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ABSTRACT

This update on aroid pollinators or inflorescence-visitors adds information on 32 genera (and 60 species). Of these, 10 aroid genera and about 36 species are newly documented or revisited under new generic names. In summary, currently available data on the subject now sums up to approximately 200 aroid species across 67 genera. An ever increasing number of studies now aim establishing the identity of effective pollinating insects among all the visitors, but also at understanding how other florivorous or phytophagous insects can affect the plant reproductive success. In recent years, many studies have integrated molecular and/or chemical data to the study of aroid pollination. Such multidisciplinary approaches further increase our knowledge of the functional and evolutionary processes involved. Aroid-insect interactions are far more complex than just plant-pollinator relationships, they include in many cases non-mutualistic partners taking advantage of the interaction to carry on with their biological cycles.

Hence interactions between these plants and their inflorescence visitors are subjected to multiple selective pressures, which ultimately drive the evolution of the component parts and the whole.

KEY WORDS

Araceae, Floral scent, Floral trait evolution, Insect Pollination, Phylogenetic approach

INTRODUCTION

It has been almost six years since the last review on aroid pollinators and inflorescence visitors was published (Gibernau, 2011), a review that was already an update of a first synthesis on the subject (Gibernau, 2003). In total, these two reviews summarized the information and data from 235 publications that to a greater or lesser degree documented the pollination biology or ecology of 58 genera and about 165 species of Araceae. These numbers are still low when faced to the richness of the family, which according to the last update encompass 125 genera and no less than 3,500 species so far (Boyce & Croat, 2016). During recent years, many studies have been published on the ecology and/or biology of aroid pollination, indicating that this field of research is becoming increasingly interesting, particularly due to an ever growing input of molecular and chemical data (see below). The protogynous inflorescences of the Araceae are mainly insect-pollinated (Gibernau, 2003, 2011) and have hence evolved several floral features adapted for entomophily particularly in relation to types (or groups) of pollinating insects (Gibernau et al., 2010), habitat colonization (Calazans et al., 2014), flower protection (Coté & Gibernau, 2012; Maldonado et al., 2015), or trapping devices (Poppinga et al., 2010). The

profuse recent use of molecular techniques has allowed the development of powerful phylogenetic approaches that help us to understand the past history and the evolution of floral traits, species distributions (past migrations) or even plant–insect interactions (Takano Takenaka et al., 2011; Bröderbauer et al., 2012; Nauheimer et al., 2012; Wong et al., 2013; de Oliveira et al., 2014; Chartier et al., 2014; Moore et al., 2015). Another field of research in rapid progress is the chemical ecology of aroid pollination. Not only more and more inflorescence odours are being chemically characterized but also the attractiveness of floral volatile compounds either singly or in combinations is being validated in behavioural assays, increasing our comprehension of the olfactory-mediated pollinator attraction and the structuring role of floral scent volatiles in aroid-pollinator interactions (Chartier et al., 2011, 2013, 2016; Dötterl et al. 2012; Schiestl & Dötterl, 2012; Maia et al., 2012, 2013b; Jürgens et al., 2013; Gottsberger et al., 2013; Leguet et al., 2014; Pereira et al., 2014; Hoe & Wong, 2016; Hoe et al., 2016).

Duckweeds are now included in the Araceae, probably as the Lemnoideae subfamily, represented by 5 genera and 38 known species (Nauheimer et al., 2012; Chartier et al., 2014; Henriquez et al., 2014; Boyce & Croat, 2016). They are not detailed in the present report since no proper study is related to their pollination (see for a mini-review Gibernau, 2011). It appears that duckweeds reproduce mainly through an efficient vegetative process (Lemon et al., 2001; Kutschera & Niklas, 2015). Flowering in these plants is uncommon, but fruits have nonetheless been observed; sexual reproduction may be induced by environmental stress and could be considered as a resistance strategy in face of less favourable conditions (Pieterse, 2013). This mode of reproduction and the extreme miniaturization of the plant bauplan might be partly due on one hand to the reduction of genes acting in the adult phase and on the other to the re-engineering of the genetic network controlling transitions to the adult and the flowering growth phases (Wang et al., 2014).

