

1 **Pollination in Melastomataceae: a family-wide update on the little we know and the much that**  
2 **remains to be discovered**

3 Agnes S. Dellinger, University of Colorado, Boulder/University of Vienna

4 Constantin Kopper, University of Vienna

5 Katharina Kagerl, University of Vienna

6 Jürg Schönenberger, University of Vienna

7

8 **Abstract**

9 Conducting a literature review of the past 31 years, we here present an update of pollinator  
10 observations in Melastomataceae following Renner's seminal work of 1989. The number of species  
11 with documented pollinators has more than doubled, to 272 species across 14 of the 18 major tribes.  
12 We detected a strong geographic bias, however, with 90% of observations from New-World species,  
13 despite 35% of Melastomataceae species diversity contained in the Old World. Further, we report  
14 that shifts from the common and most widespread pollination strategy (buzz pollination by bees, ca.  
15 95.5% of species) have occurred both in the New- and Old-World tropics, and likely more than 20  
16 times. These include shifts to nectar-foraging vertebrates (2.5%, 6 tribes), food-body-foraging  
17 vertebrates (0.9%, 1 tribe), and to generalized pollination systems (1.1%, possibly 2 tribes). Pollinator  
18 shifts commonly associate with floral trait changes, including, for instance, reward type, pollen  
19 release mechanisms, and corolla shape. We emphasize the need for more pollination biological  
20 studies particularly of Old-World species and the four hitherto unstudied clades, as well as  
21 comparative investigations across tribes and biogeographic regions to understand the extraordinary  
22 success of buzz pollination and the drivers of pollinator shifts in the family.

23

24 **I. Introduction**

25 Animal pollinators are regarded as key drivers of floral diversity and diversification across  
26 angiosperms (Sauquet & Magallón 2018). Particularly in the world's biodiversity hotspots, such as the  
27 tropical Andes, the Atlantic Rainforest, Madagascar, Sundaland or the Cape Floristic Region,  
28 pollinators may have played a key role in plant speciation by mediating reproductive isolation among  
29 incipient species (in addition to abiotic factors, fruit dispersers, etc; van der Niet & Johnson 2012;  
30 Lagomarsino et al. 2016). Our understanding of the phylogenetic history of plant radiations is  
31 continuously improving through rapid advances in sequencing technologies, allowing to more

32 completely and reliably resolve even recent speciation events. At the same time, information on the  
33 natural history of many of these species remains fragmentary or even inexistent (Hortal et al. 2015).  
34 Data on biotic interactions such as pollination is time-consuming to collect and requires careful,  
35 continuous field observations in order to differentiate illegitimate flower visitors (i.e. any animal  
36 visiting a flower but not performing pollination) from legitimate pollinators (those visitors that touch  
37 both female and male reproductive organs). Even among pollinators, however, there may be  
38 important differences in pollination efficiency, i.e. in the amount of pollen they transfer, as even  
39 frequently visiting pollinators may be poor pollinators if they only transfer small amounts of pollen  
40 (King et al. 2013).

41 Accurately collecting comparative empirical field data on pollination forms the backbone for  
42 placing any macroevolutionary study on floral traits into a meaningful pollination ecological context.  
43 Pollination syndromes represent a tool for such approaches (Dellinger 2020). Pollination syndromes  
44 are defined as suites of floral traits which have evolved under distinct pollinator selection regimes,  
45 i.e. in adaptation to a specific functional group of pollinators (Fenster et al. 2004). If detailed  
46 empirical pollinator observations are available for a subset of species spanning the taxonomic and  
47 morphological diversity of a plant lineage, pollination syndromes may be used – with care! - to  
48 predict the most likely pollinators of species for which no empirical observations are available  
49 (Dellinger 2020). One crucial pre-condition for such predictions to be reliable, however, is the  
50 identification of the floral traits most strongly associating with distinct pollination strategies in the  
51 clade studied. These floral traits may differ among clades and may be highly system specific  
52 (Dellinger et al. 2019a).

53 In Melastomataceae, the last systematic review of the pollination ecological literature was done  
54 more than 30 years ago (Renner 1989). In this seminal review, Renner presented data on 126  
55 Neotropical Melastomataceae species and their animal pollinators. The most common (and possibly  
56 ancestral) pollination strategy across the family is buzz pollination by bees, and Renner estimated  
57 98% of species to be buzz-pollinated. Buzz pollination represents a functionally highly specialized  
58 pollination strategy, where bees apply vibrations to flowers to extract pollen (Buchmann 1983). Buzz  
59 pollination is common across angiosperms (ca. 8% of species), and has evolved multiple times  
60 independently (De Luca & Vallejo-Marín 2013). With more than 5000 species likely being bee-  
61 pollinated, Melastomataceae may form the largest radiation of buzz-pollinated flowers (Melo et al.  
62 2021). In addition to buzz pollination, Renner reported observations by colleagues on shifts to  
63 alternative pollination strategies such as hummingbird-, bat- or rodent-pollination in the four  
64 Neotropical tribes Blakeeae, Melastomateae, Merianieae and Miconieae. These pollinator shifts  
65 generally go along with changes in reward type through the secretion of nectar (Varassin et al. 2008;  
66 Dellinger et al. 2019a). In the past 31 years, field investigations on pollination in Melastomataceae

67 have led to the discovery of several unexpected new pollination systems. In the Merianieae genus  
68 *Axinaea*, for example, passerine birds visit the nectarless flowers, and are rewarded by nutritional  
69 staminal food bodies, which, at the same time, function as bellows-like air-filled pollen expulsion  
70 organs (Dellinger et al. 2014). Further, recent fieldwork has shown that nectar-producing Merianieae  
71 commonly rely on pollination by mixed assemblages of both diurnal and nocturnal pollinators, such  
72 as diurnal hummingbirds and nocturnal rodents (Dellinger et al. 2019b). In the tribe Miconieae, in  
73 turn, several cases of generalist pollination have been reported, where nectar-secreting species are  
74 visited by a large number of insect taxa (Brito et al. 2016). In contrast to the New-World  
75 Melastomataceae, Old-World Melastomataceae have never been subject to a systematic literature  
76 review on pollination.

77 It is our aim in this chapter to provide an update of the published pollination records for both  
78 New- and Old-World Melastomataceae and to pinpoint tribes and geographic areas which are in  
79 particular need for future fieldwork. We then discuss broad patterns of floral trait convergence  
80 across the family based on recent work on pollination syndromes in Merianieae (Dellinger et al.  
81 2019a). Using machine-learning algorithms and multivariate statistics, Dellinger et al. (2019a) had  
82 differentiated three distinct pollination syndromes in Merianieae: a bee-buzz syndrome, a mixed-  
83 vertebrate syndrome and a passerine syndrome. Each of these syndromes is associated with a  
84 characteristic set of floral traits. We discuss the most significant of these traits and point out obvious  
85 floral trait convergences across Melastomataceae. These floral traits may serve as guides for  
86 scientists working in distinct Melastomataceae tribes to correctly predict the most probable  
87 pollinators and identify particularly interesting species for field investigations. We emphasize,  
88 however, that no prediction can substitute empirical fieldwork (Hortal et al. 2015). Finally, we give a  
89 new estimate for the percentage of buzz-pollinated versus other pollination systems in  
90 Melastomataceae based on the reviewed literature and discuss drivers of pollinator shifts across the  
91 family.

92

## 93 **II. Updated literature survey on empirical pollinator observations in Melastomataceae**

### 94 **1. Methods**

95 We performed a systematic survey of the published literature from 1990 to 2020 (following  
96 Renner's seminal work published in 1989) by searching Web of Science using the search terms  
97 "Melastomataceae & pollinat\*" on 10.10.2020 (197 hits, 70 relevant). We repeated the Web of  
98 Science search on 18.12.2020 adding the following country/continent words: "Africa", "Australia\*",  
99 "India\*", "Borneo", "China", "Madagascar", "Philippines", "Sri Lanka", "South East Asia" (37 hits, zero

100 relevant) or specific genera which had not been covered in the first search (12 relevant hits). In order  
101 to better cover the South American (particularly Brazilian) literature, we also searched SciELO  
102 (30.11.2020, 21 hits, three new and relevant) and for Asian/Chinese literature the Wanfang database  
103 (07.12.2020, 103 hits, zero new). In a pre-screening, we considered all papers containing information  
104 on flower visitors as relevant. Next, we checked whether the authors of the paper had differentiated  
105 illegitimate visitors from pollinators. Given the specialized morphology of Melastomataceae,  
106 important primary pollinators may usually be those which are capable of activating the sophisticated  
107 pollen expulsion mechanisms. We grouped these as “primary pollinators” and classified them as  
108 “buzzing bees” (including oil-collecting bees in Olistheoideae, see below), “nectar-foraging  
109 vertebrates”, “food-body-foraging vertebrates” and “generalist insects”. In the rare cases where  
110 authors had classified flower visitors as pollinators that are clearly not capable of triggering pollen  
111 release (i.e. small beetles which may occasionally touch both the stamens and the stigma), we  
112 classified those as “uncertain or secondary pollinators”. Finally, we also included “pollen thieves,  
113 robbers and illegitimate visitors” if they were specified by the authors. We also checked primary  
114 sources cited by previous authors and critically differentiated actual field observations from  
115 predictions based on floral traits. Finally, we added personal observations on flower visitors or nectar  
116 secretion by ourselves and colleagues (Yannick Klomberg, Fabián Michelangeli, Luan Passos, Darin  
117 Penneys, Mauricio Posada, Peter Quakenbush).

118 Next, we went through the obtained lists to correct species names so that they correspond to  
119 recent systematic changes following Michelangeli et al. 2021 and  
120 <http://www.melastomataceae.net/>. For calculating the percentage of available pollinator records per  
121 genus and the major 18 tribes (plus the monotypic Lithobieae), we followed the species number per  
122 tribe estimates provided in Michelangeli et al. 2021. Further, to evaluate whether the number of  
123 species with documented pollinators correlates with species diversity per continent, we used  
124 continent-wide species number estimates given by Michelangeli (2021). Please note that estimates  
125 from Michelangeli 2021 and Michelangeli et al. 2021 differ slightly, but do not change the outcome  
126 of our survey. Further, in our pollinator list, we identified those bee genera for which buzzing  
127 behaviour has been documented (Cardinal et al. 2018) and marked them in Supplementary Table 1.  
128 Finally, to visualize general patterns of pollinator shifts across Melastomataceae, we redrew the  
129 phylogenetic tree produced by Reginato et al. 2020. For illustrative purposes, we randomly  
130 subsampled each tribe (to 6.5% of species) so that tribes are represented proportionally (R-package  
131 *phytools* (Revell 2012)). We marked tribes where pollinator shifts have occurred.

