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EUGLOSSINE POLLINATION OF *SPATHIPHYLLUM* (ARACEAE)

Norris H. Williams[1] *and Robert L. Dressler*[2]

The genus *Spathiphyllum* Schott (Monsteroideae: Spathiphylleae) is found in the American tropics from Mexico south through Central America to Peru and Brazil. Bunting (1960) listed 35 species in the American tropics (with one species then thought to be endemic on Cocos Island) and one species in the western Pacific area. Nicolson (1968) discussed the species from the Phillipines and described two additional species in the genus from the western Pacific islands. Some mention has been made in the past of the attraction of male euglossine bees to *Spathiphyllum* (Dodson 1966; Dodson *et al.*, 1969; Dressler, 1967, 1968; Vogel, 1963, 1966; Zucchi *et al.*, 1969). The neotropical members of the genus seem to be pollinated mainly by male euglossine bees, although little mention has been made of species-specific attraction in the genus. The neotropical species of the genus have floral odors very similar to those found in certain groups of orchids which are also pollinated by male euglossines, such as *Catasetum* L. C. Rich., *Gongora* Ruiz & Pav., *Stanhopea* Frost ex Hook., and other members of the subtribe Catasetinae Pfitz. and the tribe Gongoreae Pfitz. (also part or all of several other subtribes). In addition to the neotropical species of *Spathiphyllum*, certain species of *Anthurium* Schott and *Xanthosoma* Schott are also pollinated by male euglossine bees.

For the past several years we have been collecting data on pollination in this group, and we present our findings here along with a review of the known observations on pollination in the genus.

MATERIALS AND METHODS

Field observations have been made in a number of localities in various parts of the American tropics. The majority of our observations have been made in central Panama. Observations were made for varying periods of time, but all observations were made during the morning hours of the day. It was known from past work on male euglossine bees associated with orchid flowers that the bees are more active from dawn to noon, rather than later in the day. All bees which visited a given species of *Spathiphyllum* were collected for identification. Voucher specimens of the bees are in the collection at the Smithsonian Tropical Research Institute (STRI) and duplicates have been distributed to various other museums when sufficient specimens existed.

Voucher specimens of the plants were collected and deposited at either the herbarium at the University of Panama, the Missouri Botanical Garden, or at the U. S. National Herbarium in Washington, D.C. Whenever possible, living specimens were transported to the garden area at STRI to be maintained in cultivation. Living plants were also established whenever possible at the greenhouses of the University of Miami, Coral Gables, Florida, at Fairchild Tropical Garden, Miami, Florida, at the Marie Selby Botanical Gardens, Sarasota, Florida, and at Florida State University, Tallahassee, Florida. It has not been possible to date to obtain gas chromatographic analyses of the floral fragrances of the species of *Spathiphyllum*

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as we have done for a number of species of orchids which are also visited and pollinated by male euglossine bees (Hills, Williams, and Dodson, 1968, 1972), but the floral fragrances of *Spathiphyllum* are very similar to the floral fragrances found in the orchids pollinated by male euglossines.

RESULTS

Our observations on visitors to *Spathiphyllum* are listed in Table 1. Table 2 lists observations on the genus *Anthurium*, and Table 3 lists reports in the literature of male euglossine visits to members of the Araceae.

The male bees visit and behave on the spadices of *Spathiphyllum* in the same manner in which they behave on the flowers of various species of orchids which they visit. The bees land, brush on the surface of the spadix with the front tarsal brushes, launch into the air and transfer the substance they have collected to their inflated hind tibiae, and return to the spadix. For a more complete discussion of the visits of male euglossines to orchid flowers, the collection of floral fragrance components, the transfer reaction, the role of floral fragrance components in attracting male euglossines to orchid flowers and various other flowers, and the identification of floral fragrance components, see Dodson, 1962, 1970, 1975; Dodson *et al.*, 1969; Dressler, 1967, 1968; Evoy and Jones, 1971; Hills, Williams, and Dodson, 1968, 1972; Vogel, 1963, 1966; Williams and Dodson, 1972.

