A SURVEY OF REPRODUCTIVE BIOLOGY IN NEOTROPICAL MELASTOMATACEAE AND MEMECYLACEAE[1]

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ABSTRACT

In the Neotropics, the Melastomataceae and Memecylaceae comprise over 3,000 species in 106 genera. Pollination observations have been reported for 126 species in 35 genera of Melastomataceae and for four species in one genus of Memecylaceae. Genetic self-incompatibility has been found in 22 Melastomataceae species, self-compatibility in 25 species. A single Memecylaceae species tested is self-compatible. Agamospermy is known in 19 New World and some Old World species of Melastomataceae. The incidence of polyploidy in Melastomataceae seems high, but only about 8% of the species have been counted. Most Melastomataceae and Memecylaceae are hermaphroditic; dioecism is known in a few species in one genus of Melastomataceae. The principal mode of promoting outcrossing in both families is spatial separation of pollen and stigma (herkogamy), achieved by the pollen being enclosed in poricidal anthers, which have to be manipulated to release pollen. New World Memecylaceae are pollinated in the same way and by some of the same bee species as most Melastomataceae. All bee species known to visit Melastomataceae and Memecylaceae are listed; they comprise a wide spectrum of the neotropical bee fauna. It is not yet clear whether the stamen dimorphism and the conspicuous connective appendages present in many Melastomataceae have a function in the pollination mechanism beyond that of enhancing the visual attractiveness of the flowers and making the stamens easier to grasp. In most Melastomataceae, flowers offer only pollen; however, some 60 species in 8 genera offer nectar as a reward for pollinators (probably, some species in at least one additional genus do, too). The nectariferous species are pollinated by birds, bats, rodents, and bees. The nectar is rich in sucrose and, as a rule, its production is correlated with floral morphological changes relating to the fact that, except for bees, nectar consumers do not vibrate the stamens to collect pollen actively. I suggest that the capacity for developing nectaries is basic in Melastomataceae but suppressed in most modern members. The staminal glands of Memecylaceae produce minute quantities of a secretion containing lipids which, however, is not collected by the pollinators; the glands may in some way enhance stamen attractiveness. In seed dispersal systems, major diversifications occurred, with 40% of the neotropical Melastomataceae having capsular fruits and wind-dispersed seeds and 60% having soft, juicy berries taken mainly by birds, but also by marsupials, monkeys, bats, other mammals, turtles, and other reptiles. All Memecylaceae have berries, and their seeds are dispersed by birds, monkeys, and fish. I conclude that the east and west Gondwanian lineages of Melastomataceae and Memecylaceae, in parallel, coevolved with the earliest bees in the lower mid-Cretaceous. This may have been the time when the ancestors of these families switched from nectar-reward flowers to pollen-reward flowers. In the further extensive radiation of both families, special adaptations to pollinators were of limited importance; diversification in seed dispersal systems, vegetative characters, and edaphic adaptations were more important.

The neotropical Melastomataceae and Memecylaceae are particularly suitable for a study of reproductive biology in view of the relative ease with which members of these families are found in the field and the availability of several recent treatments in monographs and floras. As Gleason (1932) stated, "a dozen or more species . . . grow naturally on every square mile of tropical America, unless

TABLE 1. New World Melastomataceae and Memecylaceae. Tribal arrangement following Cogniaux (1891), except for more recently described, transferred, or synonymized genera. Species numbers are those of the most recent treatment, or based on a herbarium survey (Renner, 1986). + indicates a recorded observation, citation in Table 4; − no observation presently known.

	Species Number	Pollination Observation
MELASTOMATACEAE		
BERTOLONIEAE		
Bertolonia	8	−
Boyania	1	−
Diplarpea	1	−
Macrocentrum	21	−
Maguireanthus	1	−
Monolena	15	−
Opisthocentra	1	+
Salpinga	8	+
Tateanthus	1	−
Triolena (incl. Diolena)	22	−
Tryssophyton	1	−
MERIANIEAE		
Acanthella	2	−
Adelobotrys	25	+
Axinaea	30	−
Behuria	3	−
Benevidesia	1	−
Bisglaziova	1	−
Centronia	15	+
Dolichoura	1	−
Graffenrieda (incl. Calyptrella and Ptilanthus)	44	+
Huberia	6	−
Meriania	74	+
Merianthera	3	−
Neblinanthera	1	−
Ochthephilus	1	−
Phainantha	4	−
Tessmannianthus	3	−
MICROLICIEAE		
Bucquetia	3	−
Cambessedesia (incl. Pyramia)	21	−
Castratella	1	−
Centradenia	6	+
Centradeniastrum	1	−
Chaetostoma	12	−
Eriocnema	1	−
Lavoisiera	46	+
Lithobium	1	−
Microlicia	100	−
Poteranthera	2	−
Rhynchanthera	15	+
Siphanthera (incl. Farringtonia)	16	+
Stenodon	1	−
Trembleya	11	+
TIBOUCHINEAE		
Aciotis	30	+
Acisanthera	17	+
Appendicularia	1	−
Brachyotum	50	+

TABLE 1. Continued.

	Species Number	Pollination Observation
Chaetolepis	10	−
Comolia	22	−
Comoliopsis	1	−
Desmoscelis	1	+
Ernestia	16	+
Fritzschia	1	−
Heterocentron	6	−
Loricalepis	1	−
Macairea	22	+
Mallophyton	1	−
Marcetia	23	−
Microlepis	4	−
Nepsera	1	+
Pilocosta	3	−
Pseudernestia	1	−
Pterogastra	4	+
Pterolepis	15	−
Sandemania	1	+
Schwackaea	1	−
Svitramia	1	−
Tibouchina (incl. Itatiaia and Purpurella)	243	+
Tibouchinopsis	2	−
RHEXIEAE		
Monochaetum	45	+
Pachyloma	6	−
Rhexia	13	+
MICONIEAE		
Anaectocalyx	3	−
Bellucia	7	+
Calycogonium	23	−
Catacoryne	1	−
Chalybea	1	+
Charianthus	11	−
Clidemia	117	+
Conostegia	43	−
Ekmaniocharis	1	−
Henriettea	12	+
Henriettella	51	+
Heterotrichum	10	−
Huilaea	4	+
Killipia	4	−
Kirkbridea	1	−
Leandra (incl. Platycentrum)	175	+
Llewellynia	1	−
Loreya	13	+
Maieta	2	−
Mecranium	21	−
Miconia	ca. 1,000 (at least 958)	+
Mommsenia	1	−
Myriaspora	1	+
Myrmidone	2	−
Necramium	1	−
Ossaea	91	−
Pachyanthus	16	−
Pleiochiton	7	−
Tetrazygia	21	−
Tococa	54	+

TABLE 1. Continued.

	Species Number	Polli-nation Obser-vation
CYPHOSTYLEAE		
Allomaieta	1	–
Alloneuron	7	–
Cyphostyla	1	–
BLAKEEAE		
Blakea	100	+
Topobea	62	+
MEMECYLACEAE		
Mouriri	81	+
Votomita	8	–

the land is under intense cultivation, and the various genera extend from the coastal marshes at sea-level to the high páramos above the tree line." The Melastomataceae are a large family (v.i.) and diverse in terms of habit, reproductive and vegetative architecture (Cremers, 1983), and indument (Wurdack, 1986). Memecylaceae comprise about 89 species in the Neotropics and are much less diverse in these characters.

The present survey is based on my observations of the reproductive biology of many Brazilian and some Venezuelan species and on a review of the literature. The survey is presented in five sections. First, an outline of the classification and reproductive morphological features of the Melastomataceae and Memecylaceae is given; second, breeding systems and cytology are discussed; third, the pollination spectra found in the two families are described; fourth, a brief survey is made of seed dispersal in the two families; fifth, the reproductive biological information is related to the fossil record and distributional data to contribute to a better understanding of the historical evolution of the two families.

Flowering and fruiting phenology of neotropical melastomes and Memecylaceae are not dealt with here, but reference may be made to Snow (1965), Croat (1978), Opler et al. (1980), Hilty (1980), Lumer (1982), and Renner (1984 and in prep.). Suffice it to say that synchronous, episodic flowering with the episodes of short duration (a few days) characterizes some of the arborescent species of the largest genus, Miconia, whereas extended flowering periods (several weeks or months) are characteristic of many of the shrubs, herbs, epiphytes, and some of the tree species.

CLASSIFICATION AND REPRODUCTIVE MORPHOLOGICAL FEATURES

Worldwide, the Melastomataceae A. L. Juss. (excluding the ca. ten species of Crypteronia, Axinandra, and Dactylocladus, i.e., the Crypteroniaceae; Dahlgren & Thorne, 1984) and the Memecylaceae DC. consist of ca. 190 genera and approximately 4,800 species. In the Neotropics, the Melastomataceae comprise over 3,000 species in 107 genera (Table 1) and the Memecylaceae 89 species in two genera. About half of these genera contain only one to four species, whereas one genus, Miconia, has some 1,000 species. Though the Memecylaceae are often included in the Melastomataceae as a subfamily, it has been pointed out (see Morley, 1953; Dahlgren & Thorne, 1984; Johnson & Briggs, 1984) that the differences between these families are such that their union obscures rather than reflects our knowledge of the two groups. The Memecylaceae consist of the Asian genera Memecylon (ca. 300 spp.) and Lijndenia (4 spp.) (Bremer, 1982, 1983), the African Spathandra (6 spp.) and Warneckea (31 spp.), and the neotropical Votomita (8 spp.; Morley, 1963) and Mouriri (81 spp.). There is a consensus that the Melastomataceae and Memecylaceae belong to the core families of the order Myrtales (Dahlgren & Thorne, 1984; Johnson & Briggs, 1984).

The classification of the Melastomataceae sensu stricto is essentially that of Triana (1867), who was closely followed by Cogniaux (1891). Wurdack (1980) has realigned the New World tribes in a sequence generally resembling that of A. P. de Candolle (1828). The main dichotomy in the Melastomataceae is between the capsular-fruited and the berry-fruited genera. The genera are arranged into tribes on the basis of fruit and seed characters and the presence and position of connective appendages (D. Don, 1823; Triana, 1867; Cogniaux, 1891; Gleason, 1929; comp. also Whiffin & Tomb, 1972).

