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A survey of the function of the lethal kettle traps of *Arisaema* (Araceae), with records of pollinating fungus gnats from Nepal

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Evidence from recent research combined with an evaluation of the literature indicates that *Arisaema* is adapted to pollination by fungus gnats. It apparently shares this peculiarity among aroids only with the distantly related genus *Arisarum*. In addition to previous records from Japan and North America, systematic collections from nine *Arisaema* species during several expeditions in the Himalayas in Nepal showed that, although other less efficient insect groups may participate, the nematoceran families Mycetophilidae and Sciaridae are the principal pollen vectors; they best fit the pollination apparatus of the mainly (para)dioecious kettle trap blossoms. A total of 16 fungus gnat genera (both Mycetophilidae and Sciaridae) comprising 47 identified species (among them one genus and 22 species new to science) were observed. Usually members of more than one taxon are attracted per *Arisaema* species, and both sexes of gnats are involved. Visitor sets differed to some degree, depending on host species, area, and altitude; they do not, however, represent the complete fungus gnat fauna of a region. Relevant traits of growth habit and inflorescence structure are surveyed, and a detailed description of the pollination process is given, based on observations made on specimens cultivated in Europe, where vicariant fungus gnats are the pollinators. Attraction is deceptive by mimicking olfactory, visual and tactile cues characteristic of fungi where the gnat sexes normally meet and females oviposit. Odours produced by osmophores (the spadix appendage or spathe tip) play the most important part. The identified volatile compounds are mainly short-chained aliphatic aldehydes and alcohols. Flagelliform osmophores of some species, up to several dm long, reach the substrate and serve as conducting paths. Gnats become imprisoned when they inadvertently slide down the inner wall of the spathe tube. Its surface including the spadix is covered with ablative wax particles that inactivate the insects' tarsal pulvilli. This gliding device, in some species reinforced by zones of imbricate papillae, is irreversible, and no movements of floral parts allowing escape via the spathe mouth occur. Anthesis lasts several weeks. In the male spathes, victims are forced to wade through the pollen masses that have accumulated at the spathe's bottom; there they find an exit hole formed by local gaping of the spathe rims. The female spathes lack such an aperture. After potentially depositing pollen on the stigmas during their efforts to escape, gnats are detained until death. Except for an autogamous subspecies of *A. flavum* Schott, the few

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monoecious taxa of *Arisaema* are protogynous and possibly self-sterile. In monoecious *A. tortuosum* (Wall.)Schott, exit forming is delayed until pollen release. Three *Arisarum* species that are suspected to deviate in their floral syndrome are discussed along with araceous genera possessing similar one-way pitfall mechanisms.

ADDITIONAL KEY WORDS:—floral deception – Mycetophilidae – osmophores – sapromyiophily – Sciaridae.

CONTENTS

INTRODUCTION

Arisaema Mart., constituting the tribe Arisaemateae Nakai (Subfam. Aroideae), comprises around 150 species of geophytes in habitats ranging from temperate–tropical wet montane forests to grasslands above the tree-line in the northern hemisphere. It is the third largest and the most widespread araceous genus. Its highest diversity (92% of all species) and presumed centre of evolution lie in the eastern Himalayas and in SW China (Li, 1980). In Asia, the western boundary of the genus is Afghanistan, its northern boundary the Amur region, Japan and Sakhalin, and its southern boundary S India and Java. There are some species in Yemen and in E Africa from Ethiopia down to Tanzania. Another three species occur in eastern N America down to Mexico (Engler, 1920). All these disjunct outsiders are considered to be relatively late immigrants because no endemic section of the genus has evolved there (Grayum, 1990).

The genus has been the subject of a monograph by Engler (1920). The eastern Himalayan taxa have been revised by Hara (1971); Chatterjee (1955) and Pradhan (1990) treated the Indian and Himalayan species, respectively. Van Steenis (1948) treated the Javanese representatives; the species of China were described and keyed by Li (1979), the Taiwanese by Wang (1996), the Japanese by Ohashi & Murata (1980) and Murata (1990c), and the Korean by Ko & Kim (1985). Robyns & Tournay (1955) and Mayo & Gilbert (1986) revised the African taxa, and Huttleston (1984) those of N America. The infrageneric systematics of the genus has been updated by Murata (1984, 1990a), who recognizes ten sections.

Form diversity of *Arisaema* spathes is well documented in the descriptive literature and has made these aroids favourites of amateur growers. In contrast, knowledge of their pollination ecology has remained poor and fragmentary, with the exception of one phenomenon: the change of sex that these mostly dioecious plants undergo. Functional aspects of spathe structure, the process of pollination, and pollinator behaviour have never been investigated, and no field records are available from the centre of distribution of the genus, continental SE Asia.

The present authors have jointly, but using different approaches, pursued the matter since the late 1960s. As a result, observations by S.V. on cultivated specimens in Germany, and systematic recordings of the natural pollinator fauna contributed by J.M. during his zoological expeditions to the Himalayas in Nepal, are presented here. The account is prefaced by a conspectus of relevant published data.

MATERIAL AND METHODS

Travelling in the Himalayas in West-Central and Eastern Nepal, J.M. regularly checked *Arisaema* inflorescences in 1973, 1980, 1988, and 1995, collected their insect contents, and brought corms to Europe for cultivation. Descriptions of new insect species resulting from J.M.'s collections are found in Wagner (1982), Mohrig & Martens (1987), Menzel & Martens (1995) and Kallweit & Martens (1995, but see also Strassen, 1976). Blossoms were cut from the peduncles and carefully transferred intact into a large vial containing cyanide. After 10 min, spathes were removed and dissected. Insect sets from each species were labelled and conserved in alcohol. In the 1988 expedition, insects were secured separately from each individual spathe. Insect samples are deposited in the collections of Forschungsinstitut Senckenberg, Frankfurt am Main (Dixidae; Sciaridae in part), Deutsches Entomologisches Institut, Eberswalde, now Projektgruppe Entomologie (Sciaridae in part), Staatliches Museum für Tierkunde Dresden (Mycetophilidae) and (temporarily) in J.M.'s working collection (Ceratopogonidae and all other insects listed). Inflorescences of the species involved were preserved for structural study and are now deposited at WU.

Sampling localities in Nepal (Fig. 1)

(1) Ringmo on Phoksumdo Lake, 3600 m, ascent to Pass Bagar La, 3400–3900 m, 15/16.v.1973 (Dolpo Distr.). Open habitats close to riverside and agricultural land (Phoksumdo Lake) and open pastures on deforested slopes, up to timberline. *A. jacquemontii.*

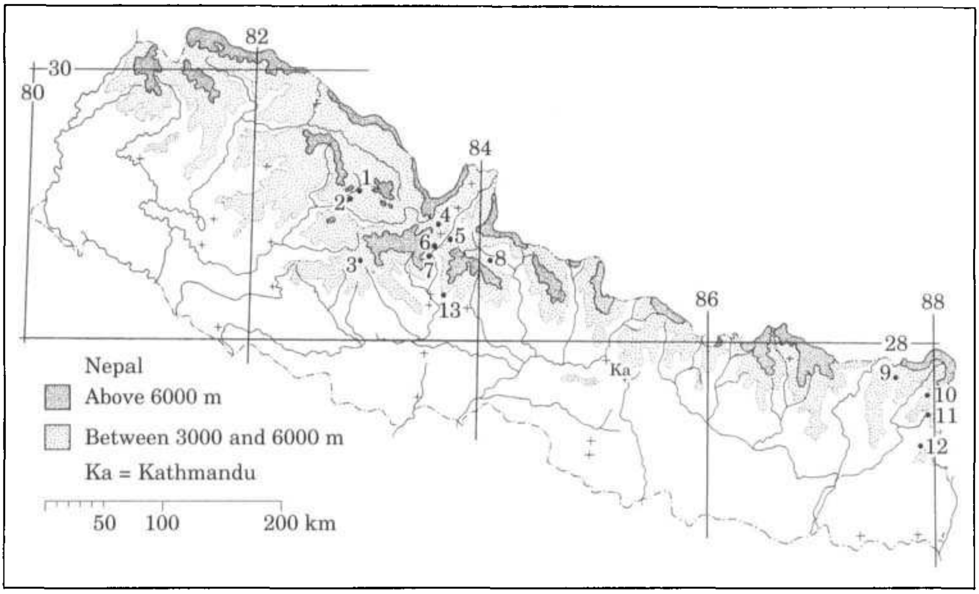

Figure 1. Collection sites of *Arisaema* species and fungus gnats in Nepal (J.M.). Figures refer to localities listed in Material and methods.

(2) Suli Gad valley, 2800 m, 9.vi.1973 (Dolpo Distr.). Deeply recessed valley floor N of the Himalayan main range, area with lower precipitation, clearings in *Picea smithiana* forest close to water. *A. jacquemontii*, *A. consanguineum*, *A. tortuosum.*

(3) Emaka NW of Dhorpatan, 2800 m, 29.v.1973 (Parbat Distr.) Edge of agricultural land, on stony ground near village, bushes. *A. tortuosum.*
Dhule NW of Dhorpatan, about 4000 m, 30.v.1973 (Parbat Distr). Barren slopes, sparse bushy vegetation. *A. utile.*

(4) Sangdak in the NE Dhaulagiri massif, 4000 m, 27.vi.1973 (Mustang Distr.). On barren ground N of the Himalayan main range, but in the convection zone of slightly higher precipitation. *A. jacquemontii*, *A. flavum.*

(5) Upper Kali Gandaki valley, forest clearing Thaksang above Tukche, 3200 m, 2–5.vii.1973 (Mustang Distr.). Slopes covered with *Pinus/Abies* forest, N of the Himalayan main range, but according to altitude, with regular but light monsoon rains. *A. jacquemontii.*

(6) Upper Kali Gandaki valley, 2500 m, 7.vii.1973 (Mustang Distr.). Between Nabrikot and Lethe in the zone of reduced monsoon precipitations; open valley floor with single trees and bushes, also in agricultural land near settlements. *A. costatum*, *A. jacquemontii.*

(7) Upper Kali Gandaki valley, Ghasa, in the transition zone between full and distinctly reduced precipitation, 2250 m, 9.vii.1973 (Mustang Distr.). Forest edge at moist places, also near cultivated land. *A. consanguineum*, *A. jacquemontii.*

(8) Upper Marsyandi valley, above Bagarchap, 2200–2550 m, 12–13.iv.1980 (Manang Distr.). Lightly grazed deciduous *Quercus/Acer* (2200 m) and *Rhododendron/Acer/Tsuga* forest (2550 m). *A. nepenthoides.*

(9) Upper Tamur valley SE Walungchung Gola, 2450 m, 19/20.v.1988 (Taplejung Distr.). Small side valley near confluence with Tamur, small pasture but no site for continuous grazing. Steep slopes with *Quercus* and *Acer*, lower limit of *Tsuga dumosa*. *A. speciosum*.

(10) Upper Simbua Khola valley, pasture Tseram, 3250 m, 10–15.v.1988 (Taplejung Distr.). Steep and deeply recessed valley with largely untouched primary forest, mainly *Abies densa* and several *Rhododendron* species. On the valley floor small pastures locally, inhabited only after mid May. Locally, large colonies of *A. utile*.

(11) Omje Khola above Yamputhin, 2200 m, 15.v.1988 (Taplejung Distr.). Luxuriant, herb- and tree-rich riverine vegetation. *A. jacquemontii*.
Yamputhin, valley floor and slopes, 1650–2000 m, 26.iv–1.v.1988 (Taplejung Distr.). Sites of *A. speciosum* along rivulets (1650–1800 m); sites of *A. jacquemontii* on clearings in partially cut-over forests in much drier localities (1800–2000 m).

(12) Dhorpar Kharka, N of Mai Majuwa. 2700 m, 14–15.iv.1988 (Ilam Distr.). Nearly undisturbed forest of *Lithocarpus*, *Quercus*, *Magnolia* and several *Rhododendron* species, but herb layer locally reduced by grazing cattle, open forest edge and adjacent pastures and groups of bushes. Large colonies of *A. nepenthoides* and *A. griffithii*.

(13) Pass Ghorapani, SW of Annapurna massif, 2800 m, 11.vii.1973 (Parbat Distr.). Mixed *Rhododendron* forest near stream. *A. utile*.

Observations on cultivated species of *Arisaema* were made by S.V. in the arboreta of the Botanical Gardens of Mainz (1963–69), Berlin-Dahlem (1974–76) and Vienna (1998). Insect contents of spathes were repeatedly collected from the same individual during anthesis, using a suctor. The tropical taxa mentioned were studied in the greenhouses of these gardens.

Analysis of odours

Odours emitted by spadix appendages were sampled by two methods:

(1) Absorption (A). Inclusion of appendage *in situ* inside a sealed glass tube that was ventilated by an air stream (generated by a membrane pump) for 6–10 h. Ambient air influx passed through a charcoal filter for cleaning, or was independently analysed for control. Absorption of volatiles by an inserted cartridge containing activated charcoal (Fa.Supelco). Elution from sorbent with pentane; eluate condensed in water bath at 40°C, and 2 µl injected using an on-column injector thermostatted at 50°C.

(2) Head Space technique (HS). From small glass vials containing 1–2 detached appendages and kept at 100°C for 20 min, 500 µl of air sample were taken and injected on column (treatment at 40°C gave no results).

Analysis was performed using a Perkin-Elmer XLS Turbomass GC-MS equipment (MS ion source at 150°C, transfer line at 250°C). GC columns used were PE 1 (60 m, 0.25 mm ø, 0.25 µm film thickness), and for head space, PE WAX (60 m, 0.25 mm ø, 0.25 µm film thickness), with helium as carrier gas (flow 0.7 ml/min). Temperature programme 70–250°C/2°C per min. Compound identification was carried out by comparison of mass spectra using the NIST/EPA/NIH mass spectral library (software vers. 1.5a, National Institute of Standards and Technology 1996).

To visualize epidermal structures including wax particles by SEM, FAP-fixed samples were CP-dried, mounted on stubs and sputtered with gold. These were examined in a Jeol T 300 Scanning electron microscope.

Species are cited with authors where first mentioned in the text (nomenclature following Stilwell, Gusman & Walton, 1997).

