Pollination in the Genus *Arum*—a Review

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ABSTRACT

The 28 species of the genus *Arum* (Araceae) attract and temporarily trap insects (mainly flies, and beetles in a few cases) during a complex pollination process. At anthesis, the appendix of the inflorescence produces heat and emits a specific odor which attracts insects. The lured insects are trapped within the floral chamber when stigmas are receptive. They will be released about 24h later after pollen emission, ensuring pollen dissemination. Studies on the reproductive biology of the genus have shown some degree of variability in the pollination strategies: morphological variations, flowering and heating periods, odor types and the type of pollinating insects.

Most species of *Arum* have never been studied in depth but data available from the literature indicate quite a high diversity of pollination strategy within this genus. Consequently, a general pollination model is not valid at the level of the whole genus. The origin of this diversity certainly results from the biogeographic history of the genus. The plants (i.e. species) have developed adaptations in response to different climatic, ecological and biotic (i.e. entomofauna) constraints (i.e. selective pressures) according to the various habitats occupied in the different regions of Europe and the Middle East. However, in the absence of phylogenetic data, it is actually impossible to determine how these different reproductive strategies have developed and evolved during the history of this genus.

KEY WORDS

insect, pollinators, inflorescence, thermogenesis, floral odor, morphology, Araceae.

INTRODUCTION

History

Arum have been known since Antiquity (Theophrastus, Pliny and Dioscorides). The description "*Arum officinarum*" appeared during the Middle-Ages because of their medicinal properties, but this term designated all kinds of aroids for about four centuries (Prime,1960; Fridlender, 1999a). During this period several authors dealt with *Arum* (see Croat, 2000 for more details). The binomial name *Arum maculatum* is attributed to Tabernaemontanus around 1590, but it has been used with a taxonomic "value" only after the classification work of Linnaeus in 1753 (Boyce, 1993). Hundreds of species were given the name of *Arum,* most of them later to be defined as new genera of Araceae, for example *Arum tenuifolium* is the type specimen for the genus *Biarum* described in 1832 by Schott (Boyce, 1993; Mayo *et al.,* 1997). Following *Arum maculatum,* the second valid species was *A. italicum,* described in 1768 by Miller (Table 1), and later Linnaeus f. described *A. pictum* in 1782. During the 19th century, period of oriental expeditions, many species were described from the East and the Mediterranean (Table 1). More recently, 7 new species have been described in the last 23 years (Boyce, 1993, 1994, 2004). Today, the genus *Arum* is considered to have 28 species (Boyce, 2004).

Table 1. History of species descriptions for the genus _Arum_ (Boyce, 1993, 2004)

Date	Species	Author	Odor
1753	_A. maculatum_	Linnaeus	Faecal/urine
1768	_A. italicum_	Miller	Urine/faecal
1782	_A. pictum_	Linnaeus fil.	Dung/pungent
1808	_A. orientale_*	Bieberstein	Dung/urine Rotting/fermenting fruit
1816	_A. dioscoridis_*	Smith	Dung/carrion[1] Ammonia ?
1836	_A. byzantinum_	Blume	Urine/putrid[%]
1836	_A. jacquemontii_	Blume	No perceptible
1844	_A. cylindraceum_	Gasparr	Putrid[2,3]
1845	_A. longispathum_	Reichenbach	Dung
1853	_A. rupicola_	Boissier	No perceptible
1853	_A. hygrophilum_	Boissier	No perceptible (sweet[%])
1853	_A. palaestinum_*	Boissier	Rotting/fermenting fruit Dung/carrion
1853	_A. creticum_*	Boissier & Heldreich	Sweet-rotting ("_Freesia_") Naphthalene mothballs
1856	_A. gratum_	Schott	Sweet ("pear drops")
1857	_A. nigrum_	Schott	Dung
1857	_A. elongatum_	Steven	Dung
1858	_A. besserianum_	Schott	Fermenting fruit[%]
1859	_A. concinnatum_	Schott	Putrid/urine
1877	_A. korolkowii_	Regel	No perceptible
1912	_A. cyrenaicum_	Hruby	Dung
1917	_A. idaeum_	Cousturier & Gandoger	No perceptible/sweet[%]
1981	_A. hainesii_	Agnew & Hadac	???
1983	_A. euxinum_	Mill	No perceptible
1983	_A. balansanum_	Mill	"Acidic apple"
1984	_A. apulum_	Bedalov	Dung
1987	_A. purpureospathum_	Boyce	Dung
1994	_A. sintenisii_	Boyce	Rotting/fermenting fruit
2004	_A. alpinariae_	Boyce	Dung[%]

* Several chemotypes exist each with different odors (Koach, 1985; Feibrun-Dothan, 1986; Boyce 1993; Drummond & Hammond, 1991, 1993).

[%] Light odor perceptible close to the inflorescence.

[1] Var. _syriacum_: odor not perceptible (Boyce, 1993).

[2] As synonym of _A. lucanum_: odor of dung/plasticine (Drummond & Boorman, 2003).

[3] As synonym of _A. alpinum_: odor not perceptible (Boyce, 1993).

Interestingly, in parallel with the taxonomic work of species description, there was a progressive discovery of insect pollination. In their 1996 book, Proctor, Yeo & Lack describe the work of Camerarius, Bradley, Miller, Logan and others during the first half of the 18th century, when botanists discovered that the "_Farina Fecundens_" produced by the stamens and the stigma were necessary to set seeds, and the first cross hand-pollinations were performed. During the second half of the 18th century biologists such as Dobbs and Kölreuter discovered that insects, and particularly bees, visited flowers in search of nectar and incidentally were carrying the "*Farina*", and thus were pollinating agents for numerous flowering plant species (Proctor *et al.*, 1996). During this period, Lamarck (1778) discovered the heat produced by spadices of *Arum italicum*. Sprengel (1793) produced the first systematic study of insect pollination on about 500 plant species and described several pollination mechanisms, in particular flowers which temporarily trap insects (e.g. *Aristolochia*).

Sixty years later (1857–1876), Darwin studied the plant variation and insect pollination systems (particularly self-pollination avoidance) within the frame of his theory of natural selection. At this time, Hildebrand (1867) wrote the first book on floral biology, followed by Delpino (1868) who proposed a flower classification (two volumes) based on different floral types in relation to pollination. Delpino studied numerous pollination mechanisms, including those of *Arum italicum* and in 1870 of *A. maculatum*. In the same way, Müller (1873) wrote three books on plant–pollinator-insect relationships, describing many pollination mechanisms, including *Arum maculatum*. In 1883, Arcangeli described the pollinating fauna of *Arum italicum* and in 1886 he studied *Arum pictum*. Knuth (1898–1905) wrote a handbook (3 volumes) on flower pollination in which *Arum italicum, A. maculatum, A. pictum* and *A. dioscoridis* are cited. The understanding of the insect trap mechanism was elucidated 40 years later thanks to experimental studies of the pollination of *Arum maculatum* and *A. nigrum* (Schmucker, 1925; Knoll, 1926). These studies showed the role of the appendix, the hairs and the floral chamber in attracting and capturing the insects, and also in seed production. During the last 60 years, only the pollination of *Arum maculatum* has been studied, and this only in England. Nevertheless the genus *Arum* is the most documented among Araceae in relation to pollination (Gibernau, 2003).

The Genus *Arum*

The genus *Arum* is composed of 28 species, largely distributed in Europe, North Africa, Middle East and Central Asia (Boyce, 1993; Mayo *et al.*, 1997). It is divided into two sub-genera: the sub-genus *Arum* which contains all the species except one, *Arum pictum*, which belongs to the sub-genus *Gymnomesium* due to the timing of its flowering (autumn instead of spring) and morphological characters of its sterile flowers and leaves.

Many *Arum* species are pollinated, or at least visited, by saprophilous or coprophilous insects, mainly flies and beetles (Boyce, 1993; Kite *et al.*, 1998; Gibernau, 2003). *Arum* inflorescences attract and trap the insects by mimicking the odor of their laying site (e.g. decaying organic matter or faeces). Thus the insects are lured by the inflorescence when pollinating and gain no reward from this interaction (Proctor *et al.*, 1996).