132

## 133 2. Results

134 Our review more than double the documented pollination reports provided in Renner (1989) to a  
135 total of 272 (4.7% of Melastomataceae). While in some clades, floral visitors have been observed in a  
136 substantial portion (> 10 %) of their species (Eriocnemeae – 14.3%, Henrietteae – 11.6%,  
137 Marcetieae – 10.1%), no visitor observations at all are available in other clades (Cypostyleae,  
138 Dissochaeteae, Lithobieae, Trioleneae) as well as in 16 unplaced species (corresponding to 3.8% of  
139 recognized species). Within clades, visitor observations are unevenly distributed, with only 55 of the  
140 currently accepted 177 Melastomataceae genera having one or more records (Table 1).

141 Of the 272 visitor records, 243 stem from the Americas (6.5% of the approximately 3723 New-  
142 World species) and 29 from the Old-World tropics (1.4% of the 2027 Old-World species). Most  
143 observations are available from known Melastomataceae diversity hotspots in the Brazilian Atlantic  
144 Rainforest and the Cerrado (131 observations), the tropical Andes (40 observations), and Costa Rica  
145 (35 observations). Among the Old-World species, 1.8% of the ca. 1352 Australasian/Indomalayan  
146 species count with pollinator observations, and only 0.8% of the 644 Afrotropical species (including  
147 Madagascar). Speciose Old-World lineages such as Sonerileae are largely deficient of observations  
148 (1.5% of species with observations). This pattern persists when comparing lineages distributed in  
149 both the New and Old World such as Melastomataceae: 10.1% of New-World species have  
150 documented floral visitors, while only 3.0% of Old-World species do (Table 1).

151 Consistent with previous reports, buzz pollination by bees is by far the most common pollination  
152 strategy in Melastomataceae, with a total of 212 out of the 272 visitor records, documented in 14  
153 out of the 15 clades with flower visitor observations, and reported for 48 (out of 175) genera. Studies  
154 where bee-pollinators were identified to lower taxonomic levels show that most Melastomataceae  
155 species were visited by a diversity of different buzzing bee taxa (Supplementary Table 1), including  
156 the genera *Bombus*, *Xylocopa*, *Melipona*, *Eulaema*, *Euglossa* and *Augochloropsis*. Other buzzing but  
157 also non-buzzing bees such as *Apis mellifera* or *Trigona* were commonly reported as secondary  
158 pollinators or pollen robbers, as well as occasionally visiting small beetles (often Curculionidae), ants  
159 or syrphid flies (note that syrphid flies may be important pollinators in generalist Miconieae,  
160 however). These visitors may contribute to pollination to a small extent if they touch the stigma  
161 when moving around the flower, i.e. to change buzzing position on single anthers, or when collecting  
162 residual pollen grains previously expelled by a buzzing bee and lying on petals (Mesquita-Neto et al.  
163 2018; Konzmann et al. 2020).

164 Shifts to nectar-foraging vertebrate pollinators have been documented in 37 species. These  
165 encompass 32 species in the four New-World tribes already reported by Renner (Blakeeae: seven  
166 spp., Merianieae: nine spp., Miconieae: eleven spp., Melastomataceae: five spp.) and, thanks to new  
167 observations by Darin Penneys and Peter Quakenbush, five species in the Old-World tribes

168 Astronieae (three spp.) and Sonerlieae (two spp., Supplementary Table 1). In New-World Blakeeae,  
169 Melastomateae and Merianieae, mixed assemblages of vertebrates were reported to visit flowers of  
170 the same species, such as hummingbirds or flowerpiercers during daytime and rodents or bats during  
171 night time. Detailed observations on the pollination efficiency of these different taxonomic pollinator  
172 groups have only been conducted in Merianieae (Dellinger et al. 2019b). In the investigated  
173 Merianieae species, both diurnal and nocturnal visitors act as effective pollinators, and the same may  
174 hold true for the other tribes. In Miconieae, flower visitation by either hummingbirds (in the Andes)  
175 or bats (in the Greater Antilles) was reported (Supplementary Table 1). Miconieae further count with  
176 a report of otherwise very rare lizard flower visitation (and possibly pollination) in the Lesser Antilles  
177 (Timmerman et al. 2008, Supplementary Table 1). While it is possible that these Miconieae species  
178 are indeed only visited by either diurnal or nocturnal pollinators, we caution that this may simply be  
179 a result of lack of observations at other times of the day. Similarly, in four species of the  
180 Melastomateae genus *Brachyotum*, only diurnal pollinators (hummingbirds and flowerpiercers) have  
181 been reported. Again, this may either be due to a lack of nocturnal observations, or it may be the  
182 result of the very narrow pseudo-tubular corolla, which is characteristic for the genus and probably  
183 limits access to birds with narrow bills and long tongues. In Old-World Astronieae, passerines such as  
184 sunbirds, spiderhunters, longbills, and honeyeaters were observed to visit flowers of two species of  
185 *Beccarianthus* (Penneys & Quakenbush, pers. com.). In addition, the same bird taxa were also  
186 reported in one species of *Astronia* (Mack & Wright 1996, Supplementary Table 1). Based on floral  
187 traits, bat-pollination is further expected for *Beccarianthus pulcherrimus* (Penneys 2013). In two  
188 *Medinilla* species (Sonerileae), nectar-foraging passerine bird visitors have also been reported in the  
189 Western Ghats of India (Sasidharan & Sujanapal 2005) and are expected for more species also in  
190 Madagascar (Quakenbush, pers. com.). To date, there are no indications of shifts to nectar-foraging  
191 vertebrate pollinators in mainland Africa. As with some of the New-World species, it remains unclear  
192 whether the shifted species are adapted to pollination by only one pollinator group or mixed  
193 assemblages of vertebrates. Generally, the few available observations on Old-World species are  
194 anecdotal and detailed comparative studies on the pollination biology of all of these Old-World  
195 clades are highly needed.

196 Pollination by food-body foraging vertebrates (birds) is restricted to the tribe Merianieae and  
197 reported for six species of the genera *Axinaea* and *Meriania*. This pollination strategy is associated  
198 with the evolution of bulbously inflated stamen appendages, which function in visual pollinator  
199 attraction, rewarding (food body) and pollen expulsion through a bellows mechanism activated when  
200 the bulbous appendages are compressed by the bird's bill (Dellinger et al. 2014). Any birds capable of  
201 activating the bellows mechanism may serve as pollinators, including passerines (tanagers,  
202 flowerpiercers, Dellinger et al. 2014) and parrots (yellow-eared parrot, Posada, pers. com.). Pollinator

203 observations are only available for Andean species, but floral morphology is suggestive of pollination  
204 by food-body foraging vertebrates also in species from the Atlantic Rainforest (Dellinger et al. 2019a).

205 In 13 species of the tribe Miconieae (some of which are nectar-secreting), generalist pollination  
206 (i.e. by representatives of several functional pollinator groups) has been documented (Brito et al.  
207 2016, Supplementary Table 1). These generalist visitor assemblages may be highly diverse and  
208 include more than 80 insect taxa such as bees, wasps, flies and beetles. In tribe Melastomateae  
209 (*Pleroma hospitum*), visitation of various insects has been reported (Bergamo et al. 2020). There also  
210 is one report of generalist insect visitation (grasshoppers, flies, beetles) in Old-World *Pternandra*  
211 *multiflora* (Kibessioideae, Momose et al. 1998, Supplementary Table 1). Since no details on reward  
212 type and pollen expulsion mechanisms are given in these publications, however, we treat these  
213 reports with care.

214

### 215 **III. Pollination syndromes: linking convergent floral traits to pollinator behaviour**

216 For a general description of the Melastomataceae flower, please see Chapter 3.

#### 217 **1. Bee buzz pollination**

218 Melastomataceae represent the largest radiation of buzz-pollinated flowers (Melo et al. 2021),  
219 and have likely evolved in tight connection with the diversity of buzzing bees. Like most other buzz-  
220 pollinated flowers, Melastomataceae are characterized by high numbers of pollen grains (e.g.  
221 300'000-1'000'000 pollen grains per flower in Merianieae, Dellinger et al. 2021) and pollen as sole  
222 reward. Unlike most others, however, they are functionally and morphologically exceptionally  
223 diverse. Many buzz-pollinated lineages across angiosperms share a single floral phenotype: the  
224 *Solanum*-type flower, with anthers forming a cone in the centre of a flower with reflexed petals  
225 (Vogel 1978; Faegri 1986; Russell et al. 2016; Vallejo-Marín et al. 2019). Bee behaviour is relatively  
226 stereotypical on this *Solanum*-type flower, with buzzing bees grasping the anther cone with their legs  
227 and mandibles to apply vibrations (Vallejo-Marín et al. 2019). The *Solanum*-type flower does also  
228 occur in Melastomataceae (i.e. *Miconia*, *Graffenrieda*), but, more commonly, buzz-pollinated  
229 Melastomataceae flowers are open, bowl-shaped flowers with zygomorphically arranged, often  
230 heterantherous stamens and highly variable in size (Fig. 1, Dellinger et al. 2019a; Melo et al. 2021).  
231 This exceptional floral diversity is commonly referred to as 'adaptive plateau' (floral trait  
232 combinations guaranteeing high evolutionary success of a lineage; Reginato & Michelangeli 2016;  
233 Dellinger et al. 2019c), and may represent adaptations to distinct bee pollinators.

234 Recent studies have showcased the diversity of interactions between buzzing bees and  
235 Melastomataceae flowers (Mesquita-Neto et al. 2018; Konzmann et al. 2020). While buzzing bees

236 have generally been regarded as one functional pollinator group, Mesquita-Neto et al. (2018)  
237 proposed to separate them into two functional groups depending on their behaviour: bees which  
238 buzz single stamens versus bees which buzz the entire androecium at once. This buzzing behaviour  
239 strongly depends on the relative size-match between the bee and the flower and bees may change  
240 from single stamen buzzing to whole androecium buzzing in different Melastomataceae flowers  
241 (Mesquita-Neto et al. 2018). Generally, only bees large enough to grasp all stamens at once can  
242 vibrate the entire flower (Mesquita-Neto et al. 2018). In very large, sturdy flowers (i.e. Andean  
243 *Meriania*), however, even large bees may only buzz single stamens by grasping single stamens by the  
244 conspicuous connective appendage (Dellinger et al. 2021). Further, to correctly evaluate whether a  
245 buzzing bee is a primary pollinator, one does not only need to consider the buzzing behaviour, but  
246 also whether the bee contacts the stigma. Large bees buzzing all stamens are usually likely to touch  
247 the stigma, but also small, single-stamen-buzzing bees may touch the stigma if they move around the  
248 flower to adjust their buzzing position (Konzmann et al. 2020).