Most Melastomataceae are characterized by poricidal anthers, the connectives of which are frequently prolonged (however, species of Miconia sects. Chaenopleura and Chaenanthera have anthers that open by 1–2 slits). They usually have a pronounced foliar venation consisting of the midvein and one to four pairs of subparallel longitudinal veins. Memecylaceae, on the other hand, mostly have pinnate venation; their anthers open by short slits or pores. In a reproductive biological context, the presence of an elliptic, concave gland on the dorsal side of the connective is a unique feature characterizing most Memecylaceae.

The flowers in both families are actinomorphic or weakly to strongly zygomorphic as a result of movements of the stamens and style immediately after the expansion of the petals (Troll, 1922; Ziegler, 1925; pers. obs.). In Melastomataceae, the flowers are usually borne in well-developed cymose inflorescences, whereas in Memecylaceae the cymes are often condensed or reduced to a few flowers in fasciculate tufts. In both families, the mostly 4- or 5-merous flowers are perigynous or epigynous with a cup-shaped hypanthium that bears on its rim the calyx lobes, petals, and stamens. The antepetalous stamens are usually longer than the antesepalous ones, which may be staminodial; this dimorphism is more or less pronounced and has given occasion to much speculation concerning its role in pollination. In Melastomataceae with poricidal anthers, the anthers are one- or two-pored, a character that is consistent at the species level but varies within genera; there is also considerable variation in the size and position of the pores. Pollen grains are usually free, small, and rather smooth, although polyads and tetrads are known in species of *Tococa* and *Miconia* (Patel et al., 1984).

BREEDING SYSTEMS

The principal mode of promoting outcrossing in most Melastomataceae and Memecylaceae is the very effective spatial separation of pollen and stigma in the flowers (herkogamy). This is achieved by the pollen being enclosed in tubular anthers with apical or subapical pores or slits, which are generally minute, and positioned well distant from the punctiform or capitate stigmas. Also, the stamens are usually shorter than the styles. In bud, the stamens are always folded over in such a way that the anther pores point downward and are maximally distant from the stigma, which lies at the tip of the bud. Thus, chances for automatic selfing before and during anthesis are very low or nil. If, however, during anthesis, an anther or the style bends in such a way that the pore is brought into contact with the stigma, automatic selfing may occur. This has been reported for *Monolena trichopoda* (Melastomataceae; Warner, 1981) where, late in anthesis, the stamens fold over and the thecae are effectively stuck to the stigmatic exudate.

No pollen escapes from the anthers unless mediated by a vector, which at least potentially may arrive bearing conspecific pollen. Almeda (1977, 1978) suggested that vigorous mechanical movement of the anthers by gusty winds or rains might release pollen in species of *Monochaetum* and *Centradenia* (Melastomataceae). Additionally, he often observed pollen in water droplets connecting anthers and stigma and suggested that this might be another possible route for selfing to occur. However, bees, which regularly collect pollen from Melastomataceae, use vibrations of around 420 Hz or higher (this frequency was found to effect ample pollen emission from the large anthers of *Bellucia*; see below). Therefore, it seems unlikely that the low-frequency vibrations produced by wind could release pollen from melastome anthers. This impression is supported by the lack of fruit set in bagged flowers of nonagamospermic species exposed to strong wind (Renner, 1984). While autogamy may be extremely rare, vector-mediated selfing (i.e., geitonogamy), a function of pollinator behavior and number of conspecific flowers available at a time, may be frequent in self-compatible species.

Temporal separation of male and female function has been suggested for species of *Monochaetum* (Almeda, 1978) in which "the ill-defined stigmatic region . . . appears to be non-receptive during the first day." This may be a rare condition because, as a rule, poricidal flowers that offer only pollen as a reward (subsequently also called "pollen-only flowers") receive foreign pollen at the same time a visitor harvests pollen from them; in female-phase flowers, there is nothing to reward visitors (only mimicry or deception might account for visits to female-phase flowers). Homogamy, i.e., the simultaneous functioning of the male and female parts, is thus to be expected in pollen-only flowers. Temporal separation of the male and female function in single flowers has been reported twice in nectariferous melastomes (Ule, 1896; Vogel, 1957); in both cases, the flowers were protandrous.

The Melastomataceae are not entirely hermaphroditic. Wurdack (1964) was the first to describe dioecism in *Miconia dioica* Wurdack; herbarium specimens of this species had female flowers with abortive stamens and male flowers with poorly developed stigmas. He also suspected dioecism in some other minute-flowered Andean species of *Miconia* (*M. dielsii* Markgraf, *M. clathrantha* Tr. ex Cogn., *M. minuta* Gleason; Wurdack, 1980: 261–262) and in *M. rubens* (Sw.) Naudin from the West Indies and Venezuela (Wurdack, 1964). Field observations on the reproductive biology of these and some other suspected dioecious melastomes are lacking.

At least one species of *Lijndenia* (Memecyla-

ceae) has hermaphrodite-flowered individuals and purely male-flowered ones (Bremen, 1982).

GENETIC COMPATIBILITY

As shown in Table 2, genetic self-incompatibility occurs in at least 22 species in the two families. As Darwin remarked (in a letter to J. D. Hooker on Nov. 28, 1871, in F. Darwin (ed.), 1903), melastomes "are troublesome beasts to fertilise." This is due to the closed anthers and mostly punctiform stigmas. In some large-flowered species, such as *Bellucia* (Melastomataceae), it is possible to collect large amounts of pollen for experimental purposes by holding a tuning fork to the stamens. Self-compatibility is found in 26 species (Table 2). Since no efforts have ever been made to distinguish pseudogamy from self-compatibility, several of the supposedly self-compatible species reported earlier (Darwin, 1876; Ziegler, 1925) may have set fruit as a result of agamospermy rather than of self-fertilization. Related species such as *Tococa guianensis* and *T. bullifera* or *Centradenia grandiflora* and *C. paradoxa* (all Melastomataceae) differ in their compatibility conditions (Table 2). The humid stigmatic surface and the binucleate pollen of the Melastomataceae and Memecylaceae (Tobe & Raven, 1984) indicate that the incompatibility system is gametophytic (Nettancourt, 1977).

AGAMOSPERMY

Experimental proof of agamospermy in melastomes is readily obtained by cutting off the style in freshly opened unvisited flowers. (To ensure that flowers are unvisited before the style is cut off, they must be bagged the evening before.) Apart from the 22 apomictic Melastomataceae listed in Table 3, polyembryony, with additional embryos being formed by nucellus or suspensor cells, has been reported from the Asiatic species *Osbeckia hispidissima* Wight, *Sonerila wallichii* Benn., and *Melastoma malabathricum* L. (Subramanyam, 1942, 1944, 1948). Polyembryony is often correlated with agamospermy (Gustafsson, 1946–47). *Mouriri nervosa* is the only member of the Memecylaceae so far tested for agamospermy, with negative results (Renner, unpubl.). In several of the neotropical species showing apomixis, for instance in *Clidemia novemnervia* and *Macairea theresiae*, the anthers contain very few pollen grains. In cultivated neotropical *Leandra cordifolia* Cogn., Subramanyam (1942) also found that a low percentage of fertile pollen grains was combined with the frequent formation of two embryo sacs. In most neotropical species, agamospermy is correlated with low stainability of fresh pollen in cotton blue with lactophenol. This stain indicates presence of callose, a saccharide found in the intine of pollen. Lack of an intine could make a grain unviable and is usually accompanied by lack of cytoplasm. However, in *Aciotis acuminifolia* and *Miconia argyrophylla*, pollen grains stain heavily, yet these species are capable of producing seeds apomictically. In *Clidemia novemnervia* and *Maieta poeppigii*, the stamens do not unflex completely upon anthesis but remain curved, and are thus not available for legitimate bee pollinators. Both species regularly set seeds apomictically.

Lumer (1982) observed that *Blakea gracilis*, *Blakea* sp. (originally identified as *B. grandiflora*), and *Topobea brenesii* ripened a large number of seedless fruits from emasculated flowers; however, in *T. pittieri*, she found that of the bagged flowers, 35% produced mature fruits containing seeds. Darwin (1876) and Ziegler (1925) observed fruit set in cultivated plants of *Monochaetum*, *Tibouchina*, *Centradenia*, *Calvoa*, and *Dissotis* in the greenhouse. Assuming that there were no bee pollinators in the greenhouses, it is likely that such fruits resulted from agamospermy rather than from autogamy, which, as pointed out above, is mechanically difficult in Melastomataceae.

The number of species investigated is still too small to draw firm conclusions about correlations between habit, habitat, and breeding system. Of the agamospermous species, 13 are shrubs of various types of savannas or of secondary vegetation; five are treelets, two are herbs, and one is a climber. The sample is clearly biased towards shrubby species, however, because of their accessibility.

CYTOLOGY

Some 300 of the over 3,000 species of neotropical Melastomataceae and only one species of Memecylaceae (*Mouriri myrtilloides*) are known cytologically (Solt & Wurdack, 1980). Only a few of these have been examined twice. Melastome chromosomes are very small (0.5–1 micron; Solt & Wurdack, 1980) and stain poorly. The most common base numbers are 9 and 17 (Wurdack & Kral, 1982). Based on Solt & Wurdack's results, the incidence of polyploidy in the Melastomataceae seems high. It cannot yet be answered whether polyploidy is more frequent in species with strong agamospermous reproduction than in those which lack apomixis, nor whether there is a correlation between polyploidy and growth habit.

POLLINATION SYSTEMS

In neotropical Melastomataceae and Memecylaceae, the most widespread pollination system

Volume 76, Number 2
1989

Renner
Reproductive Biology in Melastomataceae
& Memecylaceae

501

TABLE 2. Compatibility systems in Melastomataceae.

