The many elusive pollinators in the genus *Amorphophallus*

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Abstract

The genus *Amorphophallus* encompasses some 230 species and is one of the largest genera of the Araceae family. Most species release scents, smelling of carrion, faeces, dung and similar nauseating odours for pollinator attraction and are therefore considered to have evolved a deceptive pollination syndrome. Some of the most iconic members of the genus, such as the *A. titanum* and *A. gigas*, are considered to be carrion mimics. Copro-necrophagous insects, beetles and flies in particular, are attracted by these scents and are therefore assumed to act as pollinators. However, many reports and observations on *Amorphophallus* pollinators are anecdotal in nature or do not distinguish between legitimate pollinators and non-pollinating visitors. Moreover, some published observations are not readily accessible as they are many decades old. Therefore, the available data and information about insect visitors and/or pollinators in the genus *Amorphophallus* is compiled, reviewed and discussed.

Keywords Coleoptera · Diptera · Insects · Pollination · Scent compounds

Amorphophallus

The genus *Amorphophallus* Blume ex Decne. (Araceae) has a palaeotropical distribution with the majority of species originating in Africa, Continental Asia and Southeast Asia (Claudel et al. 2017). It currently encompasses some 230 validly published species (WCVP 2021; Bustamante et al. 2020; Tamayo et al. 2021). The *Amorphophallus* inflorescence consists of a spadix surrounded by a spathe (Mayo et al. 1997) (Fig. 1a). The spathe is usually funnel-shaped but may occasionally be differentiated into a limb and a kettle, forming a chamber or a trap (Bröderbauer et al. 2012) (Fig. 1b). The spadix is subdivided into three zones (Fig. 1b). The lowermost zone that bears the female (pistillate) flowers (Fig. 1c), the adjacent zone that bears the male (staminate) flowers and a terminal zone, consisting of the appendix (Fig. 1b) that essentially serves the purpose of

scent production and emission (Hettterscheid and Ittenbach 1996; Kite and Hettterscheid 2017).

Amorphophallus inflorescences are protogynous and anthesis usually lasts for 2 days. On the first day of anthesis the stigmas of the pistillate flowers are receptive. On the second day of anthesis, pollen is released by the staminate flowers (Fig. 1d). Once the pollen is released, the female flowers are no longer receptive and self-pollination is prevented (Mayo et al. 1997; Hesse 2006). Usually, stigma receptivity is announced by the emission of characteristic scent compounds which serve to attract pollinators. In some species, such as *A. konjac* K. Koch, *A. paeoniifolius* (Dennst.) Nicolson and *A. titanum* Becc. ex Arcang, the scent volatilisation is enhanced through heat generation by the appendix (Skubatz et al. 1990; Barthlott et al. 2009; Korotkova and Barthlott 2009; Lamprecht and Seymour 2010).

The most famous species of the genus *Amorphophallus* are the two giants of the genus, *A. titanum* and *A. gigas* Teijsm and Binnend. These species develop large leaves and inflorescences, the latter exceeding three metres height (Hettterscheid 1994; Hettterscheid and Ittenbach 1996; McPherson and Hettterscheid 2011). The inflorescences carry spathes that are inwardly purplish and are accompanied by foul smells of decomposing organic material, such as carrion, and are therefore referred to as “carrion” or “corpse flowers”

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Fig. 1 *Amorphophallus johnsonii*. **a** Inflorescence consisting of a spadix surrounded by a constricted spathe, separated into a limb and a base forming a floral chamber. **b** Same inflorescence cut open, showing the female flowers at the base, followed by the male flower zone and the appendix above. Note the broadened appendix base, which in combination with the constriction and the slippery floral chamber make it difficult for insects to leave once they have entered. **c** Close-up of the female flower zone and the male flower zone. Note the hair-like papillae covering the base inside the floral chamber. **d** Section from (c). Extrusion of pollen strands on the second day of anthesis. Scale bars: A = 10 cm. B = 5 cm. C = 1 cm. D = 0.5 cm. Photographs: Cyrille Claudel

(Barthlott and Lobin 1998; Barthlott et al. 2009; Chen et al. 2015; Jürgens and Shuttleworth 2016; Raman et al. 2017).

The scent compounds of nearly a hundred *Amorphophallus* species have been analysed (Kite and Hetterscheid 1997, 2017; Kite et al. 1998; Kakishima et al. 2011; Lamprecht and Seymour 2010; Shirasu et al. 2010; Chen et al. 2015; Raman et al. 2017) and most species release scent types that include “carion, faeces, urine, dung, fishy, sewerage, nauseating gaseous, rancid cheese,

fermenting fruit and mushrooms” (Kite and Hetterscheid 2017). These odour types are effective cues for insects that search for such substrates for feeding, mating or breeding, indicating the deceptive nature of the majority of *Amorphophallus* species (Kite et al. 1998; Jürgens et al. 2006, 2013; Vereecken and McNeil 2010; Urru et al. 2011; Johnson and Schiestl 2016; Kite and Hetterscheid 2017). The deceived targets are usually Diptera or Coleoptera (Wiens 1978; Faegri and Van der Pijl 1979; Johnson and

Schiestl 2016), defining most *Amorphophallus* species as oviposition-site mimics.

