Pollinators and Visitors of Aroid Inflorescences: an addendum

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ABSTRACT

Data on aroid pollinators or inflorescence visitors were reviewed lately by Gibernau (2003), documenting the pollinators of 49 genera and about 125 species. This addendum adds information on 35 genera, of which 9 are newly documented, and about 60 species. In summary, we have some information on pollinators or inflorescence visitors on 58 genera and about 165 species. Such numbers are very low in comparison of the family diversity (more than 110 genera and about 4,000 species). The pollination of entire groups of Araceae is still unknown. The knowledge on the pollination of each tribe is discussed.

KEY WORDS

Araceae, Coleoptera, Diptera, Hymenoptera, Pollination.

DEDICATION

I would like to dedicate this paper to Patricia Frank and Julius Boos.

I met (Pa)Tricia on a few occasions in Sarawak during the International Aroid Congress and in Miami during the 2008 annual IAS sale & show at the Fairchild Tropical Botanical Garden in Miami. I was the invited speaker and she organized perfectly my stay in Miami. She was very kind to me and always "in good humor" as we say in French. I still remember her guiding me through her marvelous garden. When I was a member of the IAS Board of Directors, we had to vote on several decisions via internet but the vote was to be printed, signed and mailed. Apparently, according to Tricia, I was the only one following the rule and she used thus to receive regularly a letter from France...

I only met Julius once in September 2008 also during the annual IAS sale & show. As many people can say, he was the kind of person who struck in your mind. Before meeting, we used to exchange e-mails, particularly on flowering or pollination questions. His last e-mail before my departure to Miami was in summary "I have prepared tens of questions for you"; and my reply has been "I will do my best to answer all of them." Effectively, we discussed on different occasions and particularly one evening during which we emptied many beers. Julius's thirst of knowledge was immense and of course I was not able to answer all his questions!!!!

INTRODUCTION

Inflorescences of Araceae are mainly insect-pollinated and a review on Aroid inflorescences visitors and pollinators has been published (Gibernau, 2003). This review presented 176 references of studies and observations on insects visiting inflorescences of 49 genera and 125 species of Araceae. Studies at the family level have shown that Aroid floral traits are adapted to the different types of pollinating insects (Chouteau *et al.*, 2008; Gibernau *et al.*, 2010b). But data on Aroid pollinators are still scarce in comparison with the family diversity with more than 115 genera and about 4,000 species (Boyce & Croat, pers. comm.). Here is an addendum to the 2003 review on Aroid inflorescences visitors and pollinators. In this paper, I summarize the data on Araceae visitors and pollinators by

completing the references since 2003 and citing several older references omitted in Gibernau (2003). The purpose of this work is not to give an exhaustive review of this subject but rather an up-to-date statement of the subject, and to develop new remarks on aroid pollination. Another important consideration is that the duckweeds (previously Lemnaceae family) are now included within the Araceae (Cabrera *et al.*, 2008) are not detailed in the present study. Just worth mentioning, no clear data are available on duckweeds pollination except that their inflorescences/flowers are protogynous as are all known aroids (Gibernau *et al.*, 2004); animal pollination is vaguely mentioned (may be water mites?) as well as water, wind or self pollination (Landolt *et al.*, 1998; Tsatsenko & Malyuga, 2002).

RESULTS

The pollinators and/or inflorescence visitors of 35 genera and about 60 species are listed in Table 1. Nine aroid genera are newly documented namely: *Anaphyllopsis*, *Dracontioides*, *Gearum*, *Lagenandra*, *Piptospatha*, *Pothos*, *Schismatoglottis*, *Scindapsus* and *Steudnera* (Table 1). Since 2003, 42 new studies have been published on aroid pollination indicating a growing interest of this topic.