It can be seen from Tables 1-3 that, although there is some overlap in the species of euglossini which visit the species of *Spathiphyllum*, for the most part each species for which we have pollination information attracts a specific pollinator or group of pollinators. The number of species of pollinators in common is shown in Table 4. Of the 26 species of euglossines which visit the species of *Spathiphyllum*, only 3 euglossines visit more than one species of *Spathiphyllum*. *Eulaema cingulata* visits the large form of *S. cannaefolium* and *S. laeve*. *Euglossa tridentata* visits the small form of *S. cannaefolium* and *S. quindiuense*. *Euglossa variabilis* visits the large and small forms of *S. cannaefolium*, *S. kochii*, and *S. quindiuense*. All those species of *Spathiphyllum* which share pollinators are either allopatric or are in different sections of the genus.

TABLE 1: POLLINATORS OF *Spathiphyllum*

PLANT SPECIES	LOCALITY	OBSERVER	POLLINATOR
S. cannaefolium (Dryand.) Schott — large form — cultivated form (native of Trinidad?)	Rio de Janeiro	Dressler	*Eulaema cingulata* (Fabricius)
	Belem, Para	Dressler	*Eulaema cingulata* *Eulaema nigrita* Lepeletier *Eufriesea pulchra* (Smith) *Exaerete smaragdina* (Guerin)
	Fusagasuga, Col.	Dodson	*Eulaema cingulata*
	Caracas, Ven.	Dressler	*Exaerete smaragdina* *Euglossa variabilis* Friese

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PLANT SPECIES

S. cannaefolium (Dryand
Schott — small form

S. humboldtii Schott
S. kalbreyeri Bunt.

S. kochii Engl. & Krause
S. laeve Engl.

S. phryniifolium Schott

S. quindiuense Engl.

S. schomburgkii Schott

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PLANT SPECIES	LOCALITY	OBSERVER	POLLINATOR
S. cannaefolium (Dryand.) Schott — small form	Rio Chicanan, Ven.	Dressler	*Euglossa analis* Westwood *Euglossa* (Dressler 572) *Euglossa* (Dressler 571) *Euplusia purpurata* (Mocsary)
	Sierra de la Macarena	Vogel	*Euglossa analis* *Euglossa viridis* (Perty) *Euglossa* sp.
	Cult. Caracas	Dressler	*Euglossa cybelia* Moure *Euglossa cordata* (L.) *Euglossa tridentata* Moure *Euglossa variabilis*
S. humboldtii Schott	Belem, Para	Dias*	*Euglossa* spp.
S. kalbreyeri Bunt.	Rio Pedro Miguel, Panama	Dressler	*Trigona* sp.
S. kochii Engl. & Krause	Cult. Caracas	Dressler	*Euglossa variabilis*
S. laeve Engl.	Cerro Campana, Panama	Williams & Dressler	*Euglossa villosa* Moure *Eulaema cingulata* *Eulaema meriana* Olivier *Euplusia ornata* (Mocsary) *Euplusia venusta* Moure
S. phryniifolium Schott	Cerro Campana, Panama	Dressler	*Euglossa deceptrix* Moure
	Cerro Jefe, Panama	Dressler & Williams	*Euglossa azureoviridis* Friese *Euglossa deceptrix* Moure *Euglossa hemichlora* Cockerell *Euglossa heterosticta* Moure
	Cerro Jefe, Panama	Dressler	*Euglossa deceptrix*
S. quindiuense Engl.	Rio Mendosa, C.Z.	Williams	*Euglossa crassipunctata* Moure *Euglossa cyanaspis* Moure *Euglossa tridentata* Moure
	Cult. Las Cumbres, Panama	Dressler	*Euglossa tridentata* *Euglossa variabilis*
S. schomburgkii Schott	Icabaru, Ven.	Dressler	*Euglossa mixta* Friese

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*Reported by Dressler, specimens in Dias collection.