GROWTH HABIT

The plants usually grow on the shady forest floor, on forest edges or in clearings, rarely (e.g. *A. leschenaultii* Blume, Barnes, 1935) as epiphytes. Their underground organ is an abbreviated, swollen corm, sympodially renewed every year, or a rhizome. The corm of many species propagates vegetatively by forming bulbils or stolons. The life period is up to 25 years (*A. triphyllum* (L.)Schott, Bierzychudek, 1982b). Tropical rhizomatous species (sect. *Fimbriata* and *Decipientia*) are evergreen and grow without dormancy, forming several floriferous ramets (Murata, 1984, 1990c). The corm of the deciduous members, before attaining the adult stage after 4 or more years, produces a single annual leaf every season. On maturity, a single, erect shoot bearing 1–3 cataphylls and 1–3 foliage leaves in distichous or spirodistichous arrangement emerges per year, ending with a single, strictly orthotropic inflorescence. The inflorescence is already laid down at the end of the preceding season. All the vegetative phyllomes are inserted at ground level, the vaginae of the foliage leaves telescopically sheath the flowering scape, jointly building a ‘pseudostem’ (Murata, 1984). The leaf number of adult plants is fairly species-constant and never exceeds three (Engler, 1920; Hara, 1971). The leaves of adult *Arisaema*, always compound, have a ternate, pedate, or radiate, usually horizontally spreading lamina. In several one-leafed species (e.g. *A. consanguineum* (L.)Schott, Fig. 2B) the blossom emerges pseudolaterally from the vagina of the erect petiole. Certain members of sect. *Trisecta* have a very short peduncle, with an inflorescence close to the bottom, overshadowed by the leaves; others reach man-size, with a peduncle superseding the foliage considerably (Fig. 2A). Most species flower in spring and early summer, and their blossom opens more or less synchronously with the leaves, while others including *A. nepenthoides* (Wall.)Mart. (Himalaya, Murata, 1991, J.M., pers. obs.) and *A. limbatum* (Nakai & F.Maek.) Serizawa (Japan) are recorded as flowering prior to the appearance of foliage in early spring (March/April). The two species of sect. *Decipientia* (China) are autumnal flowerers (Murata, 1984).

GENERAL FEATURES OF THE INFLORESCENCE

The inflorescence consists of the spadix enveloped by the spathe (Fig. 6). Its tubular portion measures from 5 to 15 cm, ranging within the medium size class among Araceae. Apart from species differences, there is considerable individual variation in size, depending on age and growth conditions. The spadix ends in a sterile appendage whose more simple clavate form superficially resembles that of *Arum*, but can be extremely diversified in terms of length, shape, and coloration. In

Figure 2. Species of *Arisaema* in their natural habitat. A, *A. tortuosum* (Nepal, Mustang Distr., near Lethe), B, *A. consanguineum* (Nepal: Suli Gad valley).

section *Fimbriatae*, the appendage bears bristly or thread-like emergences, presumably rudiments of staminodial florets—a primitive condition. The tip of the appendage overtops the spathe mouth, while the fertile zone of the spadix is always enclosed within the tubular part of the spathe. The floriferous zones represent morphogenetic units, with the numerous florets developing more or less simultaneously (Maekawa, 1927). These are apetalous and unisexual; the 150–200 ovoid pistillate florets, bearing a tufted or papillate, dry stigma, are sessile and densely crowded. The more remotely spaced staminate florets, 100–150 in number, consist of a single column topped by a congested bunch of 2–5 bilocular anthers that vary in number individually and between species. Anthers dehisce by a straight or semilunar slit, or by a pore. The sole anther of *A. exappendiculatum* Hara, which opens by circumscision, is presumed to be a fusion product of 2–3 anthers (Hara, 1971). Awl-like sterile florets may occur distally but never develop below the fertile zone. Being rather dry, the pollen does not remain in the open anthers but soon falls off and collects at the bottom of the spathe, where it forms copious cream- or light rose-coloured masses.

Most *Arisaema* species are dioecious, a condition unique in aroids. In the few monoecious members, including *A. flavum* (sect. *Dochafa*), *A. dracontium* (L.)Schott, *A. tortuosum* (sect. *Tortuosa*) and *A. filiforme* (Blume)Thwaites (sect. *Fimbriata*), the spadix bears basally the exclusively pistillate, and distally the staminate, florets; the two types form well-segregated zones along the spadix, as in *Arum*. In the dioecious species, while the spathes and spadix appendages of the two morphs do not differ, the fertile spadix zone comprises only pistillate, or only staminate, florets.

TABLE 1. Sex ratios in *Arisaema* populations

Species	♂	☿	♀	*N*	Locality	Author
A. triphyllum	62*	14	24	1874	Ohio	Schaffner, 1922
A. triphyllum	38	13	50	—	Delaware	Rust, 1980
A. triphyllum	57	11	32	9184	Ontario	Doust & Cavers, 1982
A. triphyllum	35	4	61	—	Massachusetts, Vermont	Ewing & Klein, 1982
A. triphyllum	60	0	40	2038	Massachusetts	Polycansky, 1981
A. dracontium	86	15	0	892	Ohio	Schaffner, 1922
A. thunbergii ssp. *urashima*	83–88	0	13–17	—	Japan	Takasu, 1989
A. japonicum (=*A. serratum* v. *serratum*)	73	2	26	589	Japan	Kinoshita & Shimitsu, 1978**
A. barbatum Buchet	81	3	17	36	Java	Van Steenis, 1948***
A. filiforme	70	29	2	108	Java	Van Steenis, 1948***

* Percentages of flowering individuals, rounded up; in part cumulated by authors from counts in more than one population; for comparability, figures in part converted from ratio values or absolute numbers.

** Cited from Murata, 1984.

*** Values obtained from herbarium material.

DISTRIBUTION OF GENDER

Arisaema is well known for exhibiting a sex expression that is phenotypically, rather than genetically fixed; the sexual state of an individual is labile and may change from one season to another in either direction, depending on the plant's age, size and vigour ('paradioecy', Nakai, 1936). Most of the field work on this genus has focused on this phenomenon, which is interpreted as a strategy to economize reproductive efforts, which are different in the two sexes. This is beyond the scope of the present paper and is referred to here only in brief. The North American *A. triphyllum* has been studied by Pickett (1915), Schaffner (1922), Rust (1980), Ewing & Klein (1982), Bierzychudek (1982a,b), Doust & Cavers (1982), Richardson & Clay (1995), Doust, Doust & Turi (1986) and *A. dracontium* by Clay (1993), the Japanese *A. japonicum* (=*A. serratum* var. *serratum* Schott) by Maekawa (1927), *A.serratum* Schott by Kinoshita (1986) and *A. thunbergii* Blume ssp. *urashima* Ohashi & Murata by Takasu (1987). A young adult plant is always initially male and will achieve, under favourable nutritional conditions, the female status in the following years. The relative critical size for this change (expressed in height, corm weight, etc.) was found to be species-specific (Kinoshita, 1989). A reverse response, i.e. from female to male, may follow due to exhaustion by antecedent fruiting or when internal or ambient conditions deteriorate. Connected ramets of rhizomatous species and clones are independent in sex expression (Murata, 1990a). While the switch from the purely male to purely female status is clear-cut in strictly dioecious species, certain taxa show a more or less extended transgression phase, manifested in monoecy (Policansky, 1981). This condition predominates in the aforementioned species designed as monoecious. Under these circumstances, it is not surprising that censuses of gender distribution in populations have been highly divergent within and among species. In the Nilghiri Hills, Barnes (1935) counted nine times as many male as female inflorescences in *A. leschenaultii*, while according to Hara (1971) most *A. utile* Hook. plants in a Nepal site were females. Some counts given in more detail in Table 1 show mostly male-biased and partly female-biased demographies, and in two species even a predominance of monoecious individuals over females. These gender relations cannot be more than punctual assessments, but as local soil and microclimatic conditions control the ratio, they may serve to predict the survival or disappearance of a given population over a longer time scale (Bierzychudek, 1982b).

Monoecious species may self-pollinate, as is the case with the autogamous *A. flavum*. Allogamous *A. tortuosum*, however, failed to set seed in our cultivated plants when bagged. Strict dichogamy may have been responsible for this result rather than self-incompatibility, a mechanism believed to be absent in the Araceae and which in the opinion of Bierzychudek (1982b) ". . . has never arisen in *Arisaema*". It remains to be examined whether clonal siblings of dioecious species (when diverging in age and hence sex) are interfertile.

THE SPATHE

The spathe leaf has a rather firm consistency and free margins from the very base. It is divided into a distal free and a proximal convolute, tubular portion. The tube is traversed by about 15–20 poorly branched primary bundles which spread, ramify, and anastomose in the blade. In the tubular part the margins overlap, being pressed against each other so that the tube is firmly closed; this to some degree maintains the vernation of the bud as in many other aroids. The sense of convolution may be right- or left-handed; Schaffner (1922) found a 1:1 distribution of the two types in *A. triphyllum*, as Barnes (1935) did in *A. lescheaultii*. The tube is cylindrical, neither ventricose nor constricted (globose in *A. flavum*). The dorsal free part of the spathe (vexillum, cap, hood, or helmet) is flat to galeate or even (*A. ringens* [Thunb.]Schott) cucullate; it extends for some distance horizontally over the mouth of the tube (Fig. 3). In *A. griffithii* Schott it is extremely enlarged, almost hiding the tube (Fig. 12). A few taxa bear an erect lamina (e.g. *A. candidissimum* W.Smith, *A. exappendiculatum*, *A. sikokianum* Franch.& F.A.Savatier). The tip of the lamina is in most cases aculeate, but long-tailed in some species discussed below. The lateral and anterior rim of the tube may be slightly dilated, forming a funnel, or it may extend into two broad, lateral auricles which horizontally spread like platforms or leaflets (bizarrely so in *A. biauriculatum* W.Smith and *A. omeiense* Mao).

Though of a peculiar elegance, the spathe is usually inconspicuous, light or dull green being the common colour; in some species it is lustrous brown or dull purple, especially the helmet. Contrasting white patches occur on the inner side of the helmet; more frequently, unpigmented stripes run along the main vascular bundles of the blade and the tube. These catch the light and produce a milky effect against a dark background (van der Pijl, 1953, for *A. laminatum* Blume). In addition, a narrow, transparent 'light window' usually encircles the lowermost zone of the spathe. Both features are functionally important and will be discussed below. The spadix appendage may share the colour of the spathe or contrast with it by brown or whitish tints.

All surfaces of the spathe, whose epidermis is composed of isodiametric or oblong cells and sparsely distributed stomata, are usually quite smooth. Among six species viewed microscopically, only in *A. utile* was the inner side of the helmet, and in *A. jacquemontii* Blume, in addition, the upper half of the tube interior found to be papillose, with imbricately arranged, downward-pointing, blunt epidermal papillae. Thus, gliding zones characteristic for kettle traps are formed (Fig. 7A,B). The

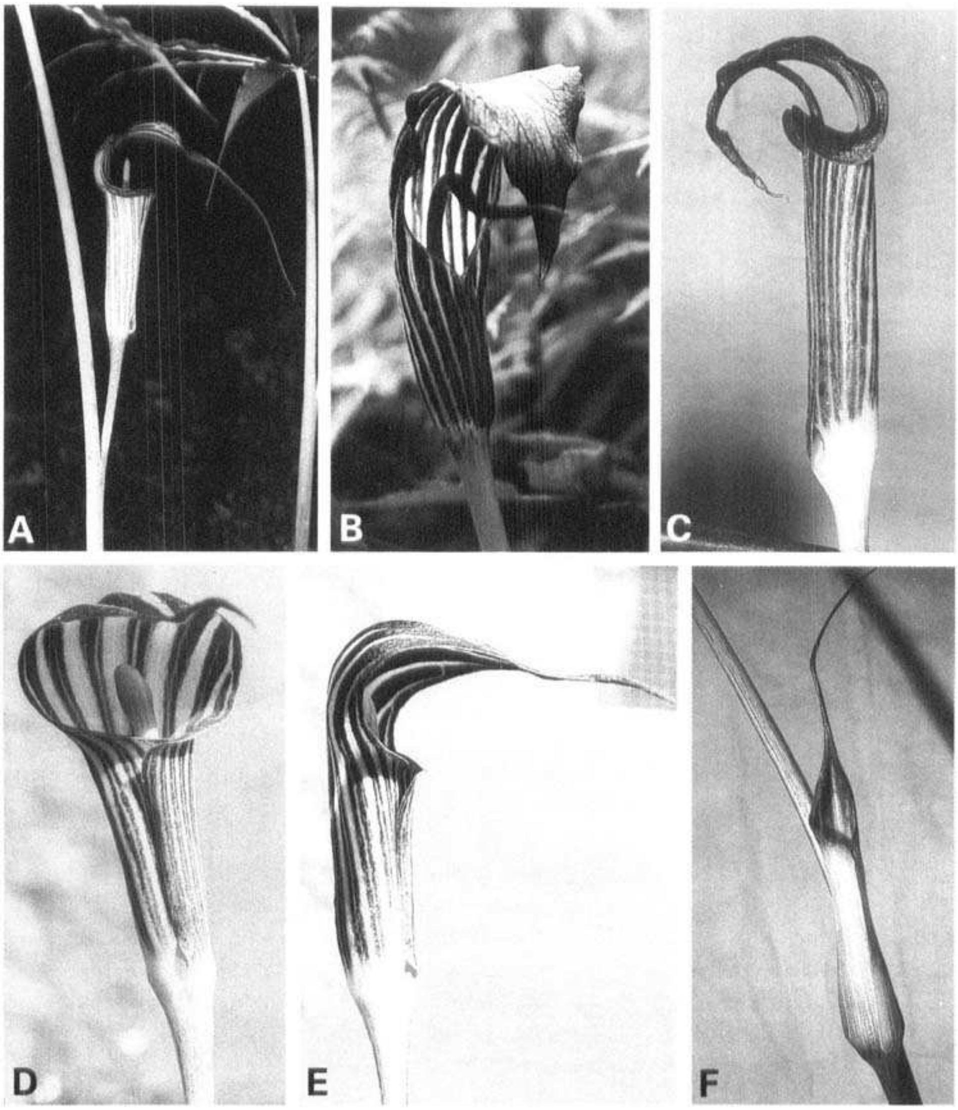

Figure 3. Inflorescences of *Arisaema* species, all males. A, *A. ciliatum* (cult.), B, *A. asperatum* (Omei Shan, Sichuan, China), C, *A. roxburghii* (Fraser's Hill, W Malaysia), D & E, *A. leschenaultii* (Horton Plains, Sri Lanka), F, *A. exappendiculatum* (cult. from Nepal).

presence or absence of this progressive trait may turn out to be useful in infrageneric taxonomy.