Inflorescence Morphology

The morphology of the *Arum* inflorescence is characteristic, made up of a spathe and a spadix. The spathe is the foliar organ around the spadix. The spadix is the central axis bearing the small unisexual flowers.

The spathe is a modified bract. Its basal part forms a tube around the fertile part of the spadix, called the floral chamber, which is closed at its top by hairs derived from sterile male flowers (Barabé *et al.*, 2003). The upper part of the spathe opens at anthesis and looks like a limb above a constriction zone. After pollination, the spathe wraps around the spadix protecting the developing fruit (i.e. the infructescence).

The spadix is divided in two zones, the basal fertile zone where the flowers are located within the floral chamber and the upper sterile zone, the appendix. Within the fertile zone, fertile female flowers (i.e. ovaries) are situated at the bottom, above them are sterile female flowers looking like hairs (i.e. pistillodes), still higher are the fertile male flowers (i.e. stamens), and finally male sterile flower also looking like hairs (i.e. staminodes). The appendix is a sterile organ situated at the apex of the spadix. It can develop heat and emits the volatile compounds attracting the pollinating insects. In *Arum italicum*, the longer the appendix, the more insects it will attract (Méndez & Obeso, 1992), and the higher will be the number of fruits initiated (Méndez & Diaz, 2001). In *A. maculatum*, if the appendix is removed, few *Psychoda* are caught and only 20% of the inflorescences are visited (Lack & Diaz, 1991). The same result had been found in inflorescences of *A. hygrophilum* with no appendix (Koach, 1985).The appendix loss (i.e. by predation) diminishes the fruit and seed productions in *A. italicum* and *A. maculatum* (Lack & Diaz, 1991; Méndez & Obeso, 1992). On the other hand, the appendix is not absolutely necessary since 40% of the *A. italicum* with no appendix produce seeds (Méndez & Obeso, 1992), and in *A. maculatum*, inflorescences still produce a reduced seed set (Lamb, 1956; Lack & Diaz, 1991).

Cryptic and Flag Species

Boyce (1993) distinguished two inflorescence types within the genus *Arum*. The species in which the inflorescence is borne on a short peduncle and in this way is situated amid or below the leaves, are called "cryptic" species. On the other hand, species where the inflorescences are above the leaf level at the end of long peduncles are called "flag" species. We will see later that these two kinds of species have different reproductive biology. Among the most studied species, *Arum maculatum, A. italicum, A. dioscoridis, A. palaestinum*, and *A. idaeum* are all "cryptic" species, while *Arum rupicola, A. hygrophilum* and *A. creticum* are "flag" species.

POLLINATION CYCLE

Cycle Steps

Arum inflorescences are protogynous: the period of stigma receptivity (female phase) starts and finishes before pollen liberation (male phase). This trait implies that inflorescences cannot self-pollinate (i.e. with their own pollen). Insects are trapped within the floral chamber during the time between the two sexual phases

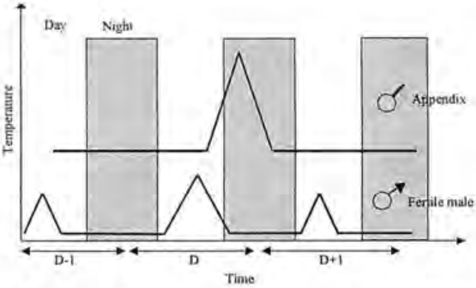

Fig. 1. Thermogenic pattern on *Arum maculatum* and *A. italicum* with four periods of heat. Two heating events occur before the spathe unfolding by the male flowers (D − 1 & D), another on the first day of anthesis by the appendix (D evening), and the last on the second day of anthesis, again by the male flowers (D + 1).

Each inflorescence produces four periods of heat during anthesis (Fig. 1). The first two are due to the male flowers. The first occurs on the day before the spathe opens (Albre *et al.*, 2003), the second on the day of the spathe opening (Skubatz *et al.*, 1990; Bermadinger-Stabentheiner & Stabentheiner, 1995). A temperature increase is perceptible at 9 A.M., several hours before the opening of the inflorescence in *A. italicum* (Arcangeli, 1886). These two heating events are not related to insect attraction but may rather be involved in the actual unfolding of the spathe (Fig. 1).

On the day of spathe opening, a third heating event occurs during the evening, but it is produced by the appendix (Fig. 1). This heating event is related to the phase of insect attraction and enhances the volatilisation of the odoriferous volatile compounds (Knoll, 1926; Bermadinger-Stabentheiner & Stabentheiner, 1995; Kite, 1995). Insects are mainly attracted by the scent, and visual cues of the spadix con-

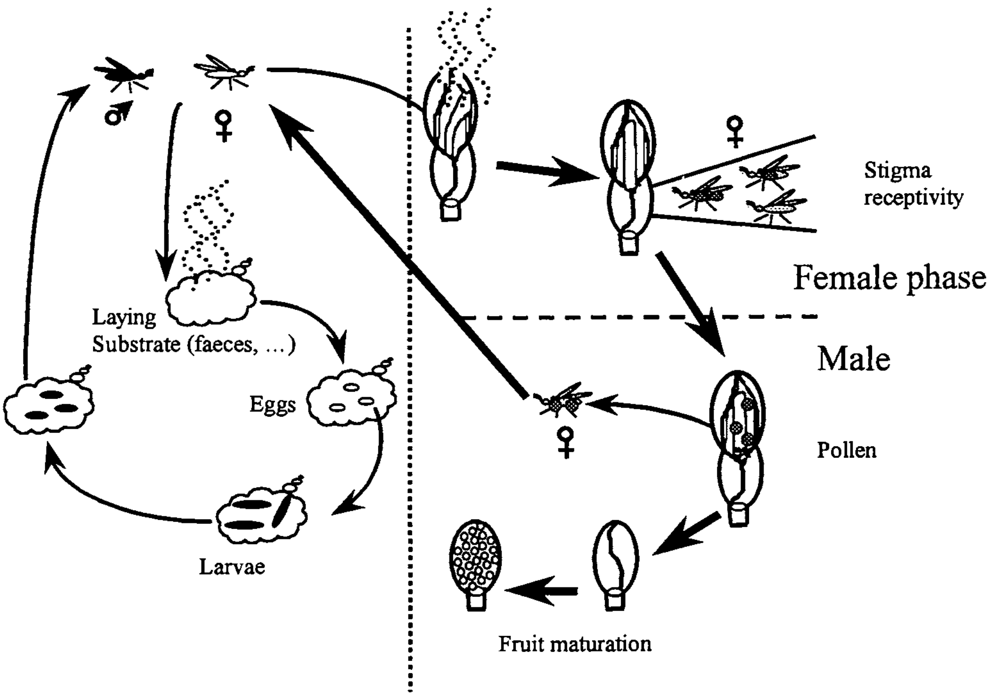

Fig 2. Biological cycle of *Psychoda* midges (left side of the vertical line), pollination of *Arum* cycle with capture of lured midges (right side of the vertical line).

trast against the spathe are secondary (Knoll, 1926; Lamb, 1956; Prime, 1960; Lack & Diaz, 1991; Kite *et al.*, 1998). Once attracted, the insects fall or enter into the floral chamber where they are trapped (Fig. 2). The upper hairs, which are modified sterile male flowers, located at the entrance of the floral chamber, are supposed to prevent the insects from escaping out and "huge" invertebrates from entering in, and/or to reduce light entrance (Knoll 1926; Dormer, 1960; Lack & Diaz, 1991; Fridlender, 1999b). Large dung flies have been observed to alight on the spadix of *A. maculatum* and *A. nigrum*, but not go further down (Church, 1908; Knoll, 1926; Dormer, 1960).

