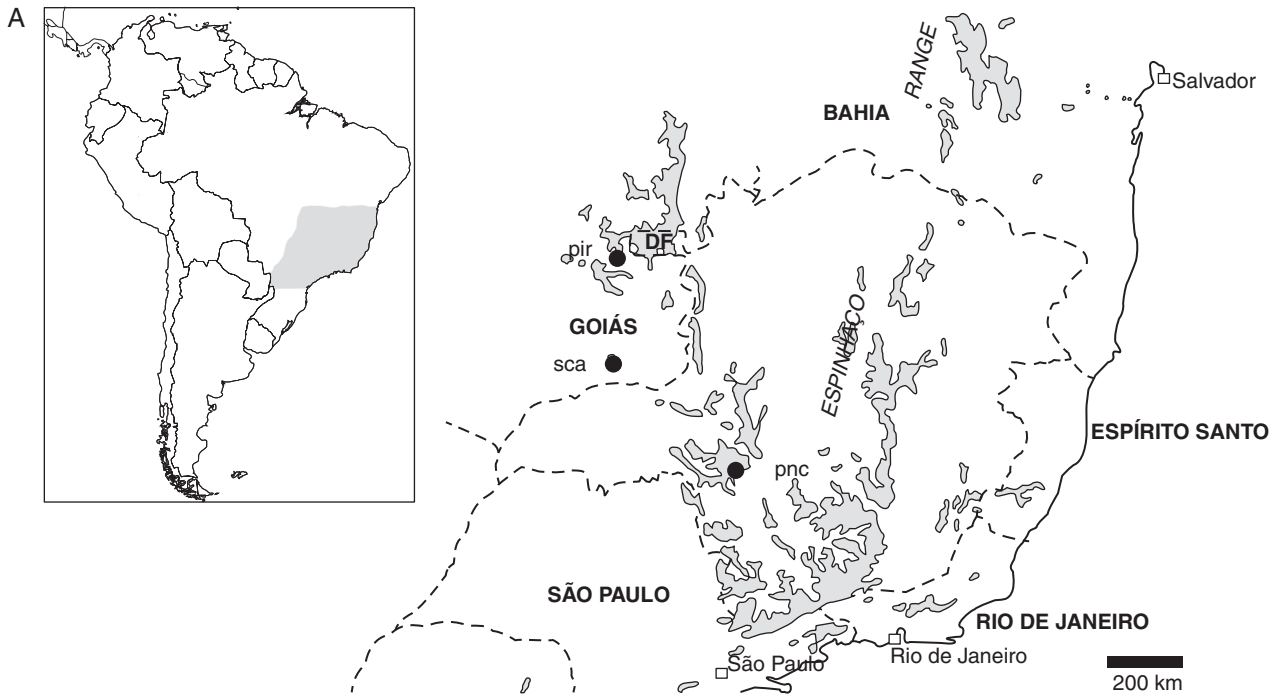
**Key words:** Apomixis, Melastomataceae, breeding system, Campo Rupestre, Cerrado, geographic distribution, rocky outcrops.

### INTRODUCTION

Different ecological and evolutionary factors such as the dispersal ability, tolerance to environment changes, population size, floral phenotypic plasticity, establishment and extinction dynamics may help to explain the geographic distribution of species (Brown *et al.*, 1996). But breeding systems have been often viewed as a factor that may affect the persistency and distribution of plant species (Eckert *et al.*, 2006; Barrett *et al.*, 2008). Since the seminal papers by Baker (e.g. Baker, 1967), self-incompatibility and self-compatibility have been associated with distinct distribution patterns (Lowry and Lester, 2006), and it is believed that the apomictic species are capable of occupying more diverse environments, due to their greater independence of pollinator services, compared with the sexual and self-incompatible species (Bierzychudek, 1987; Hörandl and Paun, 2007; Hörandl *et al.*, 2008). Although these

assumptions are mostly based on temperate plant taxa, the Pleistocene climatic changes, which seem to have driven apomictics range expansion (geographical parthenogenesis *sensu* Hörandl, 2006), also affected the southern hemisphere and the idea may help in understanding the breeding system and biogeographical association of species-rich Neotropical groups.

The Melastomataceae is the seventh largest family of flowering plants, with around 166 genera and 4500 species of which some 3000 are Neotropical (Clausing and Renner, 2001). Centres of diversity for the family are distributed in two regions with different environmental conditions: the Andes in the north of South America, and the Brazilian central–south mountain ranges (Renner, 1993). In Brazil, there are >1500 species of Melastomataceae distributed in habitats ranging from moist forests to open plant formations of Cerrado, the Neotropical savanna region in central Brazil (Renner, 1989a; Romero and Martins, 2002).



In comparison with other tropical families the Melastomataceae are relatively conservative in their floral morphology and pollination system. Most species have hermaphrodite flowers with poricidal anthers and marked herkogamy, which favour allogamy (Renner, 1989a). Usually, pollen is the only resource offered and bees able to vibrate the anthers (buzz pollination) are the main pollinators (Proença, 1992).

Although allogamy is common in the family, there are also many apomictic and self-compatible species (Renner, 1989a). Indeed, apomixis appears to be more frequent in some groups of Melastomataceae than in the angiosperms as a whole (Goldenberg and Shepherd, 1998; Melo *et al.*, 1999; Goldenberg, 2000a). In some of these species, apomixis has been related to the presence of polyembryony, polyploidy and high pollen sterility (Carman, 1997; Goldenberg and Shepherd, 1998; Mendes-Rodrigues and Oliveira, 2012).

Most of the apomictic species of Melastomataceae belong to the tribe Miconieae (88%), and they have wider distributions than the sexual species of the same tribe (Goldenberg, 2000a). If this relationship between breeding system and geographic distribution applies to the family as a whole, one would anticipate that the species of Melastomataceae with restricted distributions are likely to be sexual species, dependent on pollination for their reproductive success. However, for the moment, there are only isolated studies on the reproductive biology of these endemic species (Andrade *et al.*, 2007) to corroborate this hypothesis.

In the Cerrado region, some upland areas with rocky outcrops, the Campos Rupestres, present very specific conditions, such as shallow soils, low fertility and water availability (Vitta, 2002; Ribeiro and Walter, 2008). Such patchy and requiring environments, small distances and simple environmental barriers seem to be capable of generating considerable genetic differentiation (Lousada *et al.*, 2011), and have produced a typical flora with considerable endemism (Harley and Simmons, 1986; Giullietti *et al.*, 1987; Pirani *et al.*, 2003; Stannard, 1995; Romero and Nakajima, 1999; Vitta, 2002). The Melastomataceae is one of the most common families of Campo Rupestre vegetation, especially such genera as *Cambessedesia*, *Lavoisiera*, *Marcettia*, *Microlicia*, *Trembleya* and *Svitramia* (Romero and Martins, 2002; Faria *et al.*, 2006). However, information on the breeding biology of these taxa, and on the occurrence of apomixis, is still limited (Goldenberg, 2000a).

