INFLORESCENCE ODOURS AND POLLINATORS OF *ARUM* AND *AMORPHOPHALLUS* (ARACEAE)

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Abstract

Chemical analyses of the inflorescence odours of 11 species of *Arum*, 20 species of *Amorphophallus* and two species of *Pseudodracontium* are presented and compared to the limited published data that are available on pollinators of these species.

The chemical odour profiles of dung-smelling *Arum* species were complex, with butanoic acid esters, 1-decene, two dimethyloctadienes, *p*-cresol, indole and 2-heptanone being among the most common identified major constituents in species analysed. The fragrant odour of *Arum creticum* consisted mainly of benzyl alcohol, while ethyl acetate dominated the fruity odour of *A. palaestinum*. The odour of *A. rupicola* var. *rupicola* consisted mainly of various sesquiterpenoids.

Experiments on the pollination ecology of *A. maculatum* revealed that its major pollinator, *Psychoda phalaenoides*, was not attracted to the heat generated by the spadix. However, three important components of the odour, *p*-cresol, indole, and 2-heptanone, were attractive to species of *Psychoda* in field tests, with *p*-cresol showing most activity. Data on the phenology of flowering in *A. maculatum* and *Psychoda* flight activity suggested that any synchronisation of flowering and pollinator abundance may be disrupted by physical conditions.

The odours of *Amorphophallus* and *Pseudodracontium* species with 'gaseous' or carrion smells had a simple chemical composition, consisting mainly of dimethyl oligosulphides. The odours of other *Amorphophallus* species having different smells were also generally dominated by one or two compounds: trimethylamine in *A. brachyphyllus*, isocaproic acid in *A. elatus*, 4-methoxyphenethyl alcohol in *A. albispathus*, isoamyl acetate with ethyl acetate in *A. haematospadix*, and ocimene in *A. margaritifer*.

Two odour types associated with carrion-mimicry and dung-mimicry are proposed for the sapromyophilous species of *Arum* and *Amorphophallus*.

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Introduction

Floral odours can be important in attracting pollinators and are therefore subject to the evolutionary selective forces that act to improve a plant's reproductive success (Knudsen, 1993). The diversity of odour cues, arising from both the immense diversity of chemical compounds and the ways in which they can be combined, is potentially greater than can be achieved with other forms of pollinator signalling, such as visual and tactile cues (Knudsen *et al.*, 1993). This diversity allows for the evolution of dedicated plant-pollinator interactions in which a single pollinator type (species or higher taxon) is signalled, thereby excluding vectors that may interfere with the process of cross pollination (Williams and Dodson, 1972). Chemical signals also have the potential to act over great distances, attracting pollinators from a wide catchment area (Steiner, 1952; Williams and Dodson, 1972).

Whilst visual and tactile cues have been much documented in various pollination syndromes, such that potential pollinators can sometimes be predicted from the shape and colour of a flower, attempts to correlate floral odour types with general classes of pollinators have, until recently, relied on subjective descriptions of the scent (Fægri and van der Pijl, 1979). This is mainly due to the technical difficulties associated with the chemical analysis of floral odours and gauging the responses of the pollinators to individual odour components (Dobson, 1994). Recent data on the chemistry of odour types associated with different pollination syndromes have come mainly from extensive analyses of orchid odours (Kaiser, 1993) and surveys of the scents of moth- and bat-pollinated flowers (Knudsen and Tollsten, 1993; 1995). These studies have resulted in some broad generalisations on the chemical nature of odour types but narrower definitions of the scent chemistry have not been possible due to the complex nature of the scents and the lack of information on the sensory preferences of pollinators.

Flowers pollinated by insects that feed or breed on dung or carrion and which attract pollinators by deceit (Dafni, 1984) may provide the clearest examples of well-defined chemical odour syndromes (Dobson, 1994). Unfortunately, the odours of only a few species which potentially show this pollination syndrome have been analysed. The putrid and faecal odours produced by some orchid species in the genera *Cirrhopetalum* and *Masdevallia* appear to be due to various short chain aliphatic acids, such as butyric acid and isovaleric acid and their alcohols and esters (Kaiser, 1993), while the fetid smell of the parasitic plant *Hydnora africana* (Hydnoraceae) contains dimethyl di- and trisulphides and long chain organic acids as the major components (Burger *et al.*, 1988).

Araceae is a family renowned for having unpleasant floral odours (Vogel, 1962), although there are aroids with strongly fragrant or distinctive odours (Willis, 1952). The range of compounds reported so far as the major constituents of aroid odours reflects this diversity: various benzenoids, phenylpropanoids and organic acids in *Spathiphyllum cannifolium* (Lewis *et al.*, 1988); a novel compound, 1,3,6-trimethyl-2,5-dioxabicyclo[3.2.1.]nonane, in *Peltandra virginica* Knuth (= *P. virginica* (L.) Rafin; Patt *et al.*, 1992) and various dimethyl oligosulphides in *Sauromatum venosum* (Ait.) Kunth (reported as S. *guttatum* Schott; Borg-Karlson *et al.*, 1994). Perceived odour variation in aroids can also occur within one genus, such as *Arum* and *Amorphophallus* (Willis, 1952; Boyce, 1993). Thus, as with orchids, the family affords the opportunity to examine the volatile compounds associated with different pollination syndromes among related species, and particularly volatiles associated with pollination by dung and carrion feeding or breeding insects - part of the sapromyophilous syndrome (Fægri and van der Pijl, 1979).

In this paper we present data on the floral odours of 11 species of *Arum*, 20 species of *Amorphophallus* and two species of the related genus *Pseudodracontium*. We review information on potential pollinators in these genera in an attempt to identify some of the odour characteristics associated with sapromyophily.

Odour analysis: techniques and precautions

The technique of headspace trapping followed by thermal desorption - gas chromatography - mass spectrometry (TD-GC-MS) has become the accepted technique for the analysis of floral odours (Kaiser, 1991). This involves passing air from around a flower or inflorescence (the headspace) through an odour trap packed with a porous polymer (e.g. Tenax, Poropak) which retains the volatile organic compounds (Cole, 1980). The odour compounds are then removed from the trap in a stream of hot inert gas and passed either directly, or more usually via some cryofocussing system, onto the column of a gas chromatograph coupled to an on-line mass spectrometer to achieve both separation and identification of the components.

Floral odours contain a wide variety of compounds that may be present at greatly differing concentrations. The composition of the odour may also vary through flowering time (Lewis *et al.*, 1988). Therefore a floral odour cannot be fully described with a single analysis. Ideally, several trapping substances should be employed with different compound retention characteristics; chromatography should be undertaken on different polarity columns to achieve optimal analysis of the various odour components; odour trapping should be performed at various times during scent production; and, if minor but potentially important odour components are to be identified, serial post-chromatography re-trapping and analysis of these is required. Unfortunately, such detailed dissection of a floral scent is often not practicable due to their ephemeral nature. This is particularly true in some aroids where odour production can be brief, sometimes lasting just a couple of hours.