	System[1]	Reference
MELASTOMATACEAE		
MERIANIEAE		
Adelobotrys rachidotricha Brade	SC	Renner, 1984
Graffenrieda latifolia (Naudin) Triana	SC	Sobrevila & Arroyo, 1982
BERTOLONIEAE		
Bertolonia marmorata Naudin	SC	Ziegler, 1925
MICROLICIEAE		
Centradenia floribunda Planchon	SC	Darwin, 1876
C. grandifolia (Schldl.) Endl. ssp. *grandiflora*	SIC	Almeda, 1977
C. paradoxa (Kraenzlin) Almeda	SC	Almeda, 1977
Rhynchanthera grandiflora (Aubl.) DC.	SC	Renner, 1984
TIBOUCHINEAE		
Nepsera aquatica (Aubl.) Naudin	SIC	Renner, 1984
Monochaetum amabile Almeda	SC	Almeda, 1978
M. calcaratum (DC.) Triana (as *M. ensiferum* Hook.)	SC	Darwin, 1876
M. floribundum (Schldl.) Naudin	SC	Almeda, 1978
M. neglectum Almeda	SC	Almeda, 1978
M. talamancense Almeda	SC	Almeda, 1978
M. vulcanicum Cogn.	SC	Almeda, 1978
RHEXIEAE		
Rhexia alifanus Walter	SIC	Kral & Bostick, 1969
R. aristosa Britton	SIC	Kral & Bostick, 1969
R. cubensis Griseb.	SIC	Kral & Bostick, 1969
R. lutea Walter	SC	Kral & Bostick, 1969
R. mariana var. *interior* (Pennell) Kral & Bostick	SIC	Kral & Bostick, 1969
R. mariana L. var. *mariana*	SIC	Kral & Bostick, 1969
R. mariana var. *ventricosa* (Fern. & Griscom) Kral & Bostick	SIC	Kral & Bostick, 1969
R. nashii Small	SIC	Kral & Bostick, 1969
R. nuttallii James	SIC	Kral & Bostick, 1969
R. parviflora Chapman	SIC	Kral & Bostick, 1969
R. petiolata Walter	SC	Kral & Bostick, 1969
R. salicifolia Kral & Bostick	SIC	Kral & Bostick, 1969
R. virginica L.	SIC	Kral & Bostick, 1969
MICONIEAE		
Bellucia acutata Pilger	SIC	Renner, 1986/1987
B. dichotoma Cogn. (as *B. imperialis* Saldanha & Cogn.)	SIC	Renner, 1984
B. grossularioides (L.) Triana	SIC	Renner, 1986/1987
Conostegia macrantha Triana	SIC	Lumer, 1982
Miconia araguensis Wurdack	SC	Sobrevila & Arroyo, 1982
M. dodecandra (Desr.) Cogn.	SC	Sobrevila & Arroyo, 1982
M. laevigata (L.) DC.	SIC	Sobrevila & Arroyo, 1982
M. macrodon (Naudin) Wurd. (as *Heterotrichum macrodon* (Naudin) Planchon)	SIC	Ziegler, 1925
M. sp. 254	SIC	Renner, 1984
M. sylvatica (Schldl.) Naudin	SC	Sobrevila & Arroyo, 1982
M. tuberculata (Naudin) Triana	SIC	Arroyo & Cabrera, 1977
Tococa bullifera DC.	SC	Renner, 1984
T. longisepala Cogn.	SIC	Renner, 1984
BLAKEEAE		
Blakea anomala J. D. Smith	SC	Lumer, 1982
B. chlorantha Almeda	SC	Lumer, 1980

TABLE 2. Continued.

	System[1]	Reference
B. gracilis Hemsley	SC	Lumer, 1982
B. sp. (as *B. grandiflora* Hemsley)	SC	Lumer, 1982
B. tuberculata J. D. Smith	SC	Lumer, 1982
Topobea brenesii Standley	SC	Lumer, 1982
T. durandiana Cogn.	SC	Lumer, 1982
MEMECYLACEAE		
Mouriri nervosa Pilger	SC	Renner, 1984

[1] SC = self-compatible, SIC = self-incompatible.

involves female bees; it occurs in an estimated 98% of the species. Pollination by hummingbirds, bats, and rodents is found in an estimated 60 species of *Meriania, Centronia, Brachyotum, Tibouchina, Miconia, Huilaea, Chalybea,* and *Blakea* (Table 4), and probably also in *Axinaea* (see below). The mode of pollination is determined by the type of reward offered: Melastomataceae and Memecylaceae with pollen-only flowers are, as a rule, pollinated exclusively by bees because the morphology of the anthers excludes all other pollen-collecting vectors. In contrast, the nectar-offering species attract a wide variety of pollinators.

MELASTOMATACEAE

POLLINATION BY POLLEN-COLLECTING BEES

a) Methods of pollen collection and kinds of bees

Pollination by bees has been reported for some 120 species in 31 genera of Melastomataceae (Table 4). In addition, a few species occurring at Finca La Selva, Costa Rica, and near Kourou, French Guiana, have been observed to be pollinated by small and medium-sized bees (Bawa et al. 1985; Roubik, 1979a). Many unidentified melastomes are indicated as visited by bees in apidological studies (e.g., Sakagami et al., 1965, and Roubik, 1979b).

TABLE 3. Agamospermous Melastomataceae.

	Habit	Habitat	Reference
Aciotis acuminifolia (DC.) Triana	herb	forest understory	Renner, 1984
Clidemia capitellata (Bonpl.) D. Don	shrub	savannas and disturbed vegetation	Renner, 1984
C. epibaterium DC.	climber	forest understory	Renner, 1984
C. fendleri Cogn.	shrub	forest understory	Sobrevila & Arroyo, 1982
C. hirta (L.) D. Don	shrub	disturbed vegetation	Renner, 1984
C. novemnervia (DC.) Triana	shrub	disturbed vegetation	Renner, 1984
C. rubra (Aubl.) Mart.	shrub	savannas and disturbed vegetation	Renner, 1984
Macairea theresiae Cogn.	shrub	Amazonian white sand savannas	Renner, 1984
Maieta guianensis (Aubl.) DC	shrub	forest understory	original
Maieta poeppigii Cogn.	shrub	forest understory	original
Miconia alata (Aubl.) DC.	shrub	disturbed vegetation	Renner, 1984
M. albicans (Sw.) Triana	shrub	savannas (cerrado)	Renner, 1984
M. argyrophylla DC.	treelet	secondary forest	Renner, 1984
M. campestris (Benth.) Tr.	shrub	disturbed vegetation	Renner, 1984
M. egensis Cogn.	treelet	secondary forest	Renner, 1984
M. minutiflora (Bonpl.) DC.	treelet	secondary forest	Renner, 1984
M. prasina (Sw.) DC.	treelet	secondary forest	original
M. regelii Cogn.	treelet	secondary forest	Renner, 1984
M. spinulosa Naudin	shrub	forest understory	Sobrevila & Arroyo, 1982
M. stenostachya DC.	shrub	savannas	Renner, 1984
M. tomentosa (L. C. Rich.) D. Don ex DC.	treelet	disturbed vegetation	Renner, 1984
Rhexia mariana L.	herb	swamps, marshes	Etheridge & Herr, 1968

Volume 76, Number 2
1989

Renner
Reproductive Biology in Melastomataceae
& Memecylaceae

503

TABLE 4.   Pollinators of Melastomataceae and Memecylaceae.

	Important Pollinators[1]	References
MELASTOMATACEAE		
BERTOLONIEAE		
Opisthocentra clidemioides Hook. f.	*Euglossa intersecta*; *Melipona fulva*	Renner, 1984
Salpinga secunda DC.	*Euglossa* sp., *Eulaema nigrita*; *Melipona* sp.	Renner, 1984
MERIANIEAE		
Adelobotrys rachidotricha Brade	*Pseudaugochloropsis* sp.	Renner, 1984
Centronia phlomoides Triana	bats	Vogel, 1988
Graffenrieda fruticosa Wurdack	*Bombus* spp.; *Xylocopa* sp.; *Melipona lateralis*	Renner, in press
G. polymera Gleason subsp. *neblinensis* Wurd.	*Bombus* spp.; *Melipona lateralis*	Renner, in press
G. reticulata Wurdack	*Bombus* spp.; *Melipona lateralis*; *Dialictus* sp.; *Neocorynura* sp.	Renner, in press
Meriania longifolia Cogn.	*Xylocopa* sp.	Vogel, 1978
M. tomentosa (Cogn.) Wurd. (= *Centronia excelsa* (Bonpl.) DC.)	hummingbirds	van der Werff, pers. comm.; *Neill et al.*, label data
MICROLICIEAE		
Centradenia grandifolia (Schldl.) Endl.	*Bombus* sp.; *Melipona* sp.	Almeda, 1977
Lavoisiera cordata Cogn.	*Bombus* spp.	Renner, 1984
L. glandulifera Naudin	*Bombus* spp.	original
Rhynchanthera grandiflora (Aubl.) DC.	*Xylocopa frontalis*, *X. tegulata*, *X. muscaria*; *Centris nitens*, *C. flavifrons*; *Eulaema nigrita*; *Monoeca* sp.	Renner, 1984, and original
R. hispida Naudin	*Xylocopa transitoria*; *Centris fuscata*; *Ptiloglossa* sp.	Renner, 1984
R. sp.	*Augochloropsis scabrifrons*, *A. sparsilis*, *A. terrestris*, *Augochloropsis* sp.; *Pseudaugochloropsis graminea*	Laroca, 1970
Siphanthera cordifolia (Benth.) Gleason	*Dialictus* sp.	N. Ramirez, pers. comm., 1986
Trembleya phlogiformis DC.	*Thygater analis*; *Bombus* sp.; *Xylocopa* sp.	Renner, 1984; Semir, pers. comm., 1982
TIBOUCHINEAE		
Aciotis acuminifolia (DC.) Triana	*Megommation ogilvei*; *Paratetrapedia duckei*; *Melipona fulva*, *Melipona* sp.; *Exomalopsini*	Renner, 1984
A. annua (DC.) Triana	halictids; *Paratetrapedia* sp.	Renner, 1984
A. circaeifolia (Bonpl.) Triana	*Megommation* sp.	Renner, 1984
A. polystachya (Bonpl.) Triana	*Paratetrapedia* sp.; *Augochloropsis callichroa*, *Augochloropsis* sp.; *Euglossa* sp.	Renner, 1984, and original
Acisanthera uniflora (Vahl) Gleason	halictids	original
Brachyotum ledifolium (Desr.) Triana	hummingbirds	Lagerheim, 1899
Brachyotum ca. 40–45 species	hummingbirds	Lagerheim, 1899; Wurdack, 1954; Fitzpatrick et al., 1979; B. Stein, pers. comm., 1985
Desmoscelis villosa (Aubl.) Naudin	*Dialictus* sp.; *Augochloropsis* sp.; *Xylocopa* cf. *tegulata*; *Augochlora* sp.; *Melipona* sp.	Roubik, 1979b; Renner, 1984, and original

TABLE 4. Continued.