We investigated the breeding system of some Melastomataceae species of the central Brazilian Campos Rupestres and associated these features with their geographic distribution. We also complemented our field observations with data available in the literature for New World Melastomataceae species. We tested the hypothesis that apomixis is associated with species with wider distributions, whilst sexual breeding systems, and dependency on biotic pollinators, characterize endemic groups, such as those found in the Campo Rupestre highland flora.

## MATERIALS AND METHODS

### Study areas

The field studies were carried out in three different areas (Fig. 1A): Serra de Caldas Novas State Park and Pirineus State Park, both in Goiás state, and the Serra da Canastra National Park, in Minas Gerais (Brazil). All Parks are in the Cerrado bioma and present diverse plant formations, from forest to open savanna grasslands, but are characterized by upland Campos Rupestres areas (Fig. 1B). The Serra de Caldas Novas State Park comprises approx. 12 500 ha and is located in the south east of Goiás (17°43' to 17°50'S; 48°40' to 48°42'W). The average altitude of the mountain range is approx. 1000 m, with differences of 150 m in relation to the surrounding areas. Average annual rainfall is approx. 1500 mm, concentrated from September to April, and average annual temperature ranges from 20 to 25 °C (Almeida and Sarmiento, 1998). The Pirineus State Park comprises approx. 2800 hectares and is located in the centre of Goiás state (15°46' to 15°50'S; 48°48' to 48°53'W), at an altitude of 1300 m. The average annual rainfall is around 1200 mm, concentrated from October to April, and the average annual temperature varies from 21 to 24 °C (Oliveira *et al.*, 2002). The Serra da Canastra National Park is the second largest conservation area in Minas Gerais state. It comprises approx. 200 000 ha and includes the municipalities of São Roque de Minas, Delfinópolis and Sacramento, in the south-west of the state (20°00' to 20°30'S; 46°15' to 47°00'W). Some peaks of the mountain range reach 1500 m. The annual rainfall is above 2000 mm and the average temperature of the coldest month is <16 °C and in the warmest month it does not exceed 22 °C (MMA/IBAMA, 2005).

### Breeding system

The breeding system of 20 Melastomataceae species from Brazilian Campos Rupestres were investigated by controlled hand-pollination experiments, analysis of pollen viability and observations of pollen-tube growth (e.g. Fig. 1C–H). The sampled taxa comprised ten species of the tribe Melastomeae [*Macairea radula*, *Svitramia hatschbachii* (Fig. 1C), *S. minor*, *Svitramia* sp. (Fig. 1G), *Tibouchina anderssonii*, *T. frigidula*, *T. heteromalla*, *T. papyrus*, *T. stenocarpa* (Fig. 1F) and *T. villosissima*], nine of the tribe Microlicieae [*Cambessedesia espora*, *C. regnelliana* (Fig. 1H), *Lavoisiera imbricata*, *Microlicia fasciculata*, *M. inquinans* (Fig. 1E), *M. viminalis*, *Rhynchanthera grandiflora*, *Trembleya neopyrenaica* and *T. parviflora*] and one of the tribe Miconieae [*Miconia ferruginata* (Fig. 1D)]. Voucher specimens were deposited at Herbarium of the University of Brasilia (UB), Herbarium Uberlandense (HUFU) and the Herbarium of the State University of Campinas (UEC).

FIG. 1. Campo Rupestre areas specifically studied, environment and some of the species in these areas. (A) Shaded areas are 1000 m a.s.l. in Central Brazil where Campo Rupestre vegetation often appears (modified from Vasconcelos *et al.*, 2003). Dots show the study areas; pir, Pirinópolis State Park; sca, Serra de Caldas Novas State Park; pnc, Parque Nacional da Serra da Canastra. (B) Campo Rupestre area on rocky outcrops at Serra da Canastra; (C) *Svitramia hatschbachii* habit; (D) flowers of *Miconia rubiginosa*; (E) flowers of *Microlicia inquinans* showing yellow connectives and anthers and less conspicuous anthers (arrows); (F) *Tibouchina stenocarpa* flower; (G) bee visiting *Svitramia* sp.; (H) flower of *Cambessedesia regnelliana*.

The controlled pollination experiments were carried out using freshly opened flowers or pre-anthesis floral buds. Flowers previously isolated using nylon mesh bags were submitted to hand self-pollination, cross-pollination, and emasculation of pre-anthesis floral buds to test for autonomous apomixis (Goldenberg and Shepherd, 1998). Other flowers were bagged and left untreated to test for spontaneous self-pollination. The fruit set in all manipulated flowers was compared with that from natural pollinations of tagged flowers (Kearns and Inouye, 1993). It is important to notice, as discussed later, that this set of controlled pollinations do not allow testing for pseudogamous apomixis. But the Melastomataceae studied so far are autonomous apomictics.

The number of individuals and flowers used in controlled pollination varied among species, depending on their availability in the study areas (see Results), and the fruit development was verified about 2 months after the experiments. The ratio between the percentage of fruits resulting from self-pollination and cross-pollination was used to determine the index of self-incompatibility (ISI *sensu* Bullock, 1985) and species were considered self-incompatible whenever the ISI was lower than 0.20.

Pollen viability was estimated for each species using pollen of pre-anthesis buds fixed in FAA or ethanol 70%. Five buds were collected from different individuals and 100 pollen grains per bud were counted. Some species presented anthers in two distinct whorls, one of them with yellow appendices on the connective and less conspicuous anthers (Fig. 1E). In these cases, pollen from each whorl was analysed separately. The percentage of viable pollen grains was calculated from the ratio of stained and non-stained grains by aceto-carmin (Kearns and Inouye, 1993; Goldenberg and Shepherd, 1998) and also from pollen morphology (collapsed vs. intact grains).

