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THE NEOTROPICAL EPIPHYTIC MELASTOMATACEAE: PHYTOGEOGRAPHIC PATTERNS, FRUIT TYPES, AND FLORAL BIOLOGY

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ABSTRACT. A census of the 2,586 species of New World Melastomataceae represented in the United States National Herbarium (US) was conducted to compile a list of the epiphytic species and information on their geographical and altitudinal distribution. The 227 epiphytic species include forms that live without connection to the ground, as well as climbing species. Members of *Blakea* and *Topobea* are able to grow as climbers or as terrestrial and epiphytic shrubs or as trees. The Andean mid-elevation forests and the Colombian Chocó region are the areas richest in epiphytic melastome species. The majority of epiphytic species have restricted distributions. Of the epiphytic species 85 percent produce berries, 15 percent have capsular fruits. They are mostly bee-pollinated, offering pollen as a reward; a few epiphytes offer nectar and are pollinated by a broader range of animals. The seven epiphytic species tested are self-compatible; one is capable of agamospermy.

The Melastomataceae, the seventh largest family of flowering plants (Wurdack, 1986), are one of the most important tropical groups. Gleason (1932), an expert on the family, said about them: "A dozen or more species probably grow naturally on every square mile of tropical America, unless the land is under intense cultivation, and the various genera extend from the coastal marshes to the high páramos above the tree line."

Most species of this ecologically variable family are easily recognized by their leaf venation and tubular anthers (FIGURE 1a, b). The Melastomataceae include annual and perennial herbs, treelets, large trees (e.g., *Mouriri, Miconia, Loreya, Bellucia*), climbers (herbaceous vines and woody lianas), and true epiphytes. The majority of the species are shrubs. Instances of hemi-epiphytism in the family need confirmation.

In the Old World tropics several hundred of the close to 500 described species of *Medinilla* are epiphytic, as are a plethora of genera in the Dissochaeteae (e.g., *Plethiandra, Dalenia, Omphalopus, Pachycentria, Pogonanthera, Backeria, Neodissochaeta, Dissochaeta*), and many other small genera. Among dicotyledonous plant families the Melastomataceae together with the Piperaceae and Gesneriaceae have the largest number of epiphytic species, and earlier estimates (Madison, 1977) of the number of epiphytic melastome species are clearly too conservative. Even though many more epiphytic melastome species exist in the Old World than in the New World, only the neotropical species are considered here because they are much better known taxonomically and biologically.

MATERIALS AND METHODS

A census of the New World melastome species was conducted at the United States National Herbarium at the Smithsonian Institution in Washington, D.C. (US) in order to compile a list of the epiphytic species. In addition to information on growth habit from specimen labels, information was obtained from Dr. John J. Wurdack (US) who has extensive field experience in the Guyana Highlands and the Andes, from Dr. Frank Almeda (CAS), and from my own observations on Amazonian melastomes.

True epiphytes, which start out life perched on another plant and pass at least part of their life cycle without being connected to the ground, as well as climbing species, were included in this survey. This broad view was chosen because most species of the closely related genera *Blakea* and *Topobea* which comprise the bulk of New World epiphytic melastomes cannot be classified as either climbing or truly epiphytic; rather, these species are able to grow as lianas and as terrestrial or epiphytic shrubs. The family does not possess thorns, spines, tendrils, or develop a twining habit. All climbing melastomes develop adventitious roots, which become buried in the bark of the supporting plant. None of the neotropical epiphytic melastomes are myrmecophilous.