This paper updates the two previous reviews on visitors and pollinators of aroid inflorescences, not repeating the information or the references already published (Gibernau, 2003, 2011). The purpose of this work is not to give an exhaustive review of this subject but rather an up-to-date statement in which new remarks on aroid pollination particularly in relation to phylogenetic approaches, floral scents and the negative effects of florivorous insects are discussed in the light of the most recent findings.

RESULTS

The pollinators and/or inflorescence visitors of 32 genera and ca. 60 species are listed in Table 1. Ten aroid genera are newly documented or documented under their new taxonomic names: *Adelonema, Aridarum, Bognera, Englerarum, Epipremnum, Lasia, Leucocasia, Phymatarum, Schottarum* and *Synandrospadix* (Table 1). Since 2011, 40 new studies have been published on aroid pollination, indicating the steady interest on this topic. Furthermore, more and more studies now distinguish the insects which are efficient pollinators from the broad array of anthophilous insects commonly associated with aroid inflorescences (see Table 1).

{INSERTION OF TABLE 1}

If the information of the previous reviews (Gibernau, 2003, 2011) is combined with data synthetized in this paper, pollinators and/or inflorescence visitors have been studied or mentioned for a total of 67 aroid genera and about 200 species. Such numbers are still very low if faced with the large family diversity (more than 125 genera and about 3,500 species) implying that the pollination ecology of entire groups of Araceae is still unknown (Gibernau, 2011). Inflorescences of many aroid species are visited by numerous types of anthophilous insects;

oftentimes, only a few of these visitors – not rarely only one species – are the sole effective pollinators of a given species (see review in Gibernau, 2011, Espindola et al., 2011; Revel et al., 2012; Low et al., 2014, 2016; Hoe & Wong, 2016; Hoe et al., 2016). For several genera, the pollination of only one or a very small number of aroid species have been documented. Thus a generalization about the pollination strategies within these genera can be hazardous and may in fact hide the existence of a greater diversity in insect-aroid interactions. Finally, increasing the dataset on floral visitors has also revealed how other florivorous or phytophagous insects may affect plant reproductive success (Gibernau et al., 2002; Maia et al., 2013a; Hernandez-Ortiz & Aguirre, 2015; Low et al., 2016; Hoe et al., 2016).

DISCUSSION

Aroid pollinators - what's new?

Most of the studies presented in Table 1 confirm known pollination systems already described in detail in the last review (Gibernau, 2011). However, several data are either new or document a diversity of pollinators previously unreported; these original contributions are detailed below.

Subfamily Monsteroideae

- Tribe Spathiphylleae. Pollination in the genus *Spathiphyllum* appears to be variable. While pollination by fragrance collecting male euglossine bees has been documented in some species from South America (Hentrich et al., 2010), it appears that pollen-collecting bees (Meliponini) from the genera *Plebeia*, *Trigona* or *Apis* are effective pollinators of two species of *Spathyphillum* native to Mexico whereas male euglossine bees are rarely observed in association with the inflorescences (Diaz-Jimenez et al., 2016). Hence, the

diversity of pollinators appears to be greater than that previously documented when considering species from different geographical areas. Further studies are needed to confirm such differences and to establish their likely association to abiotic (e.g. climate…) and/or biotic (e.g. vegetation type, specialization to the locally most abundant and/or efficient pollinator) environmental factors.

Subfamily Aroideae

- Tribe Spathicarpeae. The visiting insects of the only species of the genus *Bognera* [*B. recondita (*Madison) Mayo & Nicolson] are mentioned as dynastid scarab beetles from unpublished data of E.G. Gonçalves (Bogner, 2008; Moore & Jameson, 2013). Recent studies on *Taccarum* (Maia et al., 2013a, 2013b) have shown that *T. ulei* Engl. & K. Krause is pollinated by cyclocephaline scarabs (Dynastinae) but fruit flies (Richardiidae) were also observed visiting and ovipositing on the inflorescences (see paragraph below on Floral predation).