The analyses reported here were obtained using traps packed with Tenax TA and compounds were chromatographed on a non-polar column (for details see Table 1). This method may result in very small molecules going undetected as Tenax TA is reported to have relatively poor affinity for compounds containing fewer than five carbon atoms (Bertsch *et al.*, 1974). In particular, aroid odours are reported to have aminoid components (Smith and Meeuse, 1966) and such components in other floral odours have proved difficult to confirm chemically by headspace trapping followed by TD-GC-MS (Kaiser, 1993). However, it has been shown that C_2-C_4 monoamines should be revealed by this method if they are major components of aroid odours (Kite, 1995), but ammonia will not be detected. A further technical reservation that needs to be considered when interpreting the results is that polar compounds, such as organic acids, may go undetected at low concentration due to their poor chromatography on the non-polar column used (Adams, 1995).

Inflorescence odours and pollinators in *Arum*

The genus *Arum* comprises 26 currently recognised species of temperate herbs with a distribution through Europe to W. China but centred around the Mediterranean (Boyce, 1993; 1995). It belongs to tribe Areae which is traditionally considered to be one of the most highly evolved in Araceae (Boyce, 1993). In particular, species of *Arum* have evolved complex pollination systems in which pollinating insects are temporarily trapped in a chamber at the base of the spathe containing the fertile part of the spadix (Knoll, 1926; Lack and Diaz, 1991). Their inflorescence odours, which emanate from the appendix of the spadix, are also perceived to be complex and are often described as mimicking various types of dung, although not all are reported to be scented. The species with foul odours are generally those in which the spathe is positioned near the ground (so-called 'cryptic' species): those where the spathe is held above the leaves ('flag species') are said to be scentless, except *A. creticum* which has a pungent 'lemon-freesia' scent (Boyce, 1993).

Various compounds have been implicated in the complex dung odours of *Arum* and it is likely that different analysis techniques will reveal different compounds. Skatole (3-methyl indole), methylamine and ammonia have been detected by paper chromatography of the condensates produced from cut and enclosed warm spadices of *A. italicum* and *A. dioscoridis*; additionally, several other aliphatic amines and putrescine were detected in the condensate of *A. italicum* (Smith and Meeuse, 1966). However, the odour of *A. maculatum* was found to be considerably more complex when it was analysed by non-invasive headspace odour trapping techniques (Kite, 1995). Fifty-six compounds were identified, major components being 2-heptanone, indole (each comprising 8–23% of the volatiles among the inflorescences studied) and bicyclogermacrene[1] (10–14%). *p*-Cresol was also a notable odorous component (0.2–6%) as were several ketones and esters, but simple aliphatic amines were not detected; the majority of the compounds were terpenoids. Vogel (1962) suggested previously that the odour of this species was possibly not due to amines but esters and terpenoids.

Using microheadspace techniques, Kite (1995) also revealed that the bicyclogermacrene component of the total inflorescence odour of *A. maculatum* arose solely from the chamber to give it a more pleasant character than the appendix odour. Microheadspace collections could not be refined to the extent of determining the exact source of the bicyclogermacrene within the chamber but it was assumed to emanate from the fertile region of the spadix, as no odour could be detected from the spathe. Contrasting appendix and chamber odours have also been found in *Sauromatum venosum* in which a lemon odour emanates from the club-shaped sterile organs situated above the pistillate flowers (Meeuse *et al.*, 1984). This sweet odour has been reported to consist mainly of α-pinene and limonene (Borg-Karlson *et al.*, 1994) and it has been suggested that it provides feeding and mating stimuli to the pollinators and serves to keep them inside the chamber until anthesis (Meeuse *et al.*, 1984).

Using non-invasive headspace sampling techniques, we have analysed the odours of ten other species of *Arum* (Table 1). As with *A. maculatum*, most of the odours were very complex and, while the odours of different inflorescences on the same plant had similar chemical profiles, some quantitative and qualitative variation was evident where analysis of different individuals was possible. Nevertheless, with the exception of *A. dioscoridis*, the most important constituents (in terms of absolute levels) that appeared characteristic for each species could be identified (Table 1). The data obtained to date for *A. dioscoridis* suggests that var. *dioscoridis* and var. *philistaeum* have distinct odour profiles.

The appendix odours of species analysed from *Arum* section *Dioscoridea* subsection *Dischroochiton* (Table 1) all had similar chemical profiles that were dominated by three unsaturated hydrocarbons: 1-decene and two dimethyloctadienes (absolute structures could not be determined from the mass spectra). *p*-Cresol was also an important component and methyl butyrate and methyl isobutyrate were present in all except the single analysis performed on *A. apulum*. Indole and skatole could be detected in some analyses of these four species and, apart from 2-heptanone and the ubiquitous ethanol component, the other major constituent was an uncommon sesquiterpenoid that could not be identified from searching available mass spectral libraries. In terms of mass spectrum and relative retention time, this sesquiterpenoid was identical to the major appendix sesquiterpenoid found in the appendix odour of *A. maculatum* (Kite, 1995). A high resolution GC-MS analysis of *A. nigrum* odour on a polar column also revealed numerous esters and organic acids and some alcohols, aldehydes and ketones as trace compounds. The odours of species in subsection *Dischroochiton* are generally described as being reminiscent of horse dung and are reported to attract various dung-breeding flies and beetles (Table 2).

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[1] This compound was identified as germacrene B by Kite (1995) according to published GC-MS data (Adams, 1989). The data for germacrene B has since been reassigned to bicyclogermacrene (Adams, 1995).

The appendix odour of *A. italicum* (section *Arum* subsection *Arum*) was very similar to the appendix odours of the species examined from section *Dioscoridea* subsection *Dischroochiton* in containing 1-decene and the two dimethyloctadienes as the major constituents together with methyl butyrate, methyl isobutyrate and the unidentified sesquiterpenoid. Consequently the odour was distinct from that of *A. maculatum*, another species in section *Arum*, in which 1-decene and the two dimethyloctadienes could not be detected. Mono- and sesquiterpenoids were also more important components of the odour of *A. maculatum* than in the odour of *A. italicum*. Psychodid midges are the major pollinators of *A. maculatum* (Lack and Diaz, 1991) and have also been reported to be the main insects attracted to *A. italicum* (Méndez and Obeso, 1992) even though its odour appears distinct from that of *A. maculatum*. Further observations on pollination in *A. italicum* are required.

The appendix odour of *A. creticum*, a flag species, had an entirely different chemical profile to the above cryptic, dung-smelling species, as might be anticipated from its pungent freesia-like odour (Table 1). The dominant component (in excess of 80% composition) was benzyl alcohol but the characteristics of the odour were probably imparted by some of the minor components such as geraniol, geranial and eugenol. Indole, skatole and traces of *p*-cresol were detected in some analyses but the unknown sesquiterpenoid, common to all the above cryptic species, was absent. The species is reported to attract scarab, staphylinid and bruchid beetles, but only bruchids have been observed to carry pollen (Table 2). *Arum idaeum*, a cryptic species thought to be closely related to *A. creticum* (both in section *Dioscoridea* subsection *Creticum*), had a different odour profile. Its appendix odour was composed of *p*-cresol and the *p*-cresol derivatives *p*-methyl anisole and 2-nitro-*p*-cresol. However, only one analysis was made for this species and the quantities of compounds trapped were low. The species is said to be scentless (Boyce, 1993) but Drummond (pers. comm.) reports a sweet odour akin to violets and hyacinth. Another flag species analysed, *A. rupicola* var. *rupicola*, is also claimed to be scentless, but odour analysis here revealed numerous sesquiterpenoids and trace amounts of *p*-cresol, various alcohols, esters and ketones. The species is reported to attract blood-sucking midges belonging to the genus *Cuculoides* that are parasitic on birds (Koach, 1986).

