Flowering Phenology and Beetle Pollination in *Theriophonum infaustum* N.E.Br. (Araceae)

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ABSTRACT

Theriophonum infaustum N.E.Br. (Araceae), an endemic species of SW India, consists of small tuberous plants. The species was found to have protogynous inflorescences and to be visited by several kinds of beetles. Beetles belonging to the species *Anotylus rubidus* Cameron (Coleoptera, Staphylinidae) are found to be the main potential pollinators. Other species observed were only casual visitors. A detailed account on the process of cantharophily in this species is given with explanatory illustrations.

KEY WORDS

Araceae, cantharophily, India, *Theriophonum.*

INTRODUCTION

The family Araceae is mainly tropical in distribution, with a few temperate genera, constituted of herbs and vines comprising about 105 genera and about 3,300 species (Mayo *et al.*, 1997). It is characterised by a spadix which is subtended by a spathe. *Theriophonum* Bl. of the subfamily Aroideae is a small genus of five species endemic to South and Central India with one species extending to Sri Lanka (Sivadasan & Nicolson, 1982). *Theriophonum infaustum* N.E.Br. is restricted to SW India.

Information on pollination biology of the members of Araceae is meagre as most of the information available on this aspect deals with temperate genera (Gibernau, 2003). The only tropical aroid genus that is fairly well-known in this regard is *Amorphophallus,* mainly from the work of Pijl (1937). The works of Hubbard (1895), Cleghorn (1913), Knoll (1926), Pijl (1937), Meeuse & Hatch (1960), Dormer (1960), Monteith (1973), Williams & Dressler (1976), Golubev & Volokitin (1983), Shaw & Cantrell (1983), Valerio (1984), Gottsberger & Amaral (1984), Pellmyr (1985), Young (1986), Whitehill (1993), Patt *et al.* (1995), Gibernau *et al.* (1999), & Gibernau *et al.* (2003) are some of the significant works on members of Araceae. In India not much work has been done on this aspect especially in Araceae, and only scattered and fragmentary information is available. The work of Barnes (1934) who described the mode of pollination and pollinators in *Arisaema* occurring in the Nilgiri Hills, and that of Banerji (1947) on *Typhonium trilobatum* are worth mentioning. A detailed account of cantharophily in *Amorphophallus hohenacheri* (Schott) Engl. & Gehrm., with a brief review on the general pollination biology with special reference to Araceae was provided by Sivadasan & Sabu (1989). Beath (1996) provided the details of pollination in *Amorphophallus johnsonii.* Gibernau (2003) provided an up-dated list of aroid pollinators which is the latest covering all the available data on this aspect.

According to the most far-reaching generalizations, as far as is known the Araceae are considered to be exclusively entomophilous, and in most cases the pollinators are beetles (Coleoptera) and flies (Diptera) (termed cantharophily and myophily respectively). Bees (Hymenoptera) are rarely reported as pollinators as in the case of *Spathiphyllum* (Williams & Dressler, 1976) and *Anthurium* (A Beath, T. Croat, pers. comm.), especially those with sweet-scented flowers such as the members of *Anthurium* sect. *Calomystrium*. Beetles have the oldest fossil record of any of the four anthophilous orders of insects viz., Coleoptera, Lepidoptera, Diptera and Hymenoptera. Thus, it is widely presumed that beetles were the pollinators of the earliest entomophilous angiosperms (Grayum, 1984).

Floral morphology is the most important element in determining the system of pollination of a particular type of blossom. Structural features have long been recognised as a diagnostic specialization for particular broad categories of insect-pollination. Faegri & Pijl (1979) gave an account of the syndrome of cantharophily. It included the features such as a pollination unit with few visual attractions, no nectar guide, generally large, flat, cylindric or shallow, bowl-shaped—sometimes closed, easy of access, dull colour, frequently greenish or white, and strong odour—fruity or aminoid. The beetle-pollinated flowers are protogynous. In addition to the protogyny, cantharophily is generally associated with phenomena like thermogenesis, musty odour, crowded pistillate and staminate flowers enclosed by bracts during a brief nocturnal anthesis.

Many beetles of different families are reported to be involved in the pollination of Araceae, with most of the beetles from the family Scarabeidae (Grayum, 1984). But Staphylinidae are also common in Araceae outside the New World (Gibernau, 2003).