- Tribe Philodendreae. A recent molecular phylogeny resurrected the genus *Adelonema*, grouping all the former New World species of *Homalomena*, as a sister group of *Philodendron* subgenus *Pteromischum,* and not closely related to Asian species of *Homalomena* (Wong et al., 2016). Apart from the taxonomic reassessment implied (paraphyly of *Philodendron*), it appears that *Adelonema* species are also pollinated by dynastid scarab beetles, as are all known species of *Philodendron* (Moore & Jameson, 2013).

- Tribe Homalomeneae. In my last review, I wrote "*Pollinators of* Homalomena *are not clearly identified*", because drosophilid flies were mentioned by some authors and scarab beetles by others (Gibernau, 2011). Recent studies have clarified the question and allow

re-interpretation of previous published works (Wong et al., 2013; Yafuso et al., 2015; Hoe et al., 2016). Apparently, species belonging to the Supergroups *Chamaecladon* and *Punctulata* are specifically pollinated by drosophilid flies (*Colocasiomyia* spp), whereas those belonging to the Supergroups *Cyrtocladon* and *Homalomena* are visited by both drosophilid flies and beetles but only the latter, specifically ruteline scarabs (*Parastasia* spp.; Rutelinae) and chrysomelids (*Chaloenus* spp.; Galeuricinae) are true pollinators (Kumano & Yamaoka 2006; Wong et al., 2013). Note that inflorescences of a given species may be visited by 6–12 different species of insects (Hoe et al., 2016).

- Tribe Caladieae. There is no proper study on the pollination ecology of *Chlorospatha*, but a recent revision of the genus (Croat & Hannon, 2015) mentioned staphylinid beetles and flies as floral visitors. Several observations during the course of anthesis are intriguing. The sterile flowers are apparently not eaten; the female stage occurs, according to the species, between the late morning and the late afternoon (but in some species until 20h00-22h00!); during the second day of anthesis, secretions are visible on the inner surface of the spathe (Croat & Hannon, 2015). In most species, pollination seems to take place during daytime but crepuscular-nocturnal pollination is not excluded in some species. In conclusion, the floral biology of *Chlorospatha* appears to be very different from that of other known Caladieae such as *Caladium*, *Syngonium* or *Xanthosoma,* all of which associated with crepuscular/nocturnal cyclocephaline scarabs that consume the sterile flowers.

- Tribe Schismatoglottideae. Several new Asian genera have recently been "described-out of " the former genus *Schismatoglottis* and pollination information is available for a few of them. Species belonging to *Aridarum*, *Phymatarum* and *Schottarum* are pollinated by drosophilid flies (*Colocasiomyia* spp.) even if in some cases beetles (Chrysomelidae, Hydrophilidae) are regular inflorescence visitors (Gibernau, 2011; Low et al., 2014,

2016). The inflorescences of *Schismatoglottis* are visited by numerous species of flies and beetles; however pollinators are probably drosophilid flies (*Colocasiomyia* spp.) alone or in association with hydrophilid beetles (*Cycreon* spp.*,* Hydrophilidae) according to the species (Yafuso et al., 2015; Hoe & Wong et al., 2016).

- Tribe Alocasieae. The new genus *Leucocasia* made up of the single species, the former *Colocasia gigantea* (now *L. gigantea*)*,* is known to be pollinated by drosophilid flies (*Colocasiomyia* spp.) (Takano et al.*,* 2011; Fartyal et al.*,* 2013; Yafuso et al., 2015).

- *Englerarum* is a newly described monotypic genus (former *Alocasia hypnosa*) actually not clearly linked to either of the tribes Colocasieae or Alocasieae, and arguably corresponding to an isolated lineage that may represent its own tribe within the basal *Pistia*-clade (Nauheimer & Boyce, 2014). Numerous staphylinidae beetles were observed visiting its inflorescences (Nauheimer & Boyce, 2014), and if they are confirmed as effective pollinators this may represent a significant difference between *Englerarum* and fly-pollinated *Alocasia*, *Colocasia* & *Leucocasia*.