During their stay in the floral chamber, insects may deposit pollen on the stigma, if they already carry some. Female flowers are receptive at this time and their stigmas have a drop of secretion, enhancing pollen collection. The conditions within the floral chamber allow the insect to survive until the male phase on the next day when pollen release occurs. The chamber wall is constituted of a spongy mesophyll (i.e. loosely packed cells) coupled with numerous stomata on the external wall surface (Knoll, 1926; Beck, 1983; Bermadinger-Stabentheiner & Stabentheiner, 1995). This structure of the wall tissue may facilitate the oxygen transfer necessary for insect respiration, but also may be of value to respiration of the male flowers of the spadix during heating events, particularly when the spathe is still closed. Moreover, in particular dry conditions, the relative humidity of the floral chamber can remain high independent of the external conditions (Knoll, 1926). In Israel, the mortality of *Psychoda cinerea*, pollinator of *A. hygrophilum*, is limited thanks to the humidity of the floral chamber, thus this may be of adaptive value in arid habitats (Koach, 1985).

During the second day of anthesis, the fourth heat event is produced by the stamens (Fig. 1) and may be related to the anther opening and pollen release (Bermadinger-Stabentheiner & Stabentheiner, 1995; Albre *et al.*, 2003). At this stage, the cells of the appendix, the epidermis of the floral chamber and the spadix are no longer turgid and slippery, and the hairs have wilted. Insects are able to walk up the floral chamber and to escape loaded with pollen (Knoll, 1926; Prime, 1960; Beck, 1983; Bermadinger-Stabentheiner & Stabentheiner, 1995). If these insects are captured again by a female stage inflorescence, they may deposit pollen on the receptive stigma, but the insect capture must occur in the two days following their escape, as *Arum* pollen quickly loses its viability (Gibernau *et al.*, 2003). In *A. maculatum,* about 25% of the *Psychoda* captured are attracted for the first time and thus carry no pollen (Lack & Diaz, 1991). Moreover, a *Psychoda* can only visit one inflorescence on a given day because of the trap mechanism. Thus, an inflorescence must attract a maximum of insects in order to have a high probability of pollination and thus set seed, and consequently will have a "good" pollen dissemination on the following day. On the other hand, the fruiting success of *A. maculatum* did not appear to be related to the number of insects trapped, as if just one midge carrying pollen was necessary for a full fruit set (Lack & Diaz, 1991).

The Pollinators

Pollinators are documented for 15 species in their natural habitats, about half the genus, plus three species in culture out of their distribution (Table 2). *Arum* species are mainly pollinated and visited by flies: *Nematocera* (Psychodidae, Ceratopogonidae, Chironomidae) and also *Brachycera* (Sphaeroceridae, Drosophilidae, Scatophagidae). Visiting insects can also be beetles (Staphylinidae, Bruchideae, Scarabaeideae) for a few species (Table 2).

Except for four species, namely *A. maculatum, A. italicum, A. nigrum* and *A. hygrophilum,* data on pollination are actually observations or samples of insects captured in the floral chamber, which are not necessarily efficient pollinators (Gibernau, 2003). For example *Arum maculatum* inflorescences captured many insect species, 56 recorded in Germany and at least 13 in England but the main pollinator is only *Psychoda phalaenoides* (Grensted, 1947; Beck, 1983; Diaz & Kite, 2002). In the same way in *A. italicum,* at least 9 insect species are captured but only two are efficient pollinators and two others may be opportunist secondary pollinators (Albre *et al.,* 2003). In Crete, at least 21 species of insects visited inflorescences of *A. creticum,* but only the bruchid beetles (5 species) seemed to be active enough and coated with enough pollen to be pollinators (Drummond & Hammond, 1993). The larger scarabs were coated with much more pollen, but remained quiescent at the bottom of the spathes (Drummond & Hammond, 1993). In *A. nigrum,* 50 species of insect are attracted by the inflorescences but only 4–5 species may be efficient pollinators (Knoll, 1926).

Thermogenesis

This question has been reviewed by Bay (1995): in summary the thermogenic process is triggered by the alternation of light and dark, which stimulates the primordia of the male flowers. As a result, the male flowers produce salicylic acid, which act as a calorigen hormone by stimulating thermogenic reactions. In *Arum,* there are two spadix zones (the male flowers and the appendix) which produce heat at different moments of anthesis. In summary (see the previous section "cycle step"), the thermogenic pattern in *Arum* is tetraphasic (Fig. 1). Two heating events occur before the spathe unfolding, by the male flowers, another on the first day of anthesis by the appendix, and the last on the second day of anthesis, again by the male flowers.

If temperature increases have been observed in many *Arum* species, in fact few actual temperature measurements are available. The heat production by the appendix appears to be the most spectular of the four heating events. In *A. italicum*

Table 2. Major insect taxa found in inflorescences of different species of *Arum* (in bold most abundant taxa). Unless noted, the insects are mainly females. (=) indicates that caught insects are about half males and half females. * plants in culture out of their natural distribution area.

Species	Country	Main pollinators
A. maculatum	England	*Psychoda phalaenoides, P. grisescens, P. brevicornis Smitt pratorum* (*Piophila vulgaris*)
A. maculatum	Germany	*Psychoda phalaenoides, P. grisescens*
A. italicum neglectum	England	*Psychoda phalaenoides, Smittia pratorum*
A. italicum italicum	England	*Psychoda phalaenoides, P. grisescens*
A. italicum italicum	Italy	*Psychoda nervosa, Limosina pygmaea, Ceratopog pictellum, Chironomus byssinus, Drosophila funebris*
A. italicum italicum	France	*Psychoda crassipenis, P. pusilla*
*A. italicum**	Israel*	*Psychoda cinerea*
A. pictum	Italy	*Sphaerocera equinus, Aphodius melanostictus*
A. orientale (named *petteri*)	Yugoslavia	*Coproica ferruginata, Spelobia clunipes*
A. orientale	Cyprus	*Atheta trinotata, Atheta sp* (Γ), *Drosophila subobscura* (=), *busckii* (=), *D. hydei* (=)
A. dioscoridis	Turkey	*Anotylus clypeonitens, A. inustus, Atheta atramentaria*
A. dioscoridis	Cyprus	*Coproica vagans, C. ferruginata, Anotylus inustus*
A. dioscoridis	Lebanon	*Scatophaga stercoraria, S. maculipes, Philonthu intermedius, Oxytelus sculpturatus, Onthophagus ovatus, . . .*
A. dioscoridis	Israel	Sphaeroceridae, Staphylinidae, Scarabaeideae
*A. dioscoridis**	England*	Dung insects
A. concinnatum	Crete	*Coproica ferruginata, Spelobia sp., Anotylus inustus, Athe coriaria*
*A. concinnatum**	England*	*Psychoda phalaenoides, Smittia* sp.
A. nigrum	Croatia	*Aphodius tristis, Sphaerocera subsultans, S. pusilla, equinus Coprophila pusilla*
A. creticum	Crete	*Bruchidius* spp., *Tropinota hirta, Aplocnemus* spp. Heteroptera, Melyridae
A. idaeum	Crete	Bruchidae, Melyridae, Mordellidae Heteroptera
A. rupicola (named *elongatum*)	Israel	*Culicoides circumscriptus, C. cataneii*
A. rupicola (named *conophalloides*)*	Austria*	*Culicoides aricola, Odagmia ornata*
*A. rupicola**	England*	*Culicoides brunnicans, C. vexans, C. punctatus, C. pulicaris*
A. hygrophilum	Israel	*Psychoda cinerea* (Γ), *Tinearia alternata* (Γ)
A. hygrophilum	Lebanon	*Sciria advena*

Table 2. Continued.