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 (Blackith & Blackith, 1993; Sivadasan & Kavalan, 2005; Garcia-Robledo *et al.*, 2005b; Sultana *et al.*, 2006; Takenaka *et al.*, 2006; Barriault *et al.*, 2009, 2010; Maia *et al.*, 2010; Punekar & Kumaran, 2010; Quilichini *et al.*, 2010; Tung *et al.*, 2010). 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 (Albre *et al.*, 2003; Garcia-Robledo *et al.*, 2005a; Takenaka *et al.*, 2006; Barriault *et al.*, 2009, 2010; Quilichini *et al.*, 2010). 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.

DISCUSSION

Once again, in spite of their "unique" and very constant inflorescence design, aroids have developed pollination relationships with a great diversity of insects: bees, beetles and flies. If we combine the information of the previous review (Gibernau, 2003) and the present paper, pollinators or inflorescence visitors have been studied or mentioned for a total of 58 genera and about 165 species. Such numbers are still very low in comparison to the family diversity (more than 115 genera and about 4,000 species). The pollination of entire groups of Araceae is still unknown.

Following the classification proposed by Mayo *et al.* (1997), I comment below in summary what is known on pollinators or inflorescence visitors in the several aroid subfamilies and tribes.

Subfamily Gymnostachydoideae

No mention according to my knowledge has been published on the pollination of *Gymnostachys* even if some other aspects of its biology have been studied (Shaw, 1997; Shaw *et al.*, 1997).

Subfamily Orontioideae

A few studies have dealt with *Lysichiton* and *Symplocarpus* species in both North America and East Asia. It appears that except perhaps for *L. americanus*, these genera have a mixed-pollination system implying several taxa of insect, and maybe wind-pollination (see review in Gibernau, 2003). Such a generalist pollination system has been indirectly suggested by a multivariate analysis of the floral traits associated with the pollination (Chouteau *et al.*, 2008; Gibernau *et al.*, 2010b). Almost nothing is

Table 1. Aroid pollinators/visitors cited in the literature between 2003 and 2010, plus a few older references omitted in the previous review (Gibernau, 2003).

Subfamily/tribe	Genera	Bees	Beetles	Flies	Others	References
Orontioideae	*Symplocarpus*	Honey bees				Kevan, 1989
Orontioideae	*Lysichiton*					Tanaka, 2004
Pothoideae/ Anthurieae	*Anthurium*		Curculionidae			Franz, 2003, 2007
		Euglossine				Hentrich *et al.*, 2007, 2010
Pothoideae/ Potheae	*Pothos*	hymenoptera				Yadav, 1998
Monsteroideae/ Spathiphylleae	*Spathiphyllum*	Euglossine				Hentrich *et al.*, 2010
Monsteroideae/ Monstereae	*Monstera*		Nitidulidae			Chouteau *et al.*, 2007
Monsteroideae/ Monstereae	*Scindapsus*			Drosophilidae		Sultana *et al.*, 2006
Monsteroideae/ Monstereae	*Rhaphidophora*	hymenoptera				Yadav, 1998
Lasioideae	*Dracontium*		beetles	flies		Zhu & Croat, 2004
Lasioideae	*Dracontioides*			flies		Boos, 1997 Gonçalves, 2005
Lasioideae	*Anaphyllopsis*				Nocturnal insects? Cockroaches?	Gibernau *et al.*, 2010a
Aroideae/ Spathicarpeae	*Gearum*		Dynastinae			Bogner & Gonçalves, 1999 Gonçalves & Maia, 2006
Aroideae/ Spathicarpeae	*Taccarum*		Dynastinae			Maia *et al.*, unpubl.

Table 1. Continued.