However, there are exceptions, as some *Amorphophallus* species are sweetly scented. Two clades, containing 13 of the 92 investigated species, release sweet odour types based on aromatic hydrocarbons, such as 1-phenylethanol derivatives or 4-methoxyphenethyl alcohol (Kite and Hetterscheid 1997, 2017). These odour types appear quite different from carrion, dung or other scent types that indicate decomposition of organic matter. However, it must be considered that methoxylated aromatics, 4-methoxyphenethyl alcohol in particular, are strong attractants to various beetle taxa (Dötterl et al. 2012; Tóth et al. 2017; Lohonyai et al. 2018). That said, 4-methoxyphenethyl alcohol does not appear to be related to decomposition processes. However, although pleasantly scented to the human nose, at least one 1-phenylethanol derivative, acetophenone, is a sweet odour that is released during cadaveric decomposition (Buis 2016). Therefore, these contrasting odour types may be very similar from a functional perspective, and a necrophagous insect might be similarly attracted to nauseating odours as to “the sweet stench of decay” (Ollerton and Raguso 2006).

However, the knowledge about pollinators in *Amorphophallus* is limited, particularly if the large size of the genus and its geographical spread are considered. Some reports consist in casual observations and rely on one single inflorescence. Furthermore, the distinction between insect visitors and pollinators is rarely specified, which makes it challenging to evaluate the plant-pollinator interaction in the genus *Amorphophallus*. Therefore, the available information is compiled and evaluated to bring together the observations about pollinators in *Amorphophallus* that are scattered through the literature, often extending over many decades.

Pollinators

Beetles are the main known pollinator group reported for *Amorphophallus* (Moretto et al. 2019). Commonly, but not exclusively, three Scarabaeoidea families act as *Amorphophallus* pollinators, according to Moretto et al. (2019). These are the Dynastidae, more precisely the genus *Peltonotus* in India and South East Asia, the Hybosoridae, i.e., the genus *Phaeochrous* in Southeast Asia and Africa; and the copro-necrophagous Scarabaeidae in Southeast Asia and India (Moretto et al. 2019). Some *Amorphophallus* species, such as *A. hohenackeri* (Schott) Engl. and Gehrm., *A. johnsonii* N.E. Br., *A. konkanensis* Hett., Yadav and Patil, *A. julaihi* Ipor, Tawan and P.C. Boyce, *A. sylvaticus* (Roxb.) Kunth and *A. variabilis* Bl. are considered specialists, pollinated by a single beetle species (van der Pijl 1937; Sivadasan and Sabu 1989; Beath 1996; Punekar and Kumaran 2010; Chai and Wong 2019).

However, most *Amorphophallus* species that have been investigated seem to attract a multitude of insects (van der Pijl 1937; Bogner 1976; Hetterscheid 1994; Beath 1996; Giordano 1999; Jung 2006; Punekar and Kumaran 2010; Gibernau 2011; Chaturvedi 2017; Moretto et al. 2019; Chai and Wong 2019); or, as in the case of *A. paeoniifolius*, the reported observations are contradictory (Singh and Gadgil 1995; Grimm 2009; Sites 2017). Also, considering the large size of the genus *Amorphophallus* (> 230 species; WCVP, 2021; Bustamante et al. 2020; Tamayo et al. 2021) very few actual field studies were conducted. As a consequence, actual pollination has rarely been observed and there are even fewer reports that include observations on fruit set, which could validate if the observed insects are truly the pollinators (Singh and Gadgil 1995; Beath 1996; Jung, 2006; Chai and Wong 2019).

In order to evaluate and discuss the reported insect and non-insects visitors and pollinators, all the known pollinators, putative pollinators and visitors of *Amorphophallus* are listed in Table 1. The distinction between pollinator, putative pollinator and visitor is based on several considerations, first and foremost the observations and statements provided in the references. However, not all references make a distinction between a visitor and a pollinator, and some reports are contradictory. For example, *Trigona* bees are either not categorised at all, or categorised either as visitors or as pollinators, depending on the report. Similarly, some Diptera have been observed crawling on the stigma but were not reported as pollinators. However, they might contribute to pollination and are classified as putative pollinators in such cases. As for the visitors, they are usually classified in the various reports as such, on the grounds that they never visit the female flower zone, or if they are rare and the visiting organism, such as Arachnida, does not match the pollinating type. However, such visitors may also play a role in pollination as predators.