THERIOPHONUM INFAUSTUM

Theriophonum infaustum, an endemic species of SW India grows abundantly on the Calicut University Campus and its vicinity by the commencement of SW monsoon (June–September).

It is a small, tuberous herb reaching a height of about 12 to rarely 30 cm (Fig. 1). The corm is somewhat subglobose to cylindric in shape, ca. 0.5–4.00 cm thick and 0.7–1.8 cm diam. The leaves have distinct petioles which arise from the top of the tuber. The lamina is glabrous, reticulate-veined, and is highly variable in size and shape, narrowly to broadly hastate-sagittate, rarely broadly ovate-cordate, 4.6–12 cm long, lateral lobes rounded to ovate or with acute tip. The inflorescence is borne on an erect peduncle, which arises in leaf axils, and during its early developmental stage is completely encased by the vaginate leaf-base. This species, like many others in the genus, also reproduces by vegetative means.

STUDY SITE AND METHODS

The study was carried out at the Calicut University Campus and its surroundings (latitude: 11°35′–45′N, longitude: 75°45′–50′E, at an altitude of 40–60 m; average annual rainfall of ca. 300 cm; and temperature ranging from 17–35°C). Flowering period is from June–September and begins one month after the first rains.

Flowering individuals in the study area were located and tagged. A total of 50 inflorescences were observed and data collected during the study period. Observations were made on the morphology and phenology of the inflorescences along with the details of the pollinators and their activities. Insect visitors to the inflorescences were collected, and preserved in 70% alcohol for identification. Insects were also collected from other populations along with inflorescences to verify whether the pollinators are common to all populations. Voucher specimens of all beetles are deposited at Commonwealth Institute of Entomology, London.

OBSERVATIONS

Floral Morphology

The inflorescence is solitary, completely enclosed by the petiolar sheath in the ear-

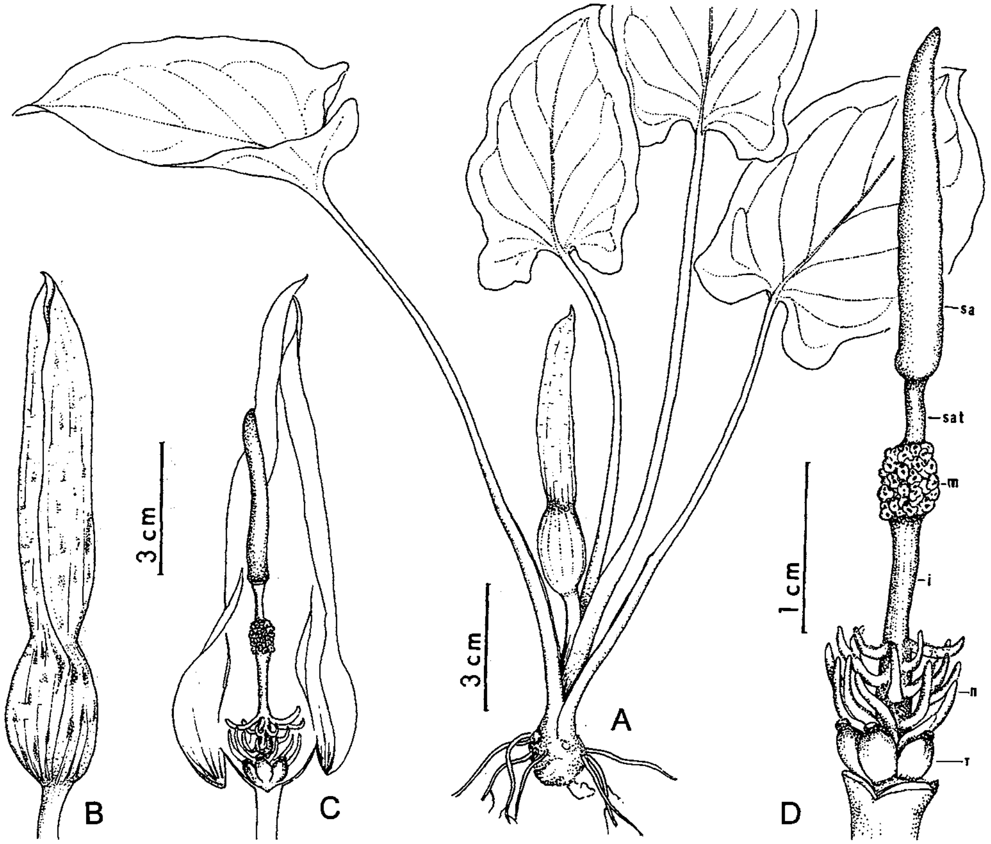

Fig. 1. *Theriophonum infaustum* N.E.Br.: A. Habit; B. Inflorescence; C. Inflorescence with spathe cut open to show spadix; D. Spadix. (f: female flowers; i: interstice; m: male flowers; n: neuter flowers; sat: stalk of spadix-appendix; sa: spadix-appendix).