Both the inner and outer spathe surfaces are dusted with a glaucous, removable wax cover. In *A. tortuosum* the external half of the spathe tube is not waxy, and marked by a rather distinct boundary. This coating also includes the appendage and axe of the spadix, and the peduncle. The wax particles were found to consist of knotty, branched rodlets about 1 µm long (Fig. 7C), similar to those of the green leaves of *Xanthosoma* as illustrated by Ensikat & Barthlott (1993), while scaly crystalloids seem to prevail elsewhere in the Araceae (Frölich & Barthlott, 1988).

Floral nectaries are missing in *Arisaema* as in most aroids, but Daumann (1930) has described the presence of extrafloral, nectar-producing spots on the upper side of the auricles and on both sides of the helmet of *A. consanguineum* and *A. amurense* Maxim. The slimy secretion of the former was analysed and found to contain a disaccharide. In this species, each droplet appeared above one stoma, while in *A. amurense* stomata were not detected in the region concerned; the nectar seemed to ooze diffusely from the leaf surface. Nectar secretion by the spathe has also been recorded in *A. flavum* (Murata *et al.*, 1993), and we have found it at the spathe mouth of *A. nepenthoides*. Nowhere was glandular tissue recognizable. Baroni (1897) noted the occurrence of extrafloral nectaries between the segments of the digitate green leaves in unspecified members of *Arisaema* which had been introduced to Italy from China. Their anatomy and relationship with the above-mentioned spathe nectaries are not known.

COURSE OF ANTHESIS

Compared with most aroids, the inflorescences of *Arisaema* are notable for their longevity, usually being anthetic up to several weeks (similar lengths of activity being known from *Anthurium*). There is no distinct sign that would indicate the end of floral activity, except for the cessation of odour. The spathe and the peduncle of the female inflorescence remain alive during most of the time of fruit formation, while the postfloral male spathes and peduncles soon wither and decay; their leaves senesce earlier than in the female plants (Doust & Cavers, 1982).

According to Barnes (1935), anthesis of *A. leschenaultii* lasted about 10 days, but there were differences depending on weather and altitude. In *A. triphyllum*, Rust (1980) reported anthesis lasting 15–20 d in male spathes and 20–35 d in the female. Monitoring cultivated plants in Europe, we observed 13–14 d in both morphs of *A. ciliatum* H.Li, 19 d in *A. speciosum* (Wall.) Mart., 21–27 d in *A. consanguineum* and *A. erubescens* (Wall.)Schott, and 30 d in *A. amurense*. No rule was found as to whether male or female spathes were the first to open within a species, but field studies by Kinoshita (1986) showed that *A. serratum* males preceded females by 3 days in onset of anthesis, and the duration of female anthesis varied depending on occurrence and date of fertilization. In the cases we observed, pollen shedding of *A. ciliatum* proceeded acropetally during the first 17 d of anthesis. The anthers of *A. consanguineum* started dehiscing at dusk. According to Barnes (1935), dehiscence in *A. leschenaultii* begins in the middle of the staminate complex, proceeding upwards and then downwards the spadix. Following Knuth's (1904) observation on *A. filiforme*, stigmas ripened acropetally. The spadix of this monoecious species was strongly protogynous (of second order), with short overlap of sex phases. We found the monoecious *A. tortuosum* to be strictly dichogamous, with the female stage lasting for 7 d and pollen shedding during 6 d of a total anthesis period of about 27 d.

The pollen grains are small (13–20 µm), rugose or spinulose (Ohashi & Murata, 1980; Murata, 1984), lacking pollenkit and maintaining their globular shape when dry. As noted above, the pollen falls and is stored at the bottom of the spathe. The occurrence of small, spinulose pollen in aroids is usually associated with pollination by dipterans since it fits hairy insects better than psilate (Grayum, 1986). In unvisited spathes, the entire amount of pollen persists here for the full length of time, apparently without losing its capacity to germinate. Thus, by secondary pollen presentation, the inflorescence remains functional during its entire blooming period, although the male florets are shrunken and non-functional during most of the time. In this light, the idea proposed by earlier observers that the peculiar hood above the mouth of the tube is adaptive in protecting the long-lasting gender function from rain, appears justified.

ODOUR PRODUCTION

The reproductive units of *Arisaema* are scented. The general type of scent is rather uniform in the genus. With some exceptions, including *A. candidissimum* and *A. odoratum* Murata & Wu, the smell is not pleasant although weak, and never as offensive as in the Areae. Barnes (1935) simply mentions an 'unpleasant' smell in *A. leschenaultii*, while Knuth (1904) compared that of *A. filiforme* with the odour of urine or mice. The smell of *A. consanguineum* and *A. amurense* reminded Daumann (1930) of fresh sea fish. This corresponds with our interpretations of the odour of these species and of *A. nepenthoides*. *A. fargesii* Buchet and *A. triphyllum* were reminiscent of ozone, while a smell similar to that of *Adoxa moschatellina* was also noted. *A. erubescens*, *A. ciliatum* and *A. speciosum* had additional fruity, yeasty, sweetish, or 'metallic' components. *A. ringens* smelled like rhubarb, while *A. sikokianum*, *A. kiushianum* Makino, *A. tortuosum* and *A. exappendiculatum* had mushroom-like aromas. The smell of *A. amurense* could be detected at a distance of 1 m, that of *A. consanguineum* of 75 cm, but in other cases (*A. serratum*, *A. roxburghii* Kunth) it was so feeble that it could not be characterized.

CHEMICAL COMPONENTS OF ODOURS

Odour samples of five taxa were collected using absorption *in situ* (A) or the Head Space sampling technique (HS), and subject to GC-MS analysis for components (see Material and methods). Due to the scarcity of material available per species and a generally very low emission rate, yields were small and results should be regarded as initial requiring confirmation (Table 2; trace amounts and unidentified substances omitted).

Among the 26 volatile compounds identified, a variety of aliphatic aldehydes and alcohols, mainly of C chain lengths 3–10, predominated. Alkanes, ketones and sulphur-containing compounds were also present. Scent compositions differed considerably in detail between species; nonanal was shared by four species. Mono- and sesquiterpenes, common elsewhere in floral scents, were not detected, and aromatic compounds were rare. The olfactory characteristics of the predominant aliphatic components correspond quite closely to the types of perceptible smells described above. However, the presence of volatiles liberated from cut tissue (HS method) which normally do not enter the floral scent, cannot be excluded; on the other hand, trace compounds ultimately crucial in attraction may have escaped recording.

TABLE 2. Components of *Arisaema* floral smells (A = Absorption method, HS = Head Space method; see Material & methods)

A. tortuosum (HS)
Octane
Pentadecane

Acetaldehyde
Nonanal

2-Methylpropanol
3-Methylpropanol
2-Methylbutanol
6-Methyl-6-hepten-3-ol

Benzophenone

Dimethylsulfide

A. tortuosum (A)

2.7.10-Trimethyl-dodecane

4.6.6-Trimethyl-bicyclo 3.1.1-hept-3-en-one

A. speciosum (HS)
8-Oxabicyclo-5. 1. 0-Octane
Nonane
1-Dodecane
1-Tetradecane
1-Hexadecane

Bis-(1-Methylethyl)-disulphide

A. lobatum (HS)
Nonanal
Decanal
Tridecanal
Tetradecanal

A. ciliatum (A)

Nonanal
Decanal

A. erubescens (HS)
Octanal
Nonanal

Nonanol

Benzaldehyde

THE OSMOPHORES

With few exceptions, the (primary) source of the scent is the spadix appendage, although this is not the only function of that organ, which contains a complex of fused axial and staminate elements. Its homology and superficial similarity with the axial club of *Arum* (lords and ladies) and *Sauromatum* has long suggested an osmophore function, which was confirmed by Vogel (1963). However, the internal structure and course of scent release are quite different. In the *Arisaema* species examined, there was no starchy storage tissue filling the club's entire volume, and no rapid respirative consumption of assimilates, accompanied by a sudden outburst of heat and smell, as typical in *Arum* and *Sauromatum*. Knuth (1904), Molisch (1926, 1930) and Troll (1928), who inferred thermogenicity in *Arisaema*, were mistaken. In *Arisaema*, no more than three glandular, starchless cell layers are present (examined by Vogel (1963) in *A. triphyllum* and *A. sikokianum*). The remainder is a voluminous medulla consisting of wide-spaced aerenchyma and a number of longitudinal, evenly dispersed bundles. The epidermal scent-generating epithelium is built of non-papillate, prismatic, columnar cells rich in lipoidal 'spherosomes'. The surface of the osmophore is smooth and wax-powdered. Scent release is moderate, without a distinct climax or periodicity; it continues throughout anthesis. It commences with some delay after unfolding of the spathe; in *A. serratum* the lag time was about 1 day, in *A. ringens* about 4.

While the appendages of most species are cylindrical or club-shaped (Fig. 3), in others the tendency of osmophores to amplify their surface is apparent. To this end, some species maintained as an ancestral feature the emergence of flower rudiments. This results in an echinate appearance of the upper part of the appendage (*A.*

echinatum [Wall.] Schott, section *Sinarisaema*) or a lamp-brush-like shape of the whole organ, as in the flaccid appendage of A. *fimbriatum* Masters (section *Fimbriata*). *A. smitinandii* S.Y. Hu, whose staminodial emergences are a few yet very long filiform threads, forms the extreme. Another way to enlarge the appendage's surface is to apically taper into a long tail, which is discussed below.

In some cases the smell does not, or not exclusively, originate from the appendage but from other parts of the inflorescence. Remarkably, in *A. flavum* which we assume is autogamous, the appendage is rudimentary; it is entirely absent in *A. exappendiculatum* (Fig. 3F). The latter species is dioecious and hence obligatorily outcrossing. It bears a helmet with a long filiform tip that produces a smell of the general type described above. Such spathe tails, often extremely long, also occur in arisaemas possessing normal, club-shaped, odoriferous spadix appendages. Some of these tails are odoriferous, too. We found the elongate helmet tip of *A. consanguineum* to be slightly scented (pers. obs., S.V., Fig. 2B). The helmet of *A. triphyllum* also shared the smell of the neighbouring appendage a little, but this may have been due to secondary adsorption of the volatiles by the wax coat covering the spathe. In *A. jacquemontii*, also observed by us in cultivation, the ozone-like smell emanated from the appendage and also from the tailed spathe tip. Barnes (1935) maintained that the tail of the spathe of *A. convolutum* (= *A. tuberculatum* C.E.C. Fischer), up to 17 cm long, was clearly the source of the smell. He did not comment on the role of the appendage of this species.

THE POLLINATORS

The first to describe an *Arisaema* inflorescence in some detail from the ecological viewpoint was Knuth (1904) in his account of *A. filiforme* from Java, with remarks on an unknown species (erroneously designated as *A. japonicum*). He found "... winzige Fliegen [minute flies]" (besides thrips) in the spathes of the former and presumed that these insects, attracted by the smell, might enter the spathe via the appendage which is extended to a 25 cm long, filiform tail in this species, and descend to the fertile part of the spadix. Molisch (1926) noted "small dipterans" in the spathes of *A. thunbergii* Blume and *A. consanguineum* in Japan, as he did (Molisch, 1930) in *A. speciosum* and *A. japonicum* (= *A. serratum*) near Darjeeling (India) "... immer nur sehr wenige Fliegen. ... meist eine kleine ... am Boden lebende häufige Diptere [always only a very few flies ... mainly a small ... common dipteran living on the ground]". Schlegel (cit. by Knuth, 1904) reported the regular presence of dead or moribund 'cecidomyid' midges in the spathes of male *A. triphyllum* inflorescences, but these insects were later identified by Lowell (cit. by Knuth, 1904) as fungus gnats (Mycetophilidae). Seven mycetophilid species (not specified) were found by Robertson (1928) as visitors of this taxon, for which fungus gnats were also recorded by Rust (1980) and Bierzychudek (1982b). Rust, however, deemed thrips, which were most abundant in the spathes, as the more efficient pollinators. Fungus gnats were also the predominant visitors of *A. leschenaultii*, observed by Barnes (1935) in the Nilghiris (India); he listed one (indet.) species each of the genera *Acnemia*, *Phronia*, *Mycetophila*, *Sciophila* and two species each of *Delopsis* and *Platyura*. In addition, sciarids (three species of *Sciara*) as well as some dolichopodid, phorid, and acalyptrate flies are mentioned. Remarkably, visitors were only encountered in the female spathes. Tanaka & Yahara (1987) mentioned in an aside the visit to an unnamed arisaema by mycetophilids in Japan, and later on, Tanaka (1990) described *A. angustatum*

Franch & P.A.L. Savat. as a "pitfall for insects". Sasakawa (1993, 1994a,b), an entomologist, made the first systematic collections of insect contents in spathes of *A. negishii* Makino, *A. yamatense* (Nakai) Nakai and *A. serratum* in Japan (Table 3). Fungus gnats predominated absolutely in *A. serratum*, with alternative preponderance of either mycetophilid (nine species) or sciarid (and keroplatid) midges (eight species) in different localities.

VISITORS TO *ARISAEMA* COLLECTED IN NEPAL

During various expeditions (1973–1995) to the Himalayas, J.M. regularly checked *Arisaema* inflorescences and collected their insect contents. For procedures applied to preserve arthropods from the blossoms without loss of individuals, see Material and methods. Floral features of the *Arisaema* species involved are indicated in Table 4.