A few species that are creeping herbs, growing and reproducing mostly on the ground, but sometimes covering rocks or fallen logs, are not included in the list of epiphytic melastome species. The morphology associated with vining, i.e., elongation of the stem, is of course the same in creeping herbs as in climbers and thus the distinction is based on the tendency to climb. Critical evaluation of the life form would require field observations. In contrast to creeping herbs, the climbing species regularly produce pendant inflorescences at several meters above the ground. A small number of herbaceous or suffrutescent species of the bertolonioid genera *Salpinga,*

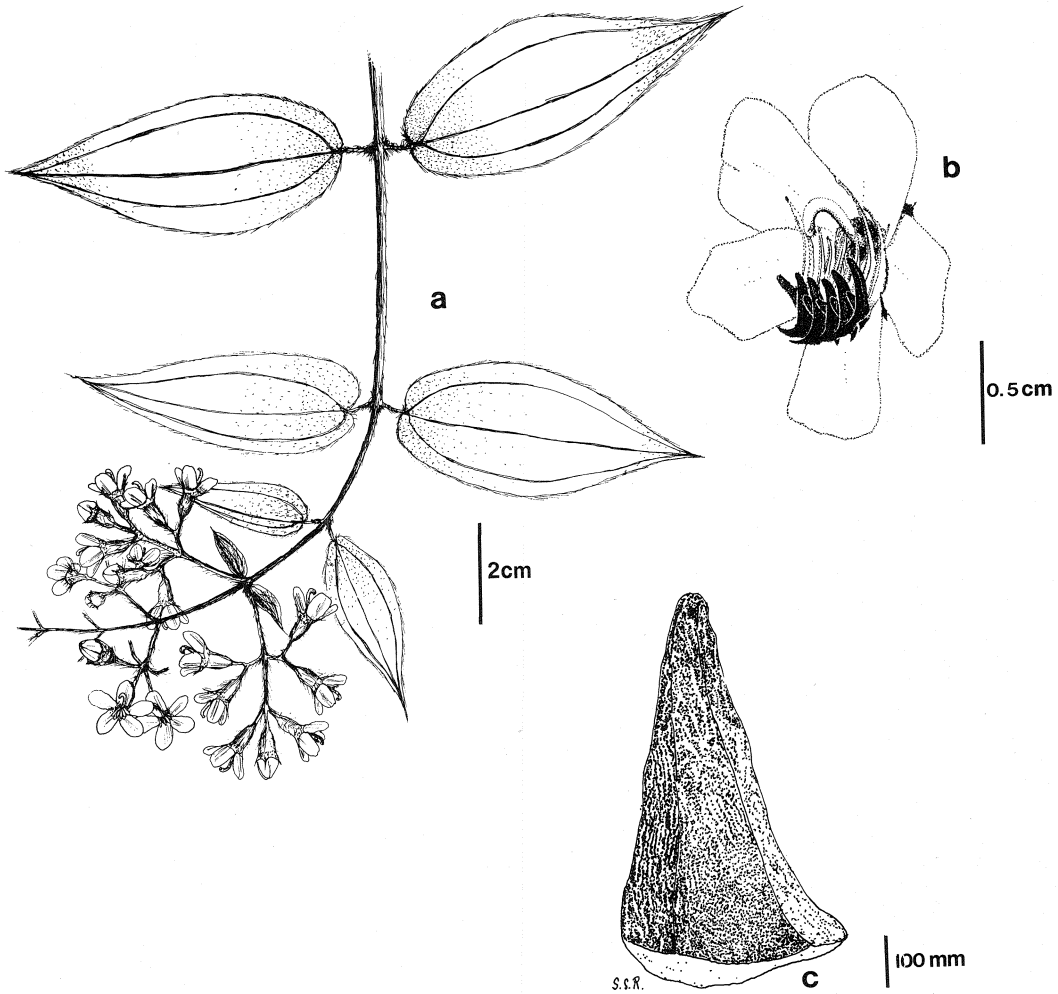

FIGURE 1. a, b, *Adelobotrys rachidotricha*: a, pendant inflorescence; b, flower, yellow connective appendices shown in black. c, *A. panamensis*: seed (drawn from scanning electron micrograph).

Macrocentrum, Bertolonia, Monolena, and *Triolena* (*Diolena*) that occasionally grow in moss mats on buttresses, stumps, and logs were also excluded except when on the majority of labels such species were described as "epiphytic."