The appendix odour of *A. dioscoridis* var. *dioscoridis* was of the *Dischroochiton* type but an initial analysis of *A. dioscoridis* var. *philistaeum* revealed that the odour contained numerous esters of butanoic acid and lacked 1-decene, dimethyloctadienes, *p*-cresol, and sesquiterpenoids. If confirmed, this divergence of odours amongst these two varieties is surprising given that the varietal status is only based on intergrading staining and patterning of the spathe. An ammonia-like odour could be perceived in the smell of *A. dioscoridis* and the production of free ammonia or amines has been demonstrated by the fumes created with hydrochloric acid placed near to the appendix (Meeuse and Raskin, 1988). As mentioned previously, free ammonia would not be detected by the methods used in the present study. *Arum palaestinum* is placed with *A. dioscoridis* in section *Dioscoridea* subsection *Poeciloporphyrochiton* but it also had a quite distinct appendix odour, consisting almost entirely of ethyl acetate, and lesser amounts of ethanol and acetic acid. The inflorescence had an odour of rotting fruit and the species is reported to attract fruit flies, *Drosophila* spp. (Koach, 1986). *Arum dioscoridis* has been described as having a donkey-dung odour, which again attracts dung-breeding flies and beetles (Table 2).

With the exception of *A. creticum*, the chamber odours of all the species for which collections were performed were found to consist of over 95% bicyclogermacrene (Table 1), as reported for *A. maculatum*. In contrast, the chamber odour of *A. creticum* consisted of a similar percentage of α-farnesene. Given the apparent consistency of the chamber odours among the other species, even between those with very different appendix odours, such as *A. dioscoridis* and *A. palaestinum*, the divergence in the chamber odour of *A. creticum* is likely to be of either taxonomic or biological significance. It would therefore be interesting to determine the chamber odour of *A. idaeum*, the species considered to be most closely related to *A. creticum*.

TABLE 1. Major components* of the appendix and chamber odours of inflorescences of *Arum* species. Odours were collected from inflorescences still attached to plants cultivated at the Royal Botanic Gardens, Kew, except for *A. maculatum* which was growing wild. The appendix odour was collected by sucking air from around a warm appendix through a trap (100 mm long × 3 mm diameter packed with 100 mg of Tenax TA 35/60 mesh) at a rate of 25 ml/min by means of a portable pump. The trap was screwed into one end of a glass tube which covered the appendix. The chamber odour was collected by sucking air at the same rate through a second identical trap attached to a Pasteur pipette that was inserted into the chamber either through the chamber entrance or wall. Sampling times varied depending on the quantity of volatile compounds being produced. The odour collected on the traps was analysed by direct thermal desorption - gas chromatography - mass spectrometry exactly as described by Kite (1995). The results summarise the data obtained from the number of plants, inflorescences and analyses indicated; chamber odours were not collected for *A. apulum*, *A. idaeum* or *A. rupicola*. Compounds that did not constitute more than 1% of the odour in any of the species examined are not listed. Data for *A. maculatum* are from Kite (1995).

Section: Subsection:		*Arum* *Arum*	*Dischroochiton*					*Dioscoridea* *Poecilophor-* *phyrochiton*	*Cretica*		*Tenui-* *filia*
HEADSPACE ANALYSED **Class of compound** Compound name (or type)	identification criteria**	*A. maculatum* L.	*A. italicum* Mill. ssp. *italicum*	*A. apulum* (Carano) P.C. Boyce	*A. cyrenaicum* Hruby	*A. nigrum* Schott	*A. purpureospathum* P.C. Boyce	*A. dioscoridis* Sm. var. *dioscoridis*	*A. palaestinum* Boiss.	*A. creticum* Boiss. & Held.	*A. idaeum* Coust. & Gandoger	*A. rupicola* Boiss. var. *rupicola*
APPENDIX												
Fatty Acid Derivatives												
1-decene	b		+++	+++	+++	+++	+++	+++				
(dimethyloctadiene)	c		+++	++	+++	+++	+++	++				
(dimethyloctadiene)	c		++	+++	+++	+++	+++	++				
(trimethylheptadiene)	c	+								++		
ethyl acetate	a								+++			
methyl butyrate	a	+	+++		++	++	++					+
methyl isobutyrate	a		++		++	++	++					
methyl 2-methyl butyrate	a	+	++		+					++		
2-heptanone	a	+++	+	+	++	++	+	++				
3-methyl butan-2-one	c	+	++									
3-methyl pentan-2-one	c	++										
6-methyl heptan-2-one	c											++
2-nonanone	b	++										
ethanol	a	+	+++	+	++	++	++	++	++	++		
propanol	a							++		++		
acetic acid	a								++			
Benzenoids												
benzyl alcohol	a									+++		
benzaldehyde	a									++		
methyl benzoate	b									++		

TABLE 1 continued

HEADSPACE ANALYSED Class of compound Compound name (or type)	identification criteria**	A. maculatum L.	A. italicum Mill. ssp. italicum	A. apulum (Carano) P.C. Boyce	A. cyrenaicum Hruby	A. nigrum Schott	A. purpureospathum P.C. Boyce	A. dioscoridis Sm. var. dioscoridis	A. palaestinum Boiss.	A. creticum Boiss. & Held.	A. idaeum Coust. & Gandoger	A. rupicola Boiss. var. rupicola
Benzenoids contd.												
methyl salicylate	b	+		+	+					++		
p-cresol	a	++	+	+++	+++	++	++	+++			+++	+++
p-methyl anisole	c										++	
Nitrogen compounds												
indole	a	+++		++	+	++				++		
skatole	b				+	++				+		
2-nitro-p-cresol	c										++	
Phenylpropanoids												
eugenol	a									++		
Terpenoids												
α-pinene	a	++										
myrcene	a	++										
limonene	a	++	++									
sabinene	a	++										
β-pinene	a	++										
terpinolene	a	++										
geraniol	b									++		
geranial	b									+		
citronellol	b	+								++		
(unidentified sesquiterpenoid)	c	+++	++	++	+++	++	++	++				
(sesquterpenoids generally)	c	+++	++	++	+	++	++	++		+		+++
CHAMBER												
Terpenoids												
bicyclogermacrene	b	++++	++++	?	++++	++++	++++	++++	++++		?	?
α-farnesene	b			?						++++	?	?
number of analyses performed		3	4	1	7	5	2	9	7	9	1	2
number of inflorescences analysed		3	2	1	3	2	1	6	2	6	1	2
number of plants analysed		3	2	1	2	1	1	1	1	3	1	1

* + signs indicate the average level of compounds in odour (determined by GC peak area):

++++ >90%

+++ 10–90%

++ 1–10%

+ <1% (indicated only if present in another species at higher level)

? chamber headspace not analysed

** compound identification criteria:

        a = comparison of mass spectrum and retention time with authentic standard

        b = comparison of mass spectrum and relative retention time with published data (Adams, 1995)

        c = comparison of mass spectrum with published data (Ausloos *et al.*, 1992)

TABLE 2. Insects reported in inflorescences of *Arum* species. Insect species specified only when they predominated.