249 Besides these legitimate buzzing interactions, pollen theft (gleaning: licking pollen out of the  
250 apical pore), and pollen robbing (destructive anther cutting), are commonly observed in non-buzzing  
251 *Trigona* bees (Renner 1983; Rego et al. 2018). Both gleaning and anther-cutting bees usually  
252 contribute little to pollination, and particularly the latter may even negatively impact reproductive  
253 success (Rego et al. 2018). Whether such interactions induce adaptive trade-offs, and, consequently,  
254 lead to the evolution of strategies discouraging flower visitation by pollen robbers in  
255 Melastomataceae, as has been reported for nectar robbers in other plant families (e.g. Barlow et al.  
256 2017), provides a challenging avenue for future research.

257 Further, in some species in the early-diverging clades Olisbeoideae, Kibessioideae and Astronieae,  
258 but also in some Miconieae, anthers dehisce through short longitudinal slits (Goldenberg et al. 2008).  
259 Longitudinal dehiscence may, in theory, open flowers to pollination by non-buzzing bees and other  
260 insects. Correspondingly, in the Kibessioideae genus *Pternandra*, floral visitation by beetles,  
261 grasshoppers and flies was reported (Momose et al. 1998, Supplementary Table 1). Anecdotal  
262 observations in *Astronia* indicate generalization, with flower visitation by non-buzzing *Apis dorsata*,  
263 ants, butterflies and beetles, but no detailed pollination studies are available (Quakenbush, pers.  
264 com.). All Olisbeoideae species with pollination studies, on the other hand, were buzz-pollinated  
265 (Supplementary Table 1). In most species, the dehiscence slits remain relatively short and pore-like,  
266 possibly confining species on buzz pollination (Oliveira et al. 2016). More work particularly in the  
267 three early-diverging clades is needed to evaluate whether these short slits in combination with  
268 pollen rewards may lead to more generalized insect pollination, or whether generalization trends are  
269 mostly driven by the evolution of nectar rewards (Brito et al. 2016).



270 Besides the exceptional diversity in floral architecture, Melastomataceae flowers are also highly  
271 variable in colour (Fig. 1). One notable feature in regard to flower colour is the common contrast  
272 between the corolla and the androecium (Fig. 2). In many lineages, petals are pink while (parts of)  
273 stamens are yellow and hence stick out markedly also in the colour vision of bees (Fig. 2, Velloso et  
274 al. 2018). It is possible that this colour contrast helps bees to quickly find the optimal buzzing position  
275 in each flower and provides a direct visual cue to pollen (which is usually white or yellow and hid  
276 inside the stamens; Lunau 2000). Particularly in heterantherous species (species presenting two  
277 distinct sets of stamens), such colour contrasts may be important in focusing the bee's foraging on  
278 the specific colour-contrasting stamen parts (Telles et al. 2020). Importantly, although often only  
279 appendages are coloured differently in human vision, the entire androecium may contrast when  
280 photographed with a UV-sensitive lens (Fig. 2). Further, colour patterns may not only function at the  
281 within-flower level in Melastomataceae but be adaptive even at the plant level. Brito et al. (2015)  
282 demonstrated that in *Tibouchina pulchra*, the retention of old flowers, which have undergone a  
283 colour change from white to pink, functions to increase visibility of and visitation to fertile first-day  
284 flowers.

285 In contrast to flower colour, floral scent has never been studied systematically in bee-pollinated  
286 Melastomataceae. Certain lineages, such as Blakeeae, have strongly scented flowers with sweet,  
287 heavy perfumes (Penneys & Judd 2013). A rose-like fragrance dominated by phenylethyl alcohol was  
288 reported in *Blakea maurofernandeziana*, and a lemon-like scent composed of monoterpenes in *B.*  
289 *anomala* (Wester et al. 2016). In Meranieae, we found weak, rose-like scents in *Meriania maxima*,  
290 dominated by the terpenoid  $\beta$ -Barbatene, and floral fragrances of *Graffenrieda penneysii* were  
291 dominated by (*E*)- $\beta$ -Caryophyllene\*, in addition to 23 terpenoids and unknown substances, but no  
292 floral scent was noticeable to the human nose (Scheer 2019). This lack in broad-scale floral scent data  
293 in Melastomataceae clearly limits our understanding of the role of traits involved in pollinator  
294 attraction (and possible pollen-robber deterrence) in the family in general. Recent investigations in  
295 buzz-pollinated *Solanum rostratum* have revealed, for example, that heterantherous stamens differ  
296 in the proportion of emitted scent compounds, with pollinating stamens producing high amounts of  
297 scents particularly attractive to bees (Solís-Montero et al. 2018). Future studies in Melastomataceae  
298 quantifying floral scents are hence direly needed in order to work out the potentially integrated and  
299 interrelated adaptive role of floral attraction traits. Further, observations in *Tibouchina* and *Meriania*  
300 indicate scent emission from stamens (Pereira et al. 2011; Dellinger, pers. obsv.), but systematic  
301 comparative data are hitherto lacking.

302 The androecium represents the morphologically and architecturally most diverse organ type in  
303 Melastomataceae flowers (Dellinger et al. 2019a, also see Chapter 27). Generally, poricidal anther  
304 dehiscence is believed to have evolved as pollen-dosing strategy to alleviate the pollen dilemma

305 arising through the dual function of pollen as reward and male reproductive agent in pollen-  
306 rewarding flowers (Konzmann et al. 2019). Our understanding of how differences in stamen traits in  
307 Melastomataceae contribute to pollen dosing in response to bee buzzes is in its infancy, however.  
308 Many buzz-pollinated species bear conspicuous connective appendages of different colour, size,  
309 shape and structure. Renner (1989) suggested that these appendages serve as handles for bees to  
310 grasp when applying vibrations, and this was also confirmed by our observations in Merianieae  
311 (Dellinger et al. 2019a). In addition, recent experimental investigations have highlighted more refined  
312 functions of stamen appendages as pollen dosing devices (Bochorny et al. 2021). Clipping the cork-  
313 screw-shaped connective appendages off stamens of *Huberia bradeana* (Pyramieae), for example,  
314 led to a significantly lower percentage of pollen released per buzz than when flowers were intact  
315 (Bochorny et al. 2021). Hence, appendages enhance pollen release in this species, possibly as an  
316 adaptation to low bee visitation rates. Further, many buzz-pollinated Melastomataceae species have  
317 sturdy stamens with strongly corrugated thecal walls (thickening of endothelial cells), which may,  
318 again, influence pollen release dynamics (Dellinger et al. 2019a). The Merianieae species *Adelobotrys*  
319 *adscendens*, for example, is heterantherous, with one set of stamens having corrugated thecal walls  
320 and the other having smooth walls. Artificially vibrating *A. adscendens* flowers, we found that higher  
321 proportions of pollen are released from the short, smooth anthers than from the long, corrugated  
322 anthers (Dellinger et al. 2019d). Further, stamen traits such as pore size and orientation of the anther  
323 tip (bearing the pore) critically influence how and in which direction pollen is released (Dellinger et  
324 al. 2019d; Konzmann et al. 2020). Experimentally removing the anther tip in *Rhynchanthera*  
325 *grandiflora*, for example, led to unfocused pollen scattering, while an intact anther tip accurately  
326 placed pollen on the bee's back (Konzmann et al. 2020).

327 Recently, much attention has been given to heteranthery, common in some Melastomataceae  
328 lineages (Melo et al. 2021). While heteranthery has classically been explained through Darwin's  
329 'division-of-labour' hypothesis, with one stamen type (feeding stamens) functioning in pollinator  
330 rewarding and the other in pollination (pollination stamens), recent investigations indicate that the  
331 functioning may be more complex. Konzmann et al. (2020) proposed that differently sized stamen  
332 types allow Melastomataceae flowers to exploit a wider range of differently sized buzzing bee  
333 pollinators, particularly if pollen is scattered widely across the bee's body. Size-matching between  
334 flower and bee is critical for successful pollen transfer (Solís-Montero & Vallejo-Marín 2018), but the  
335 relation between bee-buzzing position, pore and stigma location have rarely been investigated. Some  
336 recent, exciting findings in *Macairea radula* (Marcetieae) indicate strong selection gradients  
337 imposed by bees on style dimorphism and intermediate levels of heteranthery, favouring flowers  
338 with high amounts of pollen grains (Oliveira et al. 2020). Taken together, more experimental work on  
339 species differing in traits potentially influencing pollen release dynamics and pollen deposition, such

340 as appendage size and shape, anther length and structure, pore size and orientation or stigma-pore  
341 distances are required to more deeply resolve the functional significance of these traits.