As previously mentioned, the most common pollinators in *Amorphophallus* belong to the three beetle families Dynastidae, Hybosoridae and Scarabaeidae (Moretto et al. 2019). However, smaller beetle taxa, i.e., Nitidulidae and Staphylinidae, also visit *Amorphophallus* inflorescences and act as pollinators (van der Pijl 1937; Punekar and Kumaran 2010; Chen et al. 2015; Chai and Wong 2019). Furthermore, fly pollination has also been mentioned. *Amorphophallus angolensis* subsp. *maculatus* (N. E. Br.) Ittenb., *A. prainii*, *A. konjac*, *A. titanum* and *A. gomboczianus* were reported to be pollinated or at least visited by flies (Gombocz 1936; Bogner 1976; Soepadmo 1973; Chen et al. 2015). Whilst Gombocz (1936) and Soepadmo (1973) only casually mentioned flies as pollinators, Bogner (1976) reported them as pollinators with certainty, together with the beetle *Phaeochrous camerunensis*. Chen et al. (2015) investigated the olfactory and visual attractors in *A. konjac* and provided

Table 1 The *Amorphophallus* species and the quantity of inflorescences investigated, together the location, reference, and categories of pollinators, putative pollinators and visitors to the inflorescences

Species & inflorescence quantity	Locations & references	Pollinators	Putative pollinators	Visitors
<i>A. abyssinicus</i> subsp. <i>akeassii</i> Single inflorescence	Ivory Coast: Comoé National Park, savanna parkland of the Lola plaine (Moretto et al. 2019)	Coleoptera: Scarabaeidae, <i>Cleptocaccobius uniseriatus</i> ("main pollinator")	Coleoptera: Aphodiidae, <i>Aphodius zumpti</i> , <i>Mesentoplatys dorsalis</i> , <i>Pseudopharaphodius phalacroanthoides</i> , <i>Trichaphodius copulatus</i> , <i>Trichaphodius flavus</i> , <i>Trichaphodius maldesi</i> ; Hydrophilidae , <i>Sphaeridium</i> sp.; Scarabaeidae , <i>Caccobius auberi</i> , <i>Caccobius ivorensis</i> , <i>Cleptocaccobius convexifrons</i> , <i>Cleptocaccobius dorbignyi</i> , <i>Furcathophagus flaviclavus</i> , <i>Hyalonthophagus nigrovittatus</i> , <i>Onthophagus lutaticollis</i> , <i>Onthophagus tersipennis</i> , <i>Sisyphus goryi</i> ; Staphylinidae sp.	Coleoptera: Scarabaeidae, <i>Chalconotus suturalis</i> , <i>Digitonthophagus fimator</i>
<i>A. angolensis</i> subsp. <i>maculatus</i> Several inflorescences	Gabon: on several unspecified sites (Bogner 1976)	Coleoptera: Hybosoridae, <i>Phaeochrous camerunensis</i> ; Diptera: Calliphoridae sp.		
<i>A. bartholotii</i> Single inflorescence	Ivory Coast: Tai National Park, track leading to the Centre de Recherche en Écologie (Moretto et al. 2019)	Coleoptera: Hydrophilidae, <i>Sphaeridium</i> sp.; Scarabaeidae , <i>Onthophagus liberianus</i>		
<i>A. bulbifer</i> The number of investigated inflorescences is not specified	India: Karnataka, Anshi National Park (Punekar and Kumaran, 2010)	Coleoptera: Hybosoridae (= <i>Melolonthidae</i> ; probably <i>Apogonia</i> sp. according to Moretto et al. 2019); Nitidulidae , <i>Epuraea</i> sp.	Diptera: Drosophilidae sp.	Coleoptera: Lycidae, <i>Lyctus</i> sp.
<i>A. commutatus</i> var. <i>commutatus</i> Several investigated populations but the number of investigated inflorescences is not specified	India: Maharashtra, three localities: Ratnagiri, Vengurla, Goa (Punekar and Kumaran 2010)	Coleoptera: Bostrichidae sp.; Nitidulidae , <i>Epuraea</i> sp.; Hymenoptera: <i>Trigona</i> sp. (except Vengurla population)	Coleoptera: Rutelinae (= Rutelidae , <i>Anomala</i> sp. according to Moretto et al. 2019); Diptera: Drosophilidae sp.; Muscidae , <i>Musca domestica</i>	Coleoptera: Staphylinidae sp.; Hymenoptera: Formicidae, <i>Oecophylla smaragdina</i> , Dolichoderinae: <i>Tapinoma</i> sp.
<i>A. commutatus</i> var. <i>anmodensis</i> Single inflorescence	India: Goa, Anmode ghat (Punekar and Kumaran 2010)	Coleoptera: Scarabaeidae, <i>Onthophagus</i> sp.		
<i>A. commutatus</i> var. <i>anshiensis</i> The number of investigated inflorescences is not specified	India: Karnataka, Anshi National Park (Punekar and Kumaran 2010)	Coleoptera: Cantharidae, <i>Rhagonycha</i> sp.; Cetoniidae , black beetles; Scarabaeidae , <i>Heliocopris</i> sp., <i>Onthophagus</i> sp.	Diptera: Drosophilidae sp.	Hymenoptera: Formicidae, <i>Oecophylla smaragdina</i> ; Blaberidae , <i>Panesthiinae</i>
<i>A. commutatus</i> var. <i>wayanadensis</i> Several investigated populations but the number of investigated inflorescences is not specified	India: Maharashtra, four localities: Mulshi, Ratnagiri, Vengurla, Goa (Punekar and Kumaran 2010)	Coleoptera: Nitidulidae, <i>Epuraea</i> sp.	Diptera: Drosophilidae; Muscidae , <i>Musca domestica</i> ; Hymenoptera: <i>Trigona</i> sp. (only Goa population)	