Post-pollination pollen-tube growth in the styles was analysed in 17 out of the 20 species studied, using previously fixed pistils, softened in NaOH or cleared with sodium hypochloride, rinsed thoroughly in water, stained with buffered aniline blue, and observed under fluorescence microscopy (Martin, 1959). For such observations of pollen-tube growth into the ovary in *Cambessedesia regnelliana*, *Macairea radula*, *Miconia angelana*, *Microlicia inquinans*, *Rhynchanthera grandiflora*, *Svitramia hatschbachii*, *S. minor*, *Svitramia* sp., *Tibouchina papyrus* and *Tibouchina villosissima*, we used pistils of self- and cross-pollinated flowers fixed at 24, 48 and 72 h after pollination. For *Cambessedesia espora*, *Lavoisiera imbricata*, *Microlicia inquinans*, *M. viminalis*, *M. frigidula*, *Tibouchina heteromalla*, *T. stenocarpa*, *T. vilosissima* and *Trembleya parviflora*, we observed pollen germination at 2, 12, 24, 36, 48, 60, 72 and 84 h after both self- and cross-pollination.

#### Geographical distribution

We searched the literature for all New World species of Melastomataceae with information detailing their breeding system, and all such taxa were referred to their tribes according to the classification system proposed by Renner (1993), Goldenberg *et al.* (2008) and Penneys *et al.* (2010). The species were also grouped according to their breeding system as self-compatible, self-incompatible or apomictic. For all

species, information on their geographical distributions was compiled from taxonomic revisions, floristic studies, studies on reproductive biology and sites with databases of Brazilian and international herbaria (e.g. [www.discoverlife.org](http://www.discoverlife.org); [www.splink.cria.org.br](http://www.splink.cria.org.br); [www.zipcodezoo.com](http://www.zipcodezoo.com)).

The species were separated into two patterns of geographical distribution, based on the distance between the most distant populations, calculated using the ArcView software version 3.2. We recognized a wide distribution pattern, which included species with distance between populations >1000 km; and a restricted distribution pattern, which included species with the most distant populations <1000 km from each other. We tested if the number of species with either restricted or wide distribution was independent of the breeding system by using the chi-square independence test (Sokal and Rohlf, 1981).

## RESULTS

#### Breeding system

Most of the species studied directly in the Campo Rupestre areas (80%) were self-compatible (Table 1). The exceptions were *Tibouchina aegopogon* and *Microlicia viminalis*, which were self-incompatible, and *Miconia ferruginata* and *Microlicia fasciculata*, which were apomictic. Apomixis was described here for the tribe Microlicieae for the first time, as were the breeding system data for the highly endemic genus *Svitramia*. The number of treatments was somewhat limited for *M. viminalis* to assure self-incompatibility, but pollen tube analysis (below) seems to corroborate this conclusion. The few fruits formed after the treatment to test apomixis (emasculation of floral buds) in *Cambessedesia regnelliana*, *Microlicia inquinans*, *Svitramia hatschbachii* and *Trembleya parviflora* did not complete their development. Fruit formation from spontaneous self-pollination was observed only for some flowers in *Tibouchina papyrus* (6.8%).

Pollen viability, estimated by staining, showed a predominance of fertile pollen in populations of all sexual species (PV > 60%, Table 1). For the species with stamens in two whorls there was no difference in the estimated fertility of pollen from the anthers of the antisealous stamens in relation to antipetalous ones. Pollen viability estimated for the two apomictic species, *Miconia ferruginata* and *Microlicia fasciculata*, was very low, approx. 8% and 2%, respectively.

The analysis of pollen-tube growth showed self-incompatibility reaction along the style only in *Microlicia viminalis*. In general, pollen tubes, irrespective of pollination treatment, were observed at the base of the styles or penetrating the ovules 24 h after pollination (Table 2). Only two species, *S. hatschbachii* and *C. regnelliana*, showed slower pollen-tube growth in self- vs. cross-pollinated pistils: self-pollen tube arrival at the ovary was delayed by 24 h in the former species, and by 48 h in the latter.

#### Geographical distribution

Based on the literature survey, information on geographical distribution and the breeding system was compiled for 124 Melastomataceae species, 41 of restricted and 83 of wide distribution (Appendix). The best represented tribe was

TABLE 1. Fruit set of Melastomataceae species after controlled pollination (flowers treated inside parenthesis)

Tribe	Species*	Controlled pollinations <sup>†</sup>					ISI <sup>‡</sup>	Reproductive system <sup>§</sup>	PV <sup>¶</sup>	
		Ss	Ms	Cr	Em	Ct				
Melastomeae	<i>Macairea radula</i> <sup>2,3</sup>	0 (68)	65.3 (121)	82.9 (123)	0 (122)	89.7 (146)	0.79	SC	88.3 ± 10.3	
	<i>Svitramia hatschbachii</i> <sup>1</sup>	0 (60)	56.3 (87)	71.0 (76)	4.0 (101)	41.3 (104)	0.79	SC	92.8 ± 3.8	
	<i>S. minor</i> <sup>1</sup>	–	61.8 (76)	61.5 (78)	0 (72)	64.3 (84)	1.00	SC	96.6 ± 4.9	
	<i>Svitramia</i> sp. <sup>1</sup>	0 (81)	57.6 (66)	33.8 (65)	0 (63)	68.3 (60)	1.70	SC	96.7 ± 2.4	
	<i>Tibouchina aegopogon</i> <sup>2,3</sup>	0 (110)	0 (20)	38.5 (13)	0 (74)	62.3 (61)	0.00	SI	97.5 ± 2.1	
	<i>T. frigidula</i> <sup>1</sup>	0 (80)	65.0 (90)	75.0 (80)	0 (100)	89.0 (100)	0.87	SC	69.9 ± 12.5 (S)	
									78.5 ± 12.3 (P)	
	<i>T. heteromalla</i> <sup>1</sup>	0 (100)	72.0 (108)	80.9 (110)	0 (100)	68.0 (100)	0.89	SC	98.0 ± 1.5 (S)	
									96.0 ± 2.0 (P)	
									65.8 ± 11.8	
	<i>T. papyrus</i> <sup>3</sup>	6.8 (176)	11.7 (94)	45.0 (151)	0 (197)	30.1 (259)	0.26	SC		
	<i>T. stenocarpa</i> <sup>1</sup>	0 (88)	21.2 (85)	32.5 (89)	0 (80)	65.0 (80)	0.65	SC	78.0 ± 5.3	
	<i>T. villosissima</i> <sup>2</sup>	0 (6)	12.6 (87)	19.3 (109)	0 (50)	16.4 (116)	0.65	SC	90.1 ± 5.6	
Miconieae	<i>Miconia ferruginata</i> <sup>2,3</sup>	54.9 (408)	100.0 (24)	87.5 (32)	50.5 (406)	77.6 (308)	1.14	AP	8.0 ± 0.9	
Microlicieae	<i>Cambessedesia espora</i> <sup>1</sup>	0 (30)	72.5 (40)	82.5 (40)	0 (40)	35.0 (40)	0.88	SC	68.0 ± 12.5	
	<i>C. regnelliana</i> <sup>1</sup>	0 (20)	14.9 (74)	28.9 (83)	1.3 (74)	33.0 (106)	0.52	SC	96.7 ± 6.3	
	<i>Lavoisiera imbricata</i> <sup>1</sup>	0 (66)	58.8 (68)	88.9 (72)	0 (89)	80.4 (97)	0.66	SC	89.0 ± 5.3 (S)	
									92.0 ± 6.0 (P)	
									1.9 ± 2.3	
		<i>Microlicia fasciculata</i> <sup>2,3</sup>	–	100.0 (5)	33.3 (6)	23.0 (22)	32.0 (50)	3.00	AP	
		<i>M. inquinans</i> <sup>1</sup>	0 (40)	55.1 (98)	75.2 (105)	0 (131)	72.1 (136)	0.73	SC	98.1 ± 1.4
		<i>M. viminalis</i> <sup>1</sup>	0 (15)	0 (15)	13.3 (15)	0 (15)	40.0 (15)	0.00	SI	97.0 ± 3.8 (S)
									95.0 ± 4.4 (P)	
									78.3 ± 8.2	
	<i>Rhynchanthera grandiflora</i> <sup>2,3</sup>	–	24.5 (53)	81.0 (47)	0 (75)	43.3 (67)	0.30	SC		
	<i>Trembleya neopyrenaica</i> <sup>3</sup>	–	57.7 (78)	91.8 (61)	0 (20)	50.0 (38)	0.63	SC	59.9 ± 13.4	
	<i>T. parviflora</i> <sup>1</sup>	0 (30)	47.9 (48)	60.8 (51)	0 (60)	5.7 (70)	0.79	SC	98.0 ± 5.6 (S)	
								65.0 ± 11.0 (P)		