We present here a complete list of all insect taxa that have been found in the course of J.M.'s journeys and that have been already determined (Table 3). In all cases, the families Sciaridae and Mycetophilidae played the major role as contents of *Arisaema* inflorescences. Names of the gnats listed are from Vogel (1978b, det. by L. Matile, Paris), Mohrig & Martens (1987), Menzel & Martens (1995) and Kallweit & Martens (1995). Hitherto unpublished data were communicated by P. Chandler (in litt., 5.iv.1988, Mycetophilidae), W. Wirth (21.x.1984, Ceratopogonidae), and U. Kallweit (4.ii.1998).

While the sciarid and mycetophilid faunas of the Himalayas are still nearly unexplored, the *Arisaema* inflorescences yielded substantial numbers of specimens and species of both families for the first time. As expected, this material contained many unknown taxa. The following were described recently: one new genus (*Keilbachia* Mohrig), 13 new species of Sciaridae (Mohrig & Martens, 1987; Menzel & Martens, 1995), and nine species of Mycetophilidae (Kallweit & Martens, 1995). The collections of the 1995 expedition, which are not yet described, yielded additional new species. The only dixid species encountered was also new (Wagner, 1982).

Beside Sciaridae and Mycetophilidae, additional dipterans were found in many inflorescences (det. U. Kallweit). According to their scanty and irregular occurrence and mainly large size, they apparently do not contribute to pollination. Specimens of the following families were present (abbreviations of *Arisaema* species as follows: con, *consanguineum*; cos, *costatum* (Wall.)Mart.; fla, *flavum*; gri, *griffithii*; jac, *jacquemontii*; nep, *nepenthoides*; spe, *speciosum*; tor, *tortuosum*; uti, *utile*).

Cecidomyidae: nep, gri, jac
Ceratopogonidae: nep, tor, spe
Chironomidae: nep, jac, tor
Chloropidae: nep
Cryptochaetidae: jac
Dixidae: nep
Dolichopodidae: jac
Drosophilidae: nep
Empididae: nep
Ephydridae: nep
Keroplatidae: jac
Lonchopteridae: gri
Milichiidae: nep
Muscidae: nep
Indet.Nematocera: jac
Phoridae: nep, spe, jac
Psilidae: nep
Psychodidae: nep, jac
Simuliidae: nep
Tachinidae: jac, nep

TABLE 3. List of Sciaridae, Mycetophilidae and Keroplatidae collected from *Arisaema* inflorescences in Nepal (J. Martens) and Japan (M. Sasakawa). Abbreviations of *Arisaema* species: con, *consanguineum*; cos, *costatum*; gri, *griffithii*; jac, *jacquemontii*; neg, *negishii* Makino; nep, *nepenthoides*; ser, *serratum*; spe, *speciosum*; tor, *tortuosum*; uti, *utile*; yam, *yamatense* (Nakai)Nakai; J, Japan; N, Nepal

Dipteran taxa	*Arisaema*:	nep	jac	cos	spe	con	tor	gri	uti	ser	yam	neg	J/N
SCIARIDAE	total(♂/♀)												
BRADYSIA													
cellarum Frey	1(1/–)						1						N
delectabilis Mohrig & Menzel	2(2/–)									2			J
divaricata Sasakawa	25(25/–)									25			J
fimbriata Mohrig	20(19/1)	19	1										N
florida Mohrig	26(12/14)	26											N
gratiosa Menzel	2(2/–)	2											N
hirsutiseta Mohrig & Krivosh.	1(1/–)		1										N
individua Mohrig & Krivosh.	1(1/–)		1										N
inusitata Tuomikoski	6(4/2)	6											N
iridipennis (Zetterstedt)	2(2/–)		1	1									N
melanura Mohrig & Mamaev	13(1/12)	13											N
nitidicollis (Meigen)	1(1/–)		1										N
peraffinis Tuomikoski	1(1/–)	1											N
pyriformis nepalensis Mohrig	3(3/–)					3							N
quadrispinistylata Alam	1(1/–)			1									N
regularis Lengersdorf	1(1/–)			1									N
scabricornis Tuomikoski	6(6/–)	6											N
semihilaris Mohrig & Krivosh.	68(9/59)	68											N
1 additional species	1(–/1)		1										N
CORYNOPTERA													
antespinifera Mohrig	6(6/–)	6											N
dumosa Sasakawa	7(2/5)									7			J
immunita Menzel	1(1/–)	1											N
licina Sasakawa	22(22/–)									22			J
semicurvata Mohrig	31(31/–)	31											N
subconcinna Mohrig	3(3/–)		3										N
subcurvata Mohrig	2(2/–)	2											N
1 additional species	1(–/1)		1										N
CTENOSCIARA													
hyalipennis (Meigen)	7(2/5)	7											N
nudata Mohrig & Kozanek	2(1/1)	2											N
KEILBACHIA													
hamata Menzel	1(1/–)	1											N
nepalensis Mohrig	4(2/2)	4											N
tenerrima Menzel	1(1/–)	1											
LYCORIELLA													
fallaciosa Menzel	12(10/2)	12											N
longiculmi (Alam)	1(1/–)		1										N
1 additional species	4(–/4)	4											N
PARACTENOSCIARA													
longimentula Sasakawa	4(2/2)									4			J
PHYTOSCIARA													
arisaemae Sasakawa	20(15/5)									20			J
bistriata (Strobl)	1(1/–)	1											N
flavipes (Meigen)	6(5/1)			6									N
insolita Sasakawa	5(3/2)									5			J
megumiae Sasakawa	7(2/5)									7			J
ungulata Winnertz	8(5/3)									8			J
1 unidentified species	5(–/5)	5											N
SCATOPSCIARA	1(1/–)	1											
edwardsi Freeman	1(1/–)	1											N
geophila Tuomikoski	5(3/2)	5											N

continued

TABLE 3. *continued*

Dipteran taxa	*Arisaema*:	nep	jac	cos	spe	con	tor	gri	uti	ser	yam	neg	J/N
MYCETOPHILIDAE													
ANATELLA													
1 unidentified species	2(–/2)							2					N
BOLETINA													
menicophalloides Sas. & Kim.	1(1/–)									1			J
subnitidula Sasakawa	3(3/–)									3			J
BREVICORNU													
mathei Kallweit	3(3/–)	2						1					N
EXECHIA													
arisaemae Sasakawa	4(1/3)											4	J
pararepanda Kallweit	20(20/–)							20					N
LEIA													
ishitanii Sasakawa	25(17/8)									25			J
MONOCHLONA													
silvatica Zaitzev	1(1/–)									1			
MYCETOPHILA													
fungorum (De Geer)	1(1/–)				1								N
ishiharai Sasakawa	1(1/–)									1			J
taplejungensis Kallweit	1(1/–)		1										N
3–4 spec. of the *ruficollis* group	11(2/9)	3	4			4							N
1 spec. of the *vittipes* group	1(–/1)	1											N
4 unidentified species	9(–/9)	2	2			5							N
MYCOMIA													
fasciata (Gimmerthal)	2(–/2)									2			J
ornata Meigen	7(7/–)									1	6		J
PHRONIA													
arisaemae Kallweit	1(1/–)	1											N
bicuspidalis Kallweit	1(1/–)	1											N
longifurca Sasakawa	4(1/3)									4			J
PSEUDEXECHIA													
macrocantha Kallweit	6(2/4)	5						1					N
PSEUDOBRACHYPEZA													
floralis Kallweit	1(1/–)		1										N
RYMOSIA													
1 unidentified species	1(–/1)											1	J
SCIOPHILA													
setiterminata Sasakawa	1(1/–)									1			J
SYNAPHA													
dhorparkharkaensis Kallweit	1(1/–)	1											N
ZYGOMYIA													
1 unidentified species	1(–/1)	1											N
KEROPLATIDAE													
ZELMIRA													
angulata Sasakawa	12(5/7)									12			J
NEOPLATYURA													
2 unidentified species	2(–/2)		2										N

Along with dipterans, small numbers of other arthropods were also present, apparently strays; these may intrude into the inflorescences by chance, possibly to gain shelter. The relatively numerous Thysanoptera (cf. Strassen, 1976) may feed on the pollen masses, in which they were most often found to be 'swimming'. Representatives of the following orders were found:

Table 4. Floral features of *Arisaema* species from which visitors were collected in Nepal and Europe

Species	Section	Position	Colour of inflorescence	Length (cm) of tube	Appendage	Gender	Sampling sites*
A. griffithii	*Trisecta*	geophilic	dull purple	5–10	flagellate	dioecious	12
A. utile	*Trisecta*	geophilic	deep purple, white stripes	5–10	flagellate	dioecious	3, 10, 13
A. costatum	*Trisecta*	medium	deep purple	4–8	flagellate	dioecious	6
A. speciosum	*Trisecta*	geophilic	deep purple	3, 5–7	flagellate	dioecious	9
A. tortuosum	*Tortuosa*	tall	light green	2.5–7	erect, long exerted	monoecious	2, 3
A. jacquemontii	*Tenuipistillata*	medium	green	2.5–9	clavate	dioecious	1, 2, 4–7
A. consanguineum	*Sinarisaema*	tall	green, flushed with red	4–8	clavate	dioecious	2, 7
A. nepenthoides	*Arisaema*	tall	greenish white mottled red	3–8	clavate	dioecious	8, 12
A. flavum	*Dopafa*	dwarf	yellow	2	globular	monoecious	4
			Species observed in cultivation				
A. serratum	*Arisaema*	medium	green/white	5	clavate	dioecious	
A. amurense	*Arisaema*	medium	green/brown, white-striped	3–5	clavate	dioecious	
A. triphyllum	*Arisaema*	medium	striped purple/ white	4–8	clavate	dioecious	
A. ciliatum	*Sinarisaema*	medium	striped purple/ white	5–7	clavate	dioecious	

* Numbers refer to list of localities provided in Material and methods and Figure 1.

Heteroptera: nep
Cicadina: nep
Psylloidea: nep
Coleoptera: (all nep)
  Chrysomelidae, Halticinae
  Curculionidae
  Staphylinidae

Hymenoptera: nep
Thysanoptera : con, fla,
  jac, tor, uti, spe
Collembola: nep
Dermaptera: gri
(Araneae: Thomisidae: *Synaema* sp.)

In conclusion, Sciaridae (up to nine specimens in one spathe; *A. nepenthoides*) and Mycetophilidae (up to 20 specimens; *A. jacquemontii*) were by far the most commonly attracted to all species of *Arisaema*. An exception is *A. flavum*, in which none were found. Both families are followed quite regularly by Phoridae, which are present in considerable numbers of specimens (up to 10 in one spathe of *A. nepenthoides* [six times], *A. speciosum* [twice], *A. jacquemontii* [once]). In five *Arisaema* species, 33 identifiable sciarid species (238 specimens: 139 ♂♂, 99 ♀♀; Menzel & Martens, 1995) were reported, and from six *Arisaema* species 15 identifiable species (40 specimens: 38 ♂♂, 2 ♀♀; Mohrig & Martens, 1987). In the Mycetophilidae, 73 specimens (36 ♂♂, 37 ♀♀) represented 25 species, including 10 unidentified ones represented only by ♀♀ (Kallweit & Martens, 1995) out of four *Arisaema* species.

Within the various species of gnats, differences in host specificity are obvious, even if one takes into account that availability of flowering *Arisaema* species differed during the various expeditions, depending mainly on season and altitude. Therefore, the overall numbers of inflorescences of all *Arisaema* species checked are by no means comparable. Consequently, only a few conclusions can be drawn on host specificity.

Spathes of *A. nepenthoides* yielded the most sciarid and mycetophilid gnats: 22 sciarid (Menzel & Martens, 1995; Mohrig & Martens, 1987) and 15 mycetophilid species (Kallweit & Martens, 1995; Chandler in litt.). Sciaridae predominated in both species and specimens, in part due to the fact that *A. nepenthoides* was the most common *Arisaema* checked in the years in which J.M. travelled in Nepal.

According to the list of spathe contents (Kallweit in litt., 3 May 1994), out of 36 spathes (four *Arisaema* species) yielding insects, only four did not contain Sciaridae and/or Mycetophilidae; 13 harboured (among other families) only Mycetophilidae, 13 only Sciaridae, and four both groups. Representatives of both families combined were by far more numerous than those of all other insects.

The various *Arisaema* species seem to attract pollinating gnats differently. *A. nepenthoides* and *A. griffithii*, which were both investigated simultaneously (April 1988) at the same forest edge (Dhorpar Kharka, 2700 m) and which grew in close proximity in the same microhabitats, revealed quite different arrays of inmates: among dozens of spathes checked, only four *A. griffithii* contained dipterans at all, exclusively Mycetophilidae (30 specimens, six species). Of these six, only two were also collected from *A. nepenthoides* at the same locality. On the other hand, also at Dhorpar Kharka, 212 sciarids (21 species, 88.7% of the individuals of the 1988 collection) were secured from *A. nepenthoides*, but not a single sciarid was present in the large *A. griffithii* population flowering in the same microhabitat. The two spathe types in question differ considerably in level of exposition, morphology, and coloration (Table 4).

In other localities as well, especially in the upper Simbua Khole valley (above 3300 m), where *A. utile* was common in May 1988, only a few insects were collected (*A. nepenthoides* was absent due to altitude).

Interestingly, in one *A. nepenthoides* spathe 121 dixid flies (55 ♂♂, 66 ♀♀), all belonging to *Dixa martensi* were collected (Wagner, 1982). However, not a single additional dixid specimen turned up in dozens of spathes examined either at this heavily forested slope or anywhere else.

According to dipteran experts (Kallweit, pers. comm.), *Arisaema* spathe contents do not reflect the total local faunas, given that potentially all sciarid and mycetophilid species may be attracted by *Arisaema* odours. Many arisaemas do not grow in microhabitats which mycetophilids and sciarids prefer: extremely damp, shadowed localities under a closed canopy (see Menzel & Martens, 1995). The only inflorescence encountered in such a habitat (*A. jacquemontii*) yielded 33 dipterans of eight families including 20 Mycetophilidae (three genera, seven species) and five Sciaridae (three genera, four species). On the other hand, those *A. utile* growing along rivulets and streams quite often harboured no individuals of the above two families.