Species	Country	Main pollinators
*A. jacquemontii**	England*	*Culicoides brunnicans, C. obsoletus, Simulium ornatum*
A. palaestinum[1]	Israel	*Drosophila phalerata* (=), *D. immigrans* (=), *D. hydei* (=), *melanogaster* (=), *D. simulans* (=)
A. palaestinum[2]	Israel	Flies & beetles
*A. purpureospathum**	England*	*Copromyza equina, Smittia sp., C. similes, P. phalaenoides*
A. gratum	Turkey	Psychodidae
A. apulum	Italy	Sphaeroceridae, Chironomidae
*A. apulum**	England*	Psychodidae, Chironomidae, Sphaeroceridae
*A. cylindraceum** (*named lucanum*)	England*	Psychodidae, Culicidae
*A. cyrenaicum**	England*	Nematocera
A. euxinum	Turkey	Psychodidae, Sphaeroceridae

[1] Ecotype with fermenting fruit odor.
[2] Ecotype with dung/carrion scent.

and *A. maculatum*, the appendix becomes as much as 15–25°C warmer than the surrounding air (Lamarck, 1783; Kraus, 1882; Arcangeli, 1886; Church 1908; Prime, 1960; Skubatz *et al.*, 1990; Bermadinger-Stabentheiner & Stabentheiner, 1995; Albre *et al.*, 2003). During anthesis, and particularly during the heat production by male flowers, the floral chamber of *A. italicum* and *A. maculatum* is about 1–3°C warmer than the external air (Church, 1908; Sowter, 1949; Prime, 1960; Bermadinger-Stabentheiner & Stabentheiner, 1995; Albre *et al.*, 2003).

Apart from *A. italicum* and *A. maculatum*, incomplete data are available for a few species. In *Arum rupicola*, the spadix maintained a temperature of around 40°C, about 15–20°C above ambient air from 17h to 23h and then began to fall (Koach, 1985; Drummond & Hammond, 1993). In *A. jacquemontii*, the spadix temperature was 36.4°C at 18h 40 compared to an ambient of 15.2°C and gave no discernible odor (Drummond & Hammond, 1993). *Arum palaestinum* and *A. creticum* are weakly thermogenic with just a few degrees above ambient (Koach, 1985; Skubatz *et al.*, 1990). By contrast, male flowers and the appendix of *A. dioscoridis* are highly thermogenic, 9–10°C above ambient, some spadix part reaching 40°C (Koach, 1985; Skubatz *et al.*, 1990).

The hypothesis of pollinator attraction by the heat production has been tested in *Arum nigrum*. Heated artificial inflorescences did not capture significant number of pollinating insects, whereas artificial inflorescences with a smell were attractive (Knoll, 1926 ; Dormer, 1960). A second experiment on *Psychoda phalaenoides*, the main pollinator of *Arum maculatum*, was performed more recently. Glass tubes 10°C warmer than ambient air simulated warm inflorescences, but no insects were attracted (Kite *et al.*, 1998).

Thus, the main role of the thermogenic process (at least for the appendix) appears to be the dispersion in the air of the scented compounds, rather than to attract the insects because of the warmth. In addition, the thermogenic activities of the male flowers are not linked with pollinator attraction, but may be related to spathe unfolding, physiological processes such as pollen maturation, insect warming or pollen release (Barabé *et al.*, 2002; Albre *et al.*, 2003).

VARIATIONS IN THE REPRODUCTION BIOLOGY

According to the species of *Arum,* differences in the pollination mechanism are of greater or lesser importance. Those differences are related to the inflorescence morphology, the thermogenesis, the inflorescence odor, the type of pollinators but these variations may also occur within a species. The geographical variation in *A. maculatum* is a well known, for example, in the presence of spots, the plant size, dextral/sinestral spathes or the yellow appendices, even if there is not always a "logical" pattern (Prime, 1960).

Modes of Capture

Differences exist in the capture method between *Arum maculatum* and *A. nigrum* (Knoll, 1926; Dormer, 1960; Boyce, 1993). Both species attract several different insects including *Psychoda,* but these insects do not behave similarly. In *A. maculatum,* insects fly in a spiral around the appendix and the spadix and then land on the spadix or the staminodes (hair modified male sterile flowers), before they walk down into the floral chamber. In *A. nigrum,* on the other hand, pollinators try to land on the spathe which is slippery due to oily secretions, and fall down into the floral chamber.

Insects are hypothesized to remain captured in the floral chamber of *A. nigrum* for three reasons (Knoll, 1926):

- The upper part of the floral chamber and the spadix epidermis are slippery preventing insects from walking upwards the exit.
- The insects do not try to fly because the volume of the floral chamber is not sufficiently large to stimulate flying behaviour.
- The main light source coming from below and the insects being positively light sensitive, they might remain near the lower part of the floral chamber (where the female flowers are located). In fact, this is because the floral chamber wall is bicoloured: dark purple in its upper part (opaque) and pale green (translucent) in its lower part. This floral chamber wall characteristic is also observed in *A. orientale, A. rupicola, A. purpureospathum* and *A. elongatum,* but not in *A. maculatum, A. italicum, A. concinnatum* or *A. cylindraceum.*

Arum creticum and *A. idaeum,* two closely related species native to Crete, are the only species with no hairs blocking the entrance of the floral chamber (Boyce, 1993). Interestingly, *A. idaeum* and *A. creticum* have similar, if not the same, pollinators; and are the only *Arum* species to be pollinated principally by beetles (Drummond & Hammond, 1993; Drummond & Boorman, 2003). This lack of "closing hairs" may be related to the pollinators. Beetles are relatively strong insects, able to sneak in through small openings thanks to their smooth body and such hairs would be, in fact, inefficient in holding them. Interestingly, *A. diosocoridis*, in Lebanon, is mainly visited by 7 species of beetles and two species of flies (*Scatophaga*). All the beetles were able to move easily up and down from the floral chamber, only the *Scatophaga* flies seemed to be held inside the floral chamber by the hairs (modified sterile flowers) (Kullenberg, 1953).

It has been suggested that in general the pollinating insects collect the stigma secretion and from this get some kind of food (Prime, 1960). But Lack & Diaz (1991) stated that such behaviour was never observed in *Psychoda phalaenoides,* pollinator of *Arum maculatum.* These authors suggest that the stigmatic secretions were not nectar (i.e. produced to feed the insects) but a fluid favourable for the adherence and the germination of the pollen. Moreover, such secretion is produced on the second day of anthesis even if female flowers are no longer receptive and, by getting onto the trapped insects, may enhance pollen adhesion to their bodies (Lack & Diaz, 1991). However, in *A. itali-*

cum, the stigmas are devoid of such secretion during the second day of anthesis (Albre *et al.,* 2003). In any case, it has been suggested that *Psychoda* species are not known to feed during their short adult life (Withers cited in Lack & Diaz, 1991), which is up to 7 days for *P. phalaenoides* (Prime 1960; Withers, 1988), and about 5 days for *P. cinerea, P. trinodulosa* and *P. parthenogenetica* (Lachmann *et al.,* 2000). It is worth noting that adult *P. trinodulosa* died when deprived of sugary water whereas *P. cinerea* and *P. parthenogenetica* survived but had a lesser reproductive success (Lachmann *et al.,* 2000). In *Arum hygrophilum,* the stigmatic fluid helps the pollinators (*Psychoda cinerea*) to survive longer when in the floral chamber (Koach, 1985). This fluid may help in maintaining a humidity rate appropriate for the insects and also represent a food source. *Psychoda cinerea* fed with an aqueous solution (5% sucrose) which is similar in composition to the stigmatic fluid, survive twice as long as those fed with only water (Koach, 1985). In comparison, the fluid produced by stigmas from *A. maculatum,* had a concentration of sucrose equivalent of 9–12.5%, which was slightly more concentrated than 8% sucrose equivalent of the fluid exuded from the phloem of cut stems (Lack & Diaz, 1991). Finally, during the rearing of *Psychoda* captured in inflorescences of *Arum italicum,* the individuals were regularly observed to feed on 5% sugary water (Albre, pers. comm.).