TABLE 2: POLLINATORS OF *Anthurium**

PLANT SPECIES		LOCALITY	POLLINATOR
Anthurium crystallinum Linden & Andre	cult.	Canal Zone	*Euglossa tridentata* Moure
Anthurium hacumense Engler		Cerro Jefe. Summit Gardens, C.Z.	*Euglossa cyanura* Cockerell *Euglossa cyanura*
Anthurium magnificum Linden	cult.	Belem, Brazil	*Euglossa cordata* (L.) *Euglossa* sp. (Dressler 500)
Anthurium - Dressler 2949		El Valle	*Eulaema leucopyga* Friese
Anthurium - Dressler 2969		Cerro Campana	*Eulaema nigrita* Lepeletier
Anthurium - Dressler 4879		Rio Pequeni	*Euglossa gorgonensis* Cheesman
Anthurium - Correa & Dressler		Santa Rita	*Euglossa hansoni* Moure *Euglossa igniventris* Friese *Euglossa dressleri* Moure
Anthurium		Cerro Jefe	*Euglossa asarophora* Moure & Sakagami
Anthurium		Cerro Campana	*Euplusia venusta* Moure
Anthurium		Cerro Jefe	*Euplusia* RD 296
Anthurium		Santo Domingo, Ec.	*Eulaema bomboides* (Friese)
Anthurium	cult.	Canal Zone	*Euglossa tridentata* Moure *Euglossa variabilis* Friese
Anthurium	cult.	Summit Gardens	*Eufriesea pulchra* (Smith)
Anthurium	cult.	Summit Gardens	*Euglossa cyanura*
Anthurium	cult.	Las Concavas, C.R.	*Eulaema seabrai luteola* Moure
Anthurium	cult.	Medellin, Col.	*Eulaema polychroma* (Mocsary)
Anthurium	cult.	Medellin, Col.	*Euglossa variabilis*
Anthurium	cult.	Guayaquil, Ec.	*Eulaema polychroma* (Mocsary)
Anthurium	cult.	Rio de Janeiro, Br.	*Eulaema seabrai* Moure

*All locations in Panama unless indicated otherwise.

DISCUSSION

By attracting one or a few species of male euglossine bees, the floral fragrances of *Spathiphyllum* may serve as the isolating mechanism between closely related species in the genus. It has been shown elsewhere (Hills *et al.*, 1972) that the floral fragrances are one important isolating mechanism in the genus *Catasetum*, as well as in other genera of orchids which are pollinated by male euglossine bees. Not only is it possible for the floral fragrances to serve as the isolating mechanism between two or more closely related species of *Spathiphyllum*, but pollination by male euglossine bees may be a means by which the genus has proliferated by adapting to a number of the different species of euglossine bees which are present in the neotropics.

Spathiphyllum kalbreyeri Bunting is visited by bees of the genus *Trigona* (not a member of the euglossini) in central Panama; however, this population is possibly on the edge of the range of the species. It is possible that the necessary species of euglossine bee is absent from central Panama.

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'OLLINATOR
glossa tridentata Moure
glossa cyanura Cockerell
glossa cyanura
glossa cordata (L.)
glossa sp. (Dressler 500)
laema leucopyga Friese
laema nigrita Lepeletier
glossa gorgonensis Cheesman
glossa hansoni Moure
glossa igniventris Friese
glossa dressleri Moure
glossa asarophora Moure & Sakagami
plusia venusta Moure
plusia RD 296
laema bomboides (Friese)
glossa tridentata Moure
glossa variabilis Friese
friesea pulchra (Smith)
glossa cyanura
laema seabrai luteola Moure
laema polychroma (Mocsary)
glossa variabilis
laema polychroma (Mocsary)
laema seabrai Moure