	Important Pollinators[1]	References
Ernestia tenella (Bonpl.) DC.	*Augochloropsis* sp.	original
Macairea pachyphylla Benth.	*Melipona* sp.	N. Ramirez, pers. comm. 1986
M. parvifolia Benth.	*Euglossa* sp.	N. Ramirez, pers. comm. 1986
M. rufescens DC.	halictids	original
Monochaetum alpestre Naudin	*Bombus* sp.; *Melipona* sp.; Anthophoridae	Almeda, 1978
M. amabile Almeda	*Bombus* sp.; *Melipona* sp.; Anthophoridae	Almeda, 1978
M. compactum Almeda	*Bombus* sp.; *Melipona* sp.; Anthophoridae	Almeda, 1978
M. cordatum Almeda	*Bombus* sp.; *Melipona* sp.; Anthophoridae	Almeda, 1978
M. deppeanum (Schldl. & Cham.) Naudin	*Bombus* sp.; *Melipona* sp.; Anthophoridae	Almeda, 1978
M. exaltatum Almeda	*Bombus* sp.; *Melipona* sp.; Anthophoridae	Almeda, 1978
M. floribundum (Schldl.) Naudin	*Bombus* sp.; *Melipona* sp.; Anthophoridae	Almeda, 1978
M. linearifolium Almeda	*Bombus* sp.; *Melipona* sp.; Anthophoridae	Almeda, 1978
M. macrantherum Gleason	*Bombus* sp.; *Melipona* sp.; Anthophoridae	Almeda, 1978
M. neglectum Almeda	*Bombus* sp.; *Melipona* sp.; Anthophoridae	Almeda, 1978
M. talamancense Almeda	*Bombus* sp.; *Melipona* sp.; Anthophoridae	Almeda, 1978
M. tenellum Naudin	*Bombus* sp.; *Melipona* sp.; Anthophoridae	Almeda, 1978
M. trichophyllum Almeda	*Bombus* sp.; *Melipona* sp.; Anthophoridae	Almeda, 1978
M. vulcanicum Cogn.	*Bombus* sp.; *Melipona* sp.; Anthophoridae	Almeda, 1978
Nepsera aquatica (Aubl.) Naudin	*Megaloptidia contradicta*; *Megommation* sp.; *Melipona* sp.	Roubik, 1979b, Renner, 1984
Pterogastra divaricata (Bonpl.) Naud.	halictids	original
Purpurella see *Tibouchina*		
Sandemania hoehnei (Cogn.) Wurd.	*Megommation* sp.; *Augochloropsis callichroa*, *Augochloropsis* sp.; *Melipona fulva*	Renner, 1984, and original
Tibouchina arborea (Gardner) Cogn.	*Bombus morio*	F. Mueller, 1873
T. aspera Aubl.	*Xylocopa transitoria*; *Bombus* sp.; *Augochloropsis* sp.; *Euglossa* sp.; *Melipona* sp.; *Ptiloglossa* sp.	Roubik, 1979b, Renner, 1984
T. benthamiana (Gardner) Cogn.	*Augochloropsis* sp.	original
T. clavata (Pers.) Wurd.	*Bombus morio*; *Pseudaugochloropsis graminea*	Laroca, 1970
T. cleistoflora Ule (= *T. cleistopetala* Ule, 1896, nom. emend. = *Itatiaia cleistopetala* (Ule) Ule, 1909	*Bombus* sp.	Ule, 1896
T. frigidula (DC.) Cogn.	*Bombus* sp.; *Oxaea flavescens*; *Pseudaugochloropsis graminea*	original
T. gardneriana (Triana) Cogn.	*Trigonopedia* sp.	original
T. grandifolia Cogn.	halictids	original

Volume 76, Number 2
1989

Renner
Reproductive Biology in Melastomataceae
& Memecylaceae

505

TABLE 4. Continued.

	Important Pollinators[1]	References
T. grossa (L. f.) Cogn.	bats (*Anoura geoffroyi*); humming-birds	Vogel, 1957
T. hospita (DC.) Cogn.	halictids	original
T. longifolia (Vahl) Baillon	halictids	Renner, 1984
T. moricandiana (DC.) Baillon	*Bombus morio*	original
T. mutabilis (Vell.) Cogn.	*Bombus morio*	original
T. pilosa Cogn.	*Micrommation larocai*	Laroca, 1970
T. spruceana Cogn.	*Augochloropsis callichroa*	Renner, 1984
T. trichopoda (DC.) Baillon	*Bombus morio*	Laroca, 1970
T. ursina (Cham.) Cogn.	*Bombus atratus*; *Xylocopa augusti*; *Exomalopsis* sp.; *Augochloropsis cleopatra, A. euphrosyne, A. iris, A. leucotricha, A. scabrifrons, A. sparsilis, A. terrestris*	Laroca, 1970
RHEXIEAE		
Rhexia virginica L.	"bees"; bumblebees	Leggett, 1881; Eyde & Teeri, 1967
MICONIEAE		
Bellucia acutata Pilger	*Xylocopa frontalis*; *Centris lilacina*	Renner, 1984, 1986/1987
B. aequiloba Pilger	*Xylocopa* spp.; *Epicharis* sp.	Renner, 1986/1987
B. dichotoma Cogn. (= *B. imperialis*)	*Ptilotopus superbus*; *Centris lilacina, Centris* sp. nov.; *Oxaea flavescens*; *Epicharis conica, E. rustica, E. affinis*; *Xylocopa frontalis, X. tegulata, X. similis*; *Bombus* spp.; *Euglossa intersecta, E.* cf. *ignita*; *Eulaema meriana, Eulaema nigrita, E. moczaryi*	Renner, 1984, 1986/1987
B. grossularioides (L.) Tr.	*Xylocopa* spp.; *Centris* spp.; *Epicharis conica*; *Bombus* sp.; *Euglossa* sp.	Roubik, 1979b; Renner, 1984, 1986/1987
B. pentamera Naudin (= *B. axinanthera*)	*Xylocopa frontalis*; *Centris* spp.; *Epicharis* sp.	Renner, 1984, 1986/1987
Chalybea corymbifera Naudin (= *Pachyanthus corymbifera* (Naudin) Cogn.)	hummingbirds	B. Stein, pers. comm., 1986
Clidemia bullosa DC.	*Melipona eburnea*; *Augochloropsis* sp.	Renner, 1984, and original
C. capitellata (Bonpl.) D. Don	*Augochloropsis* sp.	Renner, 1984
C. hirta (L.) D. Don	*Augochloropsis hebescens, A. callichroa*, halictids; *Melipona fulva, M. lateralis, Melipona* spp.; *Euglossa* sp.	Renner, 1984, and original
C. japurensis DC.	*Augochloropsis* sp.; *Melipona eburnea, M. compressipes, Melipona* spp.	Renner, 1984
C. rubra (Aubl.) Mart.	halictids; *Melipona* sp.	Renner, 1984
Henriettea horridula Pilger	*Xylocopa tegulata*; *Melipona* sp.	Renner, 1984
Henriettella caudata Gleason	*Euglossa* sp.; *Melipona* sp.	Renner, 1984
Huilea macrocarpa Uribe	hummingbirds	Snow & Snow, 1980
H. penduliflora Wurd.	hummingbirds	Snow & Snow, 1980
Leandra micropetala Cogn.	*Augochloropsis* sp.; Exomalopsini	Renner, 1984
L. secundiflora (DC.) Cogn.	*Augochloropsis* sp.	Renner, 1984
Leandra sp. 884	halictids	Renner, 1984
Loreya riparia Renner	*Xylocopa frontalis*	original
L. spruceana Triana	*Eulaema meriana*; *Xylocopa frontalis*	Vogel, 1966; Renner, 1984, in press

TABLE 4. Continued.