In sciarids and mycetophilids, both sexes are attracted by *Arisaema* inflorescences, but ♂/♀ ratios encountered in the individual spathes differ and vary apparently by chance (cf. Table 3). In Nepal, of 311 sciarid specimens, 214 were ♂♂ (68.9%) and 97 were ♀♀ (31.1%) (Menzel & Martens, 1995; Mohrig & Martens [1987] treated only ♂♂). Of 124 mycetophilid specimens 78 were ♂♂ (70.7%) and 46 were ♀♀ (29.3%). The *Arisaema* species in Japan also showed similar ratios. Sasakawa (1993, 1994a,b) reported 75 ♂♂/30 ♀♀ sciarid and 38 ♂♂/24 ♀♀ mycetophilid specimens. Even though Mohrig & Martens (1987) did not consider ♀♀ there is a pronounced preponderance of the male gender in the two gnat families caught in the *Arisaema* traps.

In a photograph of the African *A. enneaphyllum* A.Rich., taken in Ethiopia by Prof. Christian Puff (Vienna), an imprisoned gnat is clearly visible, most probably a mycetophilid.

GNAT VISITATIONS IN ARISAEMAS CULTIVATED IN EUROPE

For several years, cultivated species of *Arisaema* (Table 4) have been monitored at anthesis by S.V. in the Botanical Gardens of Mainz, Berlin-Dahlem, and Vienna. Fungus gnats were present in the spathes of *A. amurense*, *A. ciliatum*, *A. fargesii*, *A. consanguineum*, *A. jacquemontii*, and *A. tortuosum*. The inmates of *A. consanguineum* and *A. amurense* were repeatedly collected for determination (Table 5).

In *A. consanguineum*, apart from two indeterminate sciarids, 10 species of mycetophilids (13 ♂♂, 2 ♀♀) were found. All six genera involved were also recorded from Nepal arisaemas (but none of them in *A. consanguineum*). In *A. amurense*, 12 mycetophilid species (8 ♂♂, 31 ♀♀) belonging to seven genera were recorded, four of which were present in Nepalese collections and two in Japan. *Mycetophila fungorum* (Fig. 8A) was the only species shared as a visitor by both cultivated plant species; it was also found in Nepal (*A. speciosum*). Among the species listed, *Exechia fusca*, *E. repanda*, and *Mycetophila fungorum* are widely distributed in the Holarctic; the remainder of species are restricted to the Palearctic, but inhabit large distributional areas as well (Kallweit, in litt.).

Visitors were only rarely encountered in the male spathes, while up to 30 individuals could be found accumulated in single pistillate inflorescences; most of these insects were dead and partly decayed, especially at the end of anthesis. Spathes of the cultivated monoecious *A. tortuosum* contained these visitors in the open as well

TABLE 5. Mycetophilids from *Arisaema* species cultivated in Europe

A. consanguineum (Mainz, June 1960) det. A. Burghele-Balacescu	*A. amurense* (Berlin-Dahlem, May 1976) det. U. Kallweit
Mycetophilids	
Exechia pallida (Stanner) 1 ♂	*Exechia fusca* (Meigen) 2 ♂♂
Pseudexechia trivittata (Staeger) 1 ♂	*Exechia repanda* (Johannsen) 1 ♂
Pseudexechia fusca (Meigen) 3 ♂♂	*Exechia separata* (Lundstroem) 1 ♂
Rhymosia fasciata (Meigen) 1 ♂	*Exechia* sp. 4 ♀♀
Allodia ornaticollis (Meigen) 1 ♂	*Allodia* sp. I 11 ♀♀
Allodia lugens (Wiedemann) 1 ♂	*Allodia* sp. II 2 ♀♀
Allodia (*Brachycampta*) sp. 1 ♂	*Brevicornu* (*Stigmatomeria*) *obscurum* (Winnertz) 1 ♂
Brevicornu griseicollis (Staeger) 1 ♂	*Mycetophila fungorum* (De Geer) 1 ♂, 12 ♀♀
Mycetophila fungorum (De Geer) 1 ♂, 1 ♀	*Cordyla sixi* (Barentrecht) 1 ♂
Mycetophila ocellus (Walker) 2 ♂♂, 1 ♀	*Cordyla crassicornis* (Meigen) 1 ♂
	Phronia sp. 1 ♀
	Mycomyia sp. 1 ♀
Sciarids	
2 indet. spp.	*Corynoptera flavicauda* 40 ♂♂, 2 ♀♀

as in the greenhouse. Inflorescences of *A. amurense*, which had already received visits from fungus gnats in the Botanical Garden of Dahlem, were transferred in a vial to a private garden, surrounded by forest; these spathes again became filled with gnats during a single night. Only *A. serratum*, also observed in Dahlem, consistently failed to attract insects, although individuals of *A. amurense* growing nearby were successful in attracting them. As mentioned above, *A. serratum* did not produce a perceivable smell, possibly due to some physiological deficiency in these plants.

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The ample development of fructescences (with red berries) in *A. consanguineum*, *A. ciliatum*, and *A. erubescens* (where both sexes were present) demonstrated the efficacy of gnat visitation.

Based on divergent reports of observers, mainly concerning *A. triphyllum*, fecundity in natural stands varies from full seed set to sterility. Seed production in the latter species was found to be so meagre in some localities of New York State that Bierzychudek (1982a) was inclined to ascribe an 'apparent maladaptiveness' to a pollination system which may have been more efficient in the evolutionary past. Swarming of gnats and the blooming time of arisaemas do not always seem to coincide. For example, gnats will be either scarce or abundant in spring, depending on whether mushrooms—their natural substrate—have been scanty or plentiful in the previous autumn. Hence, in our opinion, the occurrence of such poor conditions is quite natural. Over a longer time scale, they will be compensated in better years, and the plants apparently do cope with such fluctuations.

From the above data we conclude that mycetophilids and sciarids are the regular pollinators of *Arisaema* over its whole geographic range. There is no local specificity in terms of gnat species, and the plants are able to lure a vicariant assembly of this pollinator type even when they are growing far from their home country.

PREVIOUS OBSERVATIONS ON THE FUNCTION OF THE SPATHE

Barnes (1935) believed that the insects arrived at the bottom of the spathe deliberately by descending the spadix, thereby, in the male plants, becoming covered with pollen from the anthers. This effect was increased by the pollen masses accumulated at the bottom. Barnes made the important observation that in the male spathes the visitors are allowed to leave through a basal exit: ". . . at the bottom of the tube . . . in front where the edges (of the spathe) overlap, . . . the two edges arch away from one another, so as to form a small roundish orifice about 1–2 mm". As Barnes also noted, there is no such exit hole in the female spathes. The outer edge in the female spathe is ". . . slightly thickened and presses firmly on the under edge and overlaps it to a greater extent than in the case of male spathes". The pistillate spadix, densely beset with ovaria, has a conical shape so that the free space left between it and the spathe wall becomes increasingly narrower. Insects forcing their way down became jammed and in their efforts to free themselves they dust the stigmas with pollen carried from previously visited male plants. Following Barnes, *A. tortuosum*, *A. translucens* C.E.C. Fischer, *A. tuberculatum* and *A. tylophorum* C.E.C. Fischer showed the same organization.

NEW OBSERVATIONS ON THE POLLINATION MECHANISM

Since the observations of Barnes (1935), no other detailed study of the pollination mechanism of *Arisaema* appears to have been published, although Vogel (1965), Bierzychudek (1982b) and Bown (1988) drew attention to the deadly fate of the pollinators of the female blossoms, a point neglected by Barnes. We (S.V) recorded the presence of an exit hole in the living staminate inflorescences of *A. amurense*, *A. ciliatum*, *A. consanguineum*, *A. roxburghii* (Fig. 3C), *A. enneaphyllum*, *A. fargesii*, *A. leschenaultii* (Fig. 3D,E), *A. nepenthoides*, *A. triphyllum* and *A. scortechinii* Hook.f. Fourteen additional taxa were recognized as possessing exit holes based on published photographs. Where pistillate spathes were available, the absence of openings in them was noted. *A. fargesii* is an exception in that some of the female spathes also had a distinct basal exit (observed in two cultivated specimens). Since 23 members of six different sections are concerned, and in view of the rather uniform construction of the spathes, these data strongly suggest that this "one-way system" (Bown, 1988) of the male blossoms is a general feature of the genus. In weak individuals, the spathe margins sometimes did not diverge enough to permit larger gnats to leave. In a number of additional species seen in cultivation, only female spathes were available, or other circumstances prevented ascertaining the development of a hole in the staminate blossoms. Occasionally, incomplete unfolding may occur due to inclement weather. In *A. serratum* the hole was never clearly seen, as was the case in the sole spathe available of *A. exappendiculatum*. *A. flavum* (monoecious) lacks a hole because the spathe is congenitally fused halfway. The linkage of exit formation to the male gender is especially apparent in the allogamous, monoecious *A. tortuosum*. In the (male) dioecists the exit opens during the first or second day of anthesis. In cultivated plants of the latter species, however, the exit remained closed as long as the female phase was functional, and started to gape only at the onset of the male phase.

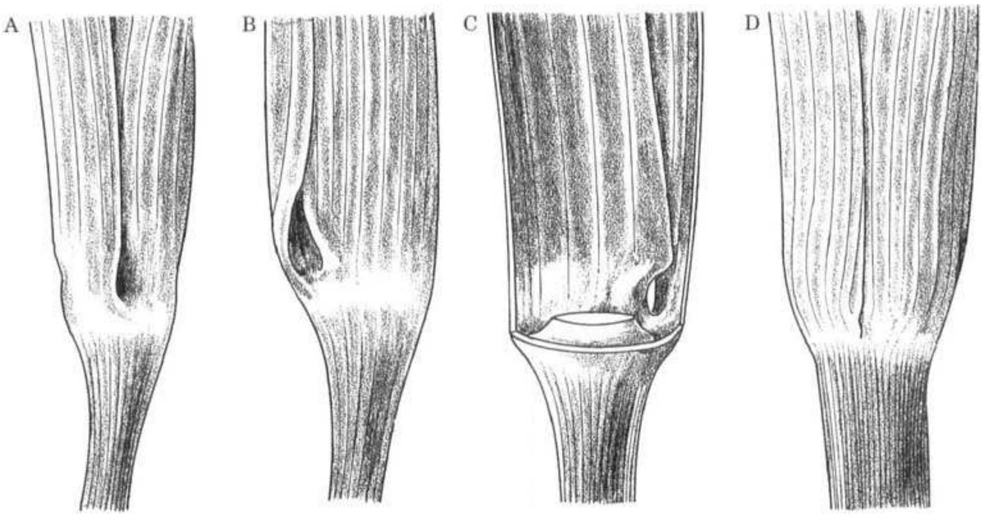

Figure 4. *Arisaema triphyllum*, lower sections of spathes. A–C, male spathe with exit hole, in C cut open, showing the interior (spadix removed), D, female spathe.

THE INFLORESCENCE AS A KETTLE TRAP: OBSERVATIONS ON *A. CONSANGUINEUM* AND *A. TORTUOSUM*

How do the fungus gnats get into the spathes, what happens inside, and how do they transfer the pollen? Up until now, no relevant data have been published, nor has a hypothesis of how the pollination apparatus functions been proposed, except for brief remarks made by Vogel (1965) and Bierzychudek (1982a,b) in a broader context.

Observations made on cultivated *A. consanguineum* may answer these questions. A group of male and female plants regularly flowered in the shady arboretum of the Mainz Botanical Garden during May and June. The inflorescences of this species, *c.* 7 cm high and 1.5 cm in diameter, are developed pseudolaterally below the lamina of the sole leaf on the strictly erect stem at a height of 30–50 cm above ground (Fig. 2B). The spathe is light green, inside flushed with red, and both its tubular and free part are ornamented with milky white (unpigmented), translucent longitudinal stripes. The helmet, bent over the entrance of the tube, tapers out into a pendent, filiform appendage 13 cm long, similar to the thread-like 'drip-tips' of the segments of the palmate leaf. The narrow auricles forming the anterior limb exude on their inner (upper) surface small drops of nectar. As stated above, the yellow appendage of the spadix is clavate to cylindrical, about 3 cm long and 5 mm thick, its rounded tip being visible in the spathe entrance. Both the laminar tail and the spadix appendage are scented. The basal opening present in the staminate morph, marked outside with maroon shades (as in some other species), resembles that figured for *A. triphyllum* (Fig. 4).

The basal opening is mainly formed by the inner rim of the spathe tube. While the outer rim remains straight, the base of the inner rim, due to local growth of tissue, bulges inwards to such an extent that a circular or semicircular 1–2 mm gap is formed. Often the hole's outer margins protrude in a collar-like manner. As

Barnes (1935) already noted in his arisaemas, the staminate spadix is, at that level, bare of florets, so that the inner space widens; this allows the gnats to circle round, wading through the pollen masses, and find the exit.

If the convolution of the tube is considered as resulting from a partial inhibition of the unfolding process (hence some kind of neoteny), then the rise of the aperture may be a local remnant of expansion that was once more complete in evolution.

As mentioned earlier, the lowermost zone of the spathe is internally illuminated by a light-window of transparent tissue; this is where the pollen masses collect in the staminate morph.

The predominant visitors were *Mycetophila fungorum*, a common species of 5 mm long fungus gnats (Fig. 8A), along with a few smaller mycetophilids (Table 5) and some other Nematocera. Especially in the evenings, the spathes were seen to be approached by the swarming gnats in an erratic flight pattern. They tried to alight on various parts of the spathe, including the outer wall of the tube and the outer and inner side of the helmet. Unable to grip the waxy surfaces, they slid down; if this happened outside, they resumed flight and attempted to land again. Some walked down from the upper side of the helmet along its margins to the horizontal flanges of the spathe mouth. This part is less slippery and allows the gnats to walk and to sip the droplets exuded from the extrafloral nectaries. The gnats were never observed to enter the interior by stepping down the tube walls; rather, they fell immediately while trying to get a foothold on the overarching (inner side of the helmet) or perpendicular parts of the spathe (interior of the flanges). The smooth, wax-dusted surface (Fig. 7C) is apparently an efficient gliding zone for mycetophilids, while most brachyceran dipterans, ants and *Forficula* are able, as experiments showed, to get hold on it. The paired tarsal pulvilli of mycetophilids (Fig. 7D) have a relatively low number of spathulate setae, which become covered by detaching wax powder and thus inactivated.