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TABLE 3: OTHER REPORTS OF EUGLOSSINE POLLINATION IN THE ARACEAE

PLANT SPECIES	BEE	SOURCE
Anthurium andraeanum Linden	*Eulaema basicincta* Moure = *E. peruviana* (Friese) *Eulaema bennetti* Moure *Eulaema terminata* (Smith)	Bennett MS, cited by Zucchi *et al.*, 1969
Anthurium regale Linden	*Euglossa cordata* (L.) *Euglossa analis* Westwood	Ducke, cited by Zucchi *et al.*, 1969
Anthurium spp. (5)	*Eulaema meriana* (Olivier)	Dodson, 1966
Anthurium spp.	*Eulaema polychroma* (Mocsary)	Dodson, 1966
Anthurium sp.	*Eulaema seabrai* Moure	Dodson, 1966
Anthurium sp.	*Eufriesea pulchra* (Smith)	Dressler, 1968
Anthurium sp.	*Euglossa cordata* *Euglossa analis*	Ducke, cited by Zucchi *et al.*, 1969
Anthurium sp.	*Euglossa ignita* Smith *Eulaema meriana* *Eulaema cingulata* Fabricius	Ducke, cited by Zucchi *et al.*, 1969
Spathiphyllum sp.	*Eulaema cingulata*	Dodson, 1966
Spathiphyllum sp.	*Euglossa analis*	Myers, cited by Zucchi *et al.*, 1969
Xanthosoma cf. *violaceum* Schott	*Eulaema cingulata*	Dodson, 1966

TABLE 4: COMMON POLLINATORS IN THE GENUS *Spathiphyllum*

Spathiphyllum SPECIES	NUMBER OF SPECIES OF POLLINATORS	SPECIES IN COMMON* WITH OTHER SPECIES
S. cannaefolium large	6	1(1), 1(1), 1(3)
S. cannaefolium small	10	1(1), 1(3)
S. humboldtii	several	0
S. kochii	1	1(3)
S. laeve	5	1(1)
S. phryniifolium	4	0
S. quindiuense	4	1(1), 1(3)
S. schomburgkii	1	0

*Numbers out of parentheses are the numbers of species of bees which are shared by the number of species in parentheses, i.e., one species *(E. tridentata)* (out of four) that visits *quindiuense* also visits one other species, and another *(E. variabilis)* species visits three other species.
Table 4 is abstracted from Table 1.

On occasion additional species of *Spathiphyllum* are visited by trigonas collecting pollen.

The knowledge that the new world members of the genus *Spathiphyllum* are pollinated almost exclusively by male euglossines (which are limited to the neotropics) provides a basis for some speculation on speciation in the genus. Of the two members of the tribe Spathiphylleae, *Holochlamys* Engl., which is limited to Papua, is thought to be more advanced than *Spathiphyllum* (Bunting, 1960). Nicolson (1960) has shown that *Holochlamys* and *Spathiphyllum* form a natural group in the Monsteriodeae Engl., based on the structure of their trichosclereids. The hypothetical primitive and advanced characters of the Spathiphylleae are listed in Table 5. Nicolson (1968) suggested that the presence of the closest relative of *Spathiphyllum* in the old world and the presence of two additional species of *Spathiphyllum* in the Papuan area would suggest an old world origin of the Spathiphylleae. The old world members of *Spathiphyllum* are all members of the section *Massowia* (K. Koch) Engl. which Bunting (1960) considered the oldest line in *Spathiphyllum*. The peculiar distribution of the members of this section was apparently the main reason for Bunting's suggestion that they are the oldest line in the genus; however, the members of the section *Massowia* possess fused tepals, which usually would be considered an advanced condition, while the other members of the genus have the tepals free at least at the apex. As Nicolson (1968) has said, "This implies the unusual hypothesis that fused tepals (found in *Holochlamys* and *Spathiphyllum* sect. *Massowia*) came before free tepals".