## 342 **2. Pollination by nectar-foraging vertebrates**

343 As we show here, shifts from bee-pollination to nectar-foraging vertebrate pollinators have  
344 occurred repeatedly, at least 15 times (and possibly more often): Astronieae: at least twice (in  
345 *Astronia* and *Beccarianthus*); Blakeeae: at least twice (in former *Chalybea* and *Blakea*);  
346 Melastomateae: possibly three times (in *Brachyotum*, *Chaetogastra* and possibly *Pleroma*, Guimarães  
347 et al. 2019); Merianieae: possibly three times (all in *Meriania*, Dellinger et al. 2021); Miconieae:  
348 possibly five times (twice in Caribbean *Miconia*, three times in *Miconia* III (plus one shift from  
349 generalist pollination in section *Cremanium*, Goldenberg et al. 2008; Kriebel & Zumbado 2014; but  
350 see Reginato et al. 2020 for different topology)); Sonerileae: possibly three times (in *Medinilla*,  
351 *Catanthera*, *Driessenia*), Fig. 1, Supplementary Table 1). Shifts to vertebrate pollinators occurred both  
352 in New-World and Old-World lineages and are associated with clear changes in floral traits, most  
353 prominently in reward type (from pollen to nectar) and pollen expulsion mechanism from buzzing to  
354 non-vibratile pollen release (Stein & Tobe 1989; Varassin et al. 2008; Dellinger et al. 2019b). There is  
355 continued controversy about the location of nectar secretion, which also differs among clades (i.e.  
356 petal nectaries in Sonerileae and possibly some Miconieae, staminal non-structural nectar secretion  
357 in other clades, Fig. 2, Vogel 1997). Field investigations are required to accurately determine the  
358 onset of nectar secretion and the location of nectar release. For example, while hypanthial nectaries  
359 have been proposed in Merianieae based on microtome sections (Varassin et al. 2008), we did not  
360 find any nectar in the hypanthium using bagging experiments in the field. Instead, in many species,  
361 nectar oozed out of horizontal dorsal filament ruptures, which formed within the first hours of  
362 anthesis when inflexed stamens folded outwards (Dellinger et al. 2019b, Fig. 2). We observed similar  
363 necrotic ruptures at the point of stamen inflexion in other nectar producing species such as  
364 *Chaetogastra grossa*, *Brachyotum ledifolium* and *B. lindenii* (both Melastomateae, Fig. 2; also  
365 reported in *Pleroma cleistoflorum* (Ule 1896) or *Miconia sintenisii* (Miconieae, also see Vogel 1997).  
366 Nectar drops formed in bagged flowers on these ruptures (Vogel 1997; Kopper 2021). In some  
367 flowers of *Meriania*, we detected stomata on connective appendages, but never observed nectar to  
368 be extruded by these stomata (Dellinger et al. 2019b). We hence disagree with Varassin et al. (2008)  
369 and argue that, at least in Merianieae, stomata are not involved in nectar production but, potentially,  
370 in scent release (see below). Nectar-sugar composition has, to our knowledge, only been studied in  
371 Merianieae. In these species, we found a textbook-example of pollination syndromes, with species  
372 pollinated by specialized nectar-feeding birds (hummingbirds) producing sucrose-rich nectar while  
373 species pollinated by generalist birds (flowerpiercers) produced nectar rich in hexose sugars

374 (Dellinger et al. 2019b). Whether these patterns hold true also for other tribes and Old-World  
375 Astronieae and Sonerileae remains to be investigated.

376 Melastomataceae flowers pollinated by nectar-foraging vertebrates are further characterized by  
377 pendant flowers with pseudo-tubular (e.g. *Astronia*, *Brachyotum*, *Miconia* (former *Charianthus*)) or  
378 pseudo-campanulate (e.g. *Blakea*, *Meriania*) corollas (Varassin et al. 2008; Dellinger et al. 2019a). At  
379 least in Merianieae, the positioning of these flowers is indicative of the pollinators: flowers projected  
380 from the surrounding foliage by long inflorescence stalks are pollinated by hovering pollinators  
381 (hummingbirds and bats) while flowers close to surrounding twigs and leaves are usually pollinated  
382 by perching birds or rodents (Dellinger et al. 2019b). Since vertebrates cannot buzz stamens, we  
383 observed convergent traits facilitating non-vibratile pollen release. While most species have retained  
384 poridical anthers (Astronieae have short slits), thecal walls have softened so that externally applied  
385 pressure when vertebrates insert their mouthparts into the flowers to take up nectar, triggers pollen  
386 release (“salt-shaker” mechanism, Stiles 1992; Dellinger et al. 2019a; b). In *Chaetogastra grossa*, we  
387 recently observed pollen release through a “bounce” mechanism, where the bifid elongated dorsal  
388 stamen appendage functions as a spring, bouncing back and triggering pollen release when the  
389 pollinator retracts its head from the flower (Kopper 2021). Otherwise, stamen appendages are often  
390 reduced in nectar-secreting species and are not directly involved in the pollination process (Dellinger  
391 et al. 2019a).

392 Floral scents have been studied in detail only in vertebrate pollinated species of Pyxidanthae and  
393 Merianieae (Wester et al. 2016; Dellinger et al. 2019b). Wester et al. found passerine- and rodent-  
394 pollinated Pyxidanthae to be unscented. In Merianieae, hummingbird- and bat-pollinated  
395 Merianieae had scent profiles dominated by aliphatics and terpenoids, while scents of hummingbird-  
396 and rodent-pollinated species were dominated by aliphatics only (Dellinger et al. 2019b).  
397 Importantly, rodent-pollinated *Meriania sanguinea* released solvent-like odours (3-hexanone, 1-  
398 hexen-3-one), which are otherwise only known from rodent-pollinated African Cytinaceae (Johnson  
399 et al. 2011). We have, however, noticed such scents in ground-flowering, nectar-producing  
400 Miconieae and the potential function of these compounds in communication with mammal  
401 pollinators provides an exciting avenue for future work. Flowers of *Chaetogastra grossa* produce  
402 garlic-like odours, while we did not notice any odour in the flowers of *Brachyotum*. No data on floral  
403 scents is available from Old-World vertebrate-pollinated species. Finally, the location of scent  
404 production remains unknown; dissecting anthetic flowers of *Meriania sanguinea* in the field and  
405 putting organs into separate Eppendorf tubes for one hour, we found only tubes containing stamens  
406 to be scented. Whether the scent is produced by the tissue underlying the stomata on the connective  
407 appendage, or comes from the nectar, remains unclear.

408 Finally, numerous Old-World lineages merit further investigation. Flower morphology of several  
409 lineages in Sonerileae is indicative of pollinator shifts. The Asian genus *Catanthera*, for example,  
410 contains species with pseudo-campanulate corollas and exerted styles, which may potentially be  
411 pollinated by birds. The species *Driessenia phasmolacuna* has cauliflorous, pseudo-campanulate  
412 white flowers (Lin 2019), possibly also indicative of a shift to vertebrate (potentially bat) pollinators.

### 413 **3. Pollination by food-body foraging vertebrates**

414 Food-body rewards have, to date, only been documented in the Merianieae, where they have  
415 evolved at least three times from bee pollination in the genera *Axinaea* and *Meriania* (Dellinger et al.  
416 2014; Valverde et al. in prep). In these food-body-rewarding species, bulbous connective appendages  
417 are co-opted into multifunctional organs serving as attractor cue and sugar reward for passerine  
418 birds (tanagers) and as “bellows”-organ for effecting pollen release (Dellinger et al. 2014). These  
419 flowers are further characterized by urceolate corollas and long, exerted styles. As in bee-pollinated  
420 species, stamen appendages form a marked colour-contrast against the corolla in most species.  
421 Stamen thecal walls are usually sturdy but smooth, likely facilitating pollen release when the bellows  
422 mechanism is activated (Dellinger et al. 2014). We believe that the rarity of this pollination  
423 mechanism across Melastomataceae may be due to a constraint for the complex bellows mechanism  
424 to evolve (Dellinger et al. 2021). Possibly, markedly enlarged, sturdy connective appendages as  
425 occurring in Merianieae are a pre-requisite for this pollination strategy to evolve. Pyxidanthaeae have  
426 similarly sturdy stamens, but lack the enlarged appendage.

### 427 **4. Generalist pollination systems**

428 Generalist pollination strategies have, to date, only been studied in detail in *Miconia*, where they  
429 evolved at least four times (clades *Miconia* III, *Miconia* IV and *Leandra*, see Chapter 11). In contrast to  
430 the other pollinator shifts, they are not always associated with changes in reward type (Brito et al.  
431 2016). Some species produce minute nectar droplets (Kriebel & Zumbado 2014). Varassin et al.  
432 (2008) and Kriebel & Zumbado (2014) suggest nectar secretion through small stomata in the proximal  
433 part of the stamen connective, and Kriebel & Zumbado (2014) and Brito et al. (2017) found small  
434 amounts of nectar on the petals and ‘lower parts of the anthers’ during field investigations. In *M.*  
435 *corymbiformis*, we found nectar secretion by filament ruptures, at the point of filament inflexion in  
436 bud stage (Fig. 2, also see Vogel 1997). Generally, nectar secretion did also increase the number of  
437 different visitor guilds documented on flowers (Brito et al. 2016). Most importantly, all species  
438 investigated show adaptations facilitating pollen release with non-vibrating insects, such as enlarged  
439 stamen pores, dehiscence through slits and shorter anthers (Brito et al. 2016). Detailed field  
440 investigations are required in the early-diverging tribes Olisbeoideae, Kibessioideae and Astronieae  
441 to clarify whether non-poricidal dehiscence in these clades is associated with generalized pollination

442 strategies. Further, generalist Miconieae flowers are small, often completely white and may produce  
443 sweet fragrances. At least from our current understanding, there seems to be some overlap between  
444 specialization on nectar-foraging vertebrates and generalization. The Antillean species *M. sintenisii*,  
445 for example, has been reported as bat pollinated (Judd 2007), but also as generalist (Kriebel &  
446 Zumbado 2014). In Ecuadorian cloud forests, we have observed bees, flies, wasps and hummingbirds  
447 as visitors of nectar-secreting *M. corymbiformis*, with insects likely being the primary pollinators  
448 (Dellinger, pers. obsv., Supplementary Table 1). Investigating under which conditions and selection  
449 regimes species adapt to a generalist (insect) pollination strategy or specialize on nectar-feeding  
450 vertebrates, and to what extent these two strategies overlap (i.e. in section *Chaenopleura*) provides a  
451 challenging and exciting avenue for future work.

## 452 **5. Potential other syndromes and unclear cases**

453 There are several lineages in Melastomataceae with trait combinations potentially indicating  
454 pollination strategies not reported yet. For example, several species with herbaceous habit and often  
455 closed flowers have evolved in shady, moist environments across the Bertolonieae, Melastomateae,  
456 Trioleneae, Sonerileae and Merianieae (Bacci et al. 2019). In three species (*Bertolonia paranaensis*, *B.*  
457 *mosenii*, Bertolonieae; *Salpinga secunda*, Merianieae), flower visitation by buzzing bees has been  
458 observed (Passos et al., submitted, Michelangeli, pers. com.), and it is possible that buzz pollination  
459 also is common in the other tribes. In addition, however, notable cases of autonomous self-  
460 pollination have been reported in Bertolonieae (Passos et al., submitted), Trioleneae (Warner 1981)  
461 and Miconieae (Kopper 2021), where pollen germinates within the stamens and grows towards the  
462 stigma. Vivipary has further been reported for Bertolonieae, Merianieae and Trioleneae (Bacci et al.  
463 2021). Clearly, additional fieldwork is needed to clarify whether there is a common reproductive  
464 strategy associated with the growth in the moist, shaded herbaceous understory (or with closed  
465 flowers). As a cautious side-note, a peculiar anecdotal observation of ‘predatophily’ is available for  
466 one such species, *Sonerila pulnyensis*, where flower movement caused by a small frog catching  
467 flower-visiting insects supposedly triggers pollen release (Karuppusamy 2019).