\* Study areas: <sup>1</sup> Serra da Canastra National Park; <sup>2</sup> Serra de Caldas Novas State Park; <sup>3</sup> Pirineus State Park.

<sup>†</sup> Ss, Spontaneous self-pollination; Ms, manual self-pollination; Cr, cross-pollination; Em, emasculation; Ct, control; –, treatment not performed; in parenthesis, the sample number in each treatment.

<sup>‡</sup> ISI, index of self-incompatibility.

<sup>§</sup> SC, Self-compatible; SI, self-incompatible; AP, apomictic.

<sup>¶</sup> PV, Pollen viability (mean ± standard deviation); S, antisepalous stamens; P, antipetalous stamens.

TABLE 2. Period between pollination and penetration of pollen tubes into the ovary and ovules after hand self-pollination (Ms), cross-pollination (Cr) or natural pollination (Np) in some Melastomataceae species of Campo Rupestre in Central Brazil

Species	Period between pollination and penetration of pollen tubes			
	<24 h	24–48 h	48–72 h	>72 h
<b>Into the ovary</b>				
<i>Cambessedesia regnelliana</i> (few pollen tubes in all styles)	X (Cr)	.	X (Ms)	.
<i>Macairea radula</i>	X (Cr)	.	.	.
<i>Miconia angelana</i>	X (Cr)	X (Ms)	.	.
<i>Microlicia inquinans</i>	X (Cr)	.	.	.
<i>Rhynchanthera grandiflora</i>	X (Cr)	.	.	.
<i>Svitramia hatschbachii</i>	X (Cr)	X (Ms)	.	.
<i>S. minor</i>	X (Cr)	.	.	.
<i>Svitramia</i> sp.	X (Cr)	.	.	.
<i>Tibouchina papyrus</i>	X (Cr)	.	.	.
<i>T. villosissima</i>	X (Cr)	.	.	.
<b>Into the ovule</b>				
<i>C. espora</i>	.	X (Np)	.	.
<i>Lavoisiera imbricata</i>	.	.	X (Np)	.
<i>Microlicia inquinans</i>	.	.	X (Np)	.
<i>M. viminalis</i>	.	.	X (Np)	.
<i>T. frigidula</i>	.	.	X (Np)	.
<i>T. heteromala</i>	.	.	X (Np)	.
<i>T. stenocarpa</i>	.	.	.	X (Np)
<i>Trembleya parviflora</i>	X (Np)	.	.	.

Miconieae, with 59 species, followed by Melastomeae (27 spp.), Microlicieae (12 spp.), Rhexieae (11 spp.), Blakeae (6 spp.), Henrietteae (3 spp.), Merianieae (3 spp.) and Bertolonieae represented by only one species. Tribe placement of the three species of *Cambessedesia* is unresolved (Fritsch et al., 2004).

Among the species analysed, 43 were apomictic and 77 were sexual. For this latter group, 24 were self-incompatible and 53 were self-compatible. Four species presented mixed or contradictory results. The analysis of the breeding systems per tribe, regardless of the geographic distribution pattern, indicated that both apomixis and self-incompatibility are common in the tribe Miconieae, respectively in 61 % and 19 % of the species studied, whereas self-compatibility is predominant in the tribes Melastomeae and Microlicieae, occurring in 78 % and 67 % of the species, respectively. Most of the apomictic and self-incompatible species, 86 % and 71 %, respectively, presented wide distributions (Fig. 2), but the chi-square test showed the differences were significant only in the case of the apomictics ( $P < 0.0001$  and  $P = 0.6848$ , respectively). A restricted distribution was predominant only among the self-compatible species (53 %) and, although some self-compatible species presented a wide distribution, distribution was significantly different when compared with the original sample ratio ( $P = 0.0022$ ).