Observations of *A. ciliatum* in the Botanical Garden of Vienna confirmed the above findings in every respect (nectaries, however, are missing in this species).

The victims' fate is quite different in the staminate and in the pistillate blossoms. In most cases, once a gnat fell into the chamber of a staminate spathe, it soon reappeared in the lower aperture, often completely dusted with pollen, and flew off immediately. On leaving the hole, the gnats swept out a good portion of free pollen that was lost and had become useless. If the helmet was cut away after a gnat had fallen into the chamber, the animal could be seen attempting to climb up the spadix (Fig. 8C), which in its upper part is unscalable as well, or the spathe walls, and finally found itself at the bottom. Here the gnats circled around in the illuminated free annular space between the wall and the lowermost, naked portion of the spadix. They waded through the pollen masses and ultimately escaped through the aperture. In one case, a gnat that had left a spathe almost immediately alighted on another. When the aperture was closed with a piece of cotton, the victims were unable to escape by another way and accumulated in the kettle.

In the pistillate traps there was no escape because the bottom is closed. In their efforts to ascend, the gnats scrambled fluttering around the pistillate part of the spadix. They also forced their way downwards, perhaps deceived by the annular window, which is fallaciously taken for an exit. By these activities, the animals contact the stigmas thoroughly and pollinate them if they previously had escaped from a male spathe. During the subsequent hours or days the inmates become exhausted and perish. Fresh victims may accumulate throughout anthesis, and the

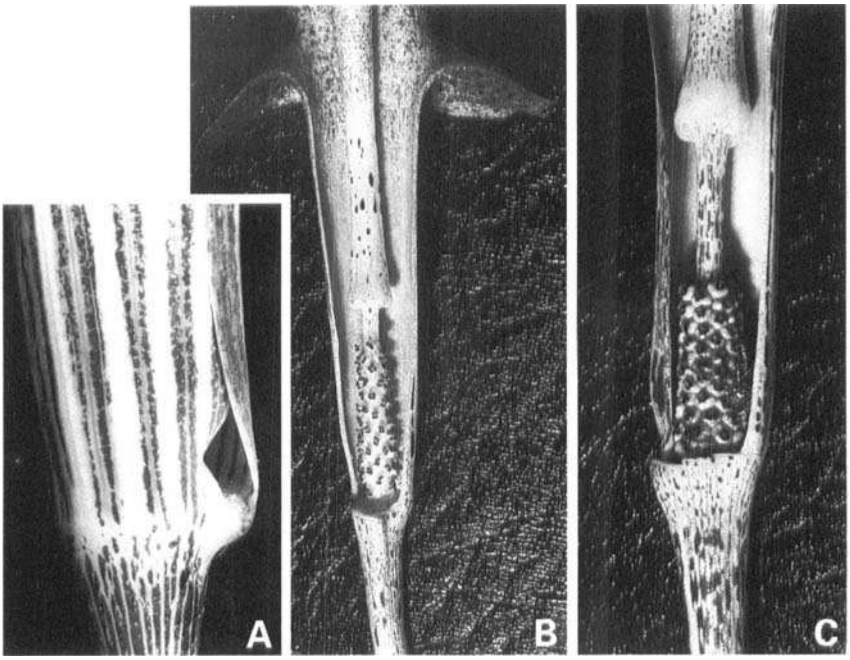

Figure 5. A, *Arisaema ciliatum*, lower part of male spathe with exit hole. B & C, *A. nepenthoides*, spathes cut lengthwise (different magnifications): B, male, C, female inflorescence (with remnants of fungus gnats).

bodies in the lowermost part of the chamber then decompose. Thus, while an individual has quickly passed through one or more staminate inflorescences, it will die in a pistillate one (Figs 5B,C, 6). If a gnat happens to visit a pistillate spathe first, it carries no pollen and its capture is thus futile.

These facts explain why gnats are seldom encountered in the male spathes, whereas the female sometimes abound with them. It also becomes plausible why the lowermost pistils tend to develop fruits more often than the upper ones, as Barnes (1935) noted in *A. leschenaultii*.

How do events proceed in the spathes of monoecious arisaemas such as *A. tortuosum*? As stated above, the inflorescences of this species, controlled by us in cultivation, are protogynous; the gaping of the exit hole is postponed until the onset of the male phase, which takes place at about day 7 of anthesis. Hence, the two modes of manipulating the visitors are combined and sequential: in the first, female, phase the agents are detained; in the second, male, phase they are allowed to escape. This conclusion is circumstantial since the gnats could not be witnessed in action but were found detained in the female stage of the spathe. Nonetheless, those captives imprisoned during the first phase will only rarely survive until the pollen is shed and the gap opens. Rather, those that export the pollen will be lucky individuals freshly attracted during the male phase.

In summary, the spathe of *Arisaema* functions as a kettle trap. Its visitors fall in unintentionally. Pollination is brought about by a functional correlation of spathe and spadix, which is more intimate than the simple construction of both parts would suggest. Previous assumptions that the midges are able to leave the kettle via the

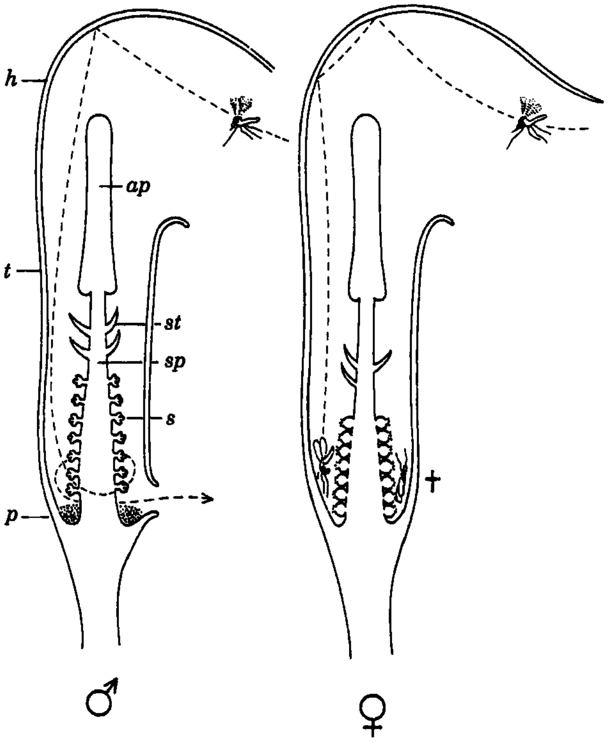

Figure 6. Scheme of pollen transfer in a dioecious *Arisaema*. After temporal entrapment in male spathes (left), gnats escape and may pollinate a female one (right), where they will be retained definitely and die. Abbreviations: h, hood of spathe, t, tube of spathe, sp, spadix, ap, spadix appendage (osmophore), st, sterile florets, s, fertile florets, p, pollen masses.

entrance or spadix are thus disproved, not counting occasional escapes by flight. The axial surface of the spadix and the tube walls are wax-covered. The florets may provide some foothold, but the naked appendage remains unsurmountable. In this connection, the abruptly truncate, concave or umbrella-like dilatation of the lower end of the appendage (which is then termed stipitate), as found in numerous species (Fig. 5B,C), also appears to aid in detaining the insects.

PECULIAR CHARACTER OF THE KETTLE TRAP

The inflorescences of *Arisaema* thus typically represent kettle traps with a suite of rather peculiar characters. Most of these are apparently related to the nature, size class, and behaviour of fungus gnats and their relatives they attract and manipulate, and whose habitat the plants share. Other kinds of insects will occasionally be captured and may even confer pollination; most, however, are able to escape prematurely, using the 'wrong' exit, or they lack the appropriate size and mobility.

Salient traits are the non-fetid, 'idiopathic' scents, long lifespan of spathes, primitiveness of gliding devices, predominant dioecy, and the different ways in which the agents are handled in the two morphs: the male spathes, being 'semitraps' with

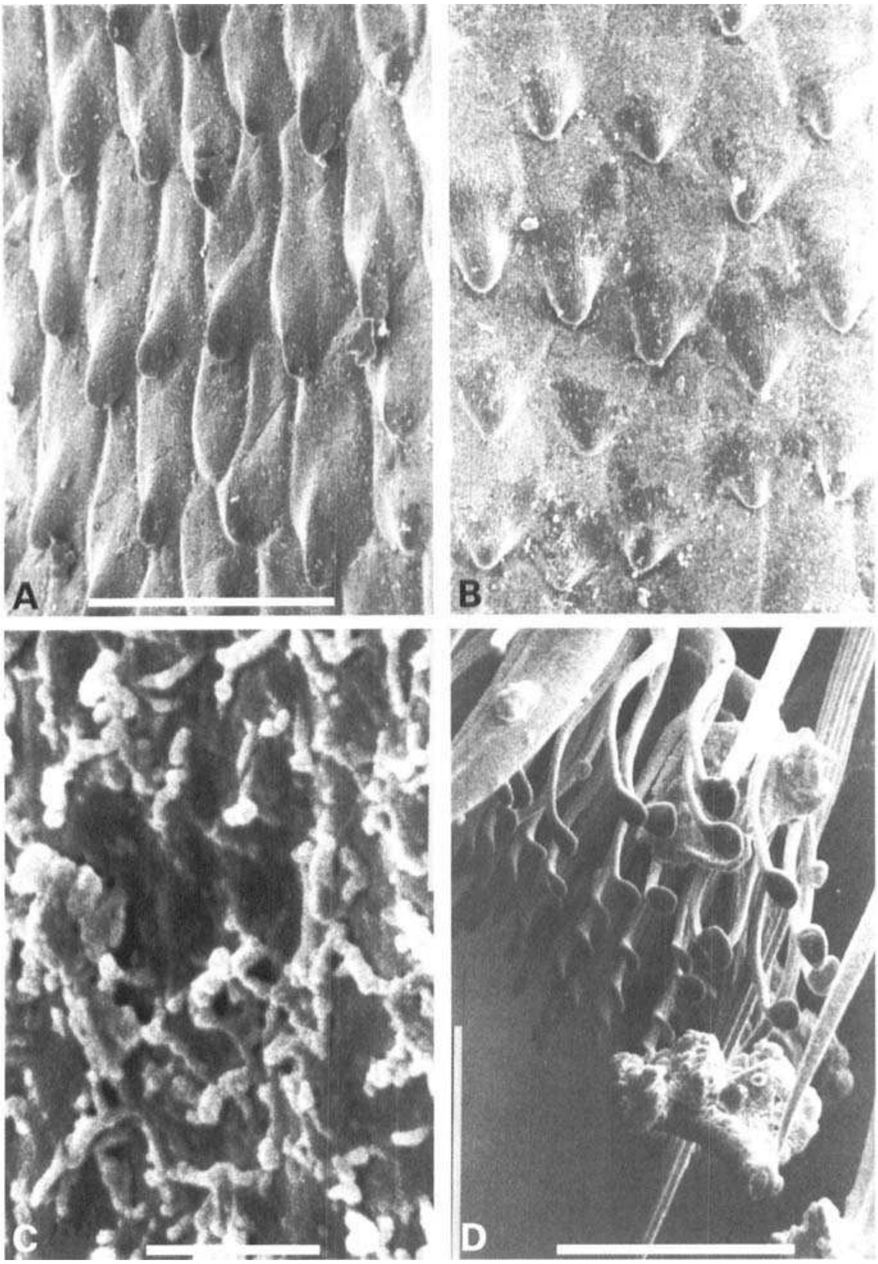

Figure 7. A–C, *Arisaema jacquemontii.* A & B, papillate gliding surface of tube, in lateral and frontal view, C, wax rodlets covering the epidermis in high magnification, D, tarsal pulvillus of a mycetophilid, spoon-like bristles soiled with clumped wax particles. Scale bars: A,B = 100 µm, C = 1 µm, D, 10 µm.

an exit, allow the insects to pass quickly, whereas the females, providing no escape, kill the potential pollen vectors. With one or two exceptions discussed below, *Arisaema* thus displays the only known type of floral trap that does not allow the captives to leave through the entrance; by permanently imprisoning them in the female spathes,

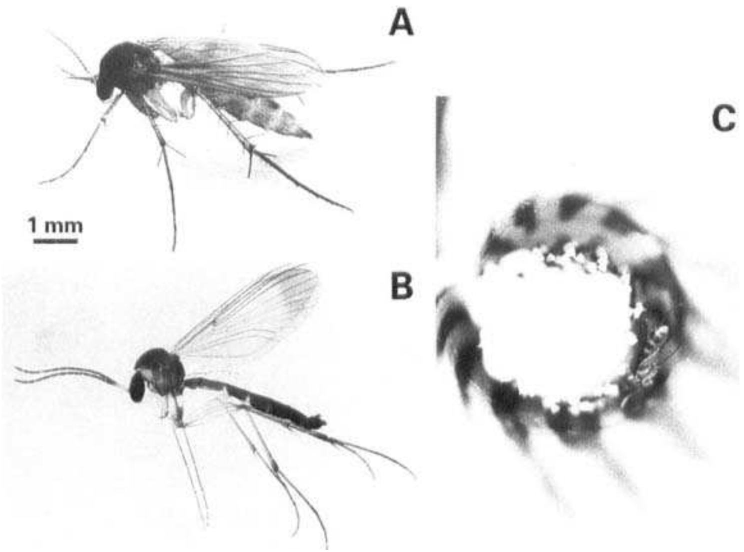

Figure 8. A & B, mycetophilid gnats. A, *Mycetophila fungorum* (live), B, *Phronia* spec. (museum specimen, photo. U. Kallweit). C, imprisoned gnat between tube wall and staminate flowers of *A. ciliatum*, viewed from the tube mouth.

it alone practises this lethal mode of parasitism. *Arisaema* contrasts herein with most genera of the related tribe Areae (*Arum*, *Sauromatum*, *Dracunculus*, *Biarum*, *Typhonium*, etc.). Although in *Helicodiceros muscivorus*, another member of this tribe, the pollination chamber is sometimes so overcrowded with carrion flies that they all perish from suffocation (Vogel, 1965), this is not intended by the functional concept of that species. The kettle traps of the Areae, designed for more alert types of insects, are short-lived, subject to strictly timed changes and movements (such as final inactivation of detaining structures), and furnished with elaborate temporal guiding and auxiliary devices, including zones of downward-pointing epidermal papillae bearing oil-drops and epidermis gaps or stomata in the kettle wall. Being monoecious and protogynous throughout, these advanced traps restrict the olfactory allurement to the pistillate phase, and by keeping the vectors as a "captive audience" (B. Meeuse) until pollen issue, they also exploit the same individuals for both import and export of pollen and releasing them via the entrance.