ly stage. Peduncle ca. 5.5 cm long and 4 mm diam., greenish to purplish. Spathe erect, to about 6 cm long, differentiated into a basal completely convolute tubular portion, and an upper initially convolute, but later with a spreading yellowish-green limb portion separated by a slight constriction between the two; the basal convolute tubular portion is 1.0–1.6 cm long, 0.6–1.2 cm diam., upper limb portion oblong, 3–5 cm long and 1–1.5 cm broad. The overlapping of the margins of the spathe is either to the right or to the left as observed earlier by Barnes (1938). The spadix is sessile, almost equalling or slightly shorter than the spathe, to ca. 4.5 cm long, with basal female portion ca. 2 mm long, contiguous with a zone of neuter flowers ca. 3 mm long, followed by naked slender interstice ca. 6 mm long, followed by male portion ca. 5 mm long and terminating in a creamy purplish sterile appendix ca. 2.5 cm long with a distinct stipe ca. 3.5 mm long. Pistillate flowers 4–8, in a single whorl; ovary ovoid, yellowish green, unilocular with 4–5 basal and apical sub-orthotropous ovules; stigma sessile, discoid. Neuter flowers subulate to subclavate, verruculose, creamy purplish, ca. 3.5 mm long. Staminate flowers 23–48, closely arranged, purplish, sessile and truncate, each with 2 distinct anther lobes, dehiscing by apical pores. Fruit a berry, 6–8 per infructescence, each to ca. 1 cm long and 5 mm diam., ovoid, green, 2–3-seeded. Seeds broadly ovoid with basal white tissue.

Phenology and Pollination Mechanism

The spadices were observed to be protogynous. The exact time of receptivity of pistillate flowers is difficult to determine because there is no clear indication to this effect. Initially the spathe is completely rolled tightly around the spadix (Fig. 2A). At maturity, the spathe unrolled and opened during the afternoon of the first day. A detailed study of the spathe opening revealed that the margin of the limb began to unfold or unroll from the top towards the base to its basal constriction Figs. 2B,2C). Generally the unfolding took place between 1.30 P.M. and 4 P.M. and the spathe attained its maximum opening with maximum width of spathe limb (Fig. 2C), between 4.00 P.M. and 6.30 P.M. The spathe limb stands erect with the tip slightly incurved and in some cases it touched the tip of the spadix-appendix. At this position, the sterile appendix of the spadix and the staminate flowers are completely exposed. The basal tubular portion of the spathe enclosing the pistillate and neuter flowers is not tightly closed at this stage so that there is space between the spathe-tube and the spadix with pistillate and neuter flowers (Fig. 2D). This facilitates easy access of small insects into the tube.

Simultaneous with the opening of the spathe, a foetid and pungent odour was emitted by the spadix-appendix. The intensity of the odour reached at its maximum when the spathe has fully opened (between 4.00 P.M. and 6.30 P.M.). The beetles carrying pollen grains from other inflorescences that they have previously visited were probably attracted by this odour and alight on either the smooth spadix-appendix or on the inner surface of the spathe-limb. The beetles alighting on them slipped off and fell down into the tube of the spathe and are trapped there. Since the flowers are protogynous, the stigma is receptive during this period. A large number of such trapped insects tried to escape from the tube, crawling up, but on every attempt they fell down because of the smoothness of the inner surface of the basal tube of the spathe. The beetles carrying pollen moved across and over the pistillate flowers, simultaneously effecting pollination. The release of odour lasted for a period of 3.5 to 6 hours, but with a relatively short period of maximum intensity. When the odour started fading, the spathe-limb began to roll and close forming a tubular structure, leaving only a small opening at the top. At this stage, the spathe at the constriction between the limb and the basal tube pressed the spadix (Fig. 2E) thereby completely closing the basal tube with the insects trapped inside the tube and unable to escape.