Reproduction

The reproductive system has been intensively studied in only two species, namely *A. maculatum* and *A. italicum.* The reproductive success depends on the flowering and pollination contexts: number of individuals, their density, the weather, the phenology, the pollinator abundance (Ollerton & Diaz, 1999; Méndez & Diaz, 2001). Inflorescences which opened on days with no other inflorescences already open (i.e. potential pollen donors) have a probability up to 45% lower to fructify than inflorescences which opened on days with inflorescences already open (Méndez & Diaz, 2001). In the same way, it appears that *A. maculatum* flowering at the beginning or the end of the flowering period, when few other inflorescences are open, have a lower probability to fructify than those flowering at the flowering peak (Ollerton & Diaz, 1999). Consequently, selection tends to synchronize flowering in *A. maculatum,* but the "mean" date fluctuates every year due to variable weather conditions (Ollerton & Diaz, 1999). In a year with "good" weather conditions, flowering of *A. maculatum* is generally synchronised with *Psychoda* flight abundance and a high fruit set occurs; whereas with "bad" weather the flowering may be delayed, the *Psychoda* flight activity reduced and few fruits are produced (Kite *et al.,* 1998). Hence, the reproductive success of *A. maculatum* and *A. italicum* appears to be pollen and pollinator limited.

The flowering phenology is unimodal (i.e. a peak) in *A. italicum* and in *A. maculatum,* with inflorescences lasting a few days (i.e. anthesis of about 24h) and withering quickly after anthesis (Méndez & Obeso, 1992; Ollerton & Diaz, 1999; Méndez & Diaz, 2001). Two exceptions are known for which inflorescences do not fade and wither rapidly, but retain their fresh appearance for several days after the spathe fully opened: about 7 days in *A. creticum* (Drummond & Hammond, 1993) and 9–10 days in *A. hygrophilum* (Koach, 1985). Once again, a long inflorescence duration in *A. creticum* may be related to beetle pollination.

In *A. italicum,* it has been shown that the sexual reproduction has a somatic cost, as tubers of reproductive plants grow 30% less than non-reproductive plants. This cost can be lower by temporal coincidence between leaves and inflorescences/infructescences (Méndez, 1999). *Arum italicum* with tubers lighter than 2.5g do not reproduce, whereas those with a tuber over 10g will reproduce each year (Méndez & Obeso, 1993). In *A. maculatum,* a size factor also exists since the tuber will not flower until they reach a weight of approximately 10g (Prime, 1960). When its vigour increases (i.e. the mass), a plant tends to produce more inflorescences which are bigger and bear more flowers (Méndez & Obeso, 1993; Méndez, 1998). An individual of *A. italicum* with several inflorescences has a higher probability to fructify than plants with only one inflorescence (Méndez & Obeso, 1992; Méndez & Diaz, 2001). In the same way, the inflorescence size (i.e. mass) is positively related to the size of the appendix and the numbers of flowers (Méndez, 1998; Méndez, 2001). On the other hand, the rank of development of the inflorescence (e.g. order of inflorescence appearance) appears to be important, since inflorescences with a higher rank (e.g. second or third inflorescences) tend to be smaller and to bear less flowers (Méndez, 1998).

In *A. italicum,* it seems that two functional reproductive strategies occur (Méndez, 1998). In fact, the reproductive outcome of individuals producing only one inflorescence is, on one hand abortion with no seed set but pollen dispersion, and on the other hand seed production but with a low pollen dispersion. The result is like a gender specialisation of the inflorescence as functionally male or female. On the contrary, plants producing two inflorescences do not tend to be male/female specialised, but are relatively as successful in pollen dispersion (i.e. male) as in seed production (i.e. female) (Méndez, 1998).

Another important reproductive character is self-compatibility. Self-pollination is rare in *Arum,* inflorescences bagged before their opening abort in *A. italicum* (Albre *et al.,* 2001), *A. maculatum* (Lamb, 1956; Prime, 1960; Lack & Diaz, 1991), *A. nigrum* (Knoll, 1926; Dormer, 1960) and *A. hygrophilum* (Koach, 1985). In contrast Fridlender (1999b) report that in *A. cylindraceum,* individuals from small populations were self-fertile whereas individuals from big populations were unable to self-pollinate. According to Ollerton & Diaz (1999), *Arum maculatum* is self-compatible, but because of the delay between the female and male phases (i.e. protogyny), self-pollination is extremely rare in natural conditions. Thus cross-pollination by insects is necessary in order to set seeds. But self-compatibility allows geitonogamous pollination, that is pollination between inflorescences of a same individual or clone, to be successful in *A. maculatum* and *A. italicum* (Diaz & Gibernau, unpubl. data), even though the contrary was previously reported (Lack & Diaz, 1991).

Pollinators

The type of the main pollinator/visitor varies according to the species (Table 2). There are five main types of pollination agents: Psychodids (5 *Arum* species), Sphaerocerids (2 *Arum* species plus 5 in association with Staphylinids), Drosophilids (2 *Arum* species), Ceratopogonids (2 *Arum* species) and Bruchids/Melyrids (2 *Arum* species). The three first types of pollination systems mimic the laying sites of their pollinators, respectively decaying matter, dung and rotting fruit. In the fourth pollination system (Ceratopogonids), the inflorescences imitate the insect host/prey. Due to the lack of data, it is unclear if the last pollination system mimics a reproductive or an alimentary site.

Recently, a study showed that *Arum maculatum* is frequently visited by females of *Smittia pratorum,* a terrestrial chironomid whose larvae develop in wet soil (Diaz & Kite, 2002). Nevertheless, this species is not a major pollinator because they carry very few pollen grains, probably because of their less pubescent bodies. They may be attracted not by the faeces/urine odor but by the stigma exudates on which they feed (Diaz & Kite, 2002). In Germany, 56 insects species were trapped in floral chambers of *A. maculatum* of which 94% were psychodid midges (Beck, 1983; Rohacek *et al.,* 1990). The main pollinators are females of *Psychoda phalaenoides* (93.5%) and of *P. grisescens* (5.3%). It's worth noting that even if *P. grisescens* globally represents a small portion of the total midges trapped, in some populations this species constitute up to half of the psychodids (Beck, 1983). Such variation has also been observed in England (Proctor *et al.*, 1996).

Pollinator variations can also occur among years. In *A. maculatum,* a population normally pollinated by *Psychoda phalaenoides,* flowered three weeks later during a year with bad weather conditions and was visited by *Piophila vulgaris* but had a low fruit set (Kite *et al.*, 1998).

In England, *A. maculatum* and *A. italicum* subsp *neglectum* both attracted mainly female *Psychoda phalaenoides* and *Smittia pratorum*; whereas *A. italicum* subsp *italicum* attracted mainly *P. phalaenoides* and *P. grisescens* (Diaz & Kite, 2002). On the other hand, *A. italicum* (subsp *italicum*) is pollinated by different species, namely *P. crassipenis* and *P. pusilla,* in Toulouse (Albre *et al.*, 2001). Interestingly, *P. crassipenis,* a rare species in England, has been recorded as a pollinator of British *A. italicum* (Withers, 1988). Consequently geographic variations of the pollinators of a same species might be frequent. Some other examples of such variations are detailed in the next section (see in the next paragraph "intraspecific variation").

In Israel, *Arum hygrophilum* is also pollinated by a *Psychoda* species, namely *P. cinerea,* but only the males are attracted (Koach, 1985). In this case, the inflorescence may not mimic the laying site of the pollinator as in *A. maculatum* or *A. italicum.* Interestingly, females of *P. cinerea* were caught by inflorescences of *A. italicum* cultivated in a botanical garden (Koach, 1985). In Lebanon, *Arum hygrophilum* is pollinated by another Psychodid, *Sciria advena* (Kullenberg, 1953).

Arum rupicola (misidentified as *A. elongatum*; [Boyce, 1993]) attracts *Culicoides* (Ceratopogonidae), an avian hematophagous parasite in Israel (Braverman & Koach 1982). This species cultivated in Austria or England also attracts other *Culicoides* or *Simulium* species, which are rather mammalophilic (Knoll, 1926; Drummond & Boorman, 2003). The inflorescence may mimic the fly host by its smell and heat and trap them once attracted. *Culicoides* was also trapped in rare occasions in *A. maculatum* (Beck, 1983)

These different kinds of interactions underline different mechanisms and adaptations of *Arum* species in order to achieve their sexual reproduction by trapping local insects.