RESULTS

Taxonomic and Geographic Distribution

Currently 2,586 species in 106 genera of New World Melastomataceae are represented by at least one specimen at US. Of these, 227 species in 12 genera are epiphytic (TABLE 1), or almost 10 percent of the total.

Among the genera a diversity of epiphytic types exists. Within a single genus all epiphytic species have the same growth habit except for *Blakea* and *Topobea*. Species of *Adelobotrys* and *Graffenrieda* are woody lianas adhering to tree trunks by adventitious roots. *Phainantha* species are climbing vines, appressed to tree trunks. Epiphytic *Monolena* and *Triolena* species are herbs most often growing on tree bases two to three meters above the ground. Besides the vining species of *Miconia* included in TABLE 1 there are a few species occasionally described as "epiphytic" but which according to the majority of collectors' notes are shrubs. This is the case for *M. intricata* Triana, *M. hymenanthera* Triana, and *M. phaeochaeta* Wurdack. *Miconia arboricola* Almeda (1984) was described as "pendent woody vine or a hemiepiphyte adhering to bark of host tree by adventitious roots." *Miconia ru-*

TABLE 1. Epiphytic herb, shrub, vine, and liana species of New World Melastomataceae.

Taxa	Phytogeographical region*	Altitudinal distribution**
1) Species with capsules		
Adelobotrys DC.		
acreana Wurdack	5	low
adscendens (Sw.) Tr.	1, 2, 3, 4, 5	low-mid
boissieriana Cogn.	3, 5	low-mid
ciliata (Naud.) Tr.	4	low
fuscescens Tr.	3	low
intonsa (Gleason) Wurdack	5	low
jefensis Almeda	1	mid
klugii Wurdack	3, 5	low-mid
linearifolia L. Uribe	5	low
macrantha Gleason	5	low
macrophylla Pilger	5	low
marginata Brade	5	low
monticola Gleason	4	mid
permixta Wurdack	4	low
praetexta Pilger	5	low
rachidotricha Brade	5	low
rotundifolia Tr.	3, 5	low
scandens (Aubl.) DC.	3, 4, 5	low
spruceana Cogn.	5	low
subsessilis Gleason	5	low
tessmanii Mgf.	4, 5	low
Graffenrieda DC.		
anomala Tr.	3	low
patens Tr.	5	low
Monolena Tr.		
dressleri Warner ined.	1	low
guatemalensis Donn. Sm.	1	mid
multiflora Warner ined.	1	low-mid
panamensis Warner ined.	1	low-mid
primulaeflora Hook. f.	1, 3	low-mid
trichopoda Warner ined.	1	low-mid
Phainantha Gleason		
laxiflora (Tr.) Gleason	4	low-mid
maguirei Wurdack	4	low-mid
myrteoloides Wurdack	4	low-mid
steyermarkii Wurdack	4	low-mid
Triolena Naud.		
pileoides (Tr.) Wurdack	1	low-mid
spicata (Tr.) L. Wms.	3	low-mid
2) Species with berries		
Blakea		
(*acostae* Wurdack)***	3	mid
(*allotricha* L. Uribe)	3	low
(*andreana* Cogn.)	3	mid-high
anomala Donn. Sm.	1	mid-high
(*argentea* Gleason)	3	high
austin-smithii Standley	1	mid-high
bella Standley	1	low
bracteata Gleason	3	low-mid
(*brasiliensis* Cogn.)	5	low
brunnea Gleason	1	mid-high
calycosa Gleason	1	mid
(*calyptrata* Gleason)	3	mid-high
campii Wurdack	3	low-mid
caudata Tr.	3	low
chlorantha Almeda	1	mid
ciliata Mgf.	5	low
crassifolia Almeda	1	mid
(*crinita* Gleason)	1	mid

TABLE 1. Continued.

