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Pollinators and Visitors of Aroid Inflorescences

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ABSTRACT

Data on aroid pollinators was first summarized by Grayum (1984) who documented 35 genera and about 90 species. A second summary was published in 1997 in *The Genera of Araceae* (Mayo *et al.,* 1997) with 38 genera and less than 100 species listed including data from Grayum (1986, 1990). This paper brings the reference list up to date since 1997, documenting the pollinators of 49 genera and about 125 species. These numbers are still very low in comparison with the diversity of the Araceae family which contains 105 genera and about 3,300 species. Some questions on aroid pollination are developed in the discussion.

KEY WORDS

Araceae, Coleoptera, Diptera, floral morphology, Hymenoptera, pollination.

INTRODUCTION

Data on aroid pollinators was first summarised by Grayum (1984) who documented 35 genera and about 90 species. A second summary was published in 1997 in *The Genera of Araceae* (Mayo *et al.,* 1997) with 38 genera and less than 100 species listed including additional data from Grayum (1986, 1990). In 13 years, the pollinators (and sometimes the pollination biology) of only three new genera and about 10 species were documented. In this paper, I summarise the data on Araceae pollinators by completing the references since 1997 and citing several omitted references earlier than 1997. The purpose of this work is not to give an exhaustive review of this subject, as Thomas Croat (2000) did in his history and current status of systematic research with Araceae, but to give, in the first place, a statement of the subject and to develop some remarks on aroid pollination.

RESULTS

Summarizing data from Grayum (1984, 1990) and Mayo *et al.* (1997), and including omitted and new publications, the pollinators of 49 genera and about 125 species are documented in Table 1. These numbers are still very low in comparison with the diversity of the Araceae family which contains 105 genera and about 3,300 species (Mayo *et al.,* 1997). Thus, pollinators are cited for only 47% of the genera.

The references not previously published document pollinators from 25 known genera and from 8 new genera namely: *Aglaonema, Biarum, Eminium, Furtadoa, Pinellia, Rhaphidophora, Sauromatum* and *Theriophonum*.

It is important to note that the list given in Table 1 does not distinguish between pollinators and visitors. Although aroid inflorescences can be visited by several types of insects, only a few—and sometimes only one—are the real pollinators for each species (Bogner, 1981; Shaw & Cantrell, 1983; Valerio, 1984; Pellmyr & Patt, 1986; Young, 1986; Patt *et al.,* 1995). Second, when there are several species of insects, efficiency in achieving pollination can differ between pollinators, some species carrying few or no pollen grains and acting as "simple" visitors (Young, 1988a).

Table 1. Adapted from Mayo *et al.* (1997), references cited after Grayum (1984, 1986, 1990) with new and update references on aroid pollinators/visitors.

Subfamily/tribe	Genera	Bees	Beetles	Flies	Others	References
Orontioideae	*Lysichiton*		Staphylinidae	Anthomyiidae Lauxaniidae Various flies		Hesse, 1980 Pellmyr & Patt, 1986 Willson & Hennon, 1997 Tanaka, 1998
Orontioideae	*Symplocarpus*	"hive bees"	Staphylinidae	Drosophilidae Psychodidae Chloropidae Ceratopogonidae Chironomidae Simuliidae Cecidomyiidae Muscidae	Wind (self-pollination) Various invertebrates	Trelease, 1879 Moodie, 1976 Grimaldi & Jaenike, 1983 Camazine & Niklas, 1984 Uemera *et al.,* 1993
Pothoideae/ Anthurieae	*Anthurium*	Euglossine	Curculionidae Staphylinidae	Cecidomyiidae Drosophilidae	Self-pollination (wind?) Hummingbird	William & Dressler, 1976 Madison, 1979 Croat, 1980 Valerio & Villalobos, 1980 Beath, 1998 Kraemer & Schmitt, 1999 Schwerdtfeger *et al.*, 2002
Monsteroideae/ Monstereae	*Monstera*	Trigone	Scarabaeidae			Madison, 1977 Ramirez & Gomez, 1978 Ramirez, 1980 Grayum, unpubl. data
Monsteroidae/ Monstereae	*Rhaphidophora*		Scarabaeidae			Beath, 1993
Monsteroideae/ Monstereae	*Rhodospatha*		"beetles"			Schatz & Grayum, unpubl. data

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Table 1. Continued.