Subfamily/tribe	Genera	Bees	Beetles	Flies	Others	References
Aroideae/ Homalomeneae	*Homalomena*			Drosophilidae		Okada, 1986, 1987
						Sultana *et al.*, 2006
			Scarabaeidae			Kumano & Yamaoka, 2006
			Chrysomelidae			Kumano-Nomura & Yamaoka, 2009
			Scarabaeidae			Tung *et al.*, 2010
Aroideae/ Homalomeneae	*Furtadoa*			Drosophilidae		Sultana *et al.*, 2006
Aroideae/ Philodendreae	*Philodendron*		Scarabaeidae			Maia *et al.*, 2010
Aroideae/Caladieae	*Xanthosoma*		Dynastinae			Garcia-Robledo *et al.*, 2004, 2005a, 2005b
						Garcia-Robledo, 2010
Aroideae/Caladieae	*Caladium*		Dynastinae			Maia & Schlindwein, 2006
Aroideae/ Thomsonieae	*Amorphophallus*			Necrophagous flies		Austen, 1896
			Beetles			Yadav, 1998
		Trigona (Apidae)	Nitidulidae	Drosophilidae		Punekar & Kumaran, 2010
			Hybosoridae	Muscidae		Hetterscheid, unpubl. Ph.D.
			Staphylinidae	Calliphoridae		
			Scarabaeidae Rutelinae			

Table 1. Continued.

Subfamily/tribe	Genera	Bees	Beetles	Flies	Others	References
Aroideae/Schisma-toglottideae	*Schismatoglottis*			Drosophilidae		Sultana *et al.*, 2006
Aroideae/Schisma-toglottideae	*Piptospatha*			Drosophilidae		Sultana *et al.*, 2006
Aroideae/ Cryptocoryneae	*Cryptocoryne*			Diptera		Yadav, 1998
Aroideae/ Cryptocoryneae	*Lagenandra*			Diptera		Yadav, 1998
Aroideae/ Colocasieae	*Alocasia*			Neurochaetidae		McAlpine, 1978, 1988
				Drosophilidae		Okada, 1986, 1987 Ivancic *et al.*, 2005 Sultana *et al.*, 2006
Aroideae/ Colocasieae	*Colocasia*			Drosophilidae		Toda & Okada, 1983 Okada, 1986, 1987, 1990 Ivancic *et al.*, 2004, 2008 Miyake & Yafuso, 2005 Sultana *et al.*, 2006
Aroideae/ Colocasieae	*Steudnera*			Drosophilidae		Takenaka *et al.*, 2006 Sultana *et al.*, 2006
Aroideae/ Arisamateae	*Arisaema*			Diptera		Yadav, 1998 Barriault *et al.*, 2009, 2010

Table 1. Continued.

Subfamily/tribe	Genera	Bees	Beetles	Flies	Others	References
Aroideae/ Ambrosineae	*Ambrosina*				Not found	Quilichini *et al.*, 2005
Aroideae/Areae	*Sauromatum*			Diptera		Yadav, 1998
Aroideae/Areae	*Theriophonum*		Staphylinidae			Sivadasan & Kavalan, 2005
Aroideae/Areae	*Typhonium*		Beetles			Yadav, 1998
Aroideae/Areae	*Helicodiceros*			Necrophagous flies		Austen, 1896
				Blowflies-Calliphoridae		Angioy *et al.*, 2004
Aroideae/Areae	*Dracunculus*			Necrophagous flies		Austen, 1896
				Calliphoridae		Blackith & Blackith, 1993
				Muscidae		
				Fanniidae		
				Piophilidae		
Aroideae/Areae	*Arum*				review	Gibernau *et al.*, 2004
		Halictidae				Diaz & Kite, 2006
			Staphylinidae	Sphaeroceridae		Linz *et al.*, 2010
				Drosophilidae		Urru *et al.*, 2010
						Stökl *et al.*, 2010
						Quilichini *et al.*, 2010
Aroideae/Areae	*Biarum*		Staphylinidae	Diptera midges		Boyce, 2008

known about the pollination of the third genus, *Orontium*. It is probably pollinated by insects, such as flies and beetles with no more indications as to specific species involved (Klotz, 1992).