The anthesis of the male flowers commenced during the afternoon of the second day between 2.30 P.M. and 5.30 P.M. The anthers dehisced by the apical pores releasing pollen grains in masses. They were deposited at the base of the tube formed by the rolled limb just above the closed basal tube. At this stage the spathe and the neuter flowers became more or less flaccid and the constriction became loose (Fig. 2F), allowing insects trapped for a day inside the tube to crawl up. While they crawled up, their bodies were covered with pollen fallen from above and also that accumulated at the base of the limb. No special organ or organs of the insects were noticed as depositories and carrier organs of pollen: Pollen grains were found all over the body of the insects. The insects carry the pollen and if they visit other inflorescences, get entrapped as mentioned earlier, and when they escape by crawling over the pistillate flowers, effect cross-pollination.

The spathe showed signs of degeneration on the third day onwards. No insects were found to remain in the inflorescence on the third day, except a few small dead ones. The first symptom of degeneration of the spathe was the inward curling of the spathe-margin (Fig. 2G) while the spathe and spadix still stand erect. Gradually the colour of the spathe started fading, the spadix-appendix shrunk, lost its colour

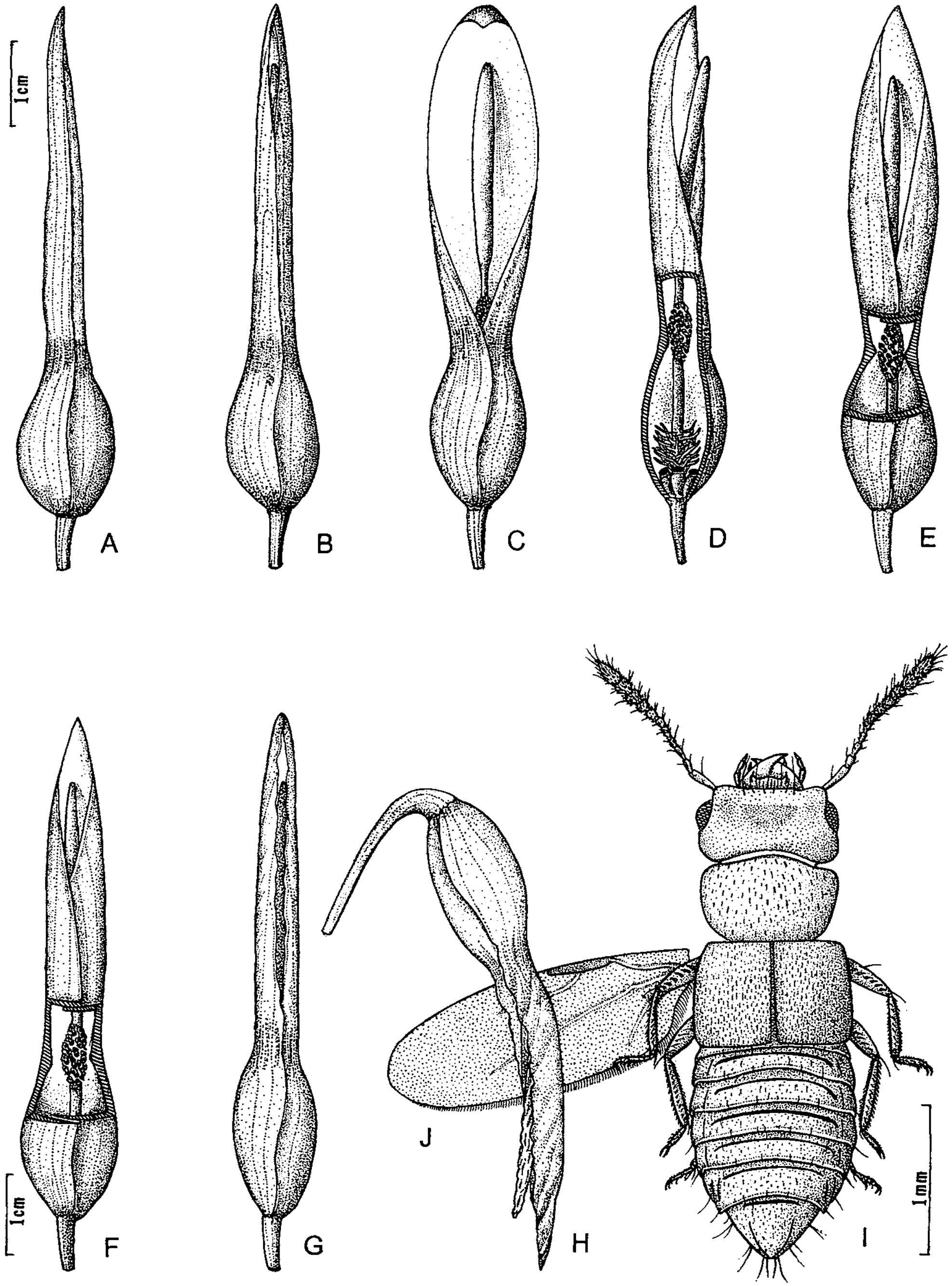

Fig. 2. A–H: Inflorescence of *Theriophonum infaustum* N.E.Br.—Different stages during and after pollination: A. Inflorescence with completely convolute spathe; B–C. Different stages of unfolding of spathe from top to the base of the limb; D. A portion of the spathe removed showing the space between the spadix and the spathe; E. A portion of the spathe removed showing the closely rolled spathe with the spadix; F. A portion of the spathe removed showing the gap between the spadix and the spathe after anthesis;

and the whole inflorescence along with the peduncle bent down (Fig. 2H) and touched the ground. Within 7–10 days all parts of the spathe and spadix degenerated except the fertilized pistillate flowers, which eventually became the fruits.

Insect Visitors

Several kinds of insects were collected from the inflorescences. Out of the six species of beetles (Coleoptera) collected from the inflorescences, only two were observed regularly in and around the inflorescences. A list of insect visitors of *Theriophonum infaustum* is presented in Table 1. The taxa of Anthocoridae of Heteroptera could not be identified.