	Important Pollinators[1]	References
Miconia alata (Aubl.) DC.	*Melipona fulva; Lophothygater decorata; Paratetrapedia* sp.; *Augochloropsis hebescens, A. cupreola, A. callichora; Pseudaugochloropsis graminea; Exomalopsis auropilosa;* gen. nov. near *Megommation*	Renner, 1984 and original
M. alborufescens Naudin	*Augochloropsis callichroa*	original
M. affinis DC.	medium-sized bees	Bawa et al., 1985
M. argentea (Sw.) DC.	"numerous spp. of bees"	Frankie, 1976
M. argyrophylla DC.	halictids	Renner, 1984
M. dispar Benth.	*Augochloropsis* sp.; *Exomalopsini; Melipona marginata; Xylocopa similis*	Renner, 1984, and original
M. egensis Cogn.	*Xylocopa ornata; Exomalopsis auropilosa; Paratetrapedia* sp.	original
M. gratissima Benth.	*Xylocopa frontalis; Melipona* sp.	Renner, 1984
M. ibaguensis (Bonpl.) Triana	*Augochloropsis* sp.; *Xylocopa tegulata, X. muscaria; Melipona* sp.; *Exomalopsini*	Renner, 1984, and original
M. minutiflora (Bonpl.) DC. (824)	*Augochloropsis callichroa;* halictids; *Melipona* sp.	Renner, 1984; Ducke, 1902; Mori & Pipoly, 1984
M. myriantha Benth.	*Melipona* sp.	Renner, 1984
M. nervosa (Smith) Triana	*Paratetrapedia* sp.; *Augochloropsis* sp.	Renner, 1984
M. pileata DC.	*Augochloropsis* spp.	Renner, 1984
M. poeppigii Triana	*Melipona fulva; Paratetrapedia* sp.	original
M. radulifolia (Benth.) Naudin	*Paratetrapedia* sp.	Renner, 1984
M. robinsoniana Cogn.	*Xylocopa darwinii*	Linsley et al., 1966; McMullen, 1985
M. rufescens (Aubl.) DC.	*Melipona eburnea; Thygater* sp.	Renner, 1984
M. splendens (Sw.) Griseb.	*Melipona* sp.	Renner, 1984
M. tomentosa (L. C. Rich.) D. Don ex DC.	*Xylocopa frontalis, X. similis; Melipona* spp.	Renner, 1984
Miconia sp. 254	*Augochloropsis* sp.	Renner, 1984
Miconia sp. 626	*Melipona* sp.	original
Miconia sp. 1004	*Xylocopa tegulata; Melipona fulva*	original
Miconia sp.	*Eulaema cingulata*	Dodson, 1966
Miconia sp.	*Melipona* sp.	Roubik, pers. comm., 1987
Myriaspora egensis DC.	*Xylocopa* sp.	original
Tococa bullifera DC.	*Euglossa intersecta, E. piliventris, E. chalybeata, E. ignita; Eulaema meriana; Melipona fulva; Paratetrapedia* sp.; *Megaloptidia* sp.	Renner, 1984
T. coronata Benth.	*Euglossa* sp., *E. intersecta; Augochloropsis* sp.	Renner, 1984 and original
T. guianensis Aubl.	*Melipona compressipes, Melipona* sp.; *Xylocopa* sp.; *Eulaema* sp.; *Augochloropsis* sp.	Roubik, 1979b; Renner, 1984
T. longisepala Cogn.	*Eulaema mocsaryi, E. meriana; Euglossa intersecta; Centris* sp.; *Xylocopa frontalis; Melipona fulva*	Renner, 1984 and original
T. pachystachya Wurd.	*Bombus* spp.; *Xylocopa* sp.	Renner, in press
T. subciliata (DC.) Triana	*Euglossa* sp.	Renner, 1984
T. tepuiensis Wurd.	*Bombus* spp.	Renner, in press

Volume 76, Number 2
1989

Renner
Reproductive Biology in Melastomataceae
& Memecylaceae

507

TABLE 4. Continued.

	Important Pollinators[1]	References
Tococa sp.	*Melipona quinquefasciata;* *Exomalopsis fulvofasciata*	Laroca, 1970
BLAKEEAE		
Blakea anomala J. D. Smith	*Bombus ephippiatus, B. volucelloides; Eulaema seabrai; Epicharis* sp.; *Melipona fasciata, M. flavipennis; Neocorynura rupa*	Lumer, 1982
B. austin-smithii Standley	rodents (Peromyscini, Oryzomini)	Lumer & Schoer, 1986
B. chlorantha Almeda	rodents (Peromyscini, Oryzomini)	Lumer, 1980, 1982
B. gracilis Hemsley	*Bombus epihippiatus, B. volucelloides; Eulaema seabrai, E. cingulata, E. polychroma; Epicharis* spp.; *Melipona fasciata; Xylocopa frontalis;* halictids	Lumer, 1982
B. penduliflora Almeda	rodents (Peromyscini, Oryzomini)	Lumer & Schoer, 1986
B. sp. (as *B. grandiflora* Hemsley)	*Bombus epihippiatus, B. volucelloides; Melipona fasciata;* halictids	Lumer, 1982
B. tuberculata J. D. Smith	*Bombus epihippiatus, B. volucelloides; Eulaema seabrai; Xylocopa frontalis*	Lumer, 1982
Topobea brenesii Standley	*Bombus epihippiatus, B. volucelloides; Eulaema seabrai, E. polychroma; Epicharis* sp.; *Melipona fasciata; Xylocopa frontalis; Crawfordopsis* sp.; *Pseudaugochloropsis nigerrima*	Lumer, 1982
T. durandiana Cogn.	*Euglossa* sp.; *Pseudaugochloropsis nigerrima*	Lumer, 1982
T. praecox Gleason	*Eulaema "mexicana"* (Surely another species, since *E. mexicana* does not occur in Panama; J. Ackerman, pers. comm., 1985)	Croat, 1978
MEMECYLACEAE		
Mouriri guianensis Aubl.	*Ceratina* sp.; *Euglossa* spp.	Renner, 1984, and original
M. brevipes Hook.	*Eulaema nigrita; Xylocopa frontalis*	original
M. myrtilloides (Sw.) Poiret	*Euglossa imperialis, E. tridentata, Euglossa* sp.; *Paratetrapedia calcarata*	Buchmann & Buchmann, 1981
M. nervosa Pilger	*Euglossa chalybeata, E. crassipunctata, E. purpurata, E. viridis; Eulaema mocsaryi, E. meriana; Xylocopa frontalis, X. similis, X. ornata; Melipona fulva, M. marginata*	Renner, 1984, and original

[1] "Important pollinators" excludes the numerous *Trigona* species, which are omnipresent pollen scavengers on Melastomataceae. Note that "halictids" stands for many different species, the correct names of which cannot be ascertained at present.

Bees gathering pollen from Melastomataceae flowers must be able to shake it out of the anthers or else pull pollen grains out through the pores with their tongues. This latter mode of exploiting melastome flowers is used by a group of *Trigona* bees and does not usually result in pollination because these bees are too small to contact the stigmas. Another subgroup of *Trigona* bees, characterized by having toothed mandibles, cuts up melastome anthers and robs their pollen (Laroca, 1970; Renner, 1983).

The method of pollen collecting used by all other bees to extract pollen from melastome anthers was first described correctly by van der Pijl (1954). When approaching a flower, in flight, the bees orient themselves with the group of stamens and the style and then straddle the stamens. They usually grasp the filaments or the bases of the anthers, quite often using their mandibles. Therefore, after having been visited, flowers often show necrotic spots on the outside of the stamens where the bees held onto them. When the bees position themselves over the androecium, their potentially pollen-bearing surface contacts the stigma even before they start exploiting the anthers. Also, they strive to establish a firm contact with as many stamens as their body size permits, going to considerable efforts in order to bundle all 8, 10, or 12 stamens. Close contact between the bee and the stamens is necessary for pollen collection by means of thorax vibrations, which are transmitted to the stamens and cause the pollen to stream out of the anther pores. Electrostatic forces due to the net positive charge of the bees and the negative charge of pollen greatly aid pollen-load adhesion (Thorp, 1979). When a pollen load, taken with forceps from a freshly captured bee, is released near this bee, it jumps back onto it (pers. obs.). The very rapid distortions of the thorax-box (with the wings at rest) are made possible by the unique contractile properties of the bees' fibrillar indirect flight muscles. Pollen collecting by this method is always accompanied by a characteristic buzzing sound and has been termed "buzzing method" (van der Pijl, 1954; Michener, 1962).

The rapid vibrations used when harvesting melastome pollen presumably produce a high temperature of the flight muscles, which may mean that this method of pollen collecting is particularly appropriate during the relatively cool early morning hours. Also, there are ecological constraints on the activity of dark-colored bees during the hottest hours. Buzz pollination continues with very high humidity of the air and even during slight rains.

In most melastomes, pollen deposition and reception is on the lower abdomen (sternotribic) or lateral on the bees (pleurotribic); it is on the back (nototribic) in a few species with downwards-curved styles (e.g., species of *Meriania*, *Adelobotrys*, *Salpinga*) and in *Desmoscelis villosa*. In these cases, bees assume quite unexpected positions in order to vibrate the stamens; in *Adelobotrys rachidotricha*, for instance, they buzz with the head pointing outward and downward. Relatively large flowers, such as those of *Blakea*, *Topobea*, and *Bellucia*, are exploited by a wide range of bees (Lumer, 1982; Renner, 1986/1987). For example, stamens of *Bellucia* are vibrated by 33-mm-long *Centris* and 8-mm-long *Augochloropsis* bees. In the case of self-compatible species, visits by bees too small to contact the stigma and deposit foreign pollen may still result in self-pollen landing on the stigma when such small bees vibrate one or a few stamens.

Bees visiting Melastomataceae exhibit considerable steadiness during individual foraging flights: pollen loads often consist of almost pure melastome pollen with very few grains from nectariferous flowers or with grains from *Cassia* mixed in (Renner, 1984). *Cassia* has buzz-pollinated flowers, and bees often visit several such flowers (see below).

In Brazilian Amazonia, I have captured 80 species of bees, including the Africanized honey bee, *Apis mellifera scutellata* Lepeletier, vibrating melastomes. (A list of all bees, including the species of *Trigona*, may be obtained upon request.) Additional species have been captured in extra-Amazonian areas and at higher altitudes. To date, at least 100 species of bees have been found pollinating melastome flowers (Table 4; this does not include the numerous species of pollen-scavenging *Trigona* bees). The relatively few groups of bees that have been successful in tropical forest environments, the euglossines, halictids, *Xylocopa*, and *Melipona* (Michener, 1979) are the most important pollinators of lowland melastomes. In savannas, Centridini, Oxaeidae, Exomalopsini, and *Ptiloglossa* (Colletidae) become important, as do bumblebees in southern Brazil and at higher altitudes. The bee fauna in neotropical forests and savannas is still incompletely known; however, based on bee inventories in Panama, Costa Rica, French Guiana, Surinam, and at the mouth of the Amazon (Heithaus, 1979; Roubik, 1979a, b; and ref. in Michener, 1979), it may be estimated that only about 300 species of bees occur in these forests, a number that includes non-flower-visiting parasitic and leaf-cutter bees. Thus, between 80 and 100 species collecting pollen from Melastomataceae represents a high proportion of the total Amazonian bee fauna.

b) Floral attractants

Melastome pollen is an important pollen source for neotropical bees. This is clear from a survey of literature on bee foraging: it is collected by female euglossines (Moure, 1970; Janzen, 1971; Michener et al., 1978; Roubik, 1979a, b; Dressler, 1982; Renner, 1984), meliponines and halictids (Ducke, 1901, 1902; Laroca, 1970; Roubik, 1979a, b; Michener et al., 1978; Absy & Kerr, 1977; Absy et al., 1980), mixed with Malpighiaceae oil by anthophorine bees (Vogel, 1974; Renner, 1984), and makes up 96–100% of the nest provision of the colletid bee *Crawfordapis* (Roubik & Michener, 1985). A chemical analysis of *Bellucia dichotoma* pollen revealed high nitrogen and total crude protein. (I am indebted to S. Buchmann for analyzing a pollen sample in 1983.) In this species, the pollen has a strong perfume resembling that of the flowers.