Subfamily Pothoideae

- Tribe Potheae. No study of pollinators for the three genera of this tribe (*Pothos*, *Pothoidium*, *Pedicellarum*), except one mention of Hymenoptera in *Pothos* (Yadav, 1998).
- Tribe Anthurieae. Only one genus is included in this tribe, *Anthurium*, but it is the most diverse of the family (with more than 1,200 species, Croat, pers. comm.). A great diversity of pollination systems exists in this genus: bees collecting resins and/or oily fragrances (Hentrich *et al.*, 2007, 2010), curculionid pollination looking for a feeding, and probably a reproductive site (Franz, 2003, 2007), and humming-bird pollination, the unique mention of vertebrate pollination in Araceae (Kraemer & Schmitt, 1999). It is not unlikely that further studies will reveal new pollination systems in this genus.

Subfamily Monsteroideae

- Tribe Spathiphylleae. No mention of pollinators for the genus *Holochlamys*. In contrast, the pollination of the genus *Spathiphyllum* appears to be variable. On one hand, bees have been observed to collect pollen, wax or oily fragrance (Hentrich *et al.*, 2010), on the other hand flies looking for nectar (and/or a reproductive site?) (see review in Gibernau, 2003).
- Tribe Anadendreae. No mention of pollinators for the genus *Anadendrum*, the unique genus of this tribe.
- Tribe Heteropsidae. No mention of pollinators for the genus *Heteropsis*, the unique genus of this tribe.
- Tribe Monstereae. The pollinators from five genera are not known (*Alloschemone*, *Amydrium*, *Epipremnum*, *Rhodospatha*, *Stenospermation*), even if beetles have been mentioned for *Rhodospatha*. Drosophilid flies have been observed to oviposit on the inflorescences of *Scindapsus* and may be pollinators (Sultana *et al.*, 2006). For *Monstera* no clear information is available, bees and beetles have been mentioned visiting their inflorescences (see review in Gibernau, 2003). The only published study has recently indicated one species, *M. obliqua*, to be pollinated by nitidulid beetles in French Guiana (Chouteau *et al.*, 2007). The pollination ecology of *Rhaphidophora africana* by a scarab beetle has been studied in West Africa, but not published (Beath, 1993), whereas Hymenoptera are mentioned for Asian species (Yadav, 1998). Interestingly, a bee-pollination system has been indirectly suggested for Monstereae based on a multivariate analysis of some floral traits associated with pollination (Chouteau *et al.*, 2008; Gibernau *et al.*, 2010b).

Subfamily Lasioideae

The pollinators from the five Asian genera are not known (*Anaphyllum*, *Cyrtosperma*, *Lasia*, *Podolasia*, *Pycnospatha*). In South America, no clear data are available on the pollinators of the four genera (*Anaphyllopsis*, *Dracontium*, *Dracontioides*, *Urospatha*). A recent study over several years was unable to determine the pollinators of *Anaphyllopsis* suggesting a very rare event or maybe night-pollination (Gibernau *et al.*, 2010a). The genera *Dracontium* and *Dracontioides* are suggested to be fly-pollinated (Boos, 1997; Zhu & Croat, 2004; Gonçalves, 2005). Nitidulid beetles have been observed in spathes of *Urospatha* (J. Boos, pers. observ.). Interestingly, the only African species, *Lasimorpha* (cited as *Cyrtosperma*) *senegalense*, is apparently pollinated by nitidulid beetles in West Africa (Knecht, 1983).

In multivariate analyses on some floral traits associated with pollination, the three studied species of Lasioid are grouped with

the two Orontioid species *Lysichiton camtschatcense* and *Symplocarpus renifolius*. This original pollination group intermediate between fly- and bee-pollination systems was hypothesized to represent a generalist (undefined?) pollination system (Chouteau *et al.*, 2008; Gibernau *et al.*, 2010b).

Subfamily Calloideae

The pollination ecology of *Calla* is not known. Old references (review in Gibernau, 2003) mentioned visiting flies. A modern study is particularly necessary to evaluate the potential attractive role of the white 'flag' spathe. Such work would be interesting in regard to the recent phylogenetic results that place *Calla* among the Aroideae taxa and not in an intermediate position between the basal taxa with bisexual flowers and the most derived ones (i.e. Aroideae) with unisexual flowers (Cabrera *et al.*, 2008).