The beetles belonging to the species *Anotylus rubidus* Cameron (Figs. 2I, 2J) of Staphylinidae (Coleoptera) and another unidentified species of this genus, and seemingly related to this species, were found to be frequent visitors and considered to be the potential pollinators. The other species of beetles appeared to be casual visitors; perhaps they might also sometimes facilitate cross-pollination, but are not considered as regular pollinators. The same species were also collected from different populations of *Theriophonum infaustum* occurring in parts of Kerala other than the present study site.

The members of the species *Philonthus flavocinctus* Motschulsky were captured only once during the study and members of Heteroptera (Table 1) were found to be only occasional visitors.

Table 1. Insect visitors of *Theriophonum infaustum*.

- COLEOPTERA
  - LEIODIDAE
    - *Ptomophaginus* sp.
  - STAPHYLINIDAE
    - *Oxytelus incisus* Motschulsky
    - *Anotylus latiusculus* (Kraatz)
    - *Anotylus rubidus* (Cameron)
    - *Anotylus* sp. nr. *A. rubidus* (Cameron)
    - *Philonthus flavocinctus* Motschulsky
    - *Atheta* sp.
- DIPTERA
  - PSYCHODIDAE
  - PSYCHODINAE
    - Genus *et* sp. *indet.*
- HEPTEROPTERA
  - ANTHOCORIDAE
    - Genus *et* sp. *indet.*
  - NABIDAE
    - *Phorticus* ? *cingalensis*

No insect-visits to the inflorescences were observed during the forenoon of the first day. The first visits were by species of *Anotylus* which arrived by the evening of the first day when the odour emitted by the spadix-appendix was strong and the spathe started to close. They easily located the inflorescence and alighted on the spadix-appendix or on the inner side of the spathe-limb in search of the source of the odour, but lost their grip and fell down into the basal tube. The beetles remained in the spathe-tube for about 24 hours. Then they began to leave the inflorescence on the evening of the second day, most leaving between 3 P.M. and 6 P.M. The *Anotylus* species captured immediately after leaving the inflorescence were found to carry large amounts of pollen on their legs and body.

DISCUSSION

Theriophonum infaustum was observed to be pollinated mainly by the beetles of the species *Anotylus rubidus* Cameron of

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G. Inflorescence with the margins of the spathe rolled; H. The inflorescence in drooping position after pollination: I. *Anotylus rubidus* (Cameron)—the pollinator beetle; J. Single hind wing—enlarged.