PARALLELS IN TRAP CONSTRUCTION OF OTHER AROIDS

A taxon that ecologically resembles *Arisaema* in many respects is the Mediterranean genus *Arisarum*, as already suggested by Pohl (1929). Its three species share with *Arisaema* the adaptation to fungus gnats and related nematocerans (Vogel, 1978b), a similar shape and makeup of their kettle traps, waxy gliding surfaces, secondary pollen deposition (Galil, 1990), and a long persistence. Where present in *Arisaema*, imbricate gliding papillae resemble those of *Arisarum*. *Arisarum vulgare* Targ.Tozz. is especially akin to *Arisaema* in possessing a clavate osmogenic appendage that produces the same type of scent; the coloration of the spathe is also green with white translucent stripes. *Arisarum* traps, however, differ by virtue of their smaller size, monoecy, homogamy, a congenitally fused spathe tube and, in turn, release of pollinators via the entrance (Faegri & van der Pijl, 1979). Based on structural and chloroplast DNA analysis, *Arisarum* is not closely related to the Arisaemateae (French, Chung & Hur, 1996), but is currently regarded as forming its own, rather distant, tribe within the subfamily Aroideae (Mayo, Bogner & Boyce, 1997). Thus, its functional style probably represents an independent convergence. This is underlined by the lack of homology of the pattern of translucent stripes in *A. vulgare*, which are intercostal in position and not, as in *Arisaema* (Vogel, 1978b), superimposed on the costae.

Pinellia ternata (Thunb.) Breitenb. is a second parallel. The spathe of this small temperate east Asian genus has in common with those of *Arisaema* its longevity, shape and green hue, a tailed osmogenic spadix appendage, and liberation of captives by basal gaping of the convolute spathe. It resembles *Arisaema tortuosum* in being monoecious and protogynous, and consequently the opening of the exit is retarded until pollen release (Vogel, 1965). The kettle trap of *Pinellia* deviates, however, by luring another type of pollinator (ceratopogonid dipterans), by its smaller size, a papillate gliding surface similar to that of *Arum*, monoecy, and a constriction of the spathe separating the distal staminate and the proximal pistillate spadix compartment (the latter being connate with the spathe). The shed pollen is deposited upon this constriction. Potential pollen carriers are imprisoned and perish during the female phase, while pollen-exporting latecomers are released.

The often cultivated *P. tripartita* (Blume) Schott is scentless and has so far never been found to be visited by insects, despite a basally similar organization. Following Uhlarz (1985) it is self-fertile, and due to overlap of sex phases, fruits are regularly set by wind-aided geitonogamy.

The Arisaemateae and Pinellieae form sister tribes in the cladistic trees of Murata (1990a) and French *et al.* (1996). The partially pernicious exploitation of vectors combined with the same type of release may have a common evolutionary origin, followed by adaptation to different pollinators and divergent advancements to dioecy in *Arisaema* and to more elaborated biotechnical devices in *Pinellia.*

The third genus inviting a comparison is *Zomicarpa*. The traps of *Z. riedelinana* Schott (Fig. 9B,C), examined by S.V. in Pernambuco (NE Brazil), very closely resemble those of a small *Arisaema*. Our biological knowledge regarding type of pollinator and its manipulation is incomplete. Flowering in the leafless state like *Arisaema nepenthoides*, the monoecious inflorescence displays a helmet, a sterile, claved osmophoric spadix appendage, and an overall green or copper-brown hue. The osmophore deviates in having a massive, starch-filled storage tissue similar to that of *Arum*. As in *Pinellia*, the proximal, female part is fused with the spathe, and a gap opens in the previously convolute tube wall. The time of opening is still unknown. The blossom has a long-lasting, protogynous anthesis. The gliding device is primitive, consisting of a wax-coated epidermis with slightly prominent cells. The spathe potentially functions like that of *Pinellia*: the first visitors to come are employed for fertilization, the subsequent ones for pollen export. Grayum (1990) already stressed the parallelism to *Arisaema* and *Arisarum* regarding common anatomical and structural features, although he considered the taxonomic status of *Zomicarpa* as unsettled. The analysis of French *et al.* (1996), based on chloroplast DNA, points to a remote position in the subfamily Colocasioideae; in the cladogram given by Mayo *et al.* (1997), which includes morphological characters, the genus forms a sister group of

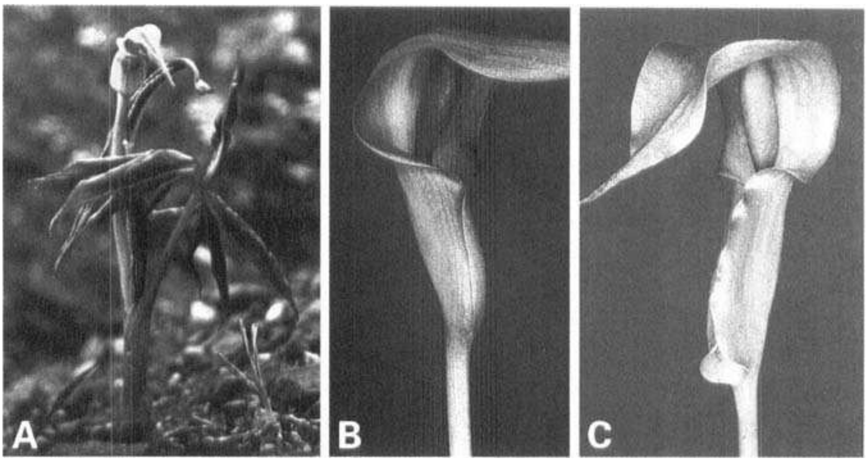

Figure 9. A, *Arisaema flavum* ssp. *abbreviatum* (Nepal, Mustang Distr., Sangdak, *c.* 4000 m), B & C, inflorescence of *Zomicarpa riedeliana* (Brazil, Serra de Ororobó, Pernambuco): B, male stage, C, female stage, with basal gaping.

the complex containing *Arisaema* and the tribe Areae. Therefore it remains dubious whether the features of *Zomicarpa* here discussed have evolved convergently or not.

POSSIBLE OUTSIDERS IN TERMS OF POLLINATION

According to a photograph taken by Shing Lam (pers. comm.), the enlarged spathe of *Arisaema cordatum* N.E. Brown from Hongkong (sect. *Tortuosa*) deviates considerably in shape and colour pattern. Its frontal rim is far extended, forming a triangular lip as a continuation of the hood, the latter being of similar shape and size. Both portions together constitute a rhomboid mouth widely gaping sideways. Its freely visible inner wall, of light ochreous ground colour stippled with deep purple, is streaked with large dull-maroon patches of irregular outline. The strong, upcurved appendage overtops the spathe tip. The makeup of the spathe suggests that carrion flies might be involved in pollination.

A. candidissimum (sect. *Franchetiana*) from China, bearing a purely white or rose-coloured erect spathe lamina, is reported by Sealy (1939) to emit a faint, sweet scent. Both features are convergently shown by *A. odoratum* (section Tortuosae) from Yunnan, whose spadix appendage produces a fragrance reminiscent of *Jasminum* or *Michelia* (Magnol.) (Murata, Wu & Yang, 1994). Such traits point to a possible association with pollen-feeding beetles or even bees as pollinators.

As noted above, *Arisaema flavum* of the monotypic section *Dochafa* is an ecological outsider in the genus. Its monoecious subspecies *abbreviatum* (Schott) Murata (Fig. 9A) exhibits by far the smallest spathe (10–15 mm long), with a globose chamber measuring about 10 × 10 mm and fused for more than half of its length; a basal exit is therefore lacking. The spadix, with a densely congested staminate/pistillate zone, has a rudimentary appendage only 4 mm high. The tissue of the helmet appears to be somewhat glandular and is perhaps involved in scent production, although no odour was detected by us. No pollinators were found in Nepal; a single inflorescence of *A. flavum* ssp. *abbreviatum*, raised from an introduced corm, yielded fruits in the Mainz Botanical Garden. These data (including the reduction of anther number per floret to one) suggest that *A. flavum* ssp. *abbreviatum* and ssp. *flavum*, both tetraploid ($n = 56$), might be homogamous, autogamous, and self-fertile derivatives, and the whole taxon not necessarily the "phenetically most primitive" member of the genus, as suggested by Grayum (1990). *A. flavum* has the widest distribution of the genus (from W China to Yemen). It displays pioneering properties, growing also in dry, open sites, and up to 4500 m. Remarkably, a third, recently discovered diploid subspecies—*A. flavum* ssp. *tibeticum* Murata ($2n = 28$, conforming to the majority of the genus, Murata & Iijima, 1983)—with larger, more conspicuous spathes—was found to exhibit dioecism and sex change (Murata, 1990b); it may represent the parental taxon of the subspecies *flavum* and *abbreviatum*. Its pollination mode remains to be determined.

SPECIAL ADAPTATIONS OF *ARISAEMA* TO FUNGUS GNATS

Most if not all of the remaining arisaemas reveal an evolutionary linkage to mycetophilids and their allies associated with fungi, exploiting their mating and ovipositing behaviour on a parasitic basis (Vogel, 1963, 1978b; Bierzychudek, 1982a, b). Fungus relations of sciarids are poorly documented; some species are recorded as being harmful in mushroom cultures (Jacobs & Renner, 1988; Scopes, 1976; Cantelo, 1976; for other substrates, see Menzel & Martens, 1995). Fungus gnats, of course, have no reciprocal adaptations and cannot be called 'flower visitors' of *Arisaema* in the usual sense. They do, however, lick nectar in allophilic flowers (Vogel, 1978a), some of which share features with *Arisaema* (Mesler, Ackerman & Lu, 1980) and may be aligned to the same sub-category of sapromyiophily.

The appeal of *Arisaema* to these insects is fairly unselective, as various different genera and families have been found in the traps of individual *Arisaema* species (Table 3).

Plants cultivated in Europe lured assemblies of mycetophilid and sciarid species vicariant to those of their homelands. The Nepal collections, however, clearly reveal that the visitor spectra of the various arisaemas were not random but to some degree differentiated, probably due to distinctive scent preferences and size classes of the fungus gnats. Specifically, different heights of flowering scapes above ground may also play a role.

Besides the more general design determinant of kettle traps, the spathes of *Arisaema* have a series of particular features addressed to fungus gnats: (1) type of gliding surface, (2) scent features, (3) occurrence of tails as guiding paths contacting the ground and (4) visual cues including three-dimensional imitations of mushrooms.

(1) The simple, wax-coated gliding surfaces selectively detain nematoceran dipterans, which have less efficient tarsal pulvilli than brachycerans. The unchangeability of such surfaces necessitates the invention of a secondary basal exit.

(2) The odour is in some cases reminiscent of mushrooms or morels, the normal brood sites of the gnats. Olfactory allurement certainly plays the major role in their attraction (Vogel, 1963, 1978a,b, 1990). The occurrence of short-chained aliphatic aldehydes and alcohols in *Arisaema* scents is in line with the compound mixtures

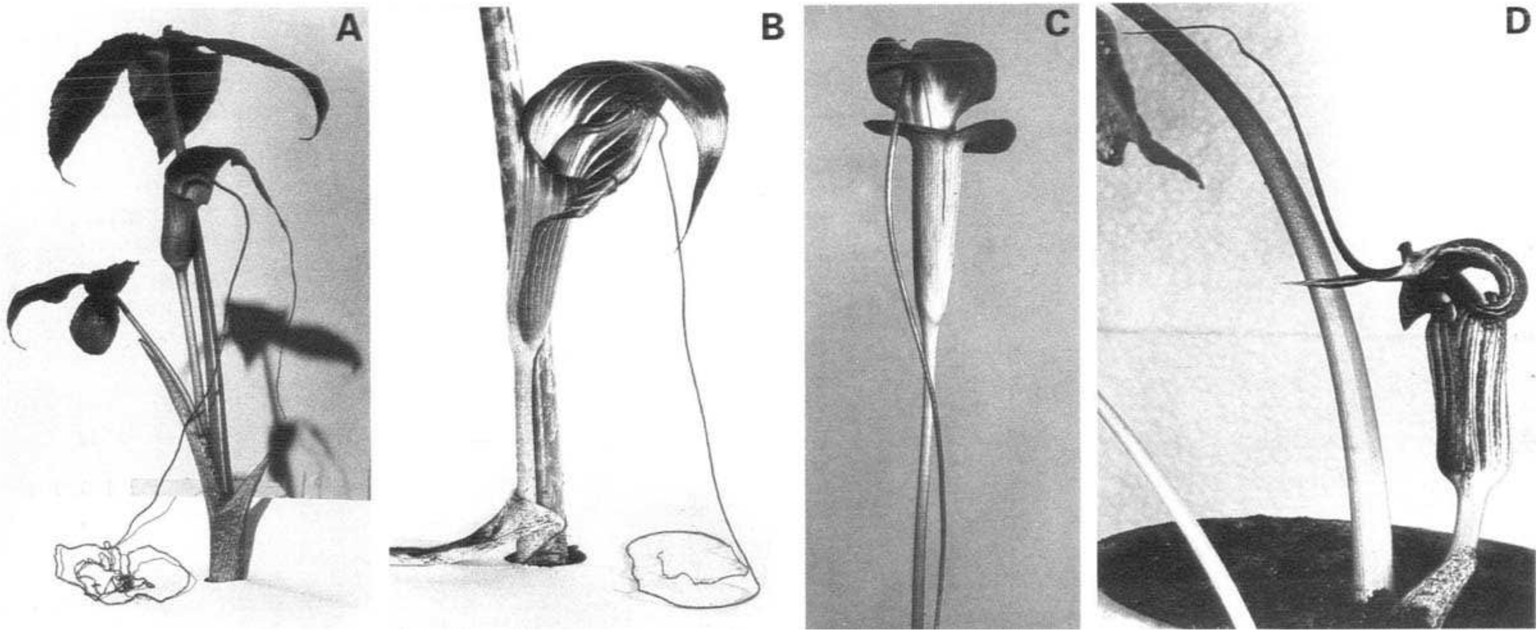

Figure 10. Species of *Arisaema* bearing flagellate spadix appendages. A & B, *A. speciosum* (cult.), C, *A. scortechinii* (Maxwell Hills, W-Malaysia), D, *A. kyushianum* (cult.).