Taxa	Phytogeographical region*	Altitudinal distribution**
cuatrecasii Gleason	1, 3	low-mid-high
cuneata Standley	1	low-mid
elliptica (Gleason) Almeda	1	mid-high
eriocalyx Wurdack	3	mid
fasciculata Gleason	3	mid
(*fissicalyx* L. Uribe)	3	high
florida L. Williams	1	low-mid
(*florifera* Gleason)	3	mid
foliacea Gleason	1	low-mid
formicaria Wurdack	3	mid
glabrescens Bentham	3	low-mid
glandulosa Gleason	3	mid-high
gracilis Hemsley	1	mid
granatensis Naud.	3	mid-high
grandiflora Hemsley	1	mid-high
grisebachii Cogn.	4	mid
guatemalensis Donn. Sm.	1	mid
harlingii Wurdack	3	mid
hirsuta Berg ex Tr.	5	low
hirsutissima (Macbr.) Wurdack	3	low-mid
hispida Mgf.	3	mid
holtonii Hochr.	3	high
hydraeformis Wurdack	3	low
incompta Mgf.	3	mid-high
involvens Mgf.	3	low-mid
(*jativae* Wurdack)	3	low
(*lanuginosa* Wurdack)	3	mid
latifolia (R. & P.) D. Don	3	mid-high
(*lindeniana* (Naud.) Tr.)	4	mid-high
litoralis L. Wms.	1	low-mid
longibracteata Cogn.	4	mid-high
(*longipes* L. Uribe)	3	high
madisonii Wurdack	3	mid
megaphylla Wurdack	3	low
mexiae Gleason	5	low-mid
micrantha Almeda	1	mid
(*monticola* Johnston)	4	mid
nodosa Wurdack	3	low
oldemanii Wurdack	3	high
orientalis Gleason	3	mid-high
ovalis (R. & P.) D. Don	5	low
paleacea Gleason	3	low
paludosa Gleason	3	mid-high
parvifolia Gleason	1	mid
pauciflora Gleason	1	mid
penduliflora Almeda	1	high
pichinchensis Wurdack	3	mid
pilosa Gleason	3	low
pittierii Cogn.	1	mid
platypoda Gleason	3	mid
podagrica Tr.	3	low-mid
(*polyantha* Wurdack)	3	mid
portentosa Wurdack	3, 5	low-mid
princeps (Linden) Cogn.	3	high
pulverulenta Vahl	2	low-mid
(*punctulata* (Tr.) Wurdack)	3	mid
purpusii Brandegee	1	high
pyxidanthus Tr.	3	mid-high
quadrangularis Tr.	3	high
quadriflora Gleason	3	mid-high
repens (R. & P.) D. Don	3	mid-high
rosea (R. & P.) D. Don	3, 5	low-mid

TABLE 1. Continued.