Species (Locality/Ecotype)	Most numerous insects found in inflorescences	Other insects found in inflorescences	Reference
Arum concinnatum Schott (Crete)	*Coproica ferruginata* (Stenhammer) (Diptera: Sphaeroceridae)	Diptera: Sphaeroceridae 2 spp. Coleoptera: Staphylinidae 2 spp.	Drummond & Hammond (1993)
A. concinnaum (UK- in cultivation)	*Psychoda phalaenoides* (L.) (Diptera: Psychodidae)	Diptera: Chironomidae 1 sp., Sphaeroceridae 1 sp.	Drummond & Hammond (1993)
A. creticum Boiss. & Held. (Crete)	Coleoptera: nine families including Scarabaeidae, Staphylinidae and Bruchidae	Diptera and Hymenoptera	Drummond & Hammond (1993)
A. dioscoridis Sm. (Lebanon)	Coleoptera: Staphylinidae 2 spp., Scarabaeidae 4 spp., Hydrophilidae 1 sp. Diptera: Scatophagidae 2 spp.		Kullenberg (1953)
A. dioscoridis (Cyprus)	*Coproica ferruginata* (Stenhammer), *C. vagans* (Haliday) (Diptera: Sphaeroceridae) *Anotylus clypeonitens* (Pand.), *A. insutus* (Grav.) (Coleoptera: Staphylinidae)	Diptera: Sphaeroceridae 6 spp., Drosophilidae 3 spp. Coleoptera: Staphylinidae 8 spp.	Drummond & Hammond (1991)
A. dioscoridis (S Turkey / lacked odour)	—	Coleoptera: Staphylinidae 5 spp.	Drummond & Hammond (1991)
A. elongatum Stev. (Israel)	*Cuculoides* spp. (Diptera: Ceratopogonidae)		Braverman & Koach (1982)
A. hygrophilum Boiss. (Israel)	Diptera: Psychodidae		Koach (1986)
A. italicum Mill. (N Spain)	Diptera: Psychodidae	Diptera: Chironomidae, Sciaridae, Sphaeroceridae, Ceratopogonidae, Heleomyzidae	Méndez & Obeso (1992); Méndez, pers. comm.
A. italicum subsp. *neglectum* (F. Towns.) Prime (S England)	Diptera: Psychodidae	Diptera: Sphaeroceridae	Prime (1954)
A. maculatum L.	*Psychoda phalaenoides* (L.) (Diptera: Psychodidae)		Müller (1883)

TABLE 2 continued

A. maculatum (UK)	*Psychoda phalaenoides* (L.)	other *Psychoda* spp.	Sowter (1949)
A. maculatum (UK)	female *Psychoda phalaenoides* (L.)		Prime (1960)
A. maculatum (S England)	female *Psychoda phalaenoides* (L.)		Lack and Diaz (1991)
A. maculatum (N Germany)	Diptera: Psychodidae	Coleoptera: Staphylinidae Other Diptera	Present study
A. maculatum (Hurley, S. England, 1994)	*Psychoda phalaenoides* (L.)	Other *Psychoda* spp.	Kite (1995)
A. maculatum (Hurley, S England, 1996)	*Piophila vulgaris* Fall. (Diptera: Piophilidae)	*Psychoda* spp. including *P. phalaenoides* (L.) Diptera: Cecidomyiidae 1 sp. Diptera: Phoridae 1 sp. *Megaselia* sp. (Diptera: Phoridae) *Fannia canicularis* L. (Diptera: Muscidae)	Present study
A. nigrum Schott (Germany - in cultivation)	Diptera: Sphaeroceridae (many e.g. *Sphaerocera* spp.) Coleoptera: Scarabaeidae (many e.g. *Aphodius* spp.), Staphylinidae (many e.g. *Atheta* spp.)	Other Diptera & Coleoptera	Knoll (1926)
A. sintenisii (Engl.) P.C. Boyce (=*A. orientale* M. Bieb) (Cyprus)	5 *Drosophila* spp. (Diptera: Drosophilidae) 4 *Atheta* spp. (Coleoptera: Staphylinidae)		Drummond & Hammond (1991)
A. palaestinum Boiss. (ecotype 1, fermenting fruit odour) (Israel)	Diptera: Drosophilidae		Koach (1986)
A. palaestinum (ecotype 2, dung and carrion odour) (Israel)	"beetles & flies"		Koach (1986)
A. purpureospathum P.C. Boyce (UK - in cultivation)	*Copromyza equina* Fallén, *C. similis* (Collin) (Diptera: Sphaeroceridae)	Diptera: Psychodidae 1 sp., Chironomidae 1 sp.	Drummond & Hammond (1993)
A. rupicola Boiss. (Germany - in cultivation)	*Cuculoides* spp. (Diptera: Ceratopogonidae),	Diptera: Simulidae	Knoll (1926)

Pollination ecology of *Arum maculatum*:
new observations and future work

The pollination of *A. maculatum* by *P. phalaenoides* and the operation of the inflorescence as a pit-fall trap have been studied in detail (Prime, 1960; Lack and Diaz, 1991). Nevertheless observations are still required on the pollination ecology of *A. maculatum* to understand further the factors affecting the success of pollinator trapping.

We have investigated the role of both the heat produced by the spadix appendix (Bermadinger-Stabentheiner and Stabentheiner, 1995) and its odour in attracting *Psychoda* species. In an experiment in which glass tubes heated to 10°C above ambient temperature were used to mimic a warm spadix appendix, *P. phalaenoides* showed avoidance of heat in two out of four experiments and no significant response in the other two (Table 3). Knoll (1926), in a study of *A. nigrum* (see Dormer, 1960), also found that an electrically heated model inflorescence failed to attract that species' pollinators while a cold model charged with stale blood and glycerine did attract various carrion insects. In these two species it appears, therefore, that the heat produced by the spadix does not attract pollinators directly. Its main function is probably to volatilise the odour (Meeuse and Raskin, 1988).

In a field-trapping experiment, *Psychoda* species were attracted to *p*-cresol, indole and 2-heptanone, three of the major chemical components of the odour of *A. maculatum*, either individually or in combination (Table 4). *p*-Cresol was the most effective individual attractant but a mixture of *p*-cresol, indole and 2-heptanone was more active than any single compound or pair of compounds. A key role for *p*-cresol in attracting *P. phalaenoides* was suggested previously from the finding that this compound was an important component of cow-dung odour (Kite, 1995). Cow dung is the normal breeding habitat of *P. phalaenoides* (Withers, 1988) and its odour is presumably mimicked by *A. maculatum*. *p*-Cresol was also present, and generally an important constituent, in the odours of all the dung-smelling species of *Arum* examined so far (Table 1) suggesting that it may be a general attractant for dung-breeding insects.