Subfamily Zamioculcadoidae

- Tribe Zamioculcadeae. No mention of pollinators for the two genera of this tribe (*Zamioculcas*, *Gonatopus*).
- Tribe Stylochaetoneae. No mention of pollinators for the genus *Stylochaeton*, the unique genus of this tribe.

Subfamily Aroideae

- Tribe Dieffenbachieae. No pollinators are known for the genus *Bognera*, on the contrary several studies have illustrated the pollination of *Dieffenbachia* species (see review in Gibernau, 2003). Scarab beetles (Dynastidae) are the pollinators of different *Dieffenbachia* species even if other insects have been observed and/or collected in the inflorescences.
- Tribe Spathicarpeae. No mention of pollinators for six genera of this tribe (*Mangonia, Asterostigma, Gorgonidium, Synandrospadix, Spathantheum, Spathicarpa*). Recent studies on two genera have shown that *Gearum* (Gonçalves & Maia, 2006) and *Taccarum* (Maia *et al.*, unpubl.) are pollinated by scarab beetles (Dynastidae).
- Tribe Philodendreae. The only genus of this tribe, *Philodendron*, has been the model of many pollination works. All the actual results indicate the same pollination system implying scarab beetles (Dynastidae) even if other insects can be found within the inflorescences (review in Gibernau, 2003; Maia *et al.*, 2010).
- Tribe Homalomeneae. Drosophilid flies have been identified as pollinators of *Furtadoa* (Sultana *et al.*, 2006). Pollinators of *Homalomena* are not clearly identified. On one hand, drosophilid flies have been observed within their inflorescences (Okada, 1986, 1987; Sultana *et al.*, 2006). On the other hand, scarab beetles were also observed (Kumano & Yamaoka, 2006; Kumano-Nomura & Yamaoka, 2009; Tung *et al.*, 2010). Thus the pollination situation in *Homalomena* needs to be clarified. In multivariate analyses on some floral traits associated with pollination, the genus *Homalomena* is distributed both within fly- and beetle-pollinated species (Chouteau *et al.*, 2008; Gibernau *et al.*, 2010b). Several hypotheses can be proposed. First, *Homalomena* species have a mixed pollination system implicating both flies and scarab beetles. Second, some *Homalomena* species are fly-pollinated and others are beetle-pollinated. Third, *Homalomena* species are pollinated by only one type of insects, flies or beetles, the second type being inflorescence visitors.
- Tribe Anubiadeae. Only one reference is available on one species from West Africa, *Anubias gigantea*, indicating nitidulid beetles as visitors and/or pollinators (Knecht, 1983).
- Tribe Schismatoglottideae. The pollinators of four genera are unknown (*Hottarum, Bucephalandra, Phymatarum, Heteroaridarum*). The two studied genera, *Piptospatha* and *Schismatoglottis*, are pollinated by drosophilid

flies (Sultana *et al.*, 2006; Toda *et al.*, 2006). The same is probable for *Aridarum nicolsonii* in Sarawak even if beetles (nitidulidae and staphylinidae) have been observed to eat the male flowers (fertile and sterile) (Gibernau & Boyce, unpubl.; Bogner, pers. observ. in Knecht, 1983). Interestingly, the genus *Schismatoglottis*, with a disjunct distribution (Asia – America), may present different pollination systems on the two continents. In multivariate analyses on some floral traits associated with pollination, the genus *Schismatoglottis* is distributed within both fly- and beetle-pollinated species (Chouteau *et al.*, 2008; Gibernau *et al.*, 2010b).

