

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

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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 nonexistent (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 Olisbeoideae, 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%, Henrietteeae – 11.6%,
137 Marcketiaeae – 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 Melastomateae: 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., Melastomateae: 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. anomala* (Wester et al. 2016). In Merianieae, we found weak, rose-like scents in *Meriania maxima*,
289 dominated by the terpenoid β-Barbatene, and floral fragrances of *Graffenrieda penneysii* were
290 dominated by (E)-β-Caryophyllene*, in addition to 23 terpenoids and unknown substances, but no
291 floral scent was noticeable to the human nose (Scheer 2019). This lack in broad-scale floral scent data
292 in Melastomataceae clearly limits our understanding of the role of traits involved in pollinator
293 attraction (and possible pollen-robbing deterrence) in the family in general. Recent investigations in
294 buzz-pollinated *Solanum rostratum* have revealed, for example, that heterantherous stamens differ
295 in the proportion of emitted scent compounds, with pollinating stamens producing high amounts of
296 scents particularly attractive to bees (Solís-Montero et al. 2018). Future studies in Melastomataceae
297 quantifying floral scents are hence direly needed in order to work out the potentially integrated and
298 interrelated adaptive role of floral attraction traits. Further, observations in *Tibouchina* and *Meriania*
299 indicate scent emission from stamens (Pereira et al. 2011; Dellinger, pers. obsv.), but systematic
300 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 associate 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 Pyxidantheae and
393 Merianieae (Wester et al. 2016; Dellinger et al. 2019b). Wester et al. found passerine- and rodent-
394 pollinated Pyxidantheae 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. Pyxidantheae 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

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

5. Potential other syndromes and unclear cases

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

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

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 (apomicts 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 (Regnato 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 dehisce 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 Western 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