Table 1 (continued)

Species & inflorescence quantity	Locations & references	Pollinators	Putative pollinators	Visitors
<i>A. gigas</i> Single inflorescence	Indonesia: North Sumatra province, Sipirok (Hettterscheid 1994)	Coleoptera: carrion beetles; dung beetles; Cetoniidae ; Staphylinidae ; Diptera: Asilidae		
<i>A. gombocianus</i> Several inflorescences	Ethiopia: Sidamo (Gombocz 1936)	Diptera spp.		
<i>A. henryi</i> Several populations and several inflorescences	Taiwan: four sampling areas (Jung 2006)	Coleoptera: Scarabaeidae , <i>Onthophagus</i> sp., <i>O. argyropygus</i> , <i>O. koshunensis</i> , <i>O. proletarius</i> , <i>O. sauteri</i> , <i>O. taurinus</i> ; Staphylinidae spp.		Coleoptera: Nitidulidae ; Scaphiidiidae ; Scarabaeidae , <i>Paragymnopleurus</i> sp.; Tenebrionidae ; Diptera: Calliphoridae , <i>Chrysomyia</i> spp.; Drosophilidae , <i>Drosophila</i> spp.; Sepsidae , <i>Sepsis</i> spp.; Hemiptera ; Homoptera: Aphididae ; Hymenoptera: Formicidae ; Isoptera: Termitidae , <i>Odonotermes formosanus</i> ; Orthoptera: Thysanoptera ; Arachnida: Araneae , Sparassidae ; Salticidae ; Blattellidae
<i>A. hewittii</i> Several inflorescences	Malaysia: Borneo, Sarawak, Gunung Mulu National Park (Chai and Wong 2019)	Coleoptera: Hybosoridae ; Silphidae , <i>Diamesus</i> sp.; Staphylinidae , <i>Creophilus</i> sp.	Hymenoptera: Trigonids	
<i>A. hohenackeri</i> Several inflorescences	India: Kerala, Calicut University campus (Sivadasan and Sabu 1989)	Coleoptera: Nitidulidae , <i>Eपुरaea motschulskii</i>		
<i>A. johnsonii</i> Several inflorescences	Ghana: Jachie Sacred Grove (Beath 1996)	Coleoptera: Hybosoridae , <i>Phaeochrous amplius</i>	Coleptera: Histeridae , <i>Pachycraterus</i> sp.	Diptera: Calliphoridae , <i>Hemigynochaeta unicolor</i> ; Platystomatidae , <i>Paryphodes tigrinus</i>
<i>A. julaihi</i> Several inflorescences	Malaysia: Borneo, Sarawak, Gunung Mulu National Park (Chai and Wong 2019)	Coleoptera: Staphylinidae , <i>Creophilus</i> sp.		
<i>A. konjac</i> Several inflorescences	China: Yunnan, Kunming (KBG: 25.127°N and 102.743°E, 1788 m. a.s.l.), several inflorescences (Chen et al. 2015)	Coleoptera: Histeridae , Nitidulidae , Staphylinidae ; Dermaptera	Diptera , Calliphoridae , Calliphoridae ssp. <i>Achoetandrus ruffiacies</i> , <i>Aldrichina grahami</i> , <i>Chrysomya</i> spp., <i>Lucilia</i> spp.; Muscidae ; Sarcophagidae	
<i>A. konkanensis</i> Not specified, apparently single inflorescence	India: Maharashtra, Sindhudurg district, Kochra (Punekar and Kumaran 2010)	Coleoptera: Nitidulidae , <i>Eपुरaea</i> sp.		
<i>A. koratensis</i> Single inflorescence	Thailand: Songkhla, Hat Yai (pers. comm. Sutthinut Soonthornkallump)		Hymenoptera: <i>Tetragonula</i> sp.	Hymenoptera: Formicidae