468 Further, while buzz pollination has been reported for seven species in Olisbeoideae  
469 (Supplementary Table 1), many species in the tribe are characterized by a small oil gland on each  
470 stamen (Buchmann & Buchmann 1981; Stone et al. 2008). Renner (1984) reported *Melipona* bees to  
471 actively collect this oil, but after further investigations, rejected this finding (Renner 1989). More  
472 recently, buzzing bees (*Melipona subnitida*) were again observed to actively collect the oil from  
473 stamens of *Mouriri guianensis* and to use it to seal the entrance to their nest overnight (Oliveira et al.  
474 2016). Since Olisbeoideae are sister to all other Melastomataceae, investigating the adaptive role of

475 this oil- and pollen-rewarding (and occasional loss thereof in *Memecylon*, Stone et al. 2008) may  
476 provide important insights into the early evolution of Melastomataceae flowers.

477 Other interesting and unexplored lineages include taxa from the high-elevation Andes such  
478 as *Bucquetia*, *Castratella*, *Chaetolepis* (all Melastomataceae), and the ground-flowering cushion plants  
479 *Miconia chionophila* (Andean) and *Miconia sphagnicola* (Antillean). While the three high-elevation  
480 genera are possibly buzz-pollinated with typical poricidal anthers, the two *Miconia* species have  
481 anthers dehiscing by slits, which, together with their ground-flowering habit, may point towards two  
482 other cases of pollinator shifts or selfing. In another ground-flowering cushion species from the  
483 Brazilian Itatiaia mountains, *Pleroma cleistoflora* (Melastomataceae), flowers do not open during  
484 anthesis, (Ule 1896). Although one may assume autonomous selfing or apomixis in such flowers, Ule  
485 (1896) reported the flowers as protandrous, with well-developed reproductive organs. Further, he  
486 documented nectar secretion through filament ruptures and often found flowers destroyed, with  
487 parts of petals lying on the ground (Ule 1896). During 14 days of field observations, he could not  
488 document any pollinators (Ule 1896; sic Renner 1989). Again, the combination of characters (ground-  
489 flowering, nectar production) and no floral visits during daytime may indicate nocturnal rodent  
490 pollination, although we have also observed tanagers destroying Melastomataceae flowers while  
491 foraging (Dellinger, pers. obsv.). Finally, Ule (1896) reported nectar secretion and campanulate  
492 corollas in two species, *Pleroma itatiaiae* and *P. hospitum*, closely related and occurring in the same  
493 area as *P. cleistoflora*, supporting the idea of additional pollinator shifts in this group. Indeed,  
494 Bergamo et al. (2020) recently reported flower visitation of various insect taxa to *P. hospitum*,  
495 suggesting a generalized pollination strategy in Melastomataceae.

496 Finally, apomixis has been reported in Miconieae (Santos et al. 2012) and Microlicieae (Viana et al.  
497 2021). Importantly, apomixis does not necessarily preclude insect visitation in Melastomataceae  
498 (Maia et al. 2016). It is hence possible that pseudogamous apomixis (apomixis in need of fertilization  
499 of polar nuclei through pollen, Hörandl 2010) went undetected by bagging experiments in other  
500 tribes (i.e. Merianieae).

501

#### 502 **IV. Concluding remarks: evolutionary trends and drivers of pollinator shifts**

503 Buzz pollination by bees clearly is the most common pollination strategy across  
504 Melastomataceae and, given that it also occurs in Olisbeoideae, the earliest-diverging lineage of the  
505 family (Reginato et al. 2020), it may be the ancestral condition for the family as a whole. On the other  
506 hand, since the early-diverging lineages (Olisbeoideae, Kibessioideae, Astronieae) sometimes have  
507 anthers dehiscence through short slits, potentially indicating more generalized pollination strategies,  
508 explicit phylogenetic analyses of pollination strategies and floral trait evolution are required.

509 Pollinator shifts have happened in at least six tribes, more than 20 times and both in the Old- and  
510 New-world tropics. In total, combining available pollinator records and information based on floral  
511 traits (pollination syndromes), we estimate that at least 4.5% of species have shifted from buzz  
512 pollination to alternative pollination strategies (146 (2.5%) pollinated by nectar-foraging vertebrates,  
513 52 (0.9%) by food-body-foraging vertebrates, and 61 (1.1%) generalist species (Table 1)). This leaves  
514 approximately 5,485 species (95.5%) as bee-pollinated. Obviously, these are vague estimates given  
515 that flower visitor observations are only available for 268 species, and we believe that future  
516 fieldwork may reveal a higher percentage of species which have shifted pollination strategy.

517 Pollinator shifts clearly associate with growth in high-elevation ecosystems and islands in all  
518 tribes, with notable exceptions in some Miconieae (e.g. Brito et al. 2016). The tropical Andes,  
519 mountain tops of the Atlantic Rainforest, Antillean mountains as well as the Whestern Ghats and  
520 island mountains in the Philippines contain species which have shifted pollination strategy  
521 (Supplementary Table 1). No pollinator observations are available from Madagascar, but pseudo-  
522 campanulate corollas in several Malagasy *Medinilla* species are indicative of pollinator shifts  
523 (Quakenbush, pers. com.). Surprisingly, there is no indication of pollinator shifts on the African  
524 continent, despite relatively high Melastomataceae species richness in mountainous areas such as  
525 Mount Cameroon (Reginato et al. 2020). Again, this may simply be the result of extremely scarce  
526 observation data for African species, or point to a different evolutionary history i.e. shaped by dry  
527 and wet periods rather than mountain uplift (Veranso-Libalah et al. 2018). Other than that, the  
528 recurring association between elevation and pollinator shifts across Melastomataceae is likely driven  
529 by the cooler, windy and often rainy weather conditions prevalent in mountains, effectively reducing  
530 bee-pollination efficiency (Brito et al. 2012; Dellinger et al. 2021).

531

## 532 **Acknowledgements**

533 We thank Darin Penneys, Peter Quakenbush, Fabián Michelangeli, Frank Almeda, Luan Passos and  
534 Mauricio Posada for sharing information on Melastomataceae flower visitors with us. We further  
535 thank Fabián Michelangeli for clarifying systematic changes in the Melastomataceae species included  
536 in our list and Vinicius Brito on discussion of generalisation. Finally, we thank the editors for putting  
537 together this book on Melastomataceae ecology and evolution! ASD, KK and JS were supported  
538 through FWF-grant AP-30669.

539

## 540 **References**



541 Bacci LF, Michelangeli FA, Goldenberg R. (2019) Revisiting the classification of Melastomataceae:  
542 implications for habit and fruit evolution. *Bot J Linn Soc*, 109:1-24.

543 Bacci LF, Goldenberg R, Michelangeli FA. (2021) First reports of vivipary in neotropical  
544 Melastomataceae. *Int. J. Plant Sci.* 182:79-83.

545 Bergamo PJ, Streher NS, Traveset A, Wolowski M, Sazima M. (2020) Pollination outcomes reveal  
546 negative density-dependence coupled with interspecific facilitation among plants. *Ecol*  
547 *Letters*, 23:129-139.

548 Bochorny T, Bacci L, Dellinger AS, Michelangeli FA, Goldenberg R, Brito V (2021) Connective  
549 appendages in *Huberia bradeana* (Melastomataceae) affect pollen release during buzz  
550 pollination. *Plant Biology*, 10.1111/plb.13244.

551 Brito VLG, Weynans K, Sazima M, Lunau K (2015) Trees as huge flowers and flowers as oversized  
552 floral guides: the role of floral color change and retention of old flowers in *Tibouchina*  
553 *pulchra*. *Frontiers in Plant Science*, 6:362.

554 Brito VLG, Rech AR, Ollerton J, Sazima M (2017) Nectar production, reproductive success and the  
555 evolution of generalised pollination within a specialised pollen-rewarding plant family: A case  
556 study using *Miconia theizans*. *Plant. Syst. Evol.*, 303:709–718.

557 Brito VLG, Sazima M (2012) *Tibouchina pulchra* (Melastomataceae): reproductive biology of a tree  
558 species at two sites of an elevational gradient in the Atlantic rainforest in Brazil. *Plant Syst.*  
559 *Evol.*, 298:1271-1279l.

560 Brito VLG, Fendrich TG, Smidt EC, Varassin IG, Goldenberg R (2016) Shifts from specialised to  
561 generalised pollination systems in Miconieae (Melastomataceae) and their relation with  
562 anther morphology and seed number. *Plant. Biol.*, 18:585–593.

563 Buchmann SL, Buchmann MD (1981) Anthecology of *Mouriri myrtilloides* (Melastomataceae:  
564 Memecyleae), an oil flower in Panama. *Biotropica*, 13:7-24.

565 Buchmann SL (1983) Buzz pollination in angiosperms. *Handbook of experimental pollination biology*,  
566 New York, NY, USA: Van Nostrand Reinold Co., 73–113.

567 Cardinal S, Buchmann SL, Russell AL (2018) The evolution of floral sonication, a pollen foraging  
568 behaviour used by bees (Anthophila). *Evolution*, 72:590–600.

569 De Luca PA, Vallejo-Marín M (2013) What's the "buzz" about? The ecology and evolutionary  
570 significance of buzz-pollination. *Curr. Opin. Plant. Biol.*, 16:429–435.

571 Dellinger AS, Penneys DS, Städler YM, Fragner L, Weckwerth W, Schönenberger J (2014) A specialized  
572 bird pollination system with a bellows mechanism for pollen transfer and staminal food body  
573 rewards. *Current Biology*, 24:1615-1619.

574 Dellinger AS, Chartier M, Fernández-Fernández D, Penneys DS, Alvear M, Almeda F, Michelangeli FA,  
575 Staedler Y, Armbruster WS, Schönenberger J (2019a) Beyond buzz-pollination – departures  
576 from an adaptive plateau lead to new pollination syndromes. *New Phytologist*, 221:1136-  
577 1149.

578 Dellinger AS, Scheer LM, Artuso S, Fernández-Fernández D, Sornoza F, Penneys DS, Tenhaken R,  
579 Dötterl S, Schönenberger J (2019b) Bimodal pollination systems in Andean Melastomataceae  
580 involving birds, bats and rodents. *American Naturalist*, 194:104-116.