A consideration of the pollinators along with a reconsideration of the floral characters and the distribution offers a different interpretation of the evolution of the genus. The primitive type of *Spathiphyllum* would have axile placentation with free perianth segments. The presence of a number of species of euglossine bees in the neotropics would provide a means by which a number of species could evolve by adapting to different species of bees as pollinators. Slight changes in the floral fragrance components would provide a means of attracting different species of male euglossines as pollinators, which could lead to isolation from the parental population (see Dodson *et al.*, 1969, for similar ideas with respect to the Orchidaceae). With enough time the isolation by selective attraction of pollinators could lead to the appearance of different characters and various modifications which are now evident in the genus. The most primitive members of the genus would have had free perianth segments, with those members of the genus with fused perianth segments arising later. This would seem to be more in line with the general trends one finds in flowering plants in general, rather than having to postulate that fused tepals came before free tepals. The placentation of *Holochlamys* is of an advanced type, with the ovules attached to the basal pad of placental tissue rather than to an axile placenta. Since *Holochlamys* with its fused tepals is considered more advanced than *Spathiphyllum* (Bunting, 1960), it seems logical to derive it from a *Spathiphyllum* of an advanced type, rather than trying to derive the members of *Spathiphyllum* with free tepals from an ancestor with fused tepals. The lack of very much speciation in the western Pacific region in the genus *Spathiphyllum*, as evidenced by only three species in the genus in that area, is probably the result of a lack of the appropriate pollinators, in this case male euglossine bees which are restricted in distribution to the neotropical regions. With an absence of euglossine bees as pollinators there would be much less chance for the members of the genus there to speciate. Although we have no data on pollination on the old world members of *Spathiphyllum*, two possibilities come to mind: 1) the old world species of *Spathiphyllum* have adapted to some other type of insect pollination, or 2) the genus is autogamous in the area of the western Pacific. Isolated populations are known to revert to autogamy in the absence of pollinators (Stebbins, 1950; van der Pijl and Dodson, 1966), but we feel that a more plausible explanation is that the old world members of *Spathiphyllum* are probably pollinated by randomly searching insects collecting pollen, just as occurs in *S. kalbreyeri* in central Panama.

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TABLE 5: PRIMITI

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We feel that the history of the group might be explained in either of the following ways: *Spathiphyllum* arose in the neotropics and underwent speciation in response to the numerous available pollinators present in the male euglossine bees. At some stage during the evolution of the genus one or more members of the section *Massowia* were the subject of long distance dispersal and reached the old world tropics. Speciation did not occur rapidly because of the lack of pollinators, but three species did evolve. Not only did three species of the section *Massowia* of *Spathiphyllum* evolve in the old world tropics, but the genus *Holochlamys* evolved from the original immigrant(s) as well. Fused tepals would have already been present in the group, having evolved in the neotropical group of species. Further speciation has been impeded by the lack of pollinators which has also caused a lack of widespread populations of the group in the old world tropics. An alternative explanation would be to have *Holochlamys* and *Spathiphyllum* originating in the old world and migrating to the new world where they underwent rapid speciation in response to the available euglossine pollinators. This rapid adaptation to the euglossine pollinators would explain the numerous species of *Spathiphyllum* in the neotropics, but still would leave unanswered the question of the fused tepals being the primitive condition of the genus. We feel that a new world origin of the Spathiphylleae obviates this question of fused tepals. We would also suggest that our explanation accounts for the presence of the most advanced genus in the tribe in the old world. The lack of a fossil record, however, makes it difficult to choose between these two hypotheses. We feel that additional study might indicate that the section *Massowia* is not the most primitive or oldest group in the genus, nor even a natural subgroup of the genus.

Work in progress on floral fragrances and anatomy will be reported later.

TABLE 5: PRIMITIVE AND ADVANCED CHARACTERS IN Spathiphylleae*

PRIMITIVE	ADVANCED
perianth free	perianth fused
perianth 4-6-sided (if fused)	perianth 4-sided
ovary 2-4-locular	ovary unilocular
axile placentation	basal placentation
spathe persistent	spathe marcescent

*Adapted from Bunting (1960) and Nicolson (1968).

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STUDIES IN A
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Missouri, St. Louis, Mo.