Taxa	Phytogeographical region*	Altitudinal distribution**
(*rostrata* Berg ex Tr.)	3	mid
sawadae Macbr.	3	mid
schlimii Tr.	3	mid-high
schultzei Mgf.	3	mid-high
spruceana Cogn.	3	mid-high
squamigera L. Uribe	3	mid
standleyana Macbr.	3	mid
stellaris Gleason	3	low
(*stipulacea* Wurdack)	3	mid
subconnata Berg	3	low-mid
subpeltata Cogn.	1	mid
(*subvaginata* Wurdack)	3	mid
truncata Gleason	3	low
tuberculata Donn. Sm.	1	mid
villosa Cogn.	3	mid-high
wilburiana Almeda	1	mid
woodsonii Gleason	1	high
trinervia L.	2	mid
Clidemia D. Don		
ablusa Wurdack	3	mid
blepharodes DC.	6	low
buntingii Wurdack	4	mid
epibaterium DC.	3, 4, 5	low
epiphytica (Tr.) Cogn.	3, 4	low-mid
fausta Wurdack	3	low-mid
longifolia Gleason	5	low
parasitica Tr.	6	low
radicans Cogn.	3	low
sandwithii Wurdack	4	low
serpens (Tr.) Cogn.	3	low
Leandra Raddi		
candelabrum (Macbr.) Wurdack	5	low
procumbens Ule	4	low
steyermarkii Wurdack	5	low
subulata Gleason	1	mid
Miconia R. & P.		
arboricola Almeda	1	low-mid
ascendens Wurdack	3	high
concinna Almeda	1	mid-high
confertiflora Almeda	1	mid-high
dioica Wurdack	4	high
grandidentata Almeda	1	mid
jorgensenii Wurdack	3	high
loreyoides Tr.	3	mid
protuberans Wurdack	3	mid
sarmentosa Cogn.	4	low
urticoides Tr.	1, 3	mid
Ossaea DC.		
araneifera Mgf.	5	low
rubescens (Tr.) Cogn.	3	mid
Pleiochiton Naudin		
ebracteatum Tr.	6	low
glaziovianum Cogn.	6	mid
longipetalum Brade	6	mid
magdalenense Brade	6	mid
micranthum Cogn.	6	low
parvifolium Cogn.	6	?
roseum Cogn.	6	low
Topobea Aublet		
(*acuminata* Wurdack)	3	mid
aeruginosa (Standley) L. Wms.	1	mid
(*albertiae* Wurdack)	3	mid

TABLE 1. Continued.

Taxa	Phytogeographical region*	Altitudinal distribution**
allenii Standley & L. Wms.	1	low
alternifolia Gleason	3	low
anisophylla Tr.	3	mid
asplundii Wurdack	3	low
brachyura (Gleason) Wurdack	3	mid-high
brenesii Standley	1	mid
brevibractea Gleason	3	mid
(*calcarata* L. Uribe)	3	low
calophylla Almeda	1	mid
calycularis Naud.	1	mid
castanedae Wurdack	3	low
(*caudata* Wurdack)	3	mid
cordata Gleason	1	mid
cutucuensis Wurdack	3	mid
dodsonorum Wurdack	3	mid
durandiana Cogn.	1	low-mid
eplingii Wurdack	3	low
ferruginea Gleason	4	mid-high
floribunda Gleason	3	low-mid
glaberrima Tr.	3	low
glabrescens Tr.	3	low
gracilis Tr.	3	low-mid
(*insignis* Tr.)	3	mid
killipii Wurdack	3	low
laevigata (D. Don) Naud.	1	low
(*latifolia* Tr.)	3	mid
longiloba Wurdack	3	high
longipes Naud.	3	low-mid
(*macbrydei* Wurdack)	3	mid
maguirei Wurdack	3	mid
maurofernandeziana Cogn.	1	low-mid
membranacea Wurdack	1, 3	low-mid
(*micrantha* Pittier)	1	high
(*modica* Wurdack)	3	mid
mortoniana Wurdack	3	mid
multiflora (D. Don) Tr.	1, 3	mid-high
parasitica Aubl.	4, 5	low-mid
pittieri Cogn.	1, 3	mid
pluvialis Standley	1, 3	mid
praecox Gleason	1	low-mid
pubescens Gleason	3	low-mid
reducta Gleason	3	low
regeliana Cogn.	1	low
setosa Tr.	3	mid
stephanochaeta Naud.	1, 3	mid
(*steyermarkii* Wurdack)	4	mid
subbarbata Wurdack	3	mid-high
subscaberula Tr.	3	low-mid
subsessiliflora Wurdack	3	low
(*superba* Naud.)	3	low-mid
tetroici Wurdack	3	mid
(*toachiensis* Wurdack)	3	mid
(*trianaei* Cogn.)	3	low-mid
urophylla Standley	1	low
(*verrucosa* Wurdack)	3	high
watsonii Cogn.	1, 3	low

* Phytogeographical regions are: 1—Central America, 2—West Indies, 3—Andes including Pacific coastal Colombia and Ecuador (Chocó region), 4—Guyana, 5—Amazon river basin, 6—Brazilian coastal mountain range.