Table 1 (continued)

Species & inflorescence quantity	Locations & references	Pollinators	Putative pollinators	Visitors
<i>A. muelleri</i> Several inflorescences	Indonesia: Java (van der Pijl 1937)	Coleoptera: Nitidulidae		Coleoptera: Melolonthidae , <i>Apogonia destructor</i>
<i>A. napalensis</i> Several inflorescences at two sites	India: Nagaland, Zunheboto, Lumami village, 880 m. a.s.l.; Mokochung, Arkong ward. Plot no. 227, 1350 m a.s.l. (Chaturvedi 2017)	Coleoptera: Scarabaeidae , <i>Parastasia</i> sp. (= <i>Dynastidae</i> , <i>Peltonotus</i> sp. according to Moretto et al. 2019)		Diptera: Drosophilidae , <i>Drosophila</i> sp.; Hymenoptera: Trigona sp.; Apidae, <i>Apis indica</i>
<i>A. paeoniifolius</i> (1) Several inflorescences, wild occurring and cultivated plants	India: Karnataka, Uttara Kannada district (Singh and Gadgil 1995)	Coleoptera: Rutelidae , <i>Adoretus</i> sp.	Hymenoptera: Melipona sp. (<i>Melipona</i> is now a neotropical genus, probably <i>Tetragonula</i> sp.)	Two unidentified insects
<i>A. paeoniifolius</i> (2) Single inflorescence	locality not specified (Giordano 1999)	Coleoptera: Hybosoridae , <i>Phaeochrous emarginatus</i>		
<i>A. paeoniifolius</i> (3) Not specified, apparently single inflorescence	India: Karnataka, Anshi National Park (Punekar and Kumaran 2010)	Coleoptera: Scarabaeidae , <i>Helicopriss</i> sp., <i>Onthophagus</i> sp.; Cetoniidae Black beetles	Coleoptera: Scarabaeidae, Rutelinae (= <i>Rutelidae</i> , <i>Anomala</i> sp. according to Moretto et al. 2019)	Diptera: Calliphoridae; Muscidae , <i>Musca domestica</i>
<i>A. paeoniifolius</i> (4) Single inflorescence	Thailand: Changwat Mae Hong son, 12 km NW Soppong (Pangmapa) (Grimm 2009)	Coleoptera: Hybosoridae, Phaeochrous dissimilis, Phaeochrous emarginatus, Phaeochrous intermedius; Scarabaeidae, Peltonotus nasutus		
<i>A. paeoniifolius</i> (5) Single inflorescence	Thailand: Nan province, Nan River at Srinan river (Sites 2017)	Coleoptera: Hybosoridae, Phaeochrous dissimilis; Scarabaeidae, Peltonotus nasutus		
<i>A. prainii</i> Single inflorescence	West Malaysia (Soepadmo 1973)		Diptera : „various flies “ are mentioned but have not been actually observed	
<i>A. sylvaticus</i> Single inflorescence	India: Maharashtra, Mumbai, Bhandup (Punekar and Kumaran 2010)	Coleoptera: Nitidulidae, Eburina sp.		
<i>A. titanum</i> (1) Several inflorescences	Sumatra: Fort de Kock (now Bukit-tinggi) (van der Pijl 1937)	Coleoptera: Silphidae, Diames <i>osculans; Staphylinidae, Creophilus villipennis</i>		
<i>A. titanum</i> (2) Single inflorescence	Indonesia: North Sumatra province, Sipirok (Hettterscheid 1994)	No insects were observed on the first day of anthesis	Hymenoptera: Trigona sp. on day two of anthesis	
<i>A. titanum</i> (3) Several inflorescences	Sumatra: (Giordano 1999)	Coleoptera: Curculionidae; Histriidae, Hybosoridae, Phaeochrous emarginatus	Coleoptera: Staphylinidae; Scarabaeidae; Diptera: Calliphoridae; Drosophilidae; Hymenoptera: Trigona geissleri; Trigona sp.	Coleoptera: Brentidae, Hormocerus compressitarsus; Arachnida; Blattodea; Formicidae

Table 1 (continued)

Species & inflorescence quantity	Locations & references	Pollinators	Putative pollinators	Visitors
<i>A. variabilis</i> (1) Several inflorescences	Java: Buitenzorg (now Bogor), (Backer 1913)	Coleoptera: Nitidulidae	Staphilinidae, <i>Philanthus crassicornis</i>	
<i>A. variabilis</i> (2) Several inflorescences	Java: Bandoeng (now Bandung) (van der Pijl 1937)	Coleoptera: Nitidulidae		

Genus and species are given in italics; family, order or other taxonomic categories are in bold

detailed experiments and observations. A total of 12 fly genera belonging to the three families Calliphoridae, Sarcophagidae and Muscidae were recorded to be attracted to *A. konjac* inflorescences, and the main visitors were species of the fly genera *Lucilia* and *Chrysomya* (Chen et al. 2015). However, Chen et al. (2015) did not investigate the fruit set. Moreover, Chen et al. (2015) also mentioned Dermaptera as well as several beetle families as natural pollinators of *A. konjac*, namely Histeridae, Staphylinidae and Nitidulidae. For the time being therefore, the effectiveness of the recorded fly genera (Chen et al. 2015) acting as pollinators for *A. konjac* remains unsubstantiated for the time being.