Thermogenesis

While almost all the species studied are known to produce some heat, this character varies among species. The main heating event can occur during the first evening or night after the spathe has opened as in: *A. italicum, A. maculatum, A. rupicola, A. jacquemontii.* On the other hand, *A. dioscoridis, A. creticum* and *A. palaestinum* produce heat during the early morning until midday (Koach, 1985; Skubatz *et al.*, 1990; Drummond & Hammond, 1993; Bermadinger-Stabentheiner & Stabentheiner, 1995; Albre *et al.*, 2003). Finally, no rise in temperature was found in *A. hygrophilum* (Koach, 1985). Another variable parameter is the intensity of heat production. The difference of temperature between the spadix and ambient can be high (15–20°C) as in *A. italicum, A. maculatum, A. rupicola, A. jacquemontii,* medium (9–10°C) in *A. dioscoridis,* low (3°C) in *A. palaestinum* and *A. creticum,* or null as in *A. hygrophilum* (Koach, 1985; Skubatz *et al.*, 1990; Drummond & Hammond, 1993; Bermadinger-Stabentheiner & Stabentheiner, 1995; Albre *et al.*, 2003).

Odors

This paragraph is mainly based on the data presented in a major work done on 11 *Arum* species (Kite *et al.*, 1998).

Odors of *Arum* species have been recorded (Table 1) and with a few exceptions are congruent among observers (Koach, 1985; Drummond & Hammond 1991, 1993; Boyce, 1993; Kite *et al.*, 1998; Drummond & Boorman, 2003; Boyce, 2004). According to Boyce (1993), "cryptic" species, except *Arum idaeum* produce odors, whereas "flag" species, except *A. creticum* are scentless, at least for a human nose.

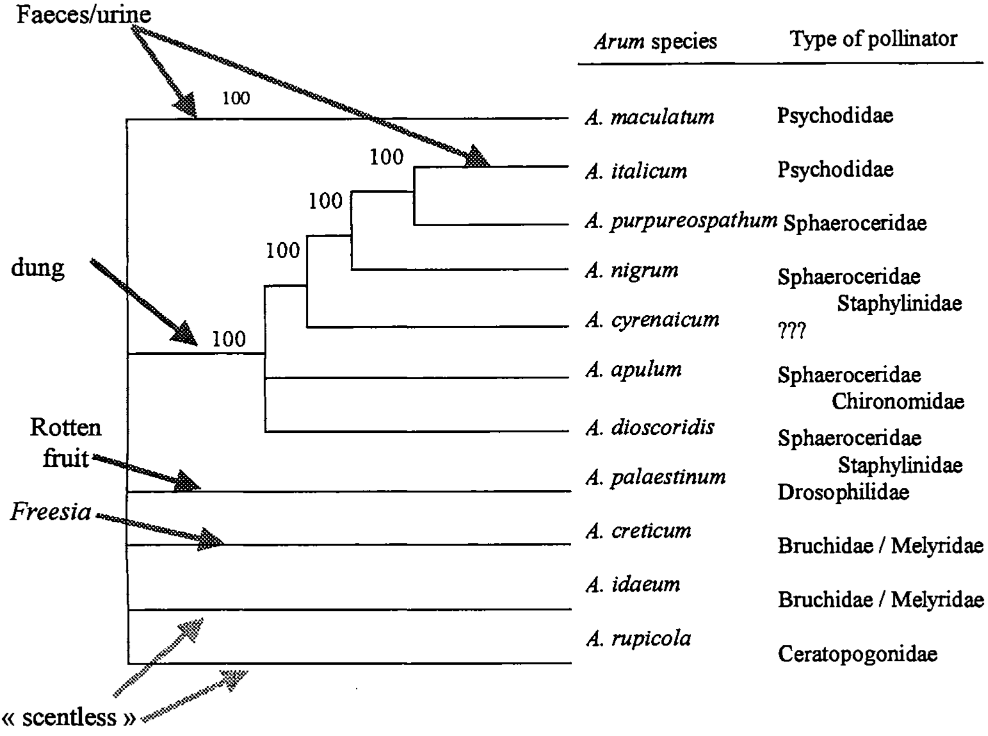

Fig. 3. Consensus strict tree ("chemogram") based on the relative abundances of the volatile compounds that composed the odor of various *Arum* species (data from Kite *et al.*, 1998; Table 3).

The odors of many *Arum* species have been studied (Kite, 1995; Kite *et al.* 1998; Diaz & Kite, 2002), in which about 36 compounds have been found (see Table 3). The volatile compounds emitted by the appendix are variable among the species, but in general their foul odor smells like faeces or decaying matter. Common compounds are butanoïc acid esters, 1-decene, terpenes (citronellene and its derivatives), *p*-cresol, methyl salicylate, indole, 2-heptanone (Table 3). Some species appear clearly different like *A. creticum* or *A. palaestinum,* whose rotten fruit odor is due to benzyl alcohol and ethyl acetate. *Arum rupicola* var. *rupicola* is also different because of a mixture of various sesquiterpenes even if *p*-cresol is abundant (Table 3).

Based on the composition of *Arum* odors published by Kite *et al.* (1998), a phylogenetic tree, that may be called a chemogram, has been produced (Fig. 3). On this "tree", *Arum* odors are grouped by chemical similarity. The integrity of one group, the 5 species with a dung odor plus *A. italicum,* is very well supported. Interestingly, *A. maculatum* and *A. italicum* which are close species with similar faecal/urine odor are not in the same group, indicating certainly an odor convergence (Kite *et al.*, 1998). *Arum maculatum* has a different odor from the "dung group" by the absence of 1-decene, β-citronellene and its derivatives: dimethyl-octadiene and trimethyl-heptadiene (Table 3, Fig. 3). Thus the faeces/urine odor of these two species have different biosynthetic origins, the one of *A. italicum* been chemically derived from a dung odor. But despite these odoriferous differences, both species are mainly pollinated by the same insect *Psychoda phalaenoides* in England (Diaz & Kite, 2002). Set apart from all others are the two species with no apparent odor (but which do emit volatile compounds!) and the two species with sweet odors similar to rotten fruit or *Freesia*. But the chemical relationships among these groups are not fully resolved.

Odors are also produced in the floral chamber, which are emitted by the fertile part of the spadix and not the chamber wall (Kite, 1995). Contrary to the odor emitted by the appendix, the floral chamber is highly homogeneous as 95% of the blend are bicyclogermacrenes for all the species studied. The exception is *A. creticum*, the only *Arum* species principally pollinated by beetles which emits α-farnesene (Kite *et al.*, 1998).

Pollinator attraction in *Arum* is mainly olfactory, thus odor change often implies different visiting/pollinating insects.

Cryptic species—Three compounds in particular are responsible for the faeces/urine odor in *Arum maculatum*: indole, *p*-cresol and 2-heptanone (Kite, 1995). But *p*-cresol is a major volatile compound of cow dung, which may explain why *A. maculatum* is pollinated 95% by females of *Psychoda phalaenoides*, since this midge lays its eggs in cow dung. Thus the midges searching by smell for a laying site may be attracted by *p*-cresol emitted by the appendix, and trapped by deceit. A field experiment showed that *Psychoda* species were attracted to traps containing *p*-cresol, 2-heptanone, indole, or any combination (Kite *et al.*, 1998). The most attractive odors were *p*-cresol alone or the mixture of the three compounds. Since *p*-cresol is present in most odors studied (Table 3), this molecule is suspected to be a general attractant for coprophilous insects (Kite *et al.*, 1998).

The odor of *A. dioscoridis* var. *dioscoridis* seems to confirm the attractive properties of 2-heptanone and *p*-cresol, since this species emitting these two compounds, attracts coprophilous staphylinid beetles and sphaerocerid flies (Drummond & Hammond, 1991). Apparently females were more numerous than males but differences were not significant as they were in the insects trapped by *A. maculatum*.

Arum palaestinum is an atypical "cryptic" species, since its appendix emits mainly ethyl acetate, producing a smell of rotten fruit. Consequently, the insects attracted are not coprophilous insects but rather different species of *Drosophila* (Koach, 1985; Kite *et al.*, 1998).