## DISCUSSION

The breeding system of the Melastomataceae studied here confirms some trends already described for these Neotropical

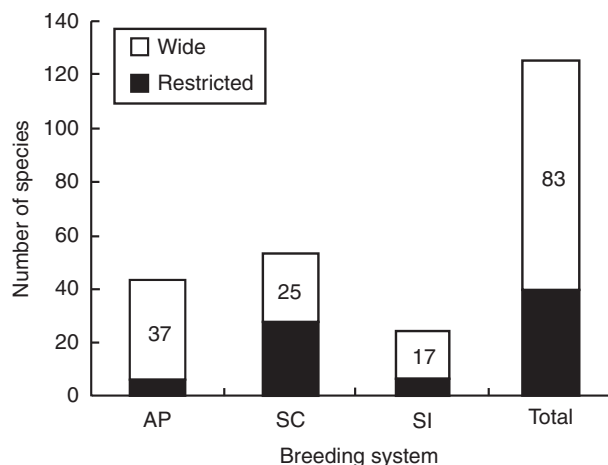


FIG. 2. Reproductive system and geographical distribution of a sample of 124 species (83 of wide and 41 of restricted distribution) of New World Melastomataceae. Abbreviations: AP, apomictic; SC, self-compatible; SI, self-incompatible species; Total, all species.

plants (Renner, 1989a): a great reproductive diversity in an apomixis-rich group. These trends may be important for understanding the general characteristics of Cerrado species as a whole, and of the endemic Campo Rupestre species in particular. The general picture, to a certain extent, parallels the geographical parthenogenesis pattern described to the northern hemisphere apomictics. We discuss below specific aspects of both parts of the study and, finally, briefly consider the consequences for the evolution of Neotropical biodiversity.

### Campo Rupestre reproductive biology

Most of the Campo Rupestre Melastomataceae studied here were self-compatible, which contrasts with the studies for other Neotropical woody species that are mostly allogamous (Oliveira and Gibbs, 2000; Machado et al., 2006; Vamosi et al., 2006). However, self-compatibility does not necessarily imply high levels of autogamy (*sensu* Richards, 1986), since autogamy is possibly restricted by poricidal anthers and herkogamy (Renner, 1989a).

Nevertheless, some spontaneous self-pollination (autonomous autogamy *sensu* Harder and Barrett, 2006) may occur when pollen released through mechanical movement of the anthers by wind or rain falls on the stigma of the flower (Renner, 1989a). *Tibouchina papyrus*, despite the poricidal anthers, produced some fruits after spontaneous self-pollination (6.8 %). Fruit set after spontaneous self-pollination was also observed in *M. angelana* (Santos et al., 2010), *M. minutiflora* (Goldenberg and Shepherd, 1998), *M. sintonisii* (Renner, 1989a) and *Rhynchanthera dichotoma* (Guimarães and Ranga, 1997). In these cases pores may be larger which would facilitate pollination (Goldenberg and Varassin, 2001).

In self-compatible species, selfing also results from pollinators' activity. The number of flowers opened at the same time is important for the reproductive success of the species dependent on biotic vectors, since it increases the attraction and visitation by pollinators (Mitchell, 1994; Williams et al., 2001). But visits will result frequently in

geitonogamous self-pollination (Williams, 2007). Hence, the high fruit set under natural conditions in some of the species of this study is probably the result of both, cross-pollination and geitonogamy. Selfing may occur less frequently in *C. regnelliana* and *S. hatschbachii* due to the difference in the speed of pollen-tube growth. As in *Miconia angelana* (Santos *et al.*, 2010), self-pollinated flowers are unlikely to form fruits, because the pollen tubes do not have sufficient time to reach and penetrate the ovules before the flower starts to senesce. This mechanism has also been reported for several species of Lythraceae and Spigeliaceae as a cryptic self-incompatibility and may reduce inbreeding (Eckert and Allen, 1997; Erbar and Leins, 1999; Erbar, 2003).

The frequency of apomictics recorded in our sample was much smaller than that recorded for the family as a whole (Renner, 1989a) and for the tribe Miconieae in particular (Goldenberg and Shepherd, 1998; Melo and Machado, 1998). But in both cases pollen viability was very low and apomixis was autonomous. Low pollen viability has been related to the occurrence of autonomous apomixis (Richards, 1986; Renner, 1989a; Carman, 1997; Goldenberg and Shepherd, 1998; Goldenberg and Varassin, 2001), but not to sporophytic pseudogamous apomixis, in which pollen viability is usually high (Mendes-Rodrigues *et al.*, 2005). Low pollen viability has been found in several apomictic Melastomataceae species, but showed unexpectedly wide variation (Baumgratz and Silva, 1988; Goldenberg and Shepherd, 1998; Goldenberg and Varassin, 2001) when compared with better studied autonomous apomictic groups (e.g. *Taraxacum*; van Baarlen *et al.*, 2000).

It is important to emphasize that the technique used to estimate the pollen viability is based on staining. Thus, stained grains are interpreted as being viable, although they are not necessarily able to germinate and sire seeds (e.g. Carvalho and Oliveira, 2003). Despite these limitations, this methodology has been used widely and allows pollen grains with cytoplasmic contents to be identified and is therefore functional either for pollination or bee foraging (Kearns and Inouye, 1993). In this sense, many autonomous apomictics are, as the Melastomataceae species studied, useless as a floral resource to pollen-collecting bees.

Pollen is the most important floral resource offered by the Campo Rupestre Melastomataceae, although some nectar may be offered in small amounts by some species (e.g. Santos *et al.*, 2010). Morphological and functional pollen dimorphism has been postulated for the Melastomataceae (Luo *et al.*, 2008), a division-of-labour hypothesis which may optimize pollen transfer. In *Lavoisiera imbricata*, *Microlicia fasciculata*, *M. inquinans*, *M. viminalis*, *Trembleya neopyrenaica* and *T. parviflora* the two conspicuously different whorls of stamens could be associated with such a functional pollen dimorphism (Faegri and van der Pijl, 1979). The results for pollen viability did not show any distinction between pollen from the different whorls, although functional dimorphism cannot be ruled out since we did not test germinability and fruit set using each kind of pollen. Similar results were reported for *Tibouchina pulchra* (Brito, 2010), other Melastomataceae (Renner, 1989a) and many other plant groups (Endress, 1994). It is possible that the two types of stamens result simply in deposition of pollen in a larger area of the visitor's body, increasing the chances of pollination.

In any case, self-compatibility and dependence on pollen-collecting bees for pollination seems to be a general trend amongst the Campo Rupestre Melastomataceae. Although somewhat isolated by this patchy environment, these species seldom rely on autogamy or apomixis for reproductive assurance.

#### Distributional correlates

The numerous studies on the breeding systems in the Melastomataceae (Renner, 1989a; Borges, 1991; Goldenberg and Shepherd, 1998; Goldenberg and Varassin, 2001; Fracasso and Sazima, 2004; Fracasso, 2008; Pereira *et al.*, 2011; Brito and Sazima, 2012) still encompass <5 % of the Neotropical species. But the present survey almost doubled the number of analysed species in Renner (1989a) and despite this still-limited sample, some trends can be clearly discerned. Apomixis is very common and apomictic species are widely distributed. The relationship between geographical distribution and breeding system for the Melastomataceae compiled here mostly comply with the pattern suggested by Goldenberg and Shepherd (1998) for the species of the tribe Miconieae.