- Tribe Areae. A study of *Dracunculus vulgaris* in Crete showed that inflorescences from two populations were highly obnoxiously scented (sulphide-rich "rotting meat" smell) and attracted several groups of carrion beetles (i.e. Staphylinidae, Dermestidae, Histeridae, Sylphidae) and carrion flies. On the contrary, inflorescences from a third population, "scentless" for the human nose despite its similar levels of floral thermogenesis, were highly attractive to a single native species of flower chafer (*Protaetia cretica*, Cetoniinae) (Lamprecht et al., 2013).

Phylogenetic studies

If the inflorescence evolutionary trends in relation to pollination and the types of interactions presented in the first review (Gibernau, 2003) are still globally true; our knowledge is now more precise and the phylogenetic approach allows us to better understand the evolution of Araceae-pollination interaction and particularly the changes that occurred during its history. Such approach has been applied to floral volatiles announcing (Schiestl & Dötterl, 2012; Wong et al., 2013) or mimicking (Urru et al., 2011; Jürgens et al., 2013) the insects' mating/oviposition sites; to floral characters (Wong et al., 2013; Chartier et al., 2014); to inflorescence trapping mechanisms (Bröderbauer et al., 2012; Chartier et al., 2014); or to evolutionary shifts of pollinators or host plants (Takano Takenaka et al., 2011; Chartier et al., 2014; Moore et al., 2015). For example, trapping aroid inflorescences can be classified in 6 different functional types occurring in 27 genera, and that they have evolved at least 10 times in correlation with fly pollination (Bröderbauer et al., 2012). Trap pollination in Aroids is most likely derived from mutualistic ancestors whose inflorescences offered brood-sites to their pollinators (Bröderbauer et al., 2012; Chartier et al., 2014).

In the tribe Spathicarpeae, basal genera, such as *Dieffenbachia* and *Gearum*, are Amazonian lowland geophytes pollinated by cyclocepahline scarabs; whereas more derived genera (*Spathantheum*, *Synandrospadix*) located in the Andean Cordillera are presumably associated with fly pollination (Gonçalves et al., 2007; Maia et al., 2013a; Gibernau, 2015a). However the most recent genera such as *Spathicarpa*, *Asterostigma* and *Taccarum* have re-colonized Amazonian lowland habitats (Gonçalves et al., 2007). Even though *Spathicarpa* apparently has maintained (ancestral) fly pollination strategy of the Andean clade, *Taccarum* probably represents a recent reversion to nocturnal cyclocephaline scarab pollination (Maia et al., 2013a). Interestingly, this point of view is supported by the fact that several floral characters observed in *Taccarum* appeared different to those of other cyclocephaline scarab-pollinated Spathicarpeae (*Gearum brasiliense*, *Dieffenbachia* spp.) (Maia et al., 2013a). A comparative

approach, including *Asterostigma* spp., would allow further advancements on the knowledge of the evolutionary correlations between biogeographical distribution and pollination systems within the Spathicarpeae (Gonçalves et al., 2007; Maia et al., 2013a).

Floral scent

Numerous recent studies have analysed the floral scents of aroids. They have not only tackled the identification of the volatile organic compounds (VOCs) that constitute the fragrant bouquet, but also the attractiveness of these floral VOCs to pollinators either singly, as mixed blends or in solvent extracts (Chartier et al., 2011, 2013, 2016; Dötterl et al. 2012; Schiestl & Dötterl, 2012; Maia et al., 2012, 2013b; Jürgens et al., 2013; Gottsberger et al., 2013; Leguet et al., 2014; Pereira et al., 2014; Hoe & Wong, 2016; Hoe et al., 2016). It has been demonstrated that floral VOCs are secreted by epidermal cells of the scented floral organs (staminate zone, appendix or other sterile zone) after accumulation in intracellular vesicles (Skubatz & Kunkel. 1999, 2000; Leguet et al., 2014).