- Tribe Cryptocoryneae. The two genera of this tribe, *Cryptocoryne* and *Lagenandra* have very similar floral morphology and ecology. No proper study on their pollination ecology has been published. But many observations and insect collections are available, suggesting fly pollination by a trap mechanism in aquatic habit (Yadav, 1998; see review in Gibernau, 2003; Jacobsen, unpubl. data)
- Tribe Zomicarpeae. No mention of pollinators for the four genera of this tribe (*Zomicarpa*, *Zomicarpella*, *Ulearum*, *Filarum*).
- Tribe Caladieae. No pollinator mention for three of the genera of this tribe (*Scaphispatha*, *Jasarum*, *Hapaline*). For the three other genera (*Caladium*, *Chlorospatha* and *Syngonium*), many studies and observations indicate a scarab beetle pollination (review in Gibernau, 2003; Maia & Schlindwein, 2006). In *Xanthosoma*, many different insects (euglossine bees, drosophilid flies, scarab beetles) have been observed in the inflorescences (review in Gibernau, 2003), but recent studies indicate that certainly only scarab beetles are pollinators, other insects have been probable visitors (Garcia-Robledo *et al.*, 2004, 2005a, 2005b; Garcia-Robledo 2010).
- Tribe Nephthytideae. The inflorescences of the three genera of this tribe *Anchomanes*, *Nephthytis* and *Pseudohydrosme* are visited by beetles (Nitidulidae) and flies. Trigona bees observed on inflorescences of *Anchomanes* might probably be only visitors (review in Gibernau, 2003). In multivariate analyses on some floral traits associated with pollination, some species of *Anchomanes* and *Nephthytis* have typical fly pollinated floral characters while other species have more mixed floral characters (Chouteau *et al.*, 2008; Gibernau *et al.*, 2010b). Further studies are needed to assess if pollination is achieved in these genera by a mixed-pollination system or by only one type of insect.
- Tribe Aglaonemateae. No pollinator mention for the genus *Aglaodorum*. On the other hand *Aglaonema* is certainly pollinated by drosophilid flies (review in Gibernau, 2003). But the results from multivariate analyses on some floral traits associated with pollination suggest that *Aglaonema* species possess floral characters typical of beetle-pollination (Chouteau *et al.*, 2008; Gibernau *et al.*, 2010b).
- Tribe Culcasieae. For the two genera of the tribe (*Culcasia*, *Cercestis*), beetles (Nitidulidae) and flies (Drosophilidae) have been collected within their inflorescences. In multivariate analyses on some floral traits associated with pollination, these two genera appear to distribute in separate positions. *Culcasia* clusters within the fly-pollinated species whereas *Cercestis* appears within the beetle-pollinated species (Chouteau *et al.*, 2008; Gibernau *et al.*, 2010b). Further studies are needed to assess if pollination is achieved in these genera by a mixed-pollination system or by only one type of insect.
- Tribe Montrichardieae. This tribe contains only the genus *Montrichardia*. Observations of bees visiting inflorescences may provide erroneous information about its pollination that is achieved by scarab beetles (review in Gibernau, 2003; Gibernau *et al.*, 2003).
- Tribe Zantedeschieae. The only genus of this tribe, *Zantedeschia*, may be

pollinated in its spontaneous distribution area by beetles, but accurate field studies are needed (see review in Gibernau, 2003).