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539

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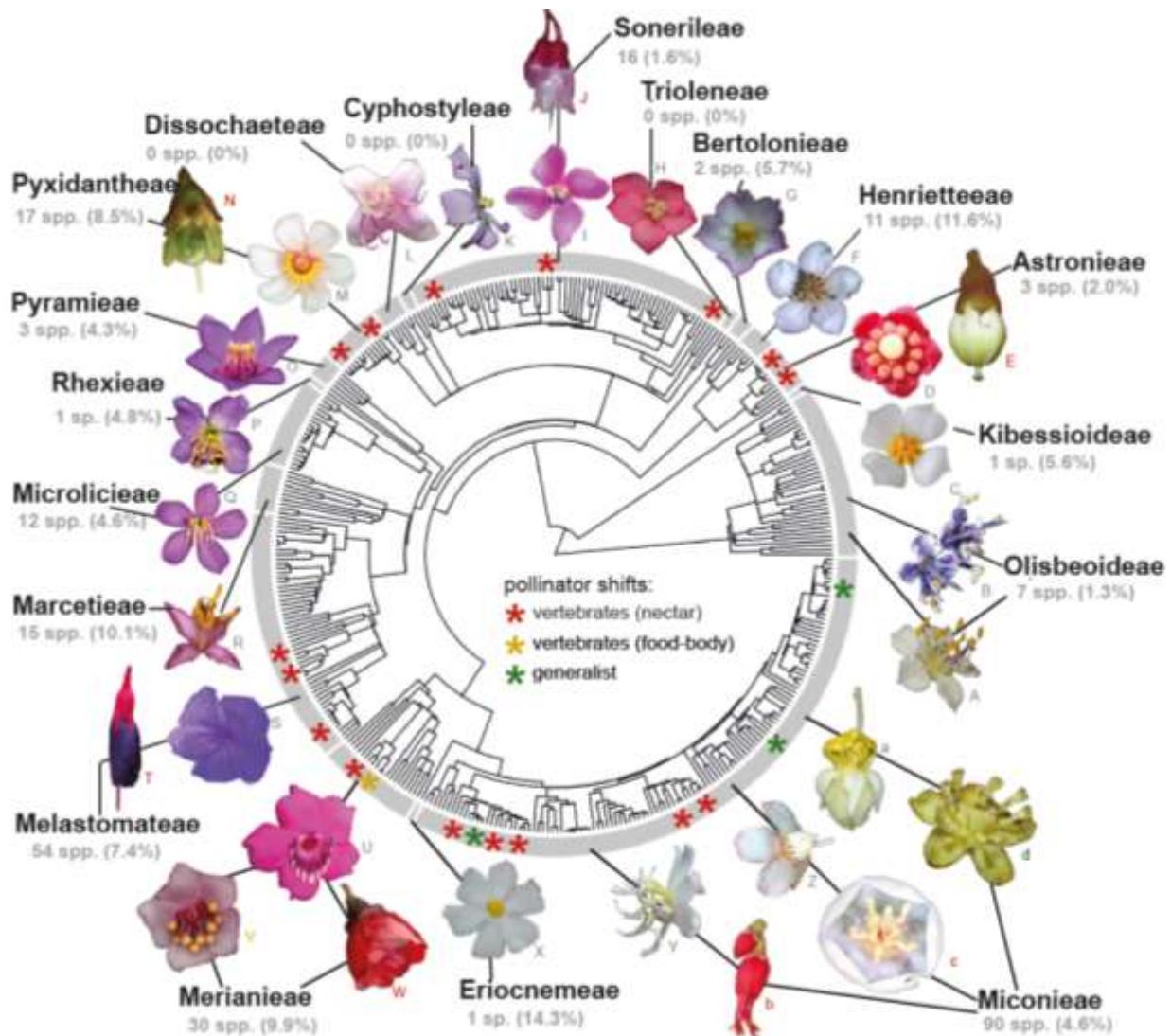
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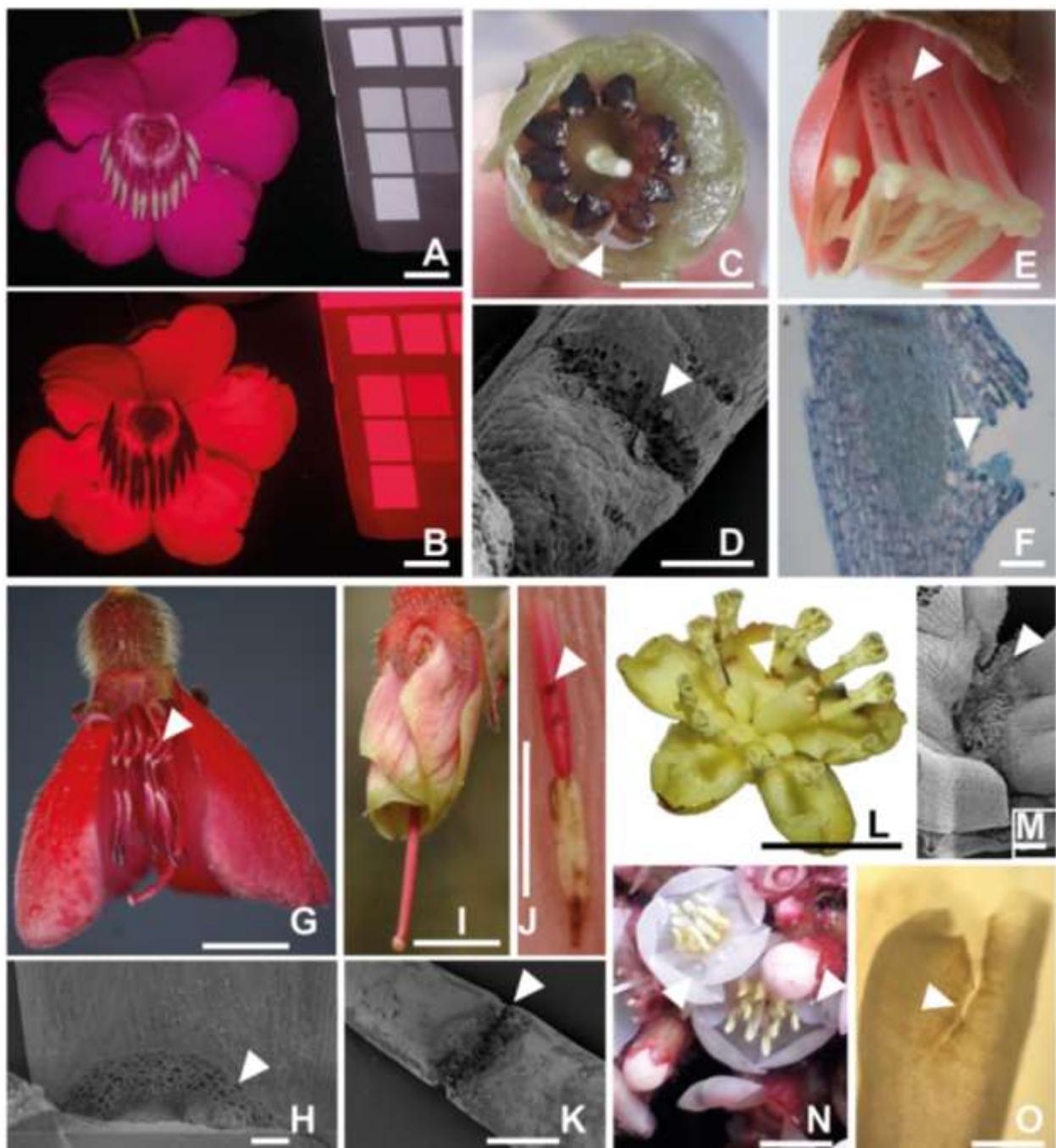
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- 749



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, Pyxidantheae,
 755 Melastomateae, Merianieae, Miconiaeae; 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 Miconiaeae (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) *Marcketia*
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 Bochorny; (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 Pyxidantheae, Merianieae, Melastomateae and Miconiae. (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
1 - Olisbeoideae	4	446	OW	1	1			*?
	2	99	NW	6	6			*?
2 - Kibessieae	1	18	OW	1	*			1
3 - Astronieae	4	141	OW	3	*	3		*?
	1	7	NW	0	*			
4 - Henrietteae	3	95	NW	11	11			
5 - Bertolonieae	1	35	NW	2	2			
6 - Trioleneae	2	43	NW	0	*			
7 - Sonerileae	42	1011	OW	15	11	2		2?
	6	15	NW	1	1			
8 - Cyphostyleae	4	24	NW	0	*			
9 - Dissochaeteae	5	99	OW	0	*			
10 - Blakeeae	2	201	NW	17	10	7		
11 - Cambessedesiaeae	4	70	NW	3	3			
12 - Rhexieae	3	21	NW	1	1			
13 - Microlicieae	7	271	NW	13	13			
14 - Marctieae	20	149	NW	15	15			
15 - Melastomateae	28	303	OW	10	10			*?
	17	497	NW	49	43	5		1?
16 - Merianieae	8	302	NW	31	16	9	6	
17 - Eriocnemeae	3	7	NW	1	1			
18 - Miconiaeae	1	1883	NW	91	68	10		13
unplaced genera	3	10	OW	0	*			
	4	7	NW	0	*			

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