Secondary attractants for bees include sweet or perfumelike floral odors produced by the petals, the connective, and the upper section of the style (as determined by neutral red staining; pers. obs.; method, Vogel, 1963), and the presence of a landing platform provided by the androecium. I have never seen bees land on the petals. Frequently, the filaments are adorned with glandular or eglandular hairs, which may make them easier for the bees to grasp. Also, direct alighting on the stamens may make visits to flowers with poricidal anthers particularly rewarding compared with flowers requiring further crawling and searching after landing.

Most Melastomataceae seem to be visited and pollinated early in the morning, sometimes 20 minutes before sunrise (F. Mueller, 1873; Frankie, 1976; Lumer, 1982; Renner, 1984), and many species close their petals by late morning. However, flowers of *Monochaetum* and *Rhynchanthera* open late, two to four hours after sunrise (Almeda, 1978; pers. obs.). Shedding of the flower parts usually starts at the end of the second day. Again, *Monochaetum* differs in having flowers that stay open for three days (Almeda, 1978), and I have seen *Graffenrieda fruticosa* flowers staying attractive for at least seven days. In the latter case, the adverse climatic conditions at 2,200 m altitude, where *Graffenrieda fruticosa* occurs, may place a high selective advantage on longer flowering periods which presumably heighten the flowers' chances of being visited.

The typical bee colors of most Melastomataceae flowers, white, purple, or pink, are due to total reflection and anthocyanins (Lowry, 1976; Bobbio et al., 1985). Yellow and orange flowers evolved repeatedly in isolated species throughout the fam-

ily. Contrasting marks at the base of the petals and color changes during anthesis are frequent in Melastomataceae (F. Mueller, 1873; Ule, 1896; Wurdack, 1980; Renner, 1984). The colors change from white to red, from yellow to red, from white to purple, or from pink to white. The bright white of the small flowers of many herbaceous understory melastomes, e.g., species of *Aciotis, Leandra, Clidemia, Miconia,* and *Ossaea,* may be of selective advantage under conditions of low light intensity. Some melastome flowers tested (using a Kodak 18A Wratten filter) did not absorb ultraviolet light (Lumer, 1982), as was to be expected from the absence of flavonols from their petals.

The androecia of many species in the capsular-fruited tribes Merianieae, Bertolonieae, Microlicieae, Tibouchineae, and Rhexieae show a strong morphological differentiation into two sets of stamens. In addition, in such flowers the connective appendages may be large and stiff, forming 5, 10, or 15 usually yellow spurs, sometimes positioned like true anthers. Based on his brother's (Fritz Mueller) observations on a southern Brazilian species of "*Heeria*," Hermann Mueller (1881, 1883) was the first to suggest that this dimorphism was the ultimate result of a "division of labor" between the two sets of stamens (his illustration shows that his brother was probably dealing with a species of *Microlicia; Heeria* is synonymous with *Heterocentron,* which does not occur in southern Brazil). According to this idea, the conspicuous anthers attract the bees and offer "food pollen" as a reward, whereas the less conspicuous ones contain "functional pollen." The "functional pollen" is supposed to be placed on a part of the bee where it will not be groomed off and used as food for larvae. It will instead function in fertilization. Hermann Mueller's idea caught on immediately (Forbes, 1882; F. Mueller, 1883) and is usually mentioned as typical of the pollination strategy of Melastomataceae (e.g., Cammerloher, 1931; Percival, 1965; Kugler, 1970; Proctor & Yeo, 1972; Baker, 1978; Faegri & van der Pijl, 1979).

A partitioning of the bee surface would be necessary for selection to favor the pollen grains from one set of stamens over those from the other and thus lead to pollen dimorphism. Pollination mechanisms involving vibration of anthers, however, may not allow a sufficiently precise placement of pollen from two sets of stamens on bees. Forbes (1882), working with unnamed species of *Melastoma,* reported that "only the pollen from the long stamens seemed [sic] to be fertile"; yet he found pollen from both types of stamens on the stigmas. To date, with the exception of Forbes's report

(1882), no morphological or physiological differences between pollen grains from dimorphic stamens have been found in any of the Melastomataceae studied (Darwin, 1876; Ziegler, 1925; Whiffin, 1973; Almeda, 1977; Renner, 1984). Further experimental fieldwork is needed to assess whether the staminal dimorphism and the stamen appendages have a function beyond that of enhancing the visual attractiveness of the flowers and making the stamens easier to grasp for bees. In view of the importance of pollen aromas for guiding bee behavior (cf. Dobson, 1987), it is uncertain if the visual cues provided by the yellow connective appendages by themselves elicit pollen-collecting behavior.

POLLINATION OF NECTAR-PRODUCING MELASTOMATACEAE
BY BIRDS, BATS, RODENTS, AND BEES

Some 60 species of *Meriania*, *Centronia*, *Brachyotum*, *Tibouchina*, *Miconia*, *Huilaea*, *Chalybea*, and *Blakea*, all of them, except the species of *Miconia*, occurring at higher altitudes (1,600–3,400 m), offer nectar as a reward for their pollinators. On the basis of their character syndrome (see below), *Meriania drakei* (Cogn.) Wurd., *M. furvanthera* Wurd., *Axinaea weberbaueri* Cogn., and several other species of *Meriania*, *Axinaea*, *Centronia*, and *Tibouchina* are expected to produce nectar, too.

The first reports on nectar production in melastomes are by Ule (1895, 1896). In three species of *Tibouchina* (Table 4) growing on the Brazilian Itatiaia mountain range, he observed that nectar was produced by the staminal vascular bundle and secreted either directly from the filaments or sometimes through a slit in the filaments. He suggested bumblebees as the probable pollinators of these species. At Ule's request, the chemist T. Peckolt analyzed the stamens of another species that did not secrete nectar (Ule gave the name as *T. glareosa* Cogn.; there is no such name, and he probably meant *T. granulosa* Cogn.). Peckolt found that sugar was present "in great quantity," which suggested to Ule (1896) that this was likely true for other species of *Tibouchina* as well. In several other nectariferous melastomes, slits in the upper ventral side of the filaments have been observed, e.g., in *Tibouchina cleistoflora* Ule (Ule, 1896; pers. obs.), *T. grossa*, *Blakea chlorantha* (Tobe et al., in prep.), *Brachyotum ledifolium*, *B. andreanum* Cogn., *B. benthamianum* Triana, and *B. rugosum* Wurd. (Lagerheim, 1899; pers. obs.). They have also been found in non-nectariferous species—such as *Centradenia grandiflora*, *Heterocentrum roseum*, *Triolena pustulata* (as *Bertolonia pubescens*)—and in paleotropical species

of *Dissotis* and *Medinilla* (Ziegler, 1925). These slits appear not to be consistently formed sutures, but rather spontaneous ruptures. The anatomy of the nectariferous tissue is being studied by Tobe et al. (in prep.).

Reports of nectar in *Miconia minutiflora* (Mori & Pipoly, 1984) are unclear, since its presence in the minute flowers (2.5 mm in diameter, style 4 mm long) was only presumed. In central Amazonia, where I have observed this species, it did not produce nectar (Renner, 1984). However, in another *Miconia* species in the Belém region at the mouth of the Amazon, Roubik measured floral nectar of ca. 20% sugar concentration and collected *Melipona* and *Apis* (!) bees (Roubik, pers. comm. 1987). Recently, nectar production has also been confirmed in the Antillean endemics *Miconia sintenisii* Cogn. and *Mecranium amygdalinum* (Desr.) Wright (Dent, pers. comm.). *Miconia robinsoniana*, also with minute white flowers, was included under "nectar sources" in a summary of flower records for *Xylocopa darwinii* by Linsley et al. (1966). McMullen, who made further observations on the floral visits of this bee on Galápagos (McMullen, 1985), has never noticed any nectar in *M. robinsoniana* (McMullen, pers. comm., 1987).

Except in *Miconia*, nectar production in Melastomataceae is correlated with floral morphological changes that relate to the fact that the nectar collectors do not vibrate the stamens. Therefore, when nectar instead of pollen is the pollinator reward, the latter must be deposited on a visitor during nectar uptake. This is achieved by the anthers having rather large pores and being stiffened, particularly at the base. Pressure on the base of the anthers exerted by the head of a bee, the bill of a bird, or the front paws of rodents clasping the flowers ejects pollen onto the visitor. Lagerheim (1899) therefore speaks of "bellow" anthers; he found that a match the thickness of a hummingbird bill pushed into the flower of *Brachyotum ledifolium* so that it pressed the anther bases brought forth a pollen cloud 3 cm long. The flowers of the nectariferous species are inclined or pendent and, in the case of the bird-pollinated ones, usually dark red, deep purple, or bluish to almost black. In *Brachyotum ledifolium* the petals are yellow, but the hypanthium is covered with bright red hairs. In nectariferous melastomes, the petals do not spread at anthesis but remain convolute almost like in bud. Vogel (1957) reported a nocturnal cabbage odor in the predominantly bat-pollinated *Tibouchina grossa*. The other nectariferous melastomes are reported as scentless.