Subfamily/tribe	Genera	Bees	Beetles	Flies	Others	References
Monsteroideae/ Spathiphylleae	*Spathiphyllum*	Euglossine Trigone Halictidae	Chrysomelidae	Drosophilidae Tephritidae		William & Dressler, 1976 Montalvo & Ackerman, 1986 Lewis *et al.,* 1988 Vogel, 1990 Chuah *et al.,* 1996 Beath, 1998
Lasioideae	*Cyrtosperma*		Nitidulidae			Knecht, 1983
Lasioideae	*Dracontium*			"myiophilous"		Grayum, pers. observ.
Lasioideae	*Urospatha*		Nitidulidae			J. Boos, pers. observ.
Calloideae	*Calla*			"small flies"		Krause, 1908 Knuth, 1909
Aroideae/ Dieffenbachieae	*Dieffenbachia*		Scarabaeidae			Madison, 1979 Bawa & Beach, 1981 Valerio, 1984 Young, 1986, 1988a, 1988 b, 1990 Seres & Ramirez, 1995 Beath, 1998, 1999 Grayum, pers. observ.
Aroideae/ Philodendreae	*Philodendron*		Scarabaeidae			Hubbard, 1895 Schrottky, 1910 Madison, 1979 Gottsberger & Amaral, 1984 Ramirez, 1989 Gottsberger & Silberbauer-Gottsberger, 1991 Seres & Ramirez, 1995 Grayum, 1996 Croat, 1997

Table 1. Continued.

Subfamily/tribe	Genera	Bees	Beetles	Flies	Others	References
						Beath, 1998 Gibernau *et al.,* 1999, 2000 Gibernau & Barabé, 2002 Grayum, pers. observ.
Aroideae/ Homalomeneae	*Furtadoa*			Drosophilidae		Mori & Okada, 2001
Aroideae/ Homalomeneae	*Homalomena*		Scarabaeidae (neotropics) Chrysomelidae In Malaya	Drosophilidae (Asia)		Yafuso & Okada, 1990 Momose *et al.,* 1998 Sultana *et al.,* 2002 Grayum, pers. observ. Schatz, pers. observ. (Malaya)
Aroideae/ Montrichardieae	*Montrichardia*	"bees"	Scarabaeidae			Madison, 1979 Ramirez & Brito, 1992 Gibernau *et al.,* 2003 Grayum & Schatz, unpubl. data
Aroideae/ Anubieae	*Anubias*		Nitidulidae Scarabaeidae			Knecht, 1983
Aroideae/ Schismatoglottideae	*Aridarum*		Nitidulidae			J. Bogner, pers. observ.
Aroideae/ Schismatoglottideae	*Piptospatha*		Staphylinidae			J. Bogner, pers. observ.
Aroideae/ Schismatoglottideae	*Schismatoglottis*			Drosophilidae		J. Bogner, pers. observ.
Aroideae/ Caladieae	*Caladium*		Scarabaeidae			Madison, 1981 Beach, 1982 Pellmyr, 1985 Pellmyr, pers. comm.

Table 1. Continued.

Subfamily/tribe	Genera	Bees	Beetles	Flies	Others	References
Aroideae/ Caladieae	*Chlorospatha*		Staphylinidae			Madison, 1981
Aroideae/ Caladieae	*Syngonium*		Scarabaeidae			Madison, 1979
						Croat, 1981
						Beath, 1998
						Grayum, pers. observ.
Aroideae/ Caladieae	*Xanthosoma*	Euglossine	Scarabaeidae (Nitidulidae)	Drosophilidae		Schrottky, 1910
						Madison, 1979
						Valerio, 1988
						Tsacas & Chassagnard, 1992
						Seres & Ramirez, 1995
						Moron, 1997
						Beath, 1998
						Goldwasser, 2000
						Garcia-Robledo *et al.,* 2003, unpubl. data
						Grayum, pers. observ.
Aroideae/ Thomsonieae	*Amorphophallus*	Trigone	Asilidae	Calliphoridae		Knuth, 1909
			Cetoniidae	Platystomatidae		Backer, 1913
			Nitidulidae			van der Pijl, 1937
			Scarabaeidae			Bogner, 1976
			Silphidae			Mayo *et al.,* 1982
			Staphylinidae			Sivadasan & Sabu, 1989
			Hybosoridae			Beath, 1993, 1996, 1998
			Histeridae			Weryszko-Chmielewska & Stpiczynska, 1995
						Kite & Hetterscheid, 1997
						van der Ham *et al.,* 1998
						Kite *et al.,* 1998

Table 1. Continued.