TABLE 3. Responses of *Psychoda phalaenoides* to heat. Between five and ten midges were introduced into the centre of a rectangular glass tank (35 × 22 × 24 cm) fitted with a cardboard lid through which protruded two boiling tubes 19 cm apart. One tube contained a thermostatic 2.3 kW heating cable which warmed the tube to 10°C above ambient; the surface of the tubes were either left dry or wrapped in wet filter paper. The number of midges in each half of the tank was then recorded every 5 min for 90 min.

Experiment		Treatment	No. midges median (range)	Wilcoxon matched pair test
Dry	1	ambient	4.0 (2 - 6)	z = -1.56
		heated	2.0 (0 - 4)	p = 0.118
	2	ambient	2.0 (1 - 4)	z = -3.00
		heated	1.0 (0 - 2)	p = 0.003
Wet	3	ambient	3.5 (2 - 5)	z = -2.80
		heated	1.0 (0 - 2)	p = 0.005
	4	ambient	1.0 (0 - 5)	z = -1.91
		heated	1.0 (0 - 3)	p = 0.056

TABLE 4. Responses of *Psychoda* species to indole, *p*-cresol and 2-heptanone. Inverted cups, containing cotton wool soaked in the stated concentration of test compound(s), were placed over water traps near to a sewage farm in Reading, Berkshire (UK). The total number of psychodid midges in 10 traps after a 24 h period was recorded.

conc. (%) of compound			
indole	2-heptanone	*p*-cresol	number of *Psychoda* trapped
0.1	–	–	49
0.01	–	–	58
–	0.1	–	76
–	0.01	–	53
–	–	0.1	452
–	–	0.01	353
0.01	–	0.01	38
–	0.01	0.01	496
0.01	0.01	0.01	785

A third factor affecting the success of pollinator trapping in *A. maculatum* is the availability of pollinators. At a site in Harrold & Odell Country Park, Bedfordshire (UK), in 1995, flowering of *A. maculatum* appeared to be synchronised with peak *Psychoda* flight abundance. However, at a site on Nene College campus, Northamptonshire (UK), in 1996 there were few *Psychoda* in flight during peak flowering (Fig. 1). *Arum* flowering at Nene was delayed by about three weeks compared to a typical year (such as 1995), as a result of unusually cold and unsettled weather conditions, which also persisted during the flowering period. *Psychoda* flight activity is reduced by heavy rain or strong winds, thus unfavourable weather conditions may adversely affect pollinator trapping, either by directly reducing *Psychoda* flight activity or uncoupling flowering of *A. maculatum* from any peak in pollinator population density. Similar unsettled weather conditions and a delay in flowering in a population of *A. maculatum* in Hurley, Berkshire (UK), in 1996 may have resulted in inflorescences trapping mainly *Piophila vulgaris* (Table 2), whereas the same population trapped *P. phalaenoides* in 1994 when flowering occurred three weeks earlier (Kite 1995). Further integrated studies on *Psychoda* abundance, *Arum* flowering phenology and climatic conditions are required.

Inflorescence odours and pollinators in *Amorphophallus* and *Pseudodracontium*

Amorphophallus comprises some 170 species distributed mainly in the tropics from West Africa eastward into Polynesia: none are found in the neotropics (Hetterscheid, 1994). They are seasonal herbs in which an underground tuber usually produces one leaf each year and species are found mostly in secondary forests or disturbed spots in primary forests and forest margins. The inflorescence, which may replace the leaf in one season or develop alongside it, is of the typical aroid type. However, *Amorphophallus* is noted for the large size of the inflorescence in some species (such as *A. titanum*) and for the production of strong and obnoxious odours. Odour production is associated with considerable heating of the spadix, notably the male zone and the appendix (Skubatch *et al.*, 1990). In many species the odour consists of a nauseating gaseous stench (like liquid petroleum gas) which in some tends
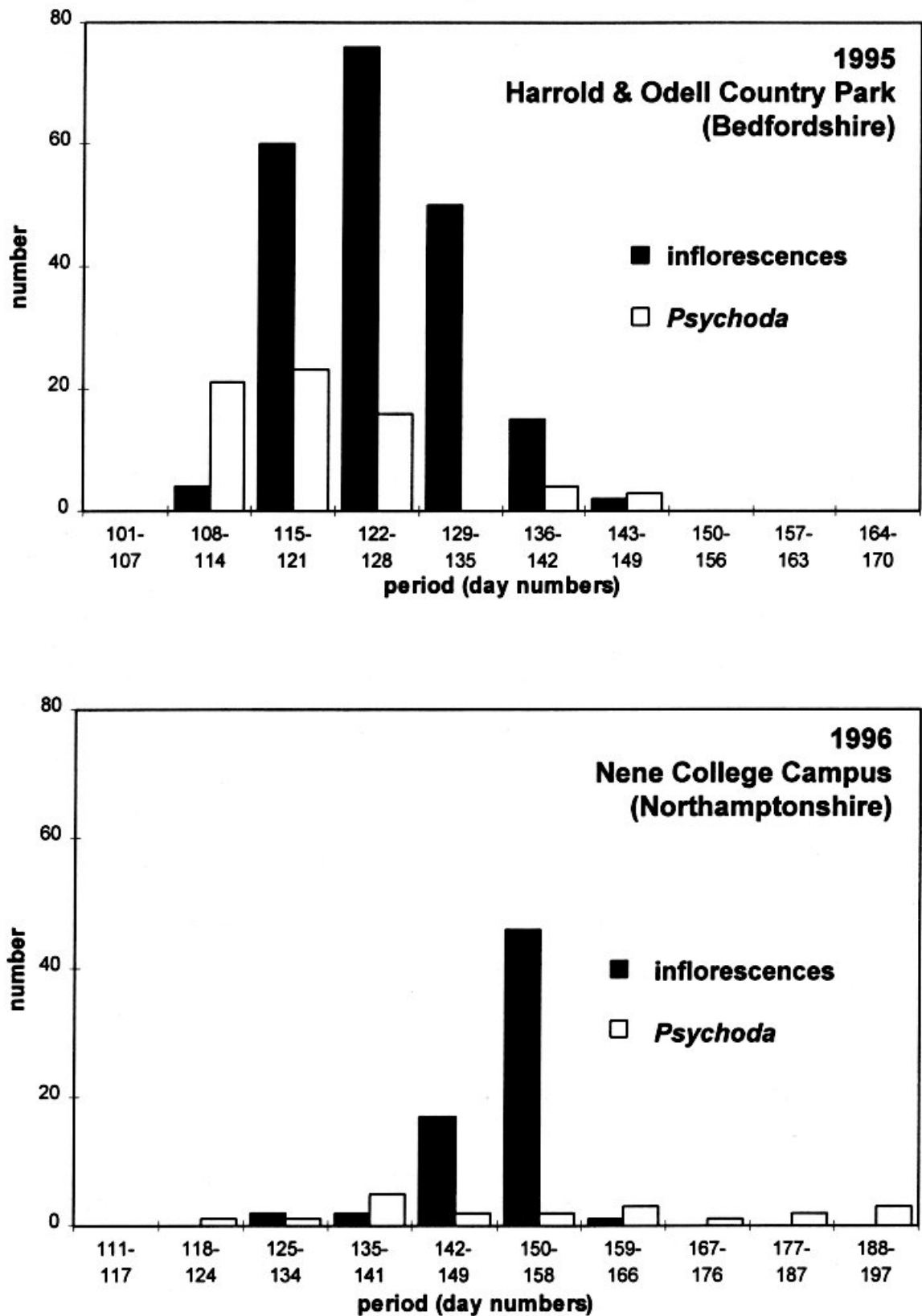
FIG. 1. Phenologies of *Arum maculatum* flowering and *Psychoda* flight activity at two sites in the UK. Numbers refer to number of inflorescences which opened and the number of *Psychoda* caught on yellow sticky traps per 100 m² during the stated period of days (day 1 = 1 Jan).

towards the odour of rotting meat: in others a diversity of odours have been noted (Table 5). In carrion-smelling species the olfactory mimicry of decay is often supported visually by the inflorescence being dark brownish and brownish-purple in colour.