TABLE 6. Maximal tail lengths recorded of flagellate *Arisaema* species. Abbreviations of section names: A, *Arisaema*; F, *Fimbriata*; S, *Sinarisaema*; T, *Trisecta*; To, *Tortuosa*

Section	Species	cm	Source
	Spadix appendix flagellate		
—	*A.* (unidentif.)	150	Kingdon-Ward (cit. from Bown, 1988)
T	*A. speciosum*	80	Hara, 1971
A	*A. thunbergii* incl. ssp. *urashima*	50	Molisch, 1930; Takasu, 1987
T	*A. griffithii* incl. var. *pradhanii* (C.E.C. Fischer) U.C. Pradhan	50	Fischer, 1936; Engler, 1920
T	*A. costatum*	50	Hara, 1971
T	*A. intermedium*	85	P. Christian (pers. comm.)
T	*A. verrucosum* Schott	30	Engler, 1920
T	*A. galeatum* N.E. Brown	26	Hooker, 1879
F	*A. filiforme*	25	Knuth, 1904
T	*A. utile*	25	Hooker, 1880; Engler, 1920
F	*A. scortechinii* Hook.f.	20	Present paper
T	*A. propinquum*	20	Hara, 1971
	Spathe tip flagellate		
T	*A. lackneri* Engl.	55	Engler, 1920; Troll, 1928
S	*A. tuberculatum*	17	Chatterjee, 1954
S	*A. taiwanense* J. Murata	40	Murata, 1985

found in the smell of *Masdevallia chestertoni* (Orchidaceae), a fungus gnat flower (Kaiser, 1993). Trans-7-hexenal is the main odorous compound in the flowers of *Adoxa moschatellina* (Adoxaceae; Brunke & Hammerschmidt, 1980), which are probably pollinated by fungus gnats.

(3) The blossoms of many arisaemas dispose of tailed appendages, which arise in a few species from the apex of the spathe, more commonly from the spadix and rarely from both. This filiform modification of non-homologous organs, axe and bract, is a convergence suggesting a common functional role, as already presumed by Knuth (1904), Molisch (1926, 1930) and Troll (1928), who interpreted these structures as guiding paths. The sigmoid appendages of *A. tortuosum* (Fig. 11B), *A. kyushianum* Makino (Fig. 10D), *A. elphas* Buchet, and others, tapering into a rather stout tail held strictly upright or ascending, is comparable with the antennal osmophores found in other myiophilous aroids, in *Aristolochia*, and orchid species. The erect or ascending tails produced from the limb of the spathe of *A. exappendiculatum*, *A. consanguineum* and *A. tuberculatum* may have the same function because they contribute to odour emission, although (clavate) spadix-borne osmophores may be present, too. They are apparently addressed to gnats on the wing.

The most spectacular thread-like spadix appendages, structures with very few parallels in the floral world (*Amorphophallus pendulus* (Araceae), *Aristolochia macroura* (Aristolochiaceae)), occur in several other Asian species which are, according to Hara (1971), not necessarily related (mainly sect. *Trisecta*, but also members of sects. *Fimbriata*, *Tortuosa*, *Sinarisaema* and *Arisaema*). These 'whip-lash' arisaemas probably arose independently in Himalayan and Chinese members of the genus (Table 6;

Figure 11. Species of *Arisaema* bearing elongate spadix appendages. A, *A. intermedium* Blume (Nepal, Taplejung Distr.) with flagellate, B, *A. tortuosum*, with upright, sigmoidal appendage (Nepal, Dolpo Distr., Suli Gad valley, Parila).

Figs 10, 11A, 12). The blossoms of this ecological group tend to have a dwarf, almost geophilic position, overshadowed by the leaves. The tail of *A. speciosum* holds the record for length, attaining 80 cm (Hara, 1971) or eleven times the tube length, though in less vigorous plants it may only measure 20 cm; our cultivated plants bore tails between 27 and 58 cm long (Fig. 10A,B). Bown (1988) even cites an unidentified arisaema found by Kingdon-Ward in Burma, with tails measuring 1.5 m. The Japanese *A. thunbergaii* ssp. *urashima* also has an enormous spadix tail, as visible in a photograph published by Hayashi, Azegami & Hishiyama (1983). In all these cases, the tails are flaccid, tapering down to 0.25 mm in diameter (*A. speciosum*); all contact the ground. Molisch (1930), commenting on the appendage of *A. speciosum* (misinterpreted by him as spathe tail), reported that on its course it entangled ". . . verschiedene Gegenstände, trockenes Gras, lebendes Laub, Halme oder Zweigstücke . . .[various objects, dry grasses, living foliage, stalks, or fragments of twigs]". Objects were even spirally entwined, making it difficult to detach the tail without severing it. The tails of *A. speciosum* we examined were slightly moist to the touch, with a glandular epidermis like that of normal osmophores; the scent, distally weak, seemed to increase toward the base. The appendages of *A. filiforme* and *A. thunbergii* ssp. *urashima* have a thick, stout basis and rise sigmoidally above the helmet and only then, tapering to a flaccid thread, curve down to the ground like a fishing rod. According to Hooker (1880), the appendage of *A. griffithii* already exceeds the spathe in length while in the bud; before expansion it is zigzag-folded inside the median of the three leaf segments. Spathe-borne flagelliform appendages attain similar lengths (Table 6).

The function of these ground-bound flagellae is self-explanatory. All authors interpreted them *unisono* as guiding paths ('Leitseile'), designed to conduct insects that live in the soil litter directly into the spathe (Fig. 12). Troll's objection (1928) that the tails may be unnecessary because most species dispense with them, underlines luxuriance and exaggeration in evolutionary trends, but does not question their apparent functional role. As pointed out elsewhere (Vogel, 1978a), mycetophilids

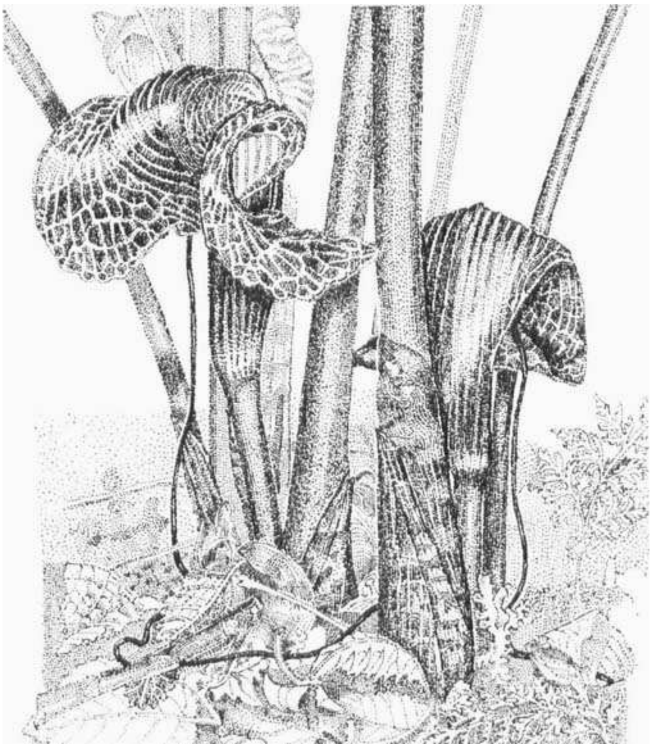

Figure 12. Inflorescences of *Arisaema griffithii* with flagellate spadix appendages intertwining leaf litter (Nepal, Marsyandi valley, Thimang). Drawn from photograph.

predominantly keep to the ground and seldom fly. They move rapidly through leaf litter by jerky movements of their spiny legs.

(4) The occurrence of conspicuous white, often translucent markings (milkglass effect) in the spathes of *Arisaema*, first noted by Barnes (1935) and van der Pijl (1953) and paralleled by other fungus gnat-pollinated flowers (Vogel, 1973, 1978a,b), points to the role of visual cues in the orientation of fungus gnats. Judging from their low number of ommatidia, probably no more than light and dark are discriminated. The white or luminous patches and stripes that occur on the spathes and especially on the helmets of many species seem to imitate the light undersides and stalks of mushrooms and toadstools, the target of swarming and ovipositing mycetophilids. The helmets of *A. murrayi* Hook., *A. wrayi* Hemsl., *A. schimperianum* Schott, *A. laminatum*, and (Huang & Wu, 1997) *A. nanjenense* T.-C. Huang & M.-J. Wu are entirely or partly milky white, some being contrasted by a black band from the green ground colour of the spathe (cf. van der Pijl, 1953). The frequent grid-like, longitudinal white striations optically resemble the hymenial lamellae where the gnats usually lay their eggs (Fig. 3B,D).

(5) Species of the section *Trisecta* (*A. utile*, *A. griffithii*, *A. propinquum* Schott, *A. costatum*) even possess three-dimensional lamellae shaped by the intercostal tissue of the spathe limb (Vogel, 1978b). They may provide a haptic cue. A white pattern on the visible inner wall of the spathe limb of *A. kyushianum* appears to depict the stalked cap of

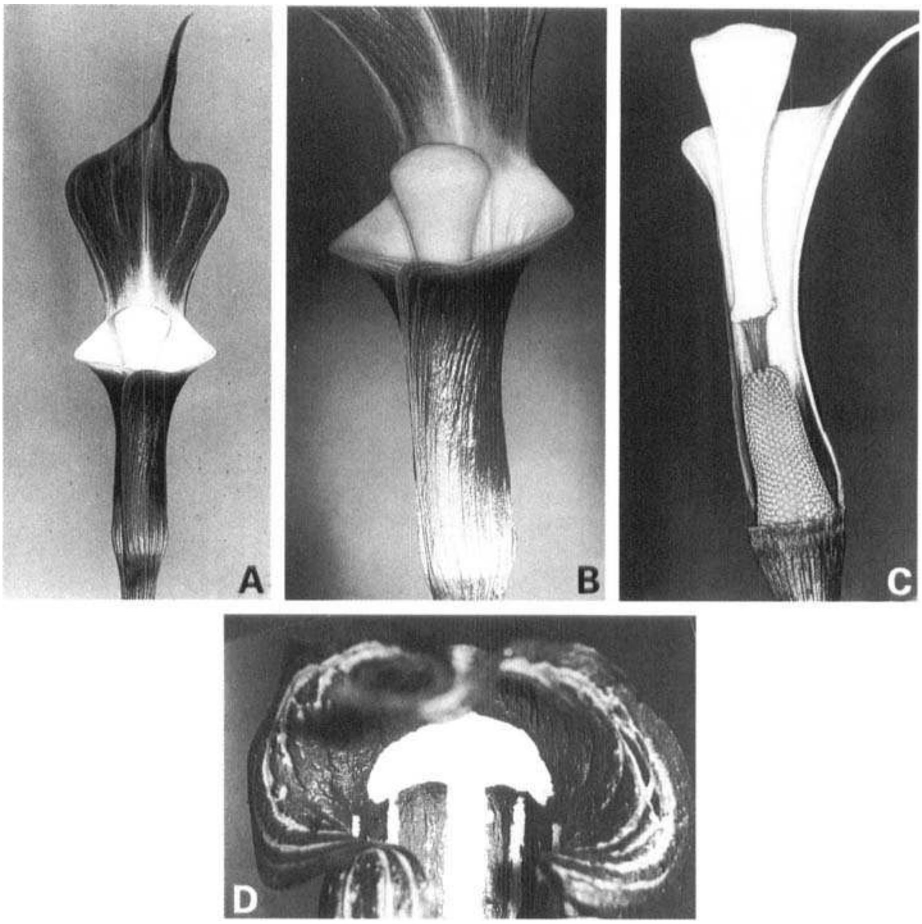

Figure 13. Inflorescences of *Arisaema* species (cult.) with three-dimensional (A–C) and two-dimensional (D) mushroom-like patterns. A–C, *A. sikokianum*. C, female spathe cut open, D, *A. kyushianum* (spathe mouth, spadix appendage removed).

a fungus (Fig. 13D); the semicircle is slightly prominent with a shiny surface, while the contrasting brown tissues are corrugated. Some spadix appendages can even be transformed into a three-dimensional dummy. In *A. intermedium* Blume the proximal portion of the appendage is inflated into an ovoid, white body almost filling the spathe mouth. The most striking plastic image, imitating an immature mushroom cap still covered by the velum universale, is realized by *A. sikokianum* (Fig. 13A–C). This part emits a distinct fungus-like smell. The surrounding funnel-shaped spathe mouth is white inside, too. Both areas are slippery. According to Mayo (1986), the appendage of *A. sikokianum* is variable; it exhibits images of minor perfection in some of its forms, a condition reminiscent of the gradual emergence of fungoid structures in the alliance of *Aristolochia arborea* (Vogel, 1978a). The fungoid appendage of gnat-pollinated *Arisarum proboscideum*, described by the same author, is an even more elaborate imitation. We predict that gnats will fall into the kettle while attempting to oviposit on these white bodies. The deep red-purple helmet of *A. griffithii* (Fig. 12), which is so enlarged and broadened that the tubular part of the spathe almost disappears below it (cf. Hooker, 1880), may also be taken for a mushroom cap.

The lower end of the appendage (above its insertion on the stipe), which is truncate in many arisaemas, has in *A. griffithii*, *A. utile*, *A. propinquum* and other members of the section *Trisecta* expanded into a large, umbrellalike disc, a structure also reminiscent of a fungus cap. Since it is not visible from the outside, however, this allusion is dubious and the disk may simply be instrumental in preventing captives from climbing up, as explained above (p. 85).

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