** Low: sea level–500 m; mid: 500–2,000 m; high: over 2,000 m.

*** *Blakea* and *Topobea* species that are poorly known (often only from a single specimen) and/or for which life form observations have not been made, but are most likely epiphytic, are included in parentheses.

fostellulata Pittier is described as a "shrub" on two collections (CAS, Almeda, pers. comm.) and as a "vine" on one US collection. *Clidemia* species included in TABLE 1 are woody lianas. *Pleiochiton* is poorly represented at US and observations on its habit are scarce. *Leandra subulata* may be an accidental epiphyte. *Ossaea* species are woody lianas; *O. resinosa* Gleason, described as a climber, is probably a synonym of *Graffenrieda anomala* Triana (Wurdack, pers. comm.). In *Blakea,* variability in life form is the greatest of any melastome genus; some species are able to grow as climbers, shrubs both terrestrial and epiphytic, treelets, and trees reaching the respectable size of 15 to 25 m. Schimper (1888: 52) describes a treelet of *Blakea* growing near another tree that sent out roots from its stem which were both partly positively geotropic growing to the ground quickly and partly without such geotropism growing and building a dense root web around the other tree. *Blakea schultzei* has been observed as a strangler. Because of the well-documented variability of habit in *Blakea* and the closely related *Topobea,* species that are poorly represented in the herbarium (most often by one specimen only) have been included in TABLE 1 (in parentheses) as probably capable of growing epiphytically, too.

The Andean mid-elevation forests and the Colombian Chocó region are by far the richest areas in epiphytic Melastomataceae with 125 species (TABLE 1). Central America with 61 species is next in diversity. The two regions hold ten species in common. The Amazon basin and Guyana, with 29 and 24 species, respectively, have fewer epiphytic melastome species, and share only three species. Only five percent of the 235 central Amazonian melastome species are epiphytic and four of 52 species (eight percent) found in 36 ha of undisturbed forest north of Manaus were growing as epiphytes (Renner, unpubl.).

Of the total 227 epiphytic neotropical melastome species, 53 percent (120 species) grow at elevations between 500 and 3,000 m; a further 19 percent (42 species) occur from sea level to 2,000 m altitude, and one species, *Blakea cuatrecasii,* as presently understood ranges from sea level to above 2,000 m; 28 percent (63 species) are found in the lowlands (below 500 m) (TABLE 1). This relative abundance in mid-elevation forests may reflect the generally higher incidence of epiphytism in cloud forests, where the epiphyte water supply depends on water condensation from mist.

The taxonomic composition of the epiphytic melastome floras of the six phytogeographical regions differs. Epiphytes belonging to *Adelobotrys* and *Graffenrieda* occur mostly in the Amazonian lowlands, whereas *Blakea, Topobea,* and *Clidemia* epiphytes are concentrated in the Andes, the Chocó, and Central America. The vast majority of epiphytic melastome species have restricted or very restricted distributions (the latter perhaps partly an artefact of the particular difficulties in collecting epiphytes). Only 18 species occur in more than one phytogeographical province, and only three are found in more than two. The few widespread species are *Adelobotrys adscendens* (which covers five of the six regions), *Clidemia epibaterium, Clidemia epiphytica,* and several species of *Adelobotrys, Blakea,* and *Topobea.*