Staphylinidae (Coleoptera), which were considered as the main potential pollinators. Other species observed were only casual visitors. Apart from Araceae, cantharophily is prominent in many families of the Magnoliales, Annonales (Faegri & Pijl, 1979; Thien, 1974, 1980; Armstrong & Drummond, 1986), Nymphaeaceae (Prance, 1980), and Palmae (Henderson, 1986).

In beetles, the sense of smell is much more highly developed than the visual sense, and 'beetle-flowers' are often white or dull in colour and frequently have strong odours. These odours are usually fruity, spicy, or like certain fermentation-odours and distinct from the sweet-odour of flowers pollinated by bees, moths and butterflies (Raven *et al.*, 1976). The combination of less striking flower (spathe) colour, (green, purple or pale green with purple tinge on the spathe-tube), strong foetid odour, absence of nectar, peculiar inflorescence structure with the spathe divided into lower chamber (tube) and an upper limb, and spadix with basal fertile portion and an apical sterile barren spadix-appendix, protogyny, etc. are the syndrome of beetle pollination. Protogyny is an essential element in the function of this type of trap-blossoms. Protandry would be the prevalent form of dichogamy in taxa pollinated by bees or flies whereas protogyny would prevail in taxa pollinated by beetles, wasps or other vectors.

The inflorescences of *Theriophonum infaustum* have a strong unpleasant smell emitted from the spadix, which is doubtless for the purpose of attracting beetles involved in their cross-pollination. The insects were irresistibly attracted by the strong odours, whether or not the blossoms offer some compensatory attractant (pollen, food bodies, etc.) (Faegri & Pijl, 1979). The importance of odour as a beetle-attractant has been demonstrated in many of the tropical aroid species of the genera like *Arisaema* (Barnes, 1934), *Typhonium* (Cleghorn, 1914; Banerji,1947; Monteith, 1973; Pijl, 1953), *Arum* (Knoll, 1926; Dormer, 1960), *Amorphophallus* (Sivadasan & Sabu, 1989) and *Philodendron* (Gottsberger & Silberbauer-Gottsberger, 1991).

Adaptation for effective pollination and subsequent trapping of beetles inside the spathe till the pollen shedding of the host were reported earlier in *Typhonium* (Banerji, 1947; Monteith, 1973; Armstrong, 1979). *Typhonium* and *Theriophonum* share many of these characteristics. Both genera are in the subtribe Arinae of the subfamily Aroideae. The inflorescence of *Typhonium* generally opened in the morning and remained odourless until late in the afternoon. On the evening of the first day, the spathe stood erect and emitted a foetid odour which attracted the dung-beetles of the genus *Onthophagus* (Scarabaeidae), which are the potential pollinators, to the blossoms. Dakwale & Bhatnagar (1997) reported that *Theriophonum crenatum* is pollinated by crepuscular Ceratopogonid flies, blood-sucking female midges, and hence has a very different pollination syndrome from that of *Theriophonum infaustum*. *Theriophonum* is closely related to *Typhonium* within the tribe Areae and they represent the basal taxa of this tribe (Renner & Zhang, 2004). The tribe Areae is composed of 9 genera (Mayo *et al.*, 1997), and except for the genus *Lazarum*, pollinators are known for each of the genera (Gibernau, 2003). Staphilinidae, associated with other beetles or flies, have been mentioned in *Biarum*, *Dracunculus*, *Eminium*, and some *Arum* (Gibernau, 2003); while *Sauromatum* appears to be pollinated by Scarabaeidae and flies, and *Helicodiceros* by only calliphorid flies. It is interesting to note that *Typhonium* is a genus pollinated only by beetles with staphylinids among them.

In contrast to the condition in *Typhonium*, the spathe opened only in the afternoon in *Theriophonum infaustum* and the odour is emitted simultaneously with the opening of the spathe, and lasts for a period of 3.5 to 6 hours. The spathe never bent backwards as in the case of *Typhonium*. Here the spathe remained erect even after anthesis of staminate flowers. This is an advantage to this species for getting pollinated by its own pollen grains and for dispersal of pollen by the pollinators. As in the case of *Typhonium*, the beetles trapped are not offered any nutritive rewards by the inflorescence. From this it is evident that the insects are attracted by the odour produced by the spadix-appendix and accidentally trapped inside the spathe-tube.

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