Chemical ecology approaches allows also to study how specialization or specificity can evolve through changes in floral traits such as the floral scent. For example, inflorescences of *Arum cylindraceum*, *A. italicum* and *A. maculatum* do not differ strongly in their floral trapping devices. However, the first two species exhibit a generalist reproductive strategy attracting different sets of insects across their distribution ranges, whereas *A. maculatum* is interpreted as a specialist, specifically attracting one of two species of fly midges (*Psychoda phalaenoides* or *Psycha grisescens*) according to the studied population (Espindola et al., 2011; Revel et al., 2012; Chartier et al., 2011, 2013, 2016). Such specialization can also be observed at the intraspecific level. Different compositions of floral scents produced by inflorescences of distinct populations (of the same species) attracting different pollen vectors may represent incipient speciation of *Dracunculus vulgaris* in Crete (Lamprecht et al., 2013). The study of the

pollination ecology of hybrids or of transplanted plants allows better understanding of the role of the floral scent and the diversity of the local entomofauna context as ecological barriers between species (Chartier et al., 2011, 2016). Another approach consists in studying the attractiveness of floral compounds in different locations to the different sets of local insects (Maia et al., 2012; Gottsberger et al., 2013). The study on *D. vulgaris* showed that even "scentless" inflorescences can be highly attractive over long distances to pollinator insects (Lamprecht et al., 2013). Volatile emissions from flowers can appear scentless to the human nose for two main reasons, dispersed VOCs : i) do not reach a minimum detection threshold ; ii) are not processed (e.g. detected) as odours by our sensory system. On the contrary, these VOCs can be perceived by insects because they possess the right receptor(s) and/or a large number of receptors able to detect trace amounts in the air. So our perception of odour intensity is not always linked with the real amount of VOCs emitted by the flowers. For examples highly odoriferous aroid inflorescences can emit relatively low quantities of VOCs (e.g. carrion-mimicking sufide-rich emissions) or some faintly scent species produce remarkably high scent emissions (e.g. several *Philodendron* and *Xanthosoma* rich in benzyl benzoate).

The structural study of the antennae of five different mothflies (Psychodinae) known to be deceived by *Arum* inflorescences revealed a total of seven types of sensillae (e.g. sensory hairs); up to six per species (Faucheux & Gibernau, 2011). The multiporous tribranched sensilla, present in all the species, are the best candidates for the reception of the odours, whereas other multiporous sensilla may be involved in the detection of CO_2 or heat (Faucheux & Gibernau, 2011). In the same way, antennae from other groups of aroid pollinators such as cyclocephaline scarabs (Scarabaeidae) or *Colocasiomyia* flies (Drosophilidae) must have olfactory receptors highly adapted to host scent perception and recognition since the inflorescences represent their mating sites (e.g. sexual partner encounters) and in some cases also the oviposition site (e.g. larvae development substrate) (Takano Takenaka et al., 2012;

Gottsberger et al., 2013; Maia et al., 2013b; Woodcock et al., 2014; Yafuso et al., 2015; Hoe & Wong, 2016; Hoe et al., 2016; Low et al., 2016). A better understanding of the insects' olfactory organs and their sensibility to chemical stimuli appear to be an original innovative field of research in the near future.

Floral predation

Finally, increasing the dataset on floral visitors has also increased our knowledge on how other florivorous or phytophagous insects can affect aroid reproductive success (Gibernau et al., 2002; Maia et al., 2013a; Hernandez-Ortiz & Aguirre, 2015; Low *et al*., 2016; Hoe et al., 2016). Florivores can use scent cues to locate their feeding and/or mating sites in the same way pollinators do, and even be specifically attracted to one or few floral VOCs present in complex scent blends (Maia et al., 2013b; Etl et al., 2016).