Subfamily/tribe	Genera	Bees	Beetles	Flies	Others	References
Aroideae/ Aglaonemateae	*Aglaonema*			Drosophilidae		Yafuso & Okada, 1990 Sultana *et al.,* 2002
Aroideae/ Zantedeschieae	*Zantedeschia*		Scarabaeidae Scydmaenidae			Letty, 1973 Singh *et al.,* 1996
Aroideae/ Nephthytideae	*Anchomanes*	Trigone	Nitidulidae	Lonchaeidae		Knecht, 1983 Thompson & Rawlins, 1986 Beath, 1993
Aroideae/ Nephthytideae	*Nephthytis*		Nitidulidae	Drosophilidae		Knecht, 1983
Aroideae/ Nephthytideae	*Pseudohydros-me*		Scaphidiidae Staphylinidae	Choridae Sphaeroceridae		Bogner, 181
Aroideae/ Culcasieae	*Cercestis*		Nitidulidae	Drosophilidae		Knecht, 1983 Beath, 1993
Aroideae/ Culcasieae	*Culcasia*		Nitidulidae	Drosophilidae		Knecht, 1983 Beath, 1993, 1998
Aroideae/ Colocasieae	*Alocasia*		Nitidulidae Scarabaeidae Staphylinidae	Drosophilidae Anthomyiidae Neurochaetidae		van der Pijl, 1933 Carson & Okada, 1982 Honda-Yafuso, 1983 Shaw & Cantrell, 1983 Okada & Yafuso, 1989 Vogel, 1990 Yafuso & Okada, 1990 Yafuso, 1993, 1994, 1999 Miyake & Yafuso, 2003
Aroideae/ Colocasieae	*Colocasia*			Drosophilidae		Cleghorn, 1913 Carson & Okada, 1982 Honda-Yafuso, 1983 Yafuso & Okada, 1990

Table 1. Continued.

Subfamily/tribe	Genera	Bees	Beetles	Flies	Others	References
Aroideae/ Cryptocoryneae	*Cryptocoryne*			Centropogonidae Ephydridae Phoridae		Petch, 1928 McCann, 1943 Vogel, 1990
Aroideae/ Peltandreae	*Peltandra*			Chloropidae Syrphidae		Goldberg, 1941 Patt *et al.,* 1995
Aroideae/ Arisamateae	*Arisaema*			Sciaridae Mycetophilidae Dolichopodidae Phoridae Keroplatidae	Thrips	Barnes, 1934 Pijl van der, 1953 Vogel, 1978, 1990 Rust, 1980 Bierzychudek, 1981, 1982, 1984 Menzel & Martens, 1995 Vogel & Martens, 2000
Aroideae/ Arisamateae	*Pinellia*			"fungus gnat" Ceratopogonidae		Hubbard, 1895 Schmucker, 1925 Vogel in Jaeger, 1976 Vogel, 1990
Aroideae/ Arisareae	*Arisarum*			Mycetophilidae Sciaridae Psychodidae Chironomidae Drosophilidae		Knuth, 1909 Vogel, 1978 Koach & Galil, 1986 Herrera, 1988
Aroideae/ Ambrosineae	*Ambrosina*			"flies"	Mites?	Knuth, 1909 Killiam, 1929, 1933
Aroideae/ Pistieae	*Pistia*		"Curculionids"?			da Silva, 1981
Aroideae/ Areae	*Arum*			Psychodidae Centropogonidae Ceratopogonidae		Arcangeli, 1886a, 1886b[1] Gaye, 1885 Church, 1908

Table 1. Continued.

Subfamily/tribe	Genera	Bees	Beetles	Flies	Others	References
				Sphaeroceridae		Knuth, 1909
				Sciaridae		Schmucker, 1925
				Simuliidae		
						Knoll, 1926
						Knoll, 1930
						Tonnoir, 1940
						Grensted, 1947
						Sowter, 1949
						Kullenberg, 1953
						Prime, 1954, 1960
						Lamb, 1956
						Dormer, 1960
						Braverman & Koach, 1982
						Koach, 1985
						Papp & Rohacek, 1987
						Withers, 1988
						Rohacek *et al.,* 1990
						Lack & Diaz, 1991
						Drummond & Hammond, 1991, 1993
						Méndez & Obeso, 1992
						Boyce, 1993
						Kite *et al.,* 1998
						Jezek, 2002
						Diaz & Kite, 2002
						Albre *et al.,* 2003
						Drummond & Boorman, 2003
						Koach & Galil, unpubl. data
						Gibernau *et al.,* unpubl. data

Table 1. Continued.