- Tribe Callopsideae. No mention of pollinators for the genus *Callopsis*, the unique genus of this tribe.
- Tribe Thomsonieae. Observations have shown that there is a great diversity of visiting insects (bees, beetles, flies) in *Amorphophallus*, but until recently only one study was published on its pollination indicating beetle pollination for the African species *A. johnsonii* (Beath, 1993). Recent observations suggest a great diversity of pollination systems in this genus implying bees, beetles and/or flies by deception or not (Punekar & Kumaran, 2010; Hetterscheid, unpubl. Ph.D). *Pseudodracontium*, a close related genus, presents floral odors and a pollen morphology very similar to *Amorphophallus* species pollinated by carrion flies and beetles, such hypothesis must be confirmed by a field study (Kite and Hetterscheid, 1997; Kite *et al.*, 1998; van der Ham *et al.*, 2005; Hetterscheid, unpubl. Ph.D).
- Tribe Arophyteae. No mention of pollinators for the three genera of this Malagasy tribe (*Arophyton*, *Carlephyton*, *Colletogyne*).
- Tribe Peltandreae. No mention of pollinators for the genus *Typhonodorum*, while pollination of *Peltandra* is highly specialized by flies (Chloropidae) ovipositing on the inflorescences (review in Gibernau, 2003).
- Tribe Arisareae. The only genus of this tribe, *Arisarum*, seems to be pollinated by diverse mycophilous or saprophilous flies (review in Gibernau, 2003).
- Tribe Ambrosineae. The only genus of this tribe, *Ambrosina*, has been recently studied. Its complex inflorescence structure suggests a complicated pollination mechanism with a small animal being able to move from a lower (dorsal) "male" chamber from one inflorescence to an upper (ventral) "female" chamber of another inflorescence (Barabé *et al.*, 2004). But field observations were not able to detect any pollinators, rare non-flying small insects or arthropods were observed visiting the inflorescences (Quilichini *et al.*, 2005).
- Tribe Areae. Only one genus of this tribe has not been studied from a pollination point of view, namely *Lazarum*. The pollination of all the other eight genera has been studied (*Arum*, *Biarum*, *Dracunculus*, *Eminium*, *Helicodiceros*, *Sauromatum*, *Theriophonum* and *Typhonium*), and it's achieved by necrophilous or saprophilous flies and/or beetles (review in Gibernau, 2003; Blackith & Blackith, 1993; Yadav, 1998; Angioy *et al.*, 2004; Gibernau *et al.*, 2004; Sivadasan & Kavalan, 2005; Boyce, 2008; Espindola *et al.*, 2010; Linz *et al.*, 2010; Stökl *et al.*, 2010; Quilichini *et al.*, 2010; Urru *et al.*, 2010) except for one known exception (Diaz & Kite, 2006; Urru *et al.*, 2010).
- Tribe Arisaemateae. The two genera of this tribe *Pinellia* and *Arisaema* are pollinated by various mycophilous and saprophilous flies (and a few beetles) and thunder bugs (Thysanoptera) (review in Gibernau, 2003; Barriault *et al.*, 2009, 2010).
- Tribe Colocasieae. No pollinator mention is available for three out of the six genera of the tribe (*Ariopsis*, *Protarum*, *Remusatia*). The pollinators of *Colocasia* and *Alocasia* species are drosophilid flies ovipositing on the inflorescences. Interestingly, each aroid inflorescence is visited by two fly species, one ovipositing on the staminate zone, the other on the pistillate one but not damaging the ovules (Toda & Okada, 1983; Okada, 1986, 1987, 1990; Ivancic *et al.*, 2004, 2005, 2008; Miyake & Yafuso, 2005; Sultana *et al.*, 2006). Other insects have been mentioned visiting the inflorescences but apparently they are not pollinators. Recently the pollination ecology of *Steudnera* has been studied indicating a similar fly pollination system except that only one fly species is present (Takenaka *et al.*, 2006).
- Tribe Pistieae. Vague mention of insects observed in the minute inflorescence of

Pistia, but no published study on its pollination is available.

In conclusion, data on the pollination ecology and biology on aroids has greatly increased in the last 10 years with about 70 papers published, compared to 145 between 1879 and 2000. But many tribes and genera are still non-documented. In several other cases, the data are not conclusive between a mixed pollination system implying at least two types of pollinators or pollination by only one type of insects associated with other visiting insects. In these cases further studies are needed to assess which is the real pollination system. An indirect approach has been recently developed through multivariate analyses based on some floral traits associated with pollination (Chouteau *et al.*, 2008; Gibernau *et al.*, 2010b). These analyses were able to separate four combinations of floral traits: generalist, bee-, fly-, beetle-pollinated taxa. Such results are exploratory. Even if these analyses can predict from a set of floral character the probable pollination type of an unknown species, they must be considered as hypotheses to be further tested in the field or experimental conditions.

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