Floral herbivory has been observed in several species of *Dieffenbachia* affecting not only the stamina but also the rachis causing the decay of the inflorescence, and even in some cases the female flowers (Gibernau, 2015a, 2015b; Hernández-Ortiz & Aguirre, 2015). Such damage could be partly attributed to the activity of pollinating cyclocephaline scarabs but it appears that the main culprits are fruit-fly larvae Richardiidae and Drosophilidae (Diptera) (Hernández-Ortiz & Aguirre, 2015). Larvae of richardiid fruit-flies have also been observed feeding on floral tissues of *Taccarum ulei* inflorescences resulting in similar severe damage when present in large numbers (Maia et al., 2013a). While damage promoted by the feeding larvae has been documented, its effects on fruit production still need to be properly assessed. Tissue injury was also observed on infructescences of *Dieffenbachia seguine* in the form of small black holes oozing resin on the spathe, promoted by weevils (Curculionidae, Gibernau, 2015b). It still is not clear whether or not the flowers are attacked, but even if they are not, the possibility that such injuries might facilitate infestation by various pathogens cannot be

excluded. The effect of weevil drill holes over the reproduction success of their aroid hosts requires further investigation. Interestingly, *Cyclanthura* curculionid beetles (Curculioninae, Acalyptini) are known to be pollinators in some *Anthurium* species (Franz & Valente, 2005; Franz, 2007). If aroid fruit dispersion by animals has been somewhat documented (Barabé & Gibernau, 2015), fruit predation or parasitism is rarely documented (Gibernau et al., 2002) and might represent a new interesting field of investigation.

CONCLUSION

The study of pollination ecology and biology of aroids is still very dynamic with no less than 40 papers published since 2011 plus several papers mentioning floral visitors; but data on many tribes and genera is still pending. Two fields of research have been recently strongly associated with pollination ecology namely molecular sciences and chemical ecology. Their addition led to a better comprehension not only of functional aspects of aroid reproduction but also evolutionary features of the interactions between these plants and anthophilous insects. Evolutionary and chemo-ecological approaches are not only helping to explain how different aroid species are associated with particular types of pollinators but also if (and how many times) these interactions have changed over evolutionary history for example through host shifts or specialization. One future research direction will be to integrate the insect physiology, behaviour and neurology of sensory perception as complementary information to pollination biology observations. Also it appears that the aroid-insect interactions are more complex that just a relationship between a pollinator and a plant; implying antagonistic species using the flowers or the pollinators to achieve their biological cycle. A second future research direction will be to integrate all these types of interactions in order to evaluate the final outcome and better understand the multiple selective pressures acting on plant-pollinator interaction and

determining its evolutionary pathway(s). A multidisciplinary approach is hence an original way to interpret classical data on pollination.

ACKNOWLEDGMENTS

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Table 1: Aroid pollinators/visitors cited in the literature between 2011 and 2016, plus a few older references omitted in the previous reviews

(Gibernau, 2003, 2011). Insect family names followed by an asterisk have been shown to be efficient pollinators while those between

brackets have been considered to be visitors rather than pollinators.

Subfamily / tribe	Genera	Bees	Beetles	Flies	Others	References
Orontioideae	*Symplocarpus*	(Honeybee)		Diptera Mycetophilidae Chironomidae	Nemouridae Thrips	Thorington, 2000 Chartier et al., 2014
Orontioideae	*Lysichiton*		Staphylinidae			Brousil et al., 2015
Monsteroideae / Spathiphylleae	*Spathiphyllum*	Meliponini* Apini Euglossini				Diaz-Jimenez et al., 2016
Monsteroideae / Monstereae	*Epipremnum*		Dynastinae	Drosophilidae		Jameson & Drumont, 2013 Fartyal et al., 2013
Monsteroideae / Monstereae	*Monstera*		Dynastinae			Ratcliffe & Moron, 1997 and Ratcliffe, 2003 *in* Moore & Jameson, 2013
Monsteroideae / Monstereae	*Rhodospatha*		Dynastinae			Ratcliffe, 1992a *in* Moore & Jameson, 2013
Monsteroideae / Monstereae	*Scindapsus*			Drosophilidae		Fartyal et al., 2013