Drosophila flies, usually not as pollinators but as visitors, have been documented in *A. bulbifer* (Roxb.) Bl., *A. commutatus* (Schott) Engl. (Punekar and Kumaran 2010), *A. henryi* N.E. Br. (Jung 2006), *A. napalensis* (Wall.) Bogner and Mayo (Chaturvedi 2017), and *A. titanum* (Giordano 1999). Likewise, flies from the Calliphoridae and the Muscidae have been observed as visitors in most of these species (Giordano 1999; Jung 2006; Punekar and Kumaran 2010). However, their exact contribution to pollination remains unclear in most cases even though they have occasionally been observed to crawl on the female flowers (Giordano 1999; Punekar and Kumaran 2010).

Moreover, ants (Formicidae) and cockroaches (Blaberidae/Panesthiinae) were observed as visitors in several Indian *Amorphophallus* species (Punekar and Kumaran 2010). Ants and cockroaches (Blattodea and Blattodea) were also found as visitors in *A. henryi* and *A. titanum* (Jung 2006; Giordano 1999) whereas ants without cockroaches were observed to crawl at the spathe base in *A. koratensis* (pers. comm. Sutthinut Soonthornkalump).

In *A. napalensis*, even honey bees (*Apis indica*) were recorded as flower visitors (Chaturvedi 2017). Also, earwigs (Dermaptera) were reported to be pollinators in *A. konjac* (Chen et al. 2015), and stingless bees (*Trigona* spp.) have been reported on several occasions as visitors or putative pollinators in several *Amorphophallus* species (Hettterscheid 1994; Singh and Gadgil 1995; Giordano 1999; Punekar and Kumaran 2010; Chaturvedi 2017). However, only one study explicitly reported that *stingless* bees (*Trigona* sp.) act as pollinators (Punekar and Kumaran 2010). Nevertheless, 14 years earlier, it was questioned if *Trigona* bees are likely to act reliably as pollinators in *Amorphophallus* (Hettterscheid and Ittenbach 1996). However, they have been repeatedly observed crawling on both male and female flowers of *A. titanum* and *A. koratensis* and carrying pollen (Hettterscheid 1994; Giordano 1999; pers. comm. Sutthinut Soonthornkalump). Moreover, considering the varied trophic preferences of stingless bees (Eltz 2001), it seems at least possible that they are attracted to *Amorphophallus* species. Recently, two fungi species of *Cladosporium* have been identified that form a fungal layer at the base of *A. titanum*

inflorescences (Ruprecht et al. 2021). Referring to Sayyad and Mulani (2016), Ruprecht et al. (2021) propose that *Cladosporium* species grow as endophytes in *A. titanum*, forming a fungal layer at the spathe base during inflorescence development. If these findings are confirmed in situ, future investigations will have to consider and investigate the impact of fungal layers on pollinator attraction, considering that *Trigona collina* stingless bees have been observed to harvest mold spores (*Rhizopus* sp.) (Eltz 2001).

As a side note, most *Trigona* bees reported as putative pollinators of *Amorphophallus* have not been identified at the species level (Hettterscheid 1994; Punekar and Kumaran 2010; Chaturvedi 2017). However, the genus *Trigona* has been extensively revised in the meantime and various Asian species have been transferred to other genera (Michener 2007). For this reason, stingless bees in general are referred to the following pages, unless the species or the genus has been specified.

Recently, stingless bees have been observed visiting the inflorescence of a cultivated plant of *A. koratensis* Gagn. in large numbers (pers. comm. Sutthinut Soonthornkalump, Prince of Songkla University, Thailand). The bees repeatedly visited the inflorescence and collected pollen, occasionally falling down into the pistillate flower zone. They were identified as *Tetragonula* species by Kanuengnit Wayo, an entomologist from Prince of Songkla University. Besides the large number of *Tetragonula* bees, S. Soonthornkalump also observed small numbers of Formicidae at the base of the floral chamber. Interestingly, the bees were still attracted to the inflorescence after it ceased to smell, at least to the human nose. This behaviour has already been observed on behalf of *A. titanum* (Hettterscheid 1994), making it unclear what exactly attracts the bees. However, pollen has been shown to release fragrances that are attractive to bees but are not perceptible by humans (Dobson and Bergström 2000; Flamini et al. 2002). This could signify that some *Amorphophallus* species putatively attract two different pollinator guilds, copro-necrophagous insects and stingless bees. However, in the case of *A. koratensis*, the question if *Tetragonula* spp. is a pollinating taxon awaits confirmation as there was only one inflorescence, and because the inflorescence is protogynous, the pollination was unsuccessful.