Subfamily/tribe	Genera	Bees	Beetles	Flies	Others	References
Aroideae/ Areae	*Biarum*		Scarabaeidae Staphylinidae	Flies? Sepsidae Empididae Drosophilidae		Koach, 1985
Aroideae/ Areae	*Dracunculus*		Staphylinidae Dermestidae Histeridae Sylphidae	Calliphoridae Muscidae Sarcophagidae		Arcangeli, 1886b, 1886c[1] Delpino, 1890a, 1890b Knuth, 1909 Schmucker, 1930 Malvesin-Fabre, 1945 Boyce, 1986 Seymour & Schultze-Motel, 1999
Aroideae/ Areae	*Eminium*		Scarabaeidae Staphylinidae	Sphaeroceridae Sepsidae Ortidae Muscidae Ulidiidae Heleomyzidae Ephydridae		Koach, 1985 Pap & Rohacek, 1987
Aroideae/ Areae	*Helicodiceros*			Calliphoridae		Schnetzler, 1879 Stensmyr *et al.,* 2002 Seymour *et al.,* 2004 Gibernau *et al.,* unpubl. data
Aroideae/ Areae	*Sauromatum*		Scarabaeidae Bruchidae	Sepsidae Muscidae Otitidae Sarcophagidae Calliphoridae		Dakwale & Bhatnagar, 1982, 1985

Table 1. Continued.

Subfamily/tribe	Genera	Bees	Beetles	Flies	Others	References
Aroideae/ Areae	*Theriophonum*			Ceratopogonidae		Dakwale & Bhatnagar, 1997
Aroideae/ Areae	*Typhonium*		Scarabaeidae Staphylinidae Nitidulidae Ptiliidae Scydmaenidae			Cleghorn, 1914 Banerji, 1947 van der Pijl, 1953 Monteith, 1973

[1] Arcangeli's papers were first published in 1883 but they were reprinted in 1886.

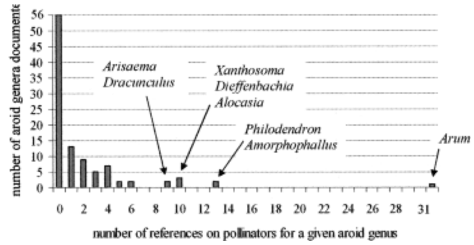

Fig. 1. ??

Third, in several cases only one or a small number of species of a given genus has been documented. Thus a generalization about the pollination of the whole genus from the reports now available becomes hazardous and may in fact hide the existence of a greater diversity in insect-aroid interactions.

The histogram below represents the number of references available on pollinators for the aroid genera. As mentioned before, for most of the aroid genera (56) there are no records of the pollinators. Most of the documented genera (59%) are only documented by one, two or three references. The genera actually named on the graph are those with the highest number of references about their pollinators: the genus *Arum* is particularly documented with 31 references.

As mentioned before, for most of the aroid genera (56), there are no records of the pollinators (i.e. the top left point). Most of the documented genera (59%) are only documented by one, two or three references (13 with one reference, nine with two, five with three and so on). The genera actually named on the graph are those with the highest number of references about their pollinators. For example, three genera, *Xanthosoma, Dieffenbachia* and *Alocasia,* each have 10 references dealing with their visitors/pollinators. The genus *Arum* is the most documented with 31 known references.

DISCUSSION

Amazingly in spite of their "unique" and very constant inflorescence design, aroids have developed pollination relationship with a great diversity of insects: bees, beetles and flies (Bown, 2000). Even vertebrates, e.g. hummingbirds, have recently been mentioned (Kraemer & Schmitt, 1999).

Inflorescence Evolutionary Trends

Aroids have a characteristic inflorescence made up of a spadix and a spathe, and all the inflorescence morphologies observed in aroids can be seen as variations around this same theme (Bown, 2000). From a pollination point of view, there are two main inflorescence evolutions:

1) Evolution of unisexual flowers that has allowed the secondary development of sterile flowers and then floral function specialisation (barrier, odor emission, thermogenesis, food-reward, . . .). On the contrary, in species with bisexual flowers, all the flowers have the same functions and participate to all the "functions" from pollinator attraction to seed fertilisation through pollen dispersion.