Finally, *A. idaeum* emits *p*-cresol and two derivatives (*p*-methyl anisole and 2-nitro-*p*-cresol) but in low quantities. This species is supposed to be scentless, but this suggests that it was never observed during the period of volatile production, or that the odor is not perceptible for the human nose. A sweet odor akin to violet and hyacinth has also been reported for this species by Drummond (in Kite *et al.*, 1998).

Flag species—These species are supposed to be non-smelling, except *Arum creticum*, whose odor recalls *Freesia* (Iridaceae) (Boyce, 1993). Nevertheless, these species do emit volatile compounds that can be detected by insects. Also, the appendix of *Arum rupicola* var. *rupicola* produces numerous sesquiterpenes, traces of *p*-cresol, various alcohols, esters and ketones (Kite *et al.*, 1998). These different compounds constitute a blend which attracts biting midges (Ceratopogonidae) of the genus *Culicoides* which are vertebrate parasites (Braverman & Koach, 1982; Koach, 1986; Drummond & Boorman, 2003).

Intraspecific variations—The odor in some species may vary among populations, particularly in species with large or fragmented geographical distribution, and the types of pollinators attracted may also vary. *Arum maculatum* is described as having a foul and urinous scent in England, whereas on continental Europe, it smells like a mixture of mouse, lemon and rotting plant material (Prime, 1960).

Arum palaestinum has two different ecotypes, the first type emits the odor of rotting fruit and attracts *Drosophila*; whereas the second type produces a smell of carrion which attracts necrophilous

Table 3. Relative abundances of volatile compounds* present in the odors emitted by the appendix or the floral chamber in 11 species of *Arum* (data from Kite *et al.,* 1998).

Chemical class compound names (or type)	*A. maculatum*	*A. italicum* spp. *Italicum*	*A. apulum*	*A. cyrenaicum*
APPENDIX				
Fatty acid Derivatives				
1-decene		+++	+++	+++
β-citronellene		+++	++	+++
(dimethyl-octadiene)		++	+++	+++
(trimethyl-heptadiene)	+			
Ethyl acetate				
Methyl butyrate	+	+++		++
Methyl isobutyrate		++		++
2-methyl methyl butyrate	+	++		+
2-heptanone	+++	+	+	++
3-methyl butan-2-one	+	++		
3-methyl pentan-2-one	++			
6-methyl heptan-2-one				
2-nonanone	++			
Ethanol	+	+++	+	++
Propanol				
Acetic acid				
Benzenics				
Benzeyl alcohol				
Benzaldehyde				
Methyl benzoate				
Methyl salicylate	+		+	+
p-cresol	++	+	+++	+++
p-methyl anisole				
Nitrogen compounds				
Indole	+++		++	+
Skatole				+
2-nitro-*p*-cresol				
Phenylpropanoids				
Eugenol				
Terpenoids				
α-pinene	++			
Myrcene	++			
Limonene	++	++		
Sabinene	++			
β-pinene	++			
Terpinolene	++			
Geraniol				
Geranial				
Citronellol	+			
(unidentified sesquiterpene)	+++	++	++	+++
Sesquiterpenes (various)	+++	++	++	+
FLORAL CHAMBER				
Terpenoids				
Bicyclogermacrene	++++	++++	?	++++
α-farnesene			?	

* ++++: >90%; +++: 10-90%; ++: 1–10%; +: <1%; ?: not analysed.

Table 3. Extended.

A. nigrum	*A. purpureo-spathum*	*A. dioscoridis*	*A. palaes-tinum*	*A. creticum*	*A. idaeum*	*A. rupicola* var. *rupicola*
+++	+++	+++				
+++	+++	++				
+++	+++	++				
				++		
			+++			
++	++					+
++	++					
				++		
++	+	++				
						++
++	++	++	++	++		
	++			++		
			++			
				+++		
				++		
				++		
				++		
++	++	+++			+++	+++
					++	
++				++		
++				+		
					++	
				++		
				++		
				+		
				++		
++	++	++				
++	++	++		+		+++
++++	++++	++++	++++		?	?
				++++	?	?

scarabs and flies (Koach 1985, 1986; Drummond & Hammond, 1993). In the same way, *A. orientale,* in Cyprus, is known to have a fruit-scented form attracting *Drosophila,* whereas a faecal-scented form attracts *Atheta* staphylinids (Drummond & Hammond, 1991). *Arum dioscoridis* has been collected frequently and represents the best documentation on geographical pollinator variation. In Turkey, this species traps coprophilous beetles (Staphylinidae: *Anotylus* and *Atheta*) whereas in Cyprus it is mainly coprophilous flies (Sphaerocerid: *Coproica*) with some *Anotylus* and *Atheta* (Drummond & Hammond, 1991). In Lebanon, *A. dioscoridis* is pollinated by other coprophilous beetles (Staphylinidae, Scarabaeideae) and scatophagid flies (Kullenberg, 1953), but none of the Lebanese species are the same as those from Turkey or Cyprus (Drummond & Hammond, 1991). In Israel the visitors are coprophilous flies (Sphaeroceridae, Sepsidae) and beetles (Staphylinidae, Scarabaeideae) (Koach, 1985; Papp & Rohacek, 1987). The odor variation has not been studied between these locations, but distinct odor profiles apparently exist between *A. dioscoridis* var. *dioscoridis* and *A. dioscoridis* var. *philistaeum* (Kite *et al.,* 1998). These different ecotypes may be an adaptation to a differential availability of pollinators among the localities.

Differences in volatile compounds have been found between the odor of the two English sub-species of *Arum italicum* (Diaz & Kite, 2002). In particular; 2,6-dimethyl-2,6-octadiene and one derivative are present in the odor of *A. italicum* subsp. *neglectum* and absent in *A. italicum* subsp. *italicum*. Moreover, *p*-cresol is more abundant in this latter sub-species. This odor difference may be related to the fact that *A. italicum* subsp. *italicum* attracts *P. phalaenoides* and *P. grisescens* whereas it is *P. phalaenoides* and *Smittia pratorum* in *A. italicum* subsp. *neglectum* (Diaz & Kite, 2002). Finally, an atypical French population of *A. maculatum* with yellow appendices may attract not only *Psychoda* but also domestic flies (Fridlender, 1999b). *Arum maculatum* populations where the percentage of yellow spadices is high (up to 50%) have been reported also in England but no data related to pollination exist (Prime, 1960).

CONCLUSION

Even if the inflorescence morphology is basically very similar among the different species of *Arum* (i.e. a spadix surrounded by a spathe which forms a floral chamber at its base), pollination systems appear to be diverse. Pollinator types attracted are in fact very different: beetles (Bruchidae, Scarabaeideae, Staphylinidae), flies (Drosophilidae, Sphaeroceridae, Psychodidae). So are the floral odors produced (sweet, faeces, urine, foetid, carrion, or none perceptible). Actually, the complete thermogenic pattern is known for only a few species, studying this character on new species may reveal variations of thermogenesis through the genus. Consequently, a general pollination model is clearly not valid for the whole genus, particularly since *A. creticum* shows several peculiarities. These differences are probably related to the biogeographical history of the genus. The species have, during their evolution, colonised various habitats in the different regions of Europe and Middle East in which they had experienced different climatic, ecological and fauna constraints and may have developed particular adaptations. However, in the absence of phylogenetic data, it is actually impossible to determine how these different reproductive strategies have developed and evolved during the history of this genus.

It is important to bear in mind that this review is based on data available on just a few species, with numerous species still to be studied. Such studies would allow testing different hypotheses on the evolution of plant-pollinators, for which the genus *Arum* appears to be a good system.

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LITERATURE CITED

Albre, J., A. Quilichini & M. Gibernau. 2003. Pollination ecology of *Arum italicum* (Araceae). *Bot. J. Linn. Soc.* 141:205–214.

Arcangeli, G. 1883. Sull'impollinazione in alcune Araceae. *Nuovo Giorn. Bot. Ital.* 15:72–97.