581 Dellinger AS, Artuso S, Pamperl S, Michelangeli FA, Penneys DS, Fernández-Fernández DM, Alvear M,  
582 Almeda F, Armbruster WS, Staedler Y, Schönenberger J (2019c) Floral modularity increases  
583 rate of evolution and adaptive success for functionally specialized pollination systems.  
584 *Communications Biology*, 2:453.

585 Dellinger AS, Pöllabauer L, Loreti M, Czurda J, Schönenberger J (2019d) Testing functional hypotheses  
586 on poricidal anther dehiscence and heteranthery in buzz-pollinated flowers. *Acta ZooBot  
587 Austria*, 159:197-214.

588 Dellinger AS (2020) Pollination syndromes in the 21st century – time to connect pollinators, flowers  
589 and phylogenies. *New Phytologist Invited Tansley review*, 228:1193-1213.

590 Dellinger AS, Pérez-Barrales R, Michelangeli F, Penneys DS, Fernández-Fernández DM, Schönenberger  
591 J. (2021) Low bee abundance explains pollinator shifts to vertebrates in tropical mountains.  
592 *New Phytologist*, 231: 864-877.

593 Faegri K (1986) The solanoid flower. *Trans Bot Soc Edinburgh*. 45:51–59.

594 Fenster CB, Armbruster WS, Wilson P, Dudash MR, Thomson JD (2004) Pollination syndromes and  
595 floral specialization. *Annual Review of Ecology, Evolution, and Systematics*, 35:375– 403.

596 Goldenberg R, Penneys DS, Almeda F, Judd WS, Michelangeli FA (2008) Phylogeny of *Miconia*  
597 (Melastomataceae): Patterns of stamen diversification in a megadiverse neotropical genus.  
598 *Int. J. Plant Sci.*, 169:963-979.

599 Guimarães PJF, Michelangeli FA, Sosa K, Gómez JRdS (2019) Systematics of *Tibouchina* and allies  
600 (Melastomataceae: Melastomateae): A new taxonomic classification. *Taxon*, 68:937-1002.

601 Hörandl E (2010) The evolution of self-fertility in apomictic plants. *Sex Plant Reprod*, 23:73-86.

602 Hortal J, de Bello F, Diniz-Filho JAF, Lewinsohn TM, Lobo JM, Ladle RJ (2015) Seven shortfalls that  
603 beset large-scale knowledge of biodiversity. *Ann Rev Ecol Evol Syst*, 46:523-549.

604 Johnson SD, Burgoyne PM, Harder LD, Dötterl S (2011) Mammal pollinators lured by scent of a  
605 parasitic plant. *Proceedings of Royal Society B*, 278:2303-2310.

606 Judd WS (2007) Revision of *Miconia* sect. *Chaenopleura* (Miconieae, Melastomataceae) in the  
607 Greater Antilles. *Systematic Botany Monographs*, 81:1-235.

608 Karuppusamy S (2019) Predatophily – a new pollination mechanism reported in Whestern Ghats.  
609 *Kong. Res J.*, 6:53-55.

610 King C, Ballantyne G, Willmer PG (2013) Why flower visitation is a poor proxy for pollination:  
611 measuring single-visit pollen deposition, with implications for pollination networks and  
612 conservation. *Methods in Ecology and Evolution*, 4:811-818.

613 Konzmann S, Koethe S, Lunau K (2019) Pollen grain morphology is not exclusively responsible for  
614 pollen collectability in bumble bees. *Scientific Reports*, 9:4705.

615 Konzmann S, Hilgendorf F, Niester C, Rech AR, Lunau K (2020) Morphological specialization of  
616 heterantherous *Rhynchanthera grandiflora* (Melastomataceae) accommodates pollinator  
617 diversity. *Plant. Biol.*, 22:583–590.

618 Kopper C (2021) Testing pollination syndromes in Melastomataceae. Master thesis.

619 Kriebel R, Zumbado MA (2014) New reports of generalist insect visitation to flowers of species of  
620 *Miconia* (Miconieae: Melastomataceae) and their evolutionary implications. *Brittonia*,  
621 66:396–404.

622 Lagomarsino LP, Condamine FL, Antonelli A, Mulch A, Cavis CC (2016) The abiotic and biotic drivers of  
623 rapid diversification in Andean bellflowers (Campanulaceae). *New Phytologist*, 1430-1442.

624 Lin CW (2019) *Driessenia phasmolacuna* (Sonerileae, Melastomataceae), a new species from Batang  
625 Ai, Sarawak, Borneo. *Taiwania*, 64:69-73.

626 Lunau K (2000) The ecology and evolution of visual pollen signals. *Plant Systematics and Evolution*  
627 222:89–11.

628 Mancera JP (2017) Morphological phylogenetic analysis of the Astronieae (Melastomataceae).  
629 Master thesis.

630 Mack AL, Wright DD (1996) Notes on occurrence and feeding of birds at Crater Mountain Biological  
631 Research station, Papua New Guinea. *Emu*, 96:89-101.

632 Maia FR, Varassin IG, Goldenberg R. (2016) Apomixis does not affect visitation to flowers of  
633 Melastomataceae, but pollen sterility does. *Plant Biol*, 18:132-138.

634 Melo LRF, Vasconcelos T, Reginato M, Caetano AP, Brito VLGd (2021) Evolution of stamen dimetrisism  
635 in Melastomataceae, a large radiation of pollen flowers. Perspectives in Plant Ecology,  
636 Evolution and Systematics, 48:125589.

637 Mendoza-Cifuentes H, Fernández-Allonso JL (2008) Evaluación de caracteres del cáliz y de los  
638 estambres en la tribu Merianieae (Melastomataceae) y definición de homologías. Rev. Acad.  
639 Colomb. Cienc., 34:143-172.

640 Mesquita-Neto JN, Blüthgen N, Schlindwein C (2018) Flowers with poricidal anthers and their  
641 complex interaction networks – Disentangling legitimate pollinators and illegitimate visitors.  
642 Functional Ecology, 32:2321-2332.

643 Michelangeli FA (2021) <https://www.youtube.com/watch?v=hwe-ombIhqU>

644 Michelangeli FA, Alemda F, Goldenberg R, Penneys DS (2021) A guide to curating New World  
645 Melastomataceae collections with a linear generic sequence to world-wide  
646 Melastomataceae. Doi: 10.20944/preprints202010.0203.v2

647 Michelangeli FA, Nicolas A, Morales-P ME, David H (2011) Phylogenetic relationships of *Allomaieta*,  
648 *Alloneuron*, *Cyphostyla*, and *Wurdastom* (Melastomataceae) and the Resurrection of the  
649 tribe Cyphosyleae. Int. J. Plant Sci., 172:1165-1178.

650 Momose K, Yumoto T, Nagamitsu T, Kato M, Nagamasu H, Sakai S, Harrison RD, Itioka T, Hamid AA,  
651 Inoue T (1998) Pollination biology in a lowland dipterocarp forest in Sarawak, Malaysia. I.  
652 Characteristics of the plant-pollinator community in a lowland Dipterocarp forest. American  
653 Journal of Botany, 85:1477-1501.

654 Oliveira FDS, Ribeiro MHM, Nunez CV, Albuquerque PMCD (2016) Flowering phenology of *Mouriri*  
655 *guianensis* (Melastomataceae) and its interaction with the crepuscular bee *Megalopta*  
656 *amoena* (Halictidae) in the restinga of Lencóis Maranhenses National Park, Brazil. Acta  
657 Amazonica, 46:281-290.

658 Oliveira LC, Teixido AL, Trevizan R, Brito VLGD (2020) Bee-mediated selection favors floral sex  
659 specialization in a heterantherous species: strategies to solve the pollen dilemma. Plants,  
660 9:1685.

661 Passos LM, Telles FJ, Goldenberg R, Maia FR (2021) "Pollen Tube Shower" in *Bertolonia* Raddi  
662 (Melastomataceae): a new delayed selfing mechanism in flowers with poricidal anthers.  
663 Botanical Journal of the Linnean Society.

664 Penneys DS, Judd WS (2013) Combined molecular and morphological phylogenetic analyses of the  
665 Blakeeae (Melastomataceae). International Journal of Plant Sciences, 174 5:802-817.

666 Penneys DS (2013) Preliminary phylogeny of the Astronieae (Melastomataceae) based on nuclear and  
667 plastid DNA sequence data, with comments on the Philippine endemic genus, *Astrocalyx*.  
668 *Philippine J. Sci.*, 142:159–168.

669 Pereira AC, da Silva JB, Goldenberg R, Melo GAR, Varassin IG (2011) Flower color change accelerated  
670 by bee pollination in *Tibouchina* (Melastomataceae). *Flora*, 206:491-497.

671 Reginato M, Michelangeli FA (2016) Diversity and constraints in the floral morphological evolution of  
672 *Leandra* s.str. (Melastomataceae). *Annals of Botany*, 118:445– 458.

673 Reginato M, Vasconcelos TN, Kriebel R, Simões AO (2020) Is dispersal mode a driver of diversification  
674 and geographic distribution in the tropical plant family Melastomataceae? *Molecular*  
675 *Phylogenetics and Evolution*, 148:106815.

676 Rego JO, Oliveira R, Jacobi CM, Schindwein C (2018) Constant flower damage caused by a common  
677 stingless bee puts survival of a threatened buzz-pollinated species at risk. *Apidologie*, 49:276-  
678 285.

679 Renner SS (1984) *Phaenologie, Blütenbiologie und Rekombinationssysteme einiger*  
680 *zentralamazonischer Melastomataceen*. Doctoral Dissertation (printed copy), Univ. Hamburg.

681 Renner SS (1983) The widespread occurrence of anther destruction by *Trigona* bees in  
682 Melastomataceae. *Biotropica*, 15:257-267.

683 Renner SS (1989) A survey of reproductive biology in neotropical Melastomataceae and  
684 Memecylaceae. *Ann. Mo. Bot. Gard.*, 76:496.

685 Revell LJ (2012) phytools: An R package for phylogenetic comparative biology (and other things).  
686 *Methods Ecol. Evol.*, 3:217-223. doi:10.1111/j.2041-210X.2011.00169.x

687 Russell AL, Golden RE, Leonard AS, Papaj DR (2016) Bees learn preferences for plant species that  
688 offer only pollen as a reward. *Behavioural Ecology*, 27:731-740.

689 Santos APMD, Fracasso CM, Santos MLD, Romero R, Sazima M, Oliveira PE (2012) Reproductive  
690 biology and species geographic distribution in the Melastomataceae: a survey based on New  
691 World taxa. *Annals of Botany*, 110:667-679.