The bulk of nectariferous melastomes seem hummingbird-pollinated (Table 4). Most of them belong to the genus *Brachyotum*, which comprises 50 species, the majority ornithophilous (Wurdack, 1965, 1980; Lagerheim, 1899; Vogel, 1957; Fitzpatrick et al., 1979; label data). Other bird-pollinated species are *Meriania tomentosa* (Cogn.) Wurd. (*Centronia excelsa* (Bonpl.) DC.; van der Werff, pers. comm.; D. Neill, pers. comm.). Nectariferous and hummingbird-pollinated species in the Miconieae are *Huilea macrocarpa*, *H. penduliflora* (Snow & Snow, 1980) and probably also *Chalybea corymbifera* (in which Stein observed nectar but no pollination events; pers. comm., 1987). The Colombian *Tibouchina grossa* is pollinated by bats and hummingbirds (Vogel, 1957; Stein, pers. comm., 1987) and certainly the same is true of *T. Stricta* Wurd. and *T. reticulata* Cogn.

New World rats and mice of the tribes Peromycini and Oryzomini pollinate at least three nectariferous species of *Blakea* in Costa Rica (Lumer, 1980, 1982; Lumer & Schoer, 1986). Lumer found that bees and hummingbirds rarely visited the flowers of these species during the day but that nectar secretion was nocturnal. The *Blakea* species involved are hemiepiphytic, and their flowers are positioned close to the stem where the rodents can reach them conveniently.

The nectar of *Blakea chlorantha* contains ca. 11% sucrose (Lumer, 1982, and pers. comm.); that of *Huilea macrocarpa* has 12–16% with a mean of 13.4% (Snow & Snow, 1980); that of *Chalybea corymbifera* 16.5%; and that of *Brachyotum ledifolium* 20–22% (Tobe et al., in prep.). It would thus be classified as relatively rich in sucrose in the nectar class system of Baker & Baker (1983), who found that sucrose-rich or sucrose-dominated nectar prevails in hummingbird flowers. Thus, nectariferous melastomes offer a reward "intended" for pollinators other than bees.

The evolutionary origin of pollination systems involving nectar in Melastomataceae is considered below.

MEMECYLACEAE

In their pollination mechanism, the neotropical Memecylaceae closely resemble the Melastomataceae, and the above description of bees' methods of pollen collecting from melastome flowers also applies to them. In *Mouriri*, the anthers are stiff, with thickened endothecial walls, and are slightly prolonged just above the insertion of the filaments. The prolongations, termed "caudae" (Morley, 1953), are used as footholds by the bees exploiting

Mouriri anthers. Pollination in four species of *Mouriri* has been observed (Table 4); the main pollinators seem to be euglossines, followed by *Xylocopa* and *Melipona* species. They are legitimate visitors, i.e., large enough to contact the stigma regularly while collecting the reward. Memecylaceae anthers differ from those of Melastomataceae in bearing dorsal concave glands, 0.3–0.8 mm long. (For illustrations of the permutations in size and position of these glands in *Mouriri* and *Votomita*, see Morley, 1953, 1976, and 1985.) None of the legitimate pollinators show any interest in the staminal glands (Buchmann & Buchmann, 1981; Renner, 1984, and unpubl.).

Earlier (1984), I reported that *Melipona marginata* and *M. fulva* sometimes collected the secretion from the glands with the front legs, and that they mixed this substance with their pollen loads between pollen-collecting bouts on the wing. Further field observations, however, have convinced me that *Melipona* does not regularly touch the glandular surface when buzzing. The bees grip the stamens by the anther caudas just below the glands, and it is difficult to see what they do with their feet or their mouth parts when vibrating because they curve tightly over the anthers to allow the pollen stream to settle on their bodies. Between buzzing bouts, *Melipona* bees (and the euglossines) rotate over the androecium so as to drum out the pollen from all ten anthers. Staining of their freshly collected corbicular loads with Fehling solution showed that the pollen had been wetted with sugar. With Sudan III (a lipid stain), *Mouriri* pollen grains stained red, but the secretion holding them together did not; this implies that the pollen contains lipids, whereas the secretion did not.

Mouriri flowers are also visited by several species of *Trigona*. These small bees do not regularly contact the stigma but rob pollen from the anthers, which they are unable to buzz. Their role as pollen scavengers and robbers in Melastomataceae is well known (Renner, 1983). When cutting up anthers of *Mouriri nervosa* to reach pollen grains further down, *Trigona williana* very rarely touched the glands (Renner, 1984, and unpubl.). Most often, *T. williana* cut off the anthers above the glands, then stopped and started cutting and robbing the pollen of another anther. This shows that this pollen robber, like the legitimate pollinators, does not regularly collect the glandular exudates. Buchmann & Buchmann (1981) have observed *T. pallens* manipulating the glands of *M. myrtilloides* with the front legs and mouth parts.

The secretion of the staminal glands is yellow, viscous, stains red in Sudan III, and tests positive

for fatty substances. That of the relatively large (0.8 mm long) glands of *M. lunatanthera* forms myelin figures in water after a drop of sodium hydroxide is added (pers. obs.; method from Vogel, 1974). The secretion in *M. myrtilloides* has been reported to be a lipoidal mixture of many compounds (e.g., phenolic compounds, small amounts of glucose and saponin, at least 13 fatty acids, and free fatty acids) and to be "extremely rich in non-lipid constituents" (Buchmann & Buchmann, 1981).

Since the secretions from the floral glands contain lipids, the relationship between *Mouriri* and oil-collecting bees is of particular interest. Floral oils are collected by bees belonging to relatively few genera of Anthophoridae (e.g., *Centris, Epicharis, Monoeca, Paratetrapedia, Tapinotaspis, Tetrapedia*; cf. Vogel, 1974; Neff & Simpson, 1981). Although many of these collect pollen from Melastomataceae (comp. Table 4), to date only a single anthophorid bee species, *Paratetrapedia calcarata*, has been observed on *Mouriri* (Buchmann & Buchmann, 1981). This bee, due to its small size (7–8 mm long), rarely vibrated more than two or three of the ten anthers in each flower and only rarely touched the stigma (l.c.). Also, Buchmann & Buchmann (1981) reported that *Paratetrapedia calcarata* was an infrequent visitor of *M. myrtilloides* (16 times during 50 hours) and not a legitimate pollinator.

The secretion of the staminal glands forms a shiny film on the gland cuticle and in this respect differs greatly from the lipid-filled blisters of other epithelial elaiophores (Vogel, 1974). *Paratetrapedia* has scrapers on the fore-basitarsi (Neff & Simpson, 1981) and ruptures the cuticle of the elaiophores from which it collects oils. While scrutinizing hundreds of stamens from *Mouriri nervosa* and *M. guianensis* under the stereoscope in order to collect their glandular secretions, I never found signs of the glands having been scraped. This was perhaps to be expected, since the secretion forms a film on the outside of the cuticle.

A further problem in understanding the role of the staminal glands is that they are so small and positioned in such a way that the collection of any exudate either with the fore-basitarsi or the mouth parts by the medium-sized bees that pollinate *Mouriri* is difficult to envisage. Visitors small enough to be attracted by the minute quantities of secretion offered (such as the *Paratetrapedia* species observed by Buchmann & Buchmann, 1981) are not large enough to touch the stigmatic surface when manipulating the glands, especially since the styles in *Mouriri* are always longer than the stamens and the stigmas are held well away from the anthers.

A possible role of the staminal glands suggested by Morley (1976) is odor production. *Mouriri* species often have a strong perfume scent (Buchmann & Buchmann, 1981; Renner, 1984). Perhaps a volatile oil would persist longer when mixed with the fatty oils and other compounds. Buchmann & Buchmann (l.c.) suggested that the glands, which absorb ultraviolet light, might visually guide the bees to the pollen. Extending this idea, one might ascribe a pseudonectary role to the staminal glands. It is interesting that in the Bonnetiaceae, at least 23 species of *Caraipa* and *Mahurea* have very similar minute urceolate glands positioned subapically on the connective (Kubitzki, 1978). The role of these glands, as of those of *Mouriri*, is obscure.

SEED DISPERSAL IN MELASTOMATACEAE

Of the neotropical Melastomataceae, 40% have capsular fruits and wind-dispersed seeds (Renner, 1986). The remaining 60% have soft, juicy berries and endozoochorous seeds. Animal-dispersed Melastomataceae are most diverse in lowlands and montane forests, whereas the capsular-fruited tribes are richest in species in various types of savannas. Melastome capsules are often sturdy and persist on the plants for many months, during which the seeds are gradually shaken out. There are no data on dispersal distances in the wind-dispersed species; however, the many striking disjunctions observed in savanna melastomes (Renner, 1987b, and in press) probably attest to their good dispersability. Small herbaceous understory species with broadly conical capsules (*Salpinga, Monolena, Bertolonia*) may also have their seeds dispersed ballistically by raindrops.

Melastome berries range in size from five to ca. 35 mm in diameter. The smaller ones are of outstanding importance for small frugivorous birds throughout the Neotropics (Huber, 1910; Snow, 1965, 1971, 1981; Ricklefs, 1977; Skutch, 1980; Lumer, 1982; Wheelwright et al., 1984; R. Bierregård, pers. comm., and many additional references). Epiphytic Melastomataceae are mostly bird-dispersed (Renner, 1986), as are many of the most successful pioneer species, for example, *Clidemia hirta*, which has become a noxious weed in Africa, Asia, and Hawaii.

Fruit attributes, such as position, size, aroma, and color, indicate that different animal classes act as the principal dispersers in different species groups. For example, black spider monkeys are the predominant consumers and likely dispersers of the green, slightly astringent and relatively large berries of the tree *Bellucia grossularioides* in Surinam (Roosmalen, pers. comm.). In French Guiana,

this species is a favorite with the *Philander opos-sum* (Atramentowicz, 1982), which also eats *Henriettea* and *Loreya* fruits. However, a search of recent literature on feeding records (Renner, 1987a) showed that Melastomataceae are not among the preferred foods of either monkeys or bats (for bats, Fleming, 1986; but compare Foresta et al., 1984, and Fleming, 1988). Perhaps because the majority of Melastomataceae are shrubs or understory trees with terminally positioned infructescences, they are unsuited for foraging monkeys and bats. Also, the taste of the mostly sweet, watery melastome berries may not be to the liking of monkeys, which apparently prefer slightly acidic fruits (Sourd & Gautier-Hion, 1986).