Monsteroideae / Monstereae	*Rhaphidophora*			Drosophilidae		Takano et al., 2011 Fartyal *et al.*, 2013 Li et al., 2014
Lasioideae	*Dracontium*			Sarcophagidae		Barabé & Gibernau, 2015
Lasioideae	*Lasia*			flies		Bröderbauer et al., 2012
Calloideae	*Calla*		small beetles	small flies		Chartier et al., 2014
Aroideae / Spathicarpeae	*Dieffenbachia*		Dynastinae*	(Richardiidae, Drosophilidae)	(Miridae)	Gibernau, 2015a, 2015b Hernandez-Ortiz & Aguirre, 2015 Etl et al., 2016
Aroideae / Spathicarpeae	*Taccarum*		Dynastinae*			Maia et al., 2013a, 2013b
Aroideae / Spathicarpeae	*Bognera*		Dynastinae			Bogner, 2008 Moore & Jameson, 2013
Aroideae / Spathicarpeae	*Synandrospadix*			flies		Chartier et al., 2014
Aroideae / Homalomeneae	*Homalomena* Supergroups: - *Chamaecladon & Punctulata* - *Cyrtocladon & Homalomena*		Scarabaeidae* Chrysomelidae*	Drosophilidae* Drosophilidae* (Drosophilidae)		Yafuso et al., 2015 Wong et al., 2013 Wong et al., 2013, Hoe et al.*,* 2016

			(Hydrophilidae) Nitidulidae			
Aroideae / Philodendreae	*Philodendron*		Dynastinae*			Dötterl et al., 2012; Gottsberger et al., 2013; Maia et al., 2013b; Pereira *et al.*, 2014; Maldonado et al., 2015
Aroideae / Philodendreae	*Adelonema*		Dynastinae			Barabé & Gibernau, 2015
Aroideae / Caladieae	*Caladium*		Dynastinae			Gasca-Alvarez, 2013; Maia et al., 2012, 2013b; Barabé & Gibernau, 2015
Aroideae / Caladieae	*Chlorospatha*		Staphylinidae small beetles	flies		Croat & Hannon, 2015
Aroideae / Schismatoglottideae	*Schismatoglottis*		Hydrophilidae* (Chrysomelidae, Staphylinidae)	Drosophilidae* Drosophilidae*		Wong & Boyce, 2014a, 2014b Yafuso et al., 2015 Hoe & Wong, 2016
Aroideae / Schismatoglottideae	*Schottarum*		(Chrysomelidae, Hydrophilidae)	Drosophilidae*		Low et al., 2014, 2016
Aroideae / Schismatoglottideae	*Aridarum*			Drosophilidae*		Low et al., 2016
Aroideae / Schismatoglottideae	*Phymatarum*			Drosophilidae*		Low et al., 2016
Aroideae /	*Englerarum*		Staphylinidae			Nauheimer & Boyce, 2014

tribe? (*Pistia* clade)						
Aroideae / Alocasieae	*Leucocasia*			Drosophilidae*		Takano et al., 2011; Fartyal et al., 2013; Yafuso et al., 2015
Aroideae / Alocasieae	*Alocasia*	(Apidae)		Drosophilidae* (Muscidae) Anthomyiidae		Takano et al., 2011; Yafuso et al., 2015 Takano et al., 2012 Woodcock et al., 2014
Aroideae / Colocasieae	*Colocasia*	(Nitidulidae)		Drosophilidae* (Chrysopidae Tephritidae)		Takano et al., 2011; Yafuso et al., 2015 Hunt et al., 2013 Bröderbauer et al., 2014
Aroideae / Colocasieae	*Steudnera*			Drosophilidae*		Takano et al., 2011
Aroideae / Areae	*Helicodiceros*			Calliphoridae Fanniidae		Gibernau & Seymour, 2014
Aroideae / Areae	*Dracunculus*		carrion beetles: Staphylinidae, Dermestidae, Histeridae, Sylphidae or Cetoniinae	flies		Lamprecht et al., 2013

Aroideae / Areae	*Arum*			Psychodidae*, Chironomidae*, Sciaridae* Ceratopogonidae Sphaeroceridae		Espindola et al., 2011; Revel et al., 2012; Chartier et al., 2011, 2013, 2016