692 Sasidharan N, Sujanal P (2005) The genus *Medinilla* Gaudich. Ex DC. (Melastomataceae) in  
693 peninsular India. *Rheedea*, 15:103-112.

694 Sauquet H, Magallón S (2018) Key questions and challenges in angiosperm macroevolution. *New*  
695 *Phytologist*, 219:1170-1187.

696 Scheer LM (2019) Pollination syndromes: floral scent and nectar composition as key factors in  
697 Ecuadorian *Meriania* taxa. Master thesis

698 Solís-Montero L, Vallejo-Marín M (2017) Does the morphological fit between flowers and pollinators  
699 affect pollen deposition? An experimental test in a buzz-pollinated species with anther  
700 dimorphism. *Ecol. Evol.*, 7:2706–2715.

701 Solís-Montero L, Cáceres-García S, Alavez-Rosas D, García-Crisóstomo JF, Vega-Polanco M, Grajales-  
702 Conesa J, Cruz-López L (2018) Pollinator preferences for floral volatiles emitted by dimorphic  
703 anthers of a buzz-pollinated herb. *Journal of Chemical Ecology*, 44:1058–1067.

704 Stein BA, Tobe H (1989) Floral nectaries in Melastomataceae and their systematic and evolutionary  
705 implications. *Ann. Miss. Bot. Gard.*, 76:519-531.

706 Stiles FG, Ayala AV, Girón M (1992) Polinización de las flores de *Brachyotum* (Melastomataceae) por  
707 dos especies de *Diglossa* (Emberizidae). *Caldasia*, 17:47-54.

708 Stone RD, Ghogue J-P, Cheek M (2008) Revised treatment of *Memecylon* sect. *Afzeliana*  
709 (Melastomataceae: Olinbeoideae), including three new species from Cameroon. *Kew Bulletin*,  
710 63:227-241.

711 Telles FJ, Klunk CL, Maia FRd, Brito VLGd, Varassin IG (2020) Towards a new understanding of the  
712 division of labour in heterantherous flowers: the case of *Pterolepis glomerata*  
713 (Melastomataceae). *Bot J Linn Soc.*, 1:1-11.

714 Timmerman A, Dalsgaard B, Olesen JM, Andersen LH, González AMM (2008) *Anolis aeneus*  
715 (Grenadian Bush Anole), *Anolis richardii* (Grenadian Tree Anole). *Nectarivory/Pollination*.  
716 *Herpetological Review*, 39:84-85.

717 Ule E (1896) Weiteres zur Blütheneinrichtung von *Purpurella cleistopetala* und Verwandten. *Ber*.  
718 *Deutsch. Bot. Ges.*, 14:169-1 78.

719 Vallejo-Marín M (2019) Buzz pollination: studying bee vibrations on flowers. *New Phytologist*,  
720 224:1068-1074.

721 Valverde-Espinoza JM, Chacón-Madriral E, Alvarado-Rodríguez O, Dellinger AS (in prep) The  
722 predictive power of pollination syndromes: passerine-pollination in heterantherous *Meriania*  
723 *macrophylla* (Benth.) Triana.

724 Van der Niet T, Johnson SD (2012) Phylogenetic evidence for pollinator-driven diversification of  
725 angiosperms. *Trends Ecol. Evol.*, 27:353–361.

726 Varassin IG, Penneys DS, Michelangeli FA (2008) Comparative anatomy and morphology of nectar-  
727 producing Melastomataceae. *Ann. Bot.*, 102:899–909.

728 Velloso MDSC, Brito VLGD, Caetano APS, Romero R (2018) Anther specializations related to the  
729 division of labor in *Microlicia cordata* (Spreng.) Cham. (Melastomataceae). Acta Botanica  
730 Brasílica, 32:349-358.

731 Veranso-Libalah MC, Couvreur TL, Stone RD, Kadereit G (2018) Multiple shifts to open habitats in  
732 Melastomataceae (Melastomataceae) congruent with the increase of African Neogene climatic  
733 aridity, Journal of Biogeography, 45:1420-1431.

734 Viana ML, Oliveira EO, Romero R, Caetano APS (2021) The best of both worlds: Apomixis and  
735 sexuality co-occur in species of *Microlicia*, Melastomataceae. Plant Species Biology, 36:476-  
736 488.

737 Vogel S (1978) Evolutionary shifts from reward to deception in pollen flowers. In: Richards AH, editor.  
738 The pollination of flowers by insects. London: Academic Press. p. 89–96.

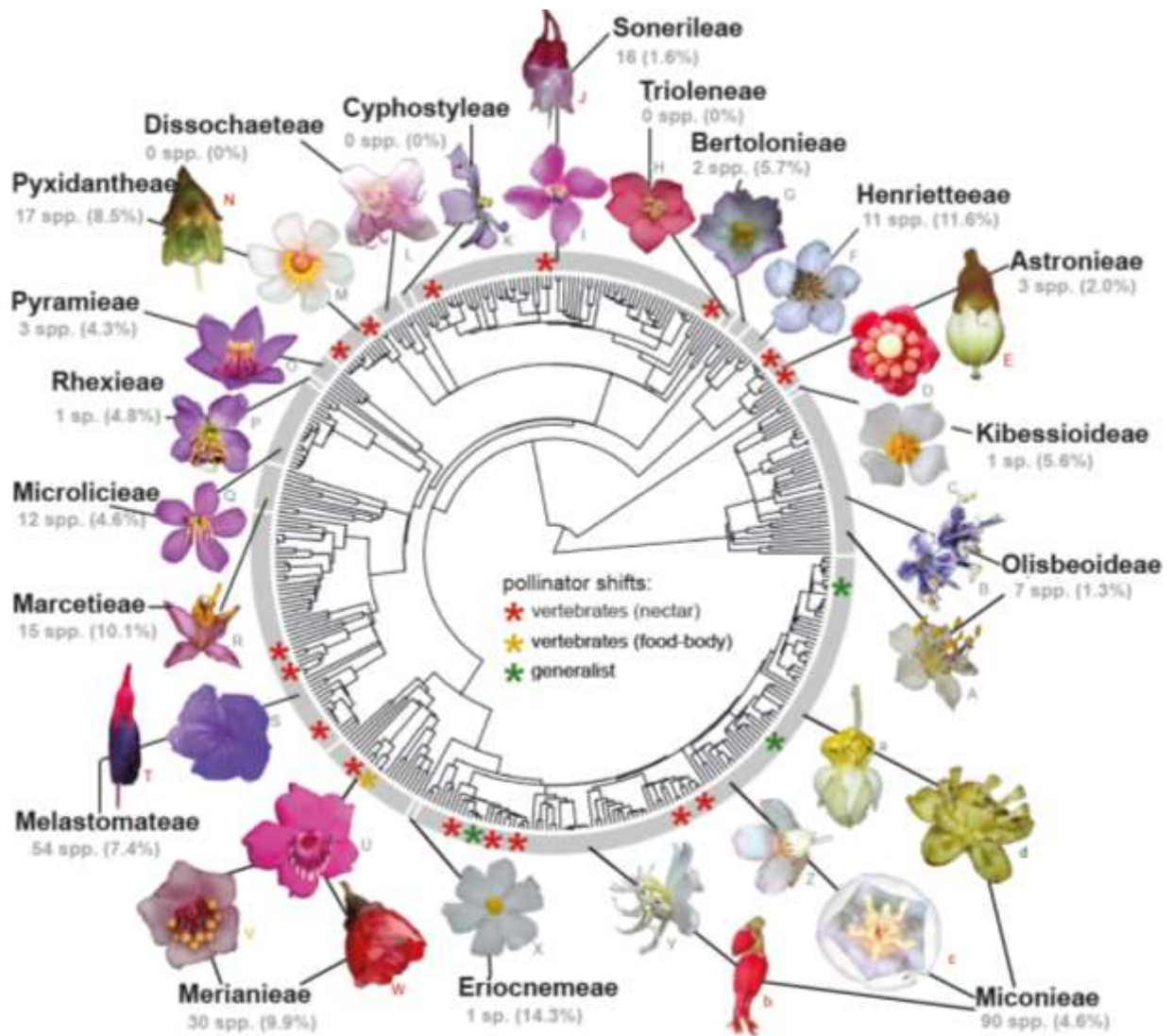
739 Vogel S (1997) Remarkable nectaries: structure, ecology, organophyletic perspectives I. Substitutive  
740 nectaries. Flora 192:305-333.

741 Warner R (1981) Systematics of Central American *Monolena* (Melastomataceae) Thesis, Univ.  
742 Minnesota, St. Paul, Minnesota.

743 Wester P, Stanway R, Pauw A (2009) Mice pollinate the Pagoda Lily, *Whiteheadia bifolia*  
744 (Hyacinthaceae) – First field observations with photographic documentation of rodent  
745 pollination in South Africa. South African Journal of Botany, 75:713-719.

746 Wester P, Filla M, Lunau K (2016) Floral scent and flower visitors of three green-flowered Costa Rican  
747 and Panamanian *Blakea* species (Melastomataceae) indicate birds rather than rodents as  
748 pollinators. Plant Ecology and Evolution, 149:319-328.