The related genus *Pseudodracontium* has been revised recently and contains seven species (Serebryanyi, 1995). They all possess an elongate underground tuber but are otherwise similar to *Amorphophallus*, although much less variable. Typically they flower alongside the leaves and have a rather inconspicuous green spathe. Hetterscheid (1994) argued that *Pseudodracontium* is actually part of *Amorphophallus* and may have to be reduced to it.

We have used headspace techniques to analyse the gaseous odour typical of many *Amorphophallus* species and found it to consist almost entirely of dimethyl oligosulphides (Table 6). Species perceived as having a rotting meat odour, such as *A. konjac* and *A. maximus*, also produced mainly dimethyl oligosulphides. These compounds also predominated in six species that were perceived to have different or additional odours: *A. titanum*, *A. arnautovii*, *A. zenkeri*, *A. eichleri*, *A. cicatricifer* and *A. opertus* (Table 6). The different odours of *A. titanum*, *A. zenkeri* and *A. arnautovii* could not be assigned to any additional compounds detectable by chemical analysis, but the faecal odour in *A. eichleri* was possibly due to the presence of 2-heptanone and indole modifying the smell of the sulphides while acetophenone and 1-phenylethyl acetate may have given the fruity quality to the *A. cicatricifer* odour. In the odour of *A. opertus*, two additional compounds could be detected that could not be identified by searching available mass spectral libraries. The gaseous odours of two species of *Pseudodracontium* were also found to be due to the presence of dimethyl oligosulphides, but both also contained 4-methoxyphenethyl alcohol, which may be responsible for the anise-like character noted in the odour of *P. lacourii* (Table 5).

In other *Amorphophallus* species, in which the inflorescence odour was quite distinct from the typical gaseous or rotting meat smell, the chemical composition was also generally entirely different. The strong fried fish odour of *A. brachyphyllus* consisted of over 90% trimethylamine while isocaproic acid (4-methyl pentanoic acid) was the only compound detectable in the strong cheesy odour of *A. elatus* (isocaproic acid has the odour of pungent cheese). The unusual banana odour of *A. haematospadix* was found to be due to isoamyl acetate ('banana oil') although there was also a major ethyl acetate component. The strong anise-like odour produced by *A. albispathus* was found to be composed of almost pure 4-methoxyphenethyl alcohol, the same compound present in the odour of the two *Pseudodracontium* species examined. Finally, the monoterpenoid ocimene (*cis* or *trans*) dominated the odour of *A. margaritifer*. This species lacks an appendix and therefore the odour presumably emanates from the flowers or staminodes. The odour's terpenoid nature likens it to the chamber odours found in *Arum* species (Table 1) and reported for *Sauromatium venosum* (Borg-Karlson *et al.*, 1994).

Few published observations exist on potential pollinators of *Amorphophallus* (Table 7) and these often pertain to insects seen trapped in the spathe rather than actually pollinating the flowers. Carrion beetles are the insects most often observed in spathes and in *A. johnsonii* and *A. hohenackeri* they have been shown to be effective pollinators (Sivadasan & Sabu, 1991; Beath, 1996). Of the species for which potential pollinator data are available, only the odours of *A. paeoniifolius* and *A. titanum* have been analysed chemically and both consist of dimethyl oligosulphides (Table 6). These sulphur compounds are likely to be effective odour cues for carrion beetles as they are present in the odour of meat (Shankaranarayana *et al.*, 1974). They have also been shown to be attractants for various carrion flies, such as several blowflies *(Calliphora, Lucilia, Sarcophaga* and *Phormia* spp.; Borg-Karlson *et al.*, 1994, Nilssen *et al.*, 1996), as well as *Musca domestica* (Mookherjee *et al.*, 1993). In fact, dimethyl disulphide is a component of the commercial screwworm-fly bait 'Swormlure' (Hall, 1995) and is used for host location by the sheep blowflies *Lucilia sericata* and *L. cuprina* (Ashworth and Wall, 1994). The odour of the stinkhorn fungus *Phallus impudicus*, which consists mainly of dimethyl oligosulphides (Borg-Karlson *et al.*, 1994), also attracts many saprophageous flies (Smith, 1956), including the black blowfly, *Phormia regina* (Stoffolano *et al.*, 1989).

TABLE 5. Perceived odours of species of *Amorphophallus* and *Pseudodracontium*.

Nauseating gaseous odour (like liquid petroleum gas)