Barabé, D., M. Gibernau & F. Forest. 2002. Zonal thermogenetic dynamics of two *Philodendron* species from two different subgenera (Araceae). *Bot. J. Linn. Soc.* 139:79–86.

Barabé, D., C. Lacroix & M. Gibernau. 2003. Development of the flower and inflorescence of *Arum italicum* (Araceae). *Can. J. Bot.* 81:622–632.

Bay, D. C. 1995. Thermogenesis in the Aroids. *Aroideana* 18:32–39.

Beck, I. 1983. Blütenökologische Untersuchungen am Aronstab (*Arum maculatum* L.). Unpublished Thesis, University of Tübingen. 122p.

Bermadinger-Stabentheiner, E. & A. Stabentheiner. 1995. Dynamics of thermogenesis and structure of epidermal tissues in inflorescences of *Arum maculatum*. *New Phytol.* 131:41–50.

Boyce, P. 1993. *The Genus Arum.* The Royal Botanic Gardens, Kew, London. 197p.

———. 2004. *Arum*–a decade of change. *The Plantsman* (In press).

Braverman, Y. & Y. Koach. 1982. Culicoides species found in the inflorescences of *Arum elongatum* in Israel. *Mosquito News* 42:516–517.

Church, A. H. 1908. *Types of Floral Mechanism: A Selection of Diagrams and Descriptions of Common Flowers Arranged as an Introduction to the Systematic Study of Angiosperms.* Clarendon Press, Oxford.

Croat, T. B. 2000. History and current status of systematic research with Araceae. web page: www.aroid.org/literature/croat/history/history_contents.html.

Diaz, A. & G. C. Kite. 2002. A comparison of the pollination ecology of *Arum maculatum* and *A. italicum* in England. *Watsonia.* 24:171–181.

Dormer, K. J. 1960. The truth about pollination in *Arum. New Scient.* 59:298–301.

Drummond, D. C. & P. M. Hammond. 1991. Insects visiting *Arum dioscoridis* SM. and *A. orientale* M. Bieb. *Entomol. Month. Mag.* 127:151–156.

———. 1993. Insects visiting *Arum creticum* Boiss. & Heldr., *A. concinnatum* Schott and *A. purpureospathum* Boyce. *Entomol. Month. Mag.* 129:245–251.

Drummond, D. C. & J. Boorman. 2003. Further records of some Arum species and their insect visitors. *Entomol. Month. Mag.* 139:163–166.

Fridlender, A. 1999a. Identification des *Arum* de la flore française. *J. Bot. Soc. bot. France* 11:29–43.

———. 1999b. Observations sur la biologie de l'*Arum cylandraceum* Gasp. (Araceae) en Corse. *Acta Bot. Gall.* 146:297–309.

Gibernau, M. 2003. Pollinators and visitors of Aroid inflorescences. *Aroideana* 26:66–83.

Gibernau, M., D. Barabé, P. Cerdan & A. Dejean. 1999. Beetle pollination of *Philodendron solimoesense* (Araceae) in French Guiana. *Int. J. Plant Sci.* 160:1135–1143.

Gibernau, M., D. Macquart & A. Diaz. 2003. Pollen viability and longevity in two species of *Arum. Aroideana* 26:27–32.

Grensted, L. W. 1947. Diptera in the spathes of Arum maculatum L. *Entomol. Month. Mag.* 83:1–3.

Kite, G. C. 1995. The floral odor of *Arum maculatum. Bioch. Syst. & Ecol.* 23(4):343–354.

Kite, G. C., W. L. A. Hetterscheid, M. J. Lewis, P. C. Boyce, J. Ollerton, E. Cocklin, A. Diaz & M. S. J. Simmonds. 1998. Inflorescence odours and pollinators of *Arum* and *Amorphophallus* (Araceae), pp. 295–315 *In* S. J. Owens & P. J. Rudall (eds.), *Reproductive Biology.* Royal Botanic Gardens, Kew.

Knoll, F. 1926. Die *Arum*—Blütenstände und ihre Besucher. *Abh. zool.-bot. Ges. Wien* 12:381.

Koach, J. 1985. Bio-ecological studies of flowering and pollination in Israeli Araceae. Unpubl. PhD Thesis, University of Tel-Aviv, Israel. In Hebrew (English abstract). 179p.

Koach, J. 1986. Araceae, pp. 330–340 *In* D. N. Feinburn (ed.), Flora Palaestina. Israel Academy of Science and Humanities, Jerusalem.

Kullenberg, B. 1953. Observationer över Arum-pollinerare i Libanons kustomade. *Svensk Botanisk Tidskrift* 47: 24–29.

Lachmann, A. D., C. Baier & M. Mierke. 2000. Life cycle of *Psychoda cinerea, P. parthenogenetica* and *P. trinodulosa* (Diptera, Psychodidae). 2. Adults. *Stud. Dipterol.* 7:533–542.

Lack, A. J. & A. Diaz. 1991. The pollination of *Arum maculatum* L.—a historical review and new observations. *Watsonia* 18:333–342.

Lamarck de, M. M. 1783. Encyclopédie méthodique—Botanique. Tome 3. Panckoucke, Paris.

Lamb, A. 1956. An investigation of the efficiency of the pollination mechanism in lords-and-ladies. *Blundell Sch. Sci. Soc. Mag.* 2:33–37.

Mayo, S. J., J. Bogner J. & P. C. Boyce. 1997. *The Genera of Araceae*. Royal Botanical Gardens, Kew. 370 p.

Méndez, M. 1998. Modification on phenotypic and functional gender in the monoecious *Arum italicum* (Araceae). *Amer. J. Bot.* 85:225–234.

———. 1999. Effects of sexual reproduction on growth and vegetative propagation in the perennial geophyte *Arum italicum* (Araceae). *Plant Biol.* 1:115–120.

———. 2001. Sexual mass allocation in species with inflorescences as pollination units: a comparison between *Arum italicum* and *Arisaema* (Araceae). *Amer. J. Bot.* 88:1781–1785.

Méndez, M. & J. R. Obeso. 1992. Influencia del osmoforo en la produccion de infrutescencias en *Arum italicum* Miller (Araceae). *An. Jard. Bota. Madrid* 50: 229–237.

Méndez, M. & J. R. Obeso. 1993. Size-dependant reproductive and vegetative allocation in *Arum italicum* (Araceae). *Can. J. Bot.* 71:309–314.

Méndez, M. & A. Diaz. 2001. Flowering dynamics in *Arum italicum* (Araceae): relative role of inflorescence traits, flowering synchrony, and pollination context of fruit initiation. *Amer. J. Bot.* 88:1774–1780.

Ollerton, J. & A. Diaz. 1999. Evidence for stabilising selection acting on flowering time in *Arum maculatum* (Araceae): the influence of phylogeny on adaptation. *Oecologia* 113:340–348.

Papp, L. & J. Rohacek. 1987. The sphaeroceridae (Diptera) of Israel. *Israel J. Entomol.* 21:77–109.

Prime, C. T. 1960. *Lords and Ladies*. Collins, London. 241p.

Proctor, M., P. Yeo & A. Lack. 1996. *The Natural History of Pollination*. Harper Collins Publishers, London. 479p.

Rohacek, J., I. Beck-Haug & K. Dobat. 1990. Sphaeroceridae associated with flowering *Arum maculatum* (Araceae) in the vicinity of Tübingen, SW-Germany. *Senckenbergiana Biol.* 71: 259–268.

Schmucker, T. 1925. Beiträge zur Biologie und Physiologie von Arum maculatum. *Flora* 118/119:460–475.

Skubatz, H., T. A. Nelson, A. M. Dong, B. J. D. Meeuse & A. J. Bendich 1990. Infrared thermography of Arum lily inflorescences. *Planta* 182:432–436.

Sowter, F. A. 1949. Arum maculatum L. *J. Ecol.* 37:207–219.

Withers, P. 1988. Revisionary notes on British species of *Psychoda* Latreille (Diptera, Psychodidae) including new synonyms and a species new to science. *Br. J. Ent. Nat. Hist.* 1:69–76.