Most apomictic species of the Melastomataceae surveyed did present wide distribution. Apomixis provides reproductive assurance and independence of pollinators, allowing uniparental reproduction favouring colonization of new areas (Baker, 1967). It also retains some advantages of seed production, such as dispersal ability and dormancy (Renner, 1989a). Moreover, many apomictics are polyembryonic and such taxa may benefit from the reproductive compensation or bet-hedging effect that polyembryony can provide (Mendes-Rodrigues and Oliveira, 2012). It is believed that, by presenting these characteristics, the apomictic species in general are able to occupy diverse environments (Bierzychudek, 1987; Hörandl and Paun, 2007). This could explain why many apomictic species of Melastomataceae are pioneers in disturbed areas and habitats, or even aggressive invasive weeds in exotic environments such as *Clidemia hirta* (Peters, 2001) and *Miconia calvescens* (Meyer, 1998; Baruch *et al.*, 2000).

Another explanation for the wider distribution of apomictic species can be found in its relation with polyploidy. Apomixis in Melastomataceae, especially in species of the tribe Miconieae, is related to polyploidy (Goldenberg and Shepherd, 1998). By joining distinct genomes in a hybrid or creating genomes with duplicated chromosomes, polyploidy can both trigger apomixis (Carman, 1997) and conserve genetic heterogeneity, which may provide the ability for these species to colonize new environments (Lowry and Lester, 2006; Hörandl and Paun, 2007). Pleistocene climatic changes (Prado and Gibbs, 1993) but also other geohistoric processes such as fire pressure in C<sub>4</sub>-dominated ecosystems (Simon *et al.*, 2009) may have provided the opportunity for the expansion of apomictic taxa.

Wide distributions were also common among self-incompatible species in our survey. These species may be better colonizers of new environments due to genetic variability provided by mandatory cross-pollination (Lowry and Lester, 2006). This breeding system ensures cross-fertilization

(Richards, 1986), allowing adaptation to the environment and evolutionary changes by increasing the genetic variability (Barrett *et al.*, 2008). But some plants with restricted distribution were also self-incompatible including some of the endemic Campo Rupestre Melastomataceae studied here.

The restricted distribution pattern predominated only in those Melastomataceae species in our survey with sexual reproduction and self-compatibility. It is believed that gene flow is limited in self-compatible species, allowing the emergence of highly specialized endemism (Lowry and Lester, 2006). In fact, this breeding system has been reported in many rare species with restricted distributions (Bernardello *et al.*, 1999; Kaye, 1999; Vieira and Grabelos, 2003; Andrade *et al.*, 2007). It conforms also with the endemism-rich Campo Rupestre areas where limited gene flow associated with selfing may lead to population differentiation and speciation (Lousada *et al.*, 2011).

However, self-compatible species present a bimodal distribution, which may obscure the effect of mating system on range size (Lowry and Lester, 2006; Williams, 2007). Some species may have their allelic variability reduced by self-compatibility and, consequently, would have lower ability to occupy different habitats and show restricted distribution. Other species may have considerable genetic variability also fixed by self-compatibility, which would also provide reproductive assurance, dispersal ability and wider distribution. Both kinds of outcomes have been reported for different taxa (Lowry and Lester, 2006). These scenarios may explain the occurrence of some self-compatible species of Melastomataceae with wide geographical distribution such as *Rynchanthera grandiflora* (Aubl.) DC. and *Leandra regnelii* (Triana) Cogn. (Goldenberg and Varassin, 2001) and *Tibouchina pulchra* Cogn. and *T. sellowiana* Cogn. (Pereira *et al.*, 2011; Brito and Sazima, 2012).

It is important to notice that the methods used here may fail to detect differences between self-compatible sexuals and pseudogamic apomictics. As many tropical apomictic species are pseudogamous sporophytic apomictics (Carman, 1997; Mendes-Rodrigues *et al.*, 2005), results for hand-pollination treatments in pseudogamous apomictics would be similar to those of self-compatible species (Oliveira *et al.*, 1992) and apomixis could be detected only by histological (Mendes-Rodrigues *et al.*, 2005) or molecular methods (Martins and Oliveira, 2003). In this sense, widely distributed self-compatible Melastomataceae could be cryptic pseudogamic apomictics, but, as mentioned before, the Melastomataceae studied so far are autonomous apomictics.

We conclude that, on the one hand, apomixis seems to be associated with ample distribution in the New World Melastomataceae, supporting the idea that this breeding system may be more important for the persistency and diversity of Neotropical plants than previously thought (Allem, 2003). As in temperate environments, these apomictics may have been favoured for occupying Cerrado and other tropical biomes, which have expanded since the last glacial maximum (Ramos *et al.*, 2009; Simon *et al.*, 2009). On the other hand, species with restricted distribution, as the Campo Rupestre endemic species studied here, are mostly sexual

and dependent on biotic pollination. Speciation and diversity in these areas seems to be driven by differentiation and restricted pollen flow, but not by autogamy or apomixis.