A. *albus* Liu & Wei

A. *asterostigmatus* Bogner & Hett.

A. *bulbifer* Blume

A. *corrugatus* N.E. Br.

A. *curvistylis* Hett.

A. *elegans* Ridl. [changing to rotting meat]

A. *glossophyllus* Hett.

A. *krausei* Engl.

A. *muelleri* Blume

A. *napalensis* (Wall.) Bogner & Mayo

A. *opertus* Hett. [also burnt rubber]

A. *paeoniifolius* (Dennst.) Nicolson [also rotting meat].

A. *parvulus* Gagnep.

A. *prainii* Hook. f.

A. *pygmaeus* Hett.

A. *sagittarius* van Steenis

A. *salmoneus* Hett.

A. *variabilis* Blume

P. *fallax* M.M. Serebryanyi

P. *gracilis* M.M. Serebryanyi

P. *lacourii* (Lind. & Andre) N.E. Br. [also anise]

P. *latifolium* M.M. Serebryanyi

Rotting meat odour

A. *angolensis* subsp. *maculatus* (Engl.) Ittenb. [becoming fishy]

A. *cirrifer* Stapf

A. *gigas* Teijsm. & Binn.

A. *kiusianus* (Makino) Makino

A. *konjac* K. Koch

A. *maximus* (Engl.) N.E. Br.

A. *maxwellii* Hett.

Anise-like odour

A. *albispathus* Hett.

A. *coudercii* (Bogner) Bogner

A. *longituberosus* Engl. & Gehrm.

Rancid cheese odour

A. *annulifer* Hett. [also rotting meat]

A. *antsingensis* Bogner & Hett. (ined.)

A. *costatus* Hett.

A. *elatus* Hook f.

A. *hayi* Hett.

A. *hirtus* N.E. Br.

A. *margaritifer* (Roxb.) Kunth [weak odour]

Dung and faecal odours

A. *abyssinicus* (Rich.) N.E. Br. [cow-dung]

A. *eichleri* (Engl.) N.E. Br. [faecal changing to shrimp-like]

A. *henryi* N.E. Br. [cow-dung]

Fishy and urine odours

A. *brachyphyllus* Hett. (ined.) [fried fish]

A. *eburneus* Bogner [fishy]

A. *lambii* Mayo & Widjaja [urine-like, later more fishy]

A. *lewallei* Malaisse & Bamps [sewage]

A. *titanum* (Becc.) Becc. ex Arcang. [urine-like or fishy]

A. *zenkeri* (Engl.) N.E. Br. [shrimp-like]

"Spicy" and chocolate odours

A. *ankarana* Hett. [spicy and chocolate]

A. *arnautovii* Hett. [spicy]

A. *manta* Hett. [chocolate]

Fruit and vegetable odours

A. *cicatricifer* Hett. [initially like shoe-polish, then changing to fruity]

A. *galbra* F.M. Bailey [fruity]

A. *haematospadix* Hook f. [bananas]

A. *odoratus* Hett. [carrots]

A. *yuloensis* H. Li [lemon]

A. *zenkeri* N.E. Br. [mushrooms]

TABLE 6. Major components* of the appendix odours of inflorescences of *Amorphallus* and *Pseudodracontium* species. Odours were collected from inflorescences still attached to plants cultivated at Leiden Botanic Garden and Aalsmeer. Appendix odours were collected and analysed as described for *Arum* in Table 1 except that the trap was simply positioned near to the appendix which, if possible, was covered by a clear nylon bag. Only one inflorescence of each species has been analysed.

compound name (identification criteria**)

Species	dimethyl disulphide (a)	dimethyl trisulphide (c)	dimethyl tetrasulphide (c)	4-methoxyphenethyl alcohol (a)	trimethylamine (a)	isoamyl acetate (a)	isocaproic acid (a)	ethyl acetate (a)	ocimene (cis or trans) (b)	2-heptanone (a)	indole (a)	acetic acid (a)	limonene (a)	acetophenone (b)	1-phenylethyl acetate (b)	1,2-dimethoxybenzene (b)	phenylethyl alcohol (a)	Odour
A. *konjac* K. Koch	+++	+++											++					rotting meat
A. *maximus* (Engl.) N.E. Br.	+++	+++																rotting meat
A. *paeoniifolius* (Dennst.) Nicolson	+++	+++	++															gaseous + rotting meat
A. *albus* Liu & Wei	+++	+++	++															gaseous
A. *bulbifer* Blume	++	++++	+															gaseous
A. *glossophyllus* Hett.	+++	+++	++															gaseous
A. *pranii* Hook. f.	+++	+++	+															gaseous
A. *sagittarius* van Steenis	+++	+++																gaseous
A. *opertus* Hett.	+++	+++																gaseous + burnt rubber
A. *titanum* (Becc.) Becc. ex Arcang.	+++	++																gaseous + urine
A. *zenkeri* N.E. Br.	+++	++												++				mushrooms
A. *arnautovii* Hett.	+++	+++												+				spicy
A. *eichleri* (Engl.) N.E. Br.	+++	+++	++							++	++					++		dung
A. *cicatricifer* Hett.	+++	+++												+++	++			gaseous + polish, fruity
P. *fallax* Serebr.	+++	+++	+++	++														gaseous
P. *lacourii* (Lind. & Andre) N.E. Br.	+++	+++	++	+++														gaseous + anise-like
A. *albispathus* Hett.				++++														anise-like
A. *brachyphyllus* Hett. (ined.)					+++													fried fish
A. *haematospadix* Hook. f						+++		+++										bananas
A. *elatus* Hook. f.							++++											strong cheese
A. *annulifer* Hett.	++					++		+++		++		++						strong cheese + rotting meat
A. *margaritifer* (Roxb.) Kunth***											+++						++	weak cheese

*+ = level of compounds in odour as described in Table 1.
** compound identification criteria as in Table 1.
*** A. *margaritifer* lacks an appendix. The odour emanated from the flowers or the staminodes and also contained various monoterpenoids at less than 1%.
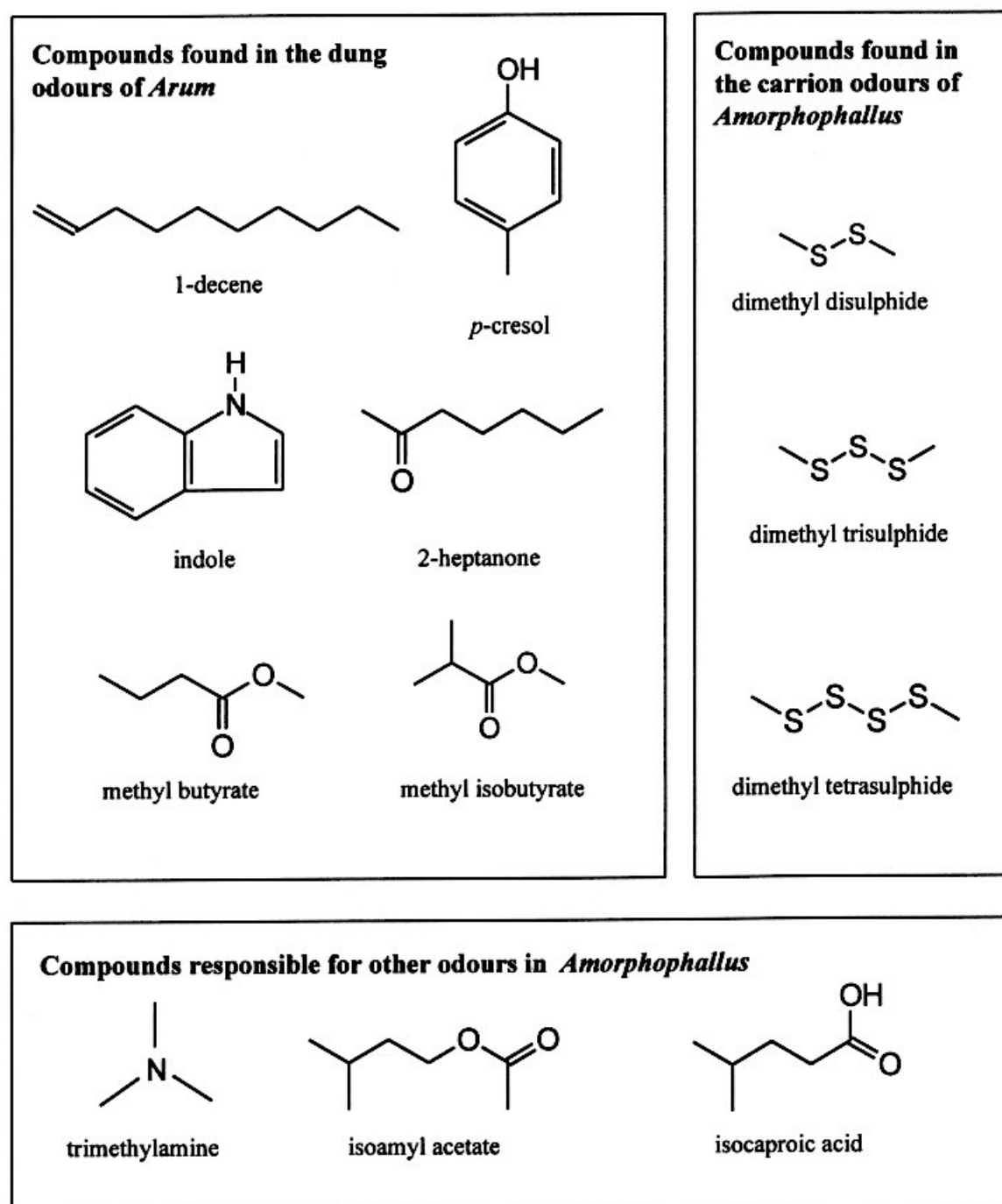
FIG. 2. Structures of odour compounds in *Arum* and *Amorphophallus*.