Fruits that have fallen to the ground are often eaten by turtles (Moskowitz, pers. comm.; Roosmalen, pers. comm.), lizards (W. Magnusson, pers. comm.), rodents (Magnusson & Sanaiotti, 1987), tapirs (Huber, 1910), and ants (pers. obs.).

SEED DISPERSAL IN MEMECYLACEAE

All Memecylaceae have berries, ranging in size from 0.5 to 10 cm long; color at maturity is most commonly yellow to red, less often it is purple-black to black (Morley, 1976). The smaller-fruited species are surely bird dispersed; some larger-fruited ones are monkey-dispersed (Roosmalen, 1985). Fish eat the fruits of at least one riverine *Mouriri* species (Goulding, 1980), which is curious, since Morley (1976) reported that two other species are used for poisoning fish.

REPRODUCTIVE BIOLOGY AND THE EVOLUTION OF MELASTOMATACEAE AND MEMECYLACEAE

Floral morphology in Melastomataceae and Memecylaceae can only be understood as the result of coevolution between the earliest ancestors of these groups and pollen-collecting bees. Flowers of the Old World members of both families have the same basic construction as those of their New World relatives and, although little information is available on their floral biology, van der Pijl's (1939) detailed description of the pollination mechanism in some species of *Osbeckia*, *Medinilla*, and *Melastoma* makes it likely that they are pollinated in the same manner as the New World ones. The pollen offered in the poricidal stamens of both families is accessible exclusively to bees, but not to many of the most common ones, such as the numerous species of *Trigona* and the paleotropical *Apis*, which apparently do not vibrate stamens. Most Melastomataceae and Memecylaceae have "modern" pollen flowers in the sense of Vogel (1978), in which the visitor is forced into a fixed position while

harvesting the reward and in which the position of the stigma is of relatively little consequence because of the deposition of pollen on a large part of the visitor's surface.

There appears to be little opportunity for partitioning the bee body. Sharing of pollinators, noted rather frequently among sympatric buzz flowers (Linsley & Cazier, 1963; Macior, 1970, 1971; Thorp & Estes, 1975; Lumer, 1982; Renner, 1984), results in hybridization in the absence of genetic barriers. This is consistent with the fact that systematists working with Melastomataceae and Memecylaceae often notice hybrids (Kral & Bostick, 1969; Whiffin, 1973; Morley, 1976; Almeda, 1978; Solt & Wurdack, 1980; Renner, in press). The data on Melastomataceae breeding systems corroborate the suggestion that apomixis may be more widespread in the tropics than formerly thought (Kaur et al., 1978; Ashton, pers. comm., 1987). Apomictic seed production would make such species independent of pollinators, while retaining the advantages of producing seeds, i.e., the potential for dispersal and dormancy. Most notably, it would give them the capacity to build up a new population from a single propagule.

Statements that "details of the structure of the anthers doubtless relate to mechanisms of pollination" (Cronquist, 1981) or "in a family, such as the Melastomataceae, where floral evolution has been extensive, one may logically conclude that the diverse floral types represent adaptations to different pollination systems" (Almeda, 1977) are not corroborated by field data. Rather, Melastomataceae seem to confirm Macior's (1971) suggestion that buzz pollination is so successful a system that, once it is established, hardly any other pollination mechanism evolves, even in species-rich groups. Compared with other families, such as Lecythidaceae, Gesneriaceae, and Bignoniaceae, for which the overall pollination spectrum is fairly well known, Melastomataceae and Memecylaceae show little diversification in floral morphology and pollination strategies. In this they resemble Malpighiaceae (Anderson, 1979) and Solanaceae (Symon, 1979), which also have relatively specialized pollination systems and faithful bee pollinators. Such lack of diversification could be interpreted as the result of being stuck on an adaptive peak.

Melastomataceae that offer nectar are pollinated by a broader range of pollinator classes, namely by hummingbirds, bats, rodents, and bees; this statement applies to the individual species as well, several of which have more than one important pollinator type, for instance birds and bats in *Tibouchina grossa* and bees and rodents in *Blakea chlorantha*. Cruden (1972) suggested, as a possible

ecological significance for nectar production at higher altitudes, that under adverse climatic conditions the homoiothermic birds and mammals may be more reliable pollinators than bees. If valid, this explanation would apply to all now known nectar-producing Melastomataceae, except the species of *Miconia*.

Whether the thousands of pollen-only Melastomataceae derived from ancestors with nectar flowers or whether the proto-Melastomataceae never possessed nectaries (as suggested by Vogel, 1978) is a difficult question. Phylogenetically, the extant nectariferous species belong to groups not closely related: *Meriania* and *Centronia* are in the capsular-fruited Merianieae (as is *Axinaea*, which probably also has some nectariferous species, see above); *Brachyotum* and *Tibouchina* are in the likewise capsular-fruited Tibouchineae; *Chalybea*, *Huilea*, and *Miconia* are in the berry-fruited Miconieae; and *Blakea* is in the also berry-fruited Blakeeae. Thus nectar production occurs in at least five evolutionary lines: the first leading to *Meriania* and *Centronia* (which are not closely related to each other), the second to *Brachyotum* and *Tibouchina* (the first genus is a segregate of the second; Wurdack, 1954), the third to *Chalybea* and *Huilea* (two intimately related genera), the fourth to *Miconia* (with 1,000 species, only two of which to date are securely known to produce nectar), and the fifth to *Blakea*. Nectaries could have originated independently in all these lineages.

The problem is confounded by the slits observed in the filaments of some non-nectariferous Melastomataceae exactly in the same position as in some of the nectariferous species, where nectar is secreted through them. They occur in species of *Heterocentron* (Tibouchineae), *Bertolonia* (Bertolonieae), and *Centradenia* (Microlicieae) and in the paleotropical genera *Medinilla* and *Dissotis* (compare above under nectariferous melastomes) and may be rudimentary, nonfunctional nectaries. Thus, to date, only in two of the neotropical tribes— the small Rhexieae with 64 species and the Cyphostyleae with nine species—are nectar production or presumed rudimentary nectaries absent. In view of the presence of nectaries in at least five neotropical lineages and the indications of their former presence in two further ones, their parallel independent origin becomes hard to accept. Instead, I suggest that the capacity for developing nectaries is basic in the Melastomataceae but suppressed in most modern members.

To understand the origin of the memecyloid connective gland, whatever the chemical composition of its secretion, the following observations seem relevant. Functioning nectaries have been observed on the hypanthia of *Memecylon edule* Roxb. (= *M. ramiflorum* Desr.; Burck, 1891) and *M. floribundum* Blume (Zimmermann, 1932). Also, I have frequently seen ants on the hypanthia of *Mouriri nervosa*, which may be an indication that this neotropical Memecylaceae also secretes sugar, albeit in minute quantities. Evolutionarily, the capacity to secrete minute quantities of exudates directly through the hypanthium epidermis, without conspicuous morphological structures, may be correlated with the development of the staminal glands. However, data on the pollinators and the chemical composition of the exudates of paleotropical Memecylaceae are needed before the significance of the staminal glands in the family as a whole can be assessed. The Memecylaceae have ca. 340 Old World and 89 New World species, and it should be noted that, in the opinion of Morley (1953), the New World Memecylaceae are more basal than the Old World ones.

There is a great amount of parallelism between the Old World and the New World tribes in the Melastomataceae: the Oxysporeae, Sonerileae, Dissochaeteae, and Osbeckieae resemble more or less closely the Merianieae, Bertolonieae, Miconieae, and Tibouchineae, respectively, of the New World (Gleason, 1932). Based on wood anatomy, the differentiation into at least some of these tribes and into Melastomataceae and Memecylaceae occurred before the breakup of Pangaea (Vliet et al., 1981). However, the coevolutionary relationships between bees and proto-Melastomataceae, which are a conditio sine qua non for the evolution of the melastome androecium, can only have begun during the mid-Cretaceous when bees arose (Michener, 1979). The mid-Cretaceous may thus have been the time when the ancestors of these families switched from nectar-reward flowers to pollen-reward flowers (with the pollen presented in poricidal anthers and available only to bees). Likely, the Melastomataceae and Memecylaceae originated during Aptian times (lower mid-Cretaceous, 110 million years before present), when the gap between Brazil and Ghana was still very narrow; their east and west Gondwanian lineages, probably coevolved in parallel with the earliest bees. The oldest fossil melastome leaves are known from the early Eocene (Hickey, 1977), about 53 million years before present, and Eocene and Miocene leaves occur widely scattered throughout the Northern Hemisphere (Wurdack & Kral, 1982). Therefore, members of the family (and some of their pollinators?) at one time may have dispersed via Europe between North America and Africa.

The Melastomataceae, with two-thirds of their species in the Neotropics, have much of their di-

versity centered in areas of varied topography—
the Andes, Guayana, and south-central Brazil. The
neotropical Memecylaceae, on the other hand, are
centered in the Amazonian lowlands, where they
appear adapted to different soil types (pers. obs.).
The very early shift from anemochory to zoochory
in the Melastomataceae was probably one of the
reasons for their success in the understory of closed
forests, where animal dispersal is more advanta-
geous than wind dispersal. (The capsular-fruited
tribes are much more diverse in open habitats and
have relatively few species in forests.) The crucial
points in the radiation of large groups within the
Melastomataceae, besides their different seed-dis-
persal strategies, have been the acquisition of par-
ticular plant architectural, indument, and leaf ve-
nation characters. Because adaptations to different
pollinator types played such a limited role in the
radiation within the two families, the floral biolog-
ical data cannot be used to support either of the
two suggested phylogenies for the Melastomataceae
(Wurdack in Welle & Koek-Noorman, 1981; Vliet
et al., 1981).

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