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## APPENDIX

## Reproductive system and geographical distribution of New World Melastomataceae species

Tribe*	Species	Reproductive system†			Reference‡	Geographical distribution	Reference‡
		SC	SI	AP			
Bertolonieae	<i>Bertonia marmorata</i> (Naudin) Naudin	X			33	Restricted (Bahia; Pernambuco, BR)	7
Blakeeae	<i>Blakea anomala</i> Donn. Sm.	X			23	Restricted (Costa Rica)	45
	<i>B. chlorantha</i> Almeda	X			22	Restricted (Costa Rica)	45
	<i>B. gracilis</i> Hemsl.	X			23	Restricted (Nicaragua; Costa Rica; Panamá)	45
	<i>B. tuberculata</i> Donn. Sm.	X			23	Restricted (Costa Rica; Panamá)	45
	<i>Topobea brenesii</i> Standl.	X			23	Restricted (Costa Rica)	45
	<i>T. maurofernandeziana</i> Cogn.	X			23	Restricted (Nicaragua; Costa Rica; Panamá)	45
Henrietteae	<i>Bellucia acutata</i> Pilg.		X		33	Wide	34
	<i>B. grossularioides</i> (L.) Triana		X		33	Wide	34
	<i>Henriettea succosa</i> (Aubl.) DC.			X	25	Wide	48
Melastomeae	<i>Aciotis acuminifolia</i> (Mart. ex DC.) Triana			X	33	Wide	12
	<i>Desmocelis villosa</i> (Aubl.) Naudin	X			28	Wide	48
	<i>Macairea radula</i> (Bonpl.) DC.	X			1	Wide	34
	<i>M. theresiae</i> Cogn.			X	33	Restricted (Pará; Amazonas, BR)	34
	<i>Marcetia taxifolia</i> (A.St.-Hil) DC.	X			30	Wide	24
	<i>Melastoma affine</i> D.Don	X			17	Wide	17
	<i>Monochaetum amabile</i> Almeda	X			3	Restricted (Costa Rica)	45
	<i>M. floribundum</i> Naudin	X			3	Wide	45
	<i>M. neglectum</i> Almeda	X			3	Restricted (Costa Rica; Panamá)	45
	<i>M. talamancense</i> Almeda	X			3	Restricted (Costa Rica)	45
	<i>M. vulcanicum</i> Cogn.	X			3	Restricted (Costa Rica)	45
	<i>Nepsera aquatica</i> (Aubl.) Naudin			X	33	Wide	48
	<i>Pterolepis glomerata</i> (Rottb.) Miq.			X	31	Wide	36
	<i>Sandemania hoehnei</i> (Cogn.) Wurdack			X	33	Wide	32
	<i>Svitramia hatschbachii</i> Wurdack	X			1	Restricted (South and Southwest of Minas Gerais, BR)	37
	<i>S. minor</i> R. Romero & A.B. Martins	X			1	Restricted (Serra da Canastra-Minas Gerais, BR)	37
	<i>Svitramia</i> sp.	X			1	Restricted (Serra da Canastra-Minas Gerais, BR)	37
	<i>Tibouchina aegopogon</i> (Naudin) Cogn.		X		1	Wide	18
	<i>T. cerastifolia</i> Cogn.	X			16	Wide	18
	<i>T. frigidula</i> (DC.) Cogn.	X			1	Wide	18
	<i>T. heteromalla</i> (D.Don) Cogn.	X			1	Wide	18
	<i>T. papyrus</i> (Pohl) Toledo	X			1	Restricted (Pirineus-Goiás, BR)	18
	<i>T. sellowiana</i> Cogn.	X			16	Wide	18
	<i>T. semidecandra</i> (Schrank & Mart. ex DC.) Cogn.	X			16	Restricted (São Paulo; Minas Gerais; Rio de Janeiro, BR)	18
	<i>T. stenocarpa</i> (Schrank & Mart. ex DC.) Cogn.	X			1; 15	Wide	18
	<i>T. trichopoda</i> (DC.) Baill.	X			30	Wide	18
	<i>T. villosissima</i> (Triana) Cogn.	X			1	Restricted (Minas Gerais; Goiás, BR)	18
Merianieae	<i>Adelobotrys rachidotricha</i> Brade	X			33	Restricted (Amazonas, BR)	46
	<i>Graffenrieda latifolia</i> (Naudin) Triana	X			42	Restricted (Venezuela; Eastern Caribbean)	57
Miconieae	<i>Clidemia bullosa</i> DC.			X	27	Wide	48
	<i>C. capitellata</i> (Bonpl.) D.Don			X	31	Wide	48
	<i>C. epibaterium</i> DC.			X	33	Wide	48
	<i>C. fendleri</i> Cogn.			X	42	Restricted (Venezuela)	48
	<i>C. hirta</i> (L.) D.Don			X	27	Wide	48
	<i>C. novemneria</i> (DC.) Triana			X	33	Wide	48
	<i>C. rubra</i> (Aubl.) Mart.			X	33	Wide	48
	<i>C. ruddae</i> Wurdack			X	4	Restricted (México)	45
	<i>Conostegia macrantha</i> O.Berg ex Triana		X		22	Restricted (Costa Rica; Panamá)	45
	<i>Eriocnema fulva</i> Naudin	X			5	Restricted (Nova Lima-Minas Gerais, BR)	5
	<i>Leandra australis</i> (Cham.) Cogn.			X	16	Wide	43
	<i>L. dasytricha</i> (A.Gray) Cogn.	X			16	Wide	43
	<i>L. involucrata</i> DC.			X	41	Restricted (Minas Gerais, BR)	43
	<i>L. lacunosa</i> Cogn.			X	15	Wide	43
	<i>L. melastomoides</i> Raddi			X	16	Wide	43
	<i>L. purpurascens</i> (DC.) Cogn.			X	16	Wide	43
<i>L. regnellii</i> (Triana) Cogn.	X			16	Wide	43	