2) Development of an enclosing spathe with secondary appearance of a constriction allowing the capture of insects in contact with the flowers. Consequently, the relationship with the pollinators has evolved from a "two-phases" interaction to a "one-phase" interaction (Meeuse, 1978). In species lacking a floral chamber, pollinators cannot "stay" or be captured near the flowers, they have to come and depart repeatedly. Thus one attraction phase is necessary during the female phase to attract pollen vectors and achieve ovule fertilisation. A second attraction phase is needed later during the male phase to ensure pollen collection and its dispersion.

In aroids with exposed inflorescences and long anthesis, the inflorescence "needs" to attract (e.g. with odour and heat production) the pollinators every day of anthesis. In species with a floral chamber, once pollinators have been attracted during the female stage, they are then kept within the floral chamber by trap mechanisms or rewards (shelter from light, food, sexual partners, . . .) until the end of the anthesis (e.g. pollen release) hours or a few days later.

Three Types of Interactions

As in all pollination systems, pollinators visit flowers looking for a resource. It can be an alimentary resource (stigmatic fluid, pollen, floral parts, . . .) or a "reproductive resource" (mating, laying site). Flowers in return have developed adaptations to transform this pollinator behaviour (e.g. resource seeking) into a "pollinating act", and thus ensure their reproduction. One interesting point is that not a single species is known to offer nectar as a reward (Schwerdtfeger *et al.,* 2002). Nectar, a high-energy supply, is not produced in Araceae and the stigmatic exudate (e.g. fluid) is supposedly a poor substitute from the energetic point of view. Stigmate exudates may have been the first type of nectar in flowering plants and occur in many primitive flowering plants (Lloyd & Wells, 1992).

From the flower-pollinator interaction point of view, three situations exist in Araceae.

1) "classical" flower—pollinator interaction. The inflorescence doesn't play any role in the pollinator reproduction. The pollinator visits the inflorescence looking for a resource (stigmatic fluid, pollen) achieving thereby the pollination (e.g. *Symplocarpus, Calla,* some *Anthurium).*

2) The inflorescence becomes part of the reproductive cycle of the pollinator. Insects visit Araceae inflorescences not only for food rewards (nectar, pollen or floral tissue) but also to meet sexual congeners, achieve copulations and sometimes lay their eggs (e.g. *Philodendron, Dieffenbachia, Peltandra, Colocasia*).

3) The inflorescence dupes the pollinators by mimicking the laying site of the pollinator (faeces, mushrooms, dead animal, . . .). Hence, the insects visit the inflorescence in order to complete their reproductive cycle. Through this deceptive attraction, the insects achieve pollination but without actually receiving any reward (e.g. *Arum, Helicodiceros*).

One can think of a fourth situation in which the pollinator dupes the flower, taking the resource but not achieving pollination. A well-known example is nectar thieving by bees or bumblebees and even birds. Such interaction exists in about 14 plant families although in some instances pollination is after all achieved (reviewed in Maloof & Inouye, 2000). Interestingly, flower exploitation by pollinators is not documented in Araceae, but this does not mean that it does not exist in this family. Further studies are needed to look for its existence or to argue why flower exploitation by pollinator has not evolved using Araceae.

Observations in Natural/Introduced Populations

Observations and experiments in natural populations are very important since the results will inform us on the "normal" reproductive biology of a given species.

On the other hand, if observations and experiments on introduced populations appear artificial or secondary at first, such results can also be very interesting even if they need different kinds of interpretation. Knowing how an aroid is pollinated and reproduces outside its natural distribution range allows an understanding of how a species can adapt to new habitats with a different pollinating fauna. For example *Arum concinnatum* growing in Crete is visited by flies (Sphaeroceridae) and beetles (Staphylinidae) associated with faeces while in England it attracts the same (female) midges (*Psychoda*: Psychodidae and *Smittia*: Chironomidae) as the two local *Arum*: *A. maculatum* and *A. italicum* (Drummond & Hammond, 1993; Diaz & Kite, 2002). Some species may change their reproductive strategy, favouring vegetative over sexual reproduction when pollinators are lacking, and may potentially become invasive like *Zantedeschia* in some humid habitats of La Réunion.

In conclusion, I encourage you to have a look inside the inflorescence for insects next time you see an aroid in bloom and, for people who have observations and experimental results, to publish them in order to document a domain still poorly known for Araceae.

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