Perhaps more intriguing than the pollinators of the species having gaseous or rotten meat odours is the identity of the pollinators in species for which odour mimicry is not so obvious, such as the cheesy odour of *A. elatus*, due to isocaproic acid. Indications as to the type of potential pollinator may come from plants in which similar compounds have been detected in the floral odour. For example, isovaleric acid, the lower homologue of isocaproic acid, occurs as the major constituent in the odour of the foul-smelling succulent *Senecio articulatus* (Compositae; Kite and Smith, 1997) and has been reported in the odours of several other foul-smelling flowers such as some *Masdevallia* species (Orchidaceae; Kaiser, 1993), *Deherainia*

TABLE 7. Insects reported in inflorescences of *Amorphophallus* species.

Species	Insects	Reference
A. hohenackeri (Schott) Engl. & Gehrm.	*Haptoncus (=Haptoncurina) motschulshii* Reitter (Coleoptera: Nitidulidae)	Sivadasan & Sabu (1991)
A. johnsonii N.E. Br.	*Phaeochrous amplus* Arrow (Coleoptera: Scarabaeidae)	Beath (1996)
A. maculatus N.E. Br.	*Phaeochrous camerunensis* Arrow (Coleoptera: Scarabaeidae)	Bogner (1976)
A. oncophyllus Prain	Coleoptera: Nitidulidae	van der Pijl (1937)
A. paeoniifolius (Dennst.) Nicolson	*Adoretus* sp. (Coleoptera: Scarabaeidae) *Melipona* sp. (Hymenoptera: Apidae)	Singh & Gadgil (1996)
A. titanum (Becc.) Becc. ex Arcang.	*Diamesus osculans* Vigors (Coleoptera: Silphidae) *Creophilus villipennis* Kraatz (Coleoptera: Staphylinidae)	van der Pijl (1937)
A. variabilis Blume	Coleoptera: Nitidulidae	van der Pijl (1937)

smaragdina, Theophrasta americana (Theophrastaceae; Knudsen and Stahl, 1994) and *Leontopodium alpinum* (Erhardt, 1993). Flies have been implicated as pollinators in all these species. Similarly 4-methoxybenzyl alcohol, the lower homologue of 4-methoxyphenethyl alcohol produced by *A. albispathus*, occurs in the inflorescence odour of another aroid, *Spathiphyllum cannifolium* (Lewis *et al.*, 1988). This and other benzenoid compounds have been shown to be attractive to tephritid fruitflies (Chuah *et al.*, 1996). Finally, the trimethyl-amine produced by *A. brachyphyllus* probably attracts carrion insects; trimethylamine is an indicator of decay in fish (Krzymien and Elias, 1990) and has been shown to be an attractant for houseflies (*Fannia* spp.; Mulla *et al.*, 1984).

The inflorescence odours of *Amorphophallus* may have taxonomic significance. The species producing dimethyl oligosulphides are thought to form two related groups and the anise-like odour of *A. albispathus* is also perceived in two species thought to be closely related to it, *A. longituberosus* and *A. coudercii*. Furthermore, species of *Pseuodracontium* are possibly most closely related to these anise-like scented *Amorphophallus* species, a hypothesis supported by the presence of 4-methoxyphenethyl alcohol in the odours of *P. fallax*, *P. lacourii* and *A. albispathus*.

Conclusions

There appear to be two major odour types among sapromyophilous species of *Arum* and *Amorphophallus* associated with attraction of either dung or carrion insects. Odours of dung-smelling *Arum* species are complex, containing numerous compounds belonging to several classes, while odours of carrion-smelling *Amorphophallus* species have a simple composition, consisting mainly of dimethyl oligosulphides (Fig. 2). Within dung odours of *Arum* a further subdivision is evident, since the odour of *A. maculatum* has a different chemical profile from the other dung-smelling species, whereas all the carrion odours of *Amorphophallus* are consistently dominated by dimethyl oligosulphides. This may reflect the possibility that carrion

exhibits less odour variation than dung, or that the semiochemicals used by carrion insects are more consistent than those used by dung insects. Certainly, the dung of different animals have perceptibly different odours and dung odours can also vary according to diet (Aii *et al.*, 1980).

Dung mimicry and carrion mimicry are not mutually exclusive odour types; for example, the odour of *Amorphophallus eichleri* contains both dimethyl oligosulphides and two compounds, indole and 2-heptanone, associated with the dung odours of *Arum*. A similar mixture of sulphides and nitrogen-compounds has been reported in another aroid *Sauromatum venosum* (Borg-Karlson *et al.*, 1994)[2]. Nevertheless, the model of at least two chemical odour types associated with dung or carrion mimicry is a useful one to test in studies of other species pollinated by dung or carrion insects. For example, analysis of the parasitic plant *Hydnora africana* (Hydnoraceae), which is said to smell of rotting hide, has revealed that the odour is dominated by dimethyl oligosulphides and therefore appears to be of the carrion-mimicking type, although the pollinators are not known (Burger *et al.*, 1988). However, not all plants with odours dominated by dimethyl oligosulphides belong to the sapromyophilous syndrome, since the odours of two presumed bat-pollinated flowers, *Crescentia cujete* (Bignoniaceae) and *Pilosocereus tweedyanus* (Cactaceae), have been found to contain high levels of dimethyl trisulphide (Knudsen and Tollsten, 1995).

Another odour type in the syndrome of sapromyophily is possibly the production of alcohols with fungus odours which seems to be associated with pollination by fungus insects; e.g. in *Theophrasta americana* (Knudsen and Stahl, 1994) and orchids of the genus *Dracula* (Kaiser, 1993). Thus, chemical odour types of sapromyophilous plants appear to show greater association with the nature of the substrate being mimicked than any particular taxonomic group of pollinators. Therefore, attempts to consider such plants as either fly or beetle pollinated may be unhelpful. In presumed sapromyophilous species with more unusual odours it is possible that only selected key pollinator-signalling chemicals are being produced and data on the pollinator species and their natural history will be required to determine the identity of the substrate being mimicked.

Acknowledgements

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[2] However, a more recent analysis of *S. venosum* suggested that monoterpenes predominated (Skubatz *et al.*, 1996), although dimethyl oligosulphides and indole were detected.

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