Continued

APPENDIX *Continued*

Tribe*	Species	Reproductive system <sup>†</sup>			Reference <sup>‡</sup>	Geographical distribution	Reference <sup>‡</sup>
		SC	SI	AP			
	<i>Maieta guianensis</i> Aubl.			X	33	Wide	29
	<i>Miconia alata</i> (Aubl.) DC.				X	Wide	14
	<i>M. albicans</i> (Sw.) Triana				X	Wide	14
	<i>M. angelana</i> R.Romero & R.Goldenberg	X				Restricted (Serra da Canastra-Minas Gerais, BR)	38
	<i>M. araguensis</i> Wurdack	X				Restricted (Venezuela)	48
	<i>M. argyrophylla</i> DC.			X	33	Wide	14
	<i>M. campestris</i> Benth. & Triana				X	Wide	14
	<i>M. chamissois</i> Naudin		X			Wide	14
	<i>M. ciliata</i> (Rich.) DC.		X			Wide	14
	<i>M. discolor</i> DC.		X	X	8	Wide	14
	<i>M. dodecandra</i> Cogn.	X				Wide	14
	<i>M. egenesis</i> Cogn.			X	33	Wide	14
	<i>M. elegans</i> Cogn.		X			Wide	14
	<i>M. fallax</i> DC.			X	15	Wide	14
	<i>M. ferruginata</i> DC.			X	1	Wide	14
	<i>M. ibaguensis</i> (Bonpl.) Triana				X	Wide	14
	<i>M. langsdorffii</i> Cogn.		X	X	15; 41	Wide	14
	<i>M. latecrenata</i> (DC.) Naudin			X	16	Wide	14
	<i>M. lepidota</i> DC.		X			Wide	14
	<i>M. ligustroides</i> (DC.) Naudin			X	15	Wide	14
	<i>M. minutiflora</i> (Bonpl.) DC.	X				Wide	14
	<i>M. pepericarpa</i> DC.		X			Wide	14
	<i>M. petropolitana</i> Cogn.			X	16	Wide	14
	<i>M. pohliana</i> Cogn.			X	15	Wide	14
	<i>M. prasina</i> (Sw.) DC.			X	10; 33	Wide	14
	<i>M. pusilliflora</i> (DC.) Naudin		X			Wide	14
	<i>M. rubiginosa</i> (Bonpl.) DC.			X	15	Wide	14
	<i>M. sellowiana</i> Naudin			X	41	Wide	14
	<i>M. sintenisii</i> Cogn.	X				Restricted (Porto Rico)	45
	<i>M. spinulosa</i> Naudin			X	42	Restricted (Venezuela)	48
	<i>M. stenostachya</i> DC.			X	15	Wide	14
	<i>M. stephananthera</i> Ule			X	31	Wide	14
	<i>M. sylvatica</i> Schldl.	X				Wide	48
	<i>M. theaezans</i> (Bonpl.) Cogn.		X			Wide	14
	<i>M. tomentosa</i> (Rich.) D.Don			X	33	Wide	14
	<i>M. trianae</i> Cogn.			X	33	Restricted (São Paulo; Minas Gerais; Espírito Santo, BR)	14
	<i>M. tuberculata</i> (Naudin) Triana		X			Restricted (Venezuela)	48
	<i>Ossaea amygdaloides</i> (DC.) Triana			X	16	Wide	43
	<i>O. confertiflora</i> (DC.) Triana			X	16	Wide	43
	<i>Tococa bullifera</i> Mart. & Schrank ex DC.	X				Wide	28
	<i>Tococa guianensis</i> Aubl. (syn. <i>T. formicaria</i> Mart.)		X			Wide	28
	<i>Tococa coronata</i> Benth. (syn. <i>T. longispala</i> Cogn.)		X			Restricted (Amazônia, BR)	28
Microlicieae	<i>Centradenia floribunda</i> Planch.	X				Restricted (Guatemala; El Salvador; Honduras)	45
	<i>C. grandifolia</i> Endl. ex Walp.		X			Restricted (South of México; Costa Rica)	45
	<i>C. paradoxa</i> (Kraenzl.) Almeda	X				Restricted (Costa Rica; Panamá)	45
	<i>Lavoisiera imbricata</i> (Thunb.) DC.	X				Wide	48
	<i>Microlicia fasciculata</i> Mart. ex Naudin			X		Wide	39
	<i>M. inquinans</i> Naudin	X				Restricted (Serra da Canastra-Minas Gerais, BR)	37
	<i>M. viminalis</i> (DC.) Triana		X			Wide	39
	<i>Rhynchanthera dichotoma</i> (Desr.) DC.	X				Wide	35
	<i>R. grandiflora</i> (Aubl.) DC.	X				Wide	35
	<i>R. novemneria</i> DC.	X				Wide	35
	<i>Trembleya neopyrenaica</i> Naudin	X				Restricted (Goiás, BR)	24
	<i>T. parviflora</i> (D.Don) Cogn.	X		X	1; 44	Wide	24
Rhexieae	<i>Rhexia alifanus</i> Walt.		X			Wide	20
	<i>R. aristosa</i> Britton		X			Wide	20
	<i>R. cubensis</i> Griseb.		X			Wide	20

*Continued*

## APPENDIX Continued

Tribe*	Species	Reproductive system <sup>†</sup>			Reference <sup>‡</sup>	Geographical distribution	Reference <sup>‡</sup>
		SC	SI	AP			
	<i>R. lutea</i> Walt.	X			20	Wide	20
	<i>R. mariana</i> L.			X	33	Wide	20
	<i>R. nashii</i> Small		X		20	Wide	20
	<i>R. nuttallii</i> James		X		20	Restricted (Flórida, USA)	20
	<i>R. parviflora</i> Chapm.		X		20	Restricted (Flórida, USA)	20
	<i>R. petiolata</i> Walt.	X			20	Wide	20
	<i>R. salicifolia</i> Kral & Bostick		X		20	Restricted (Flórida, USA)	20
	<i>R. virginica</i> L.	X	X		20; 21	Wide	20
**	<i>Cambessedesia espora</i> (A.St.-Hil. ex Bonpl.) DC.	X			1	Wide	24
**	<i>C. hilariana</i> (Kunth) DC.	X			11	Wide	24
**	<i>C. regnelliana</i> Cogn.	X			1	Restricted (Minas Gerais; Goiás, BR)	24

\* Classification in tribe according to Renner (1993), Penneys *et al.* (2010) and Fritsch *et al.* (2004); \*\* unresolved polytomy (Fritsch *et al.*, 2004).

<sup>†</sup> SC, Self-compatible; SI, self-incompatible; AP, apomictic.

<sup>‡</sup> Source references: 1, This study; 2, Almeda (1977); 3, Almeda (1978); 4, Almeda and Chuang (1992); 5, Andrade *et al.* (2007); 6, Arroyo and Cabrera (1977); 7, Baumgratz (1989); 8, Borges (1991); 9, Borges (2000); 10, Dent-Acosta and Breckon (1991); 11, Fracasso and Sazima (2004); 12, Freire-Fierro (2002); 13, Goldenberg (1994); 14, Goldenberg (2000b); 15, Goldenberg and Shepherd (1998); 16, Goldenberg and Varassin (2001); 17, Gross (1993); 18, Guimarães (1997); 19, Guimarães and Ranga (1997); 20, Kral and Bostick (1969); 21, Larson and Barrett (1999); 22, Lumer (1980); 23, Lumer, 1982; 24, Martins (1997); 25, Melo and Machado (1996); 26, Melo and Machado (1998); 27, Melo *et al.* (1999); 28, Michelangeli (2005); 29, Michelangeli (2010); 30, Pinheiro (1995); 31, Ramirez and Brito, 1990; 32, Renner (1987); 33, Renner (1989a); 34, Renner (1989b); 35, Renner (1990); 36, Renner (1994); 37, Romero (2000); 38, Romero and Goldenberg (1999); 39, Romero and Woodgyer (2010); 40, Santos *et al.* (2010); 41, Saraiva *et al.*, 1996; 42, Sobrevila and Arroyo, 1982; 43, Souza and Baumgratz (2004); 44, Souza-Silva (2000); 45, Flora Mesoamericana ([www.tropicos.org/Project/FM](http://www.tropicos.org/Project/FM)); 46, The International Plant Names Index ([www.ipni.org](http://www.ipni.org)); 47, Plants of the Eastern Caribbean ([www.ecflora.cavehill.uwi.edu](http://www.ecflora.cavehill.uwi.edu)); 48, [www.tropicos.org](http://www.tropicos.org).