749

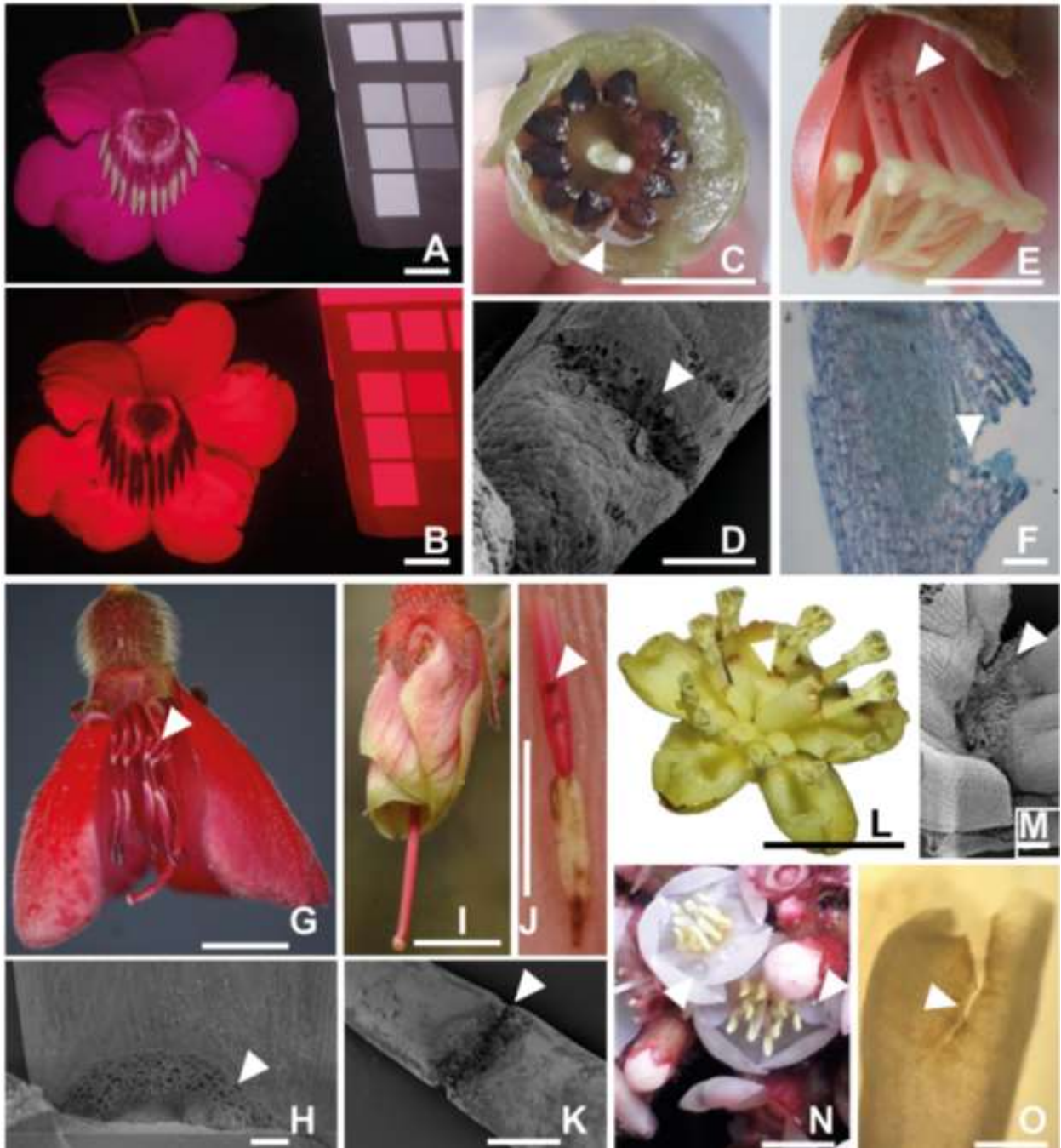


750

751 **Figure 1. Flower diversity and pollinator shifts across Melastomataceae.** Buzz-bee-pollinated  
 752 flowers are most common (inner circle, grey letters), with generally reflexed corollas and actino- or  
 753 zygomorphically arranged, often visually contrasting androecia offering pollen rewards. Shifts to  
 754 nectar-foraging vertebrates have occurred in six tribes (Astronieae, Sonerileae, Pyxidanthaeae,  
 755 Melastomateae, Merianieae, Miconieae; outer circle, red letters) and go along with shifts to nectar  
 756 rewards and pseudo-tubular or pseudo-campanulate corollas. Shifts to food-body-foraging  
 757 vertebrates occurred only in tribe Merianieae (outer circle, yellow letter), with the evolution of  
 758 bulbously-inflated sugary stamen appendages and bowl-shaped to urceolate corollas. Shifts to  
 759 generalist pollination are documented in tribe Miconieae (outer circle, green letter), often with  
 760 nectar secretion, open corollas, actinomorphic androecia and enlarged stamen pores. The 18 tribes  
 761 are represented corresponding to their size, number and proportion of species per tribe with flower  
 762 visitor observations are given. Shifts are indicated by \* approximately where they occurred on the  
 763 phylogeny (note that in Merianieae, two additional shifts to nectar-foraging vertebrates and two  
 764 additional shifts to food-body-foraging vertebrates occurred, but are not indicated due to limited



765 space). Lines connecting flower images do not indicate evolutionary sequences of shifts. A) *Mouriri*  
766 *emarginata*, B) *Lijndenia darainensis*, C) *Pternandra echinata*, D) *Astronia* cf. *meyeri*, E) *Beccarianthus*  
767 *pulcherrimus*, F) *Bellucia grossularioides*, G) *Bertolonia formosa*, H) *Triolena* cf. *hirsuta*, I) *Medinilla*  
768 sp., J) *Medinilla papillosa*, K) *Allomaieta* sp., L) *Dissochaetea macrosepala*, M) *Blakea anomala*, N)  
769 *Blakea chlorantha*, O) *Huberia kollmannii*, P) *Rhexia virginica*, Q) *Microlicia confertiflora*, R) *Marcetia*  
770 *taxifolia*, S) *Tibouchina urvilleana*, T) *Brachyotum* sp., U) *Meriania maguirei*, V) *Axinaea* sp., W) *M.*  
771 *tetragona*, X) *Physeterostemon aonae*, Y) *Miconia mirabilis*, Z) *M. conglomerata*, a) *M. subseriata*, b)  
772 *M. purpurea*, c) *M. barbipetiolata*, j) *M. corymbiformis*. © (A, F, K, P, R, a) Fabián Michelangeli; (B) L.  
773 Gautier in Stone 2017; (C, D, E, L) Darin Penneys; (G, H) Lucas Bacci; (I, J) Peter Quakenbush; (O)  
774 Thuane Bochorney; (X) Renato Goldenberg; (b) Carol Ann Gracie; (d) Marcela Alvear.



775

776 **Figure 2. Flower colour-contrast in buzz-bee-pollinated *Meriania maguirei* and common sites of**  
 777 **nectar secretion in Pyxidanthaeae, Merianieae, Melastomateae and Miconieae. (A) Flower of**  
 778 ***Meriania maguirei* viewed in normal light and (B) through a UV-sensitive lens, with the entire**  
 779 **androecium clearly visually contrasting against the corolla. (C) Pseudo-campanulate, pendant flower**  
 780 **of *Blakea chlorantha*, nectar accumulating between corolla and filaments. (D) Ventral filament**  
 781 **rupture in *B. chlorantha*, and site of nectar secretion. (E) Flower of *Meriania tomentosa*, with petals**  
 782 **partly removed, nectar accumulation on dorsal filament ruptures which form within the first six**  
 783 **hours of anthesis. (F) Longitudinal section of filament of *M. tomentosa*, the dorsal filament rupture**  
 784 **reaches the vascular bundle, from which nectar is secreted. (G) Pseudo-campanulate flower of**

785 *Chaetogastra grossa*, arrow indicating site of nectar secretion at ventral filament bent. (H) Detail of  
786 (G), reaching vascular bundle. (I) Pseudo-tubular flower of *Brachyotum* sp. (J) Ventral filament  
787 ruptures on stamen of *Brachyotum* sp. (K) Detail of (J), reaching vascular bundle. (L) Generalist  
788 *Miconia corymbiformis* with nectar secretion from filament ruptures indicated by arrow. (M) Detail of  
789 (L), reaching vascular bundle. (N) Nectar-secreting *Miconia barbipetiolata*, nectar droplets  
790 aggregating in each involute petal tip (arrows). (O) Involute petal of *M. barbipetiolata* with necrotic  
791 tissue rupture through vascular bundles, likely site of nectar secretion. Scale bars: A, B, C, E, G, I, L, N  
792 – 1 cm; D – 200 µm; F, H – 100 µm; O – 300 µm; K, L – 500 µm.

793

794

795 **Table 1. Number of species per tribe with flower visitor observations** in relation to clade size  
796 (number of genera, number of species) and distribution (OW – Old World; NW – New World,  
797 following Michelangeli et al. 2020); we separated pollinators into four major groups. \* indicate most  
798 probable pollination syndrome (based on general floral morphology), \*? indicates uncertainty in  
799 pollination syndrome.

tribe	no of genera	no of spp.	occ.	no of obs.	buzz- bee	vertebrate (nectar)	vertebrate (food body)	generalist
<b>1 - Olisbeoideae</b>	4	446	OW	1	1			*?
	2	99	NW	6	6			*?
<b>2 - Kibessieae</b>	1	18	OW	1	*			1
<b>3 - Astronieae</b>	4	141	OW	3	*	3		*?
	1	7	NW	0	*			
<b>4 - Henrietteae</b>	3	95	NW	11	11			
<b>5 - Bertolieae</b>	1	35	NW	2	2			
<b>6 - Trioleneae</b>	2	43	NW	0	*			
<b>7 - Sonerileae</b>	42	1011	OW	15	11	2		2?
	6	15	NW	1	1			
<b>8 - Cyphostyleae</b>	4	24	NW	0	*			
<b>9 - Dissochaeteae</b>	5	99	OW	0	*			
<b>10 - Blakeeae</b>	2	201	NW	17	10	7		
<b>11 - Cambessedesieae</b>	4	70	NW	3	3			
<b>12 - Rhexieae</b>	3	21	NW	1	1			
<b>13 - Microlicieae</b>	7	271	NW	13	13			
<b>14 - Marcetieae</b>	20	149	NW	15	15			
<b>15 - Melastomateae</b>	28	303	OW	10	10			*?
	17	497	NW	49	43	5		1?
<b>16 - Merianieae</b>	8	302	NW	31	16	9	6	
<b>17 - Eriocnemeae</b>	3	7	NW	1	1			
<b>18 - Miconieae</b>	1	1883	NW	91	68	10		13
<b>unplaced genera</b>	3	10	OW	0	*			
	4	7	NW	0	*			

800

- 801 **Dellinger, Agnes Sophie**, Department of Botany and Biodiversity Research, University of Vienna,  
802 Rennweg 14, 1030 Vienna, Austria; agnes.dellinger@univie.ac.at
- 803 **Kagerl, Katharina**, Department of Botany and Biodiversity Research, University of Vienna, Rennweg  
804 14, 1030 Vienna, Austria; k.Kagerl@gmx.at
- 805 **Kopper, Constantin**, Department of Botany and Biodiversity Research, University of Vienna, Rennweg  
806 14, 1030 Vienna, Austria; constantin\_kopper@gmx.at
- 807 **Schönenberger, Jürg**, Department of Botany and Biodiversity Research, University of Vienna,  
808 Rennweg 14, 1030 Vienna, Austria; juerg.schoenenberger@univie.ac.at