Fruit Types

The Melastomataceae possess two fruit types: berries and capsules. Of the 227 neotropical epiphytic melastome species 85 percent (193 species) produce fruits that are berries; only 15 percent (33 species) have capsules. Melastome seeds cannot be classified as "dust-like," and neither *Adelobotrys* (FIGURE 1c) nor *Phainantha* has winged seeds (cf. Madison, 1977). Despite the fact that 60 percent of the New World melastomes possess berries, the high proportion of fleshy fruits in epiphytic species corroborates earlier findings that many epiphytes rely on birds for dispersal to suitable habitats (Schimper, 1888; Ridley, 1930; Richards, 1952; Gentry, 1983a, 1983b). These plants start out life on tree branches where their seeds germinate in the sticky excreta dropped by a bird. Berries of *Blakea* contain nearly a thousand smooth pyramidal seeds (Lumer, 1983) and the capsules of *Adelobotrys* lianas approximately a hundred (pers. obs.). Seeds of the latter genus are elongate-pyramidal and aerodynamically streamlined for plummeting downwards (FIGURE 1c). Whereas all truly epiphytic melastomes have berries, all epiphytic species with capsular fruits are climbers or may be considered to be "accidental" epiphytes confined to low sites such as the species of the genera *Triolena* and *Monolena.* The data thus suggest that seeds from the capsules are not carried far by air currents.

Floral Biology

Few observations exist on pollination mechanisms in epiphytic melastomes. Spruce (1908) satisfied himself that no pollen escaped from the anthers of *Blakea subconnata.* He did not observe bees visiting the flowers and assumed that the beetles eating the inner parts of the anthers must pollinate the flowers in the process. Several Amazonian lowland species belonging to the genera *Adelobotrys* and *Clidemia* are bee-pollinated. Pollen is harvested by female bees as food for larvae. Various bees have learned to use vibra-

tions of their strong (indirect) flight muscles to cause pollen grains to be shaken out of the tubular anther pores (Renner, 1984). For the body vibrations to be transmitted onto the anthers a close contact between insect and stamens is essential. Many melastome flowers provide a landing platform because the stamens are usually bunched into a compact group, and often bear appendices serving as a hold for the bees' legs (FIGURE 1b). As the bees position themselves on the stamens, they contact the stigmatic surface and potentially pollinate the flower. *Adelobotrys rachidotricha,* which has a strongly zygomorphic androecium (FIGURE 1b), was found to be pollinated by halictid bees (*Pseudaugochloropsis* sp.). This species is self-compatible, but as in most melastomes the floral morphology precludes automatic selfing. *Monolena trichopoda* is possibly capable of selfing because late in anthesis the stamens fold over bringing the anther pore in contact with the stigma; the thecae are then effectively stuck to the stigmatic exudate (Warner, 1981). *Clidemia epibaterium* is capable of apomictic seed formation (Renner, 1984).

Whereas lowland Melastomataceae appear to rely exclusively on pollen as a reward for the bee pollinators, some melastomes of higher elevations provide nectar as a reward. Among the approximately 50 species of neotropical Melastomataceae known to produce nectar are four epiphytes, *Blakea austin-smithii, B. chlorantha, B. purpusii,* and *B. penduliflora* (Lumer, 1980; Almeda, pers. comm.). *Blakea chlorantha* is pollinated during the night by several species of rodents, while during the day it is visited by bumble bees and hummingbirds. Vertebrates that visit nectar-producing melastomes do not vibrate the stamens; in these species nectar production is associated with a set of morphological and physiological characters allowing pollination by visitors other than bees. The six epiphytic species of *Blakea* and *Topobea* studied by Lumer (1983, pers. comm.) are self-compatible.

CONCLUSIONS

Neotropical epiphytic Melastomataceae occur mostly in mid-elevation forests of the Andes and Central America. They are mostly bird-dispersed and bee-pollinated. The switch to nectar production allows some epiphytic species to use a different set of pollinators which may be advantageous at the higher altitudes where these species occur (Cruden, 1972; Heinrich & Raven, 1972). All seven epiphytic species (belonging to three genera) tested thus far are self-compatible.

The Melastomataceae, although lacking specific characteristics for epiphytism, do possess some features, such as animal-pollination and fleshy fruits, that have allowed them to evolve the epiphytic habit repeatedly. They may be a good example of Schimper's notion (1888: 118) of opportunistic epiphytism.

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