It has been reported in several cases that the pollinating beetles are trapped in the floral chamber until pollen shedding (Sivadasan and Sabu 1989; Beath 1996; Moretto et al. 2019). Although most *Amorphophallus* species do not form complex traps (Bröderbauer et al. 2012), some still capture visitors or pollinators by means of slippery spathes and/or a floral chamber with a strong constriction, making it difficult for most trapped insects to leave the inflorescence (Sivadasan and Sabu 1989; Beath 1996; Chai and Wong 2019; Moretto et al. 2019). Similarly, or additionally, in some species, such as in *A. johnsonii* (Beath 1996) (Fig. 1) and

A. titanum (van der Pijl 1937), the base of the appendix is broadened and forms an overhanging wall, functioning as an effective obstacle to insects that try to leave. Still, it has also been observed on several occasions that visitors and pollinators were “disinclined” to leave for no apparent reason (Chai and Wong 2019), and according to Beath (1996), it must be assumed that the pollinators are kept by the smell.

Moreover, recent research indicates that some beetles respond differently to scent compounds, depending on their life-stage. Trumbo and Steiger (2020) investigated the attractiveness of five single scent compounds, as well as mixtures of these five compounds on burying beetles from the genus *Nicrophorus*. They showed that freshly emerged beetles respond to the scent signatures of well-rotted carcasses whereas beetles in search of a suitable breeding site respond to the scent signatures of fresh carcasses which may serve as food for their own brood. Moreover, flying beetles in search of a breeding place were actually deterred by some compounds, such as dimethyl trisulphide (Trumbo and Steiger 2020). Four out of five of these scent compounds, namely dimethyl monosulphide, dimethyl disulphide, dimethyl trisulphide and s-methyl thioacetate are emitted by *Amorphophallus* species (Kite and Hettterscheid 1997, 2017). Nearly half of the *Amorphophallus* species studied by Kite and Hettterscheid (1997, 2017) emit oligosulphides as major scent compounds, often accompanied by s-methyl-thioesters. This underlines the necessity for future research as the specific ratio of the scent compounds might have very different effects on putative pollinators.

In some species, such as *A. johnsonii*, *A. paeoniifolius* and *A. titanum*, the floral chamber was used by insects as a mating place (Beath 1996; Giordano 1999; Grimm 2009; Chai and Wong 2019). Moreover, it has been observed that both the appendix and the pollen has been consumed or harvested by pollinators in *A. napalensis* (Chaturvedi 2017) and *A. commutatus* (Punekar and Kumaran 2010). Likewise, fruit bodies are offered in *A. hohenackeri* (Sivadasan and Sabu 1989; Punekar and Kumaran 2010) and *A. konkanensis* (Punekar and Kumaran 2010), as is food tissue in *A. variabilis* (van der Pijl 1937) and stigmatic fluid in *A. bulbifer* (Punekar and Kumaran 2010), indicating that plant-pollinator interactions in the genus *Amorphophallus* are diverse and can be based on several, not necessarily mutually exclusive strategies, such as deceit, trapping, provision of a reward or possibly even mutualism. Obviously, some insects are in search of food, whereas others use the floral chamber as a mating place, or both; a behavioural trait known from other plant-pollinator interactions, such as Glaphyridae beetles feeding and mating on large bowl-shaped flowers from *Anemone coronaria* L. and *Papaver umbonatum* Boiss. (Keasar et al. 2010). Besides visiting the inflorescence in search of females, some visitors are simply using the inflorescence as a shelter (Wasserman and Itagaki 2003; Fishman

and Hadany 2013). However, the purpose of other visitors or pollinators in *Amorphophallus* remains obscure (van der Pijl 1937; Chai and Wong 2019).

Moreover, the picture is very heterogeneous. For example, one of the species, *A. commutatus* comprises four subspecies and the spectrum of insect visitors or pollinators differs markedly between the four subspecies (Table 1). Judging by the reported visitors/pollinators, it would seem that *A. commutatus* var. *anmodensis* is exclusively pollinated by a single beetle species whereas the other three subspecies are visited by a broad spectrum of different taxa (Table 1). It seems surprising that one subspecies is apparently a specialist when it comes to pollinator attraction whereas the other three subspecies are generalists. That said, it is unclear if more than one inflorescence of *A. commutatus* var. *anmodensis* has been investigated and therefore more observations are required to validate these observations.

Similarly, there are three species that have been sampled by different investigators. Firstly, *A. paeoniifolius* that has been sampled five times (Table 1). Although Hybosoridae and Scarabaeidae prevail in most of these reports, other Coleoptera and Diptera have also been observed to visit the inflorescences. However, *A. paeoniifolius* is a crop plant that is widely distributed in the tropics and its natural distribution is not known (Hettterscheid 2012). It is therefore debatable if the reported insects can be regarded as the natural pollinators, especially as one of the reports explicitly state that some of the wild occurring *A. paeoniifolius* plants, and all of the cultivated plants, failed to develop fruits (Singh and Gadgil 1995).

Another example is *A. titanum* in which insect visitors/pollinators in situ have been observed on three occasions, with markedly different results. Hettterscheid (1994) observed only stingless bees during the second day of anthesis but no insects at all on the first day of anthesis. In contrast, van der Pijl report that *Diamesus osculans* beetles (Silphidae) in particular, as well as *Creophilus villipennis* beetles (Staphylinidae) have been observed to visit several inflorescences of *A. titanum*. Lastly, Giordano (1999) observed several *A. titanum* specimens and reported a multitude of different taxa, including Coleoptera, Diptera and Hymenoptera and also ants, cockroaches and spiders (Table 1).

Lastly, *A. variabilis*, which has been investigated by Backer (1913) and van der Pijl (1937). At least in this species both authors report a beetle from the Nitidulidae family as the main pollinator. Nonetheless, Backer also reports a second visitor, namely the beetle *Philanthus crassicornis* (Staphylinidae) that was not observed by van der Pijl (1937).

Another difficulty is that the numbers of sampled specimens per site is not always referenced (Bogner 1976; Puneekar and Kumaran 2010) and it remains unclear on how many inflorescences these observations are based.

In some species, several specimens per population (Beath 1996; Giordano 1999) or several populations per species have been investigated (Bogner 1976; Jung 2006; Puneekar and Kumaran 2010). However, other observations rely on observations gathered on behalf of one single inflorescence per *Amorphophallus* species (Soepadmo 1973; Hettterscheid 1994; Giordano 1999; Grimm 2009; Puneekar and Kumaran 2010; Sites 2017; Moretto et al. 2019).

Pollinating predators

One motive, which so far has been widely neglected, is that visitors and pollinators do not approach either the substrate (dung, carrion, etc.) or the mimic (the inflorescence) in themselves, but arrive there to prey on the feeding or mating insects, or insects larvae (Moretto et al. 2019). Apparently, some *Amorphophallus* species, such as *A. titanum* (Giordano 1999; Moretto et al. 2019), *A. henryi* (Jung 2006) and *A. commutatus* (Puneekar and Kumaran 2010), attract different insect groups as well as other arthropods. The attracted and deceived insects might feed on plant resources such as pollen, etc., or use the floral chamber as a mating place or as a shelter. However, some of the attracted insects or arthropods, exemplified by Arachnida, Blattaria, and predatory beetles (Giordano 1999; Jung 2006; Puneekar and Kumaran 2010), do not arrive for the plant resources, etc., but rather to prey on the visiting insects.

For example, *Creophilus* beetles (Staphylinidae) are reported as exclusive pollinators in *A. julaihi*. However, *Creophilus* species are well investigated, as they provide useful forensic information; and *Creophilus* species are generally predators feeding on copro-necrophagous adult insects and on their larvae (Frątczak-Łagiewska et al. 2020). Similar predatory visitors have also been observed in *A. titanum* (Giordano 1999; Moretto et al. 2019). Fittingly, insect larvae, more specifically maggots, have been reported in inflorescences of *A. variabilis* and *A. commutatus* var. *commutatus* (van der Pijl 1937; Puneekar and Kumaran 2010).

Although these records constitute only a few observations, it must be noted that predators such as Arachnida, Blattodea and Formicidae are reported in all of the more detailed observations and investigations (Giordano 1999; Jung 2006; Puneekar and Kumaran 2010). This could signify a complex interplay between the inflorescence and its visitors, and it begs the question, which group contributes the most to actual pollination? The insects that are deceived and not rewarded, those feeding on plant resources, or those predating the first two insect groups? And if predators are attracted first in a significant numbers, would other visitors still alight on the inflorescence? A most fascinating scenario would consist of a multitude of attracted insects that constitute the actual reward for a predatory beetle, with

prey and predator both potentially acting as pollinators. If such a relationship could be confirmed it would certainly add another dimension to the complexity of deceit flowers. Remarkably, this scenario was proposed as early as 1889 but has not received much attention ever since (Delpino 1889). Engler (1920, pp. 18 and 19 and references herein) gives a brief summary on a scientific dispute between Arcangeli and Delpino. Delpino had observed that *Dracunculus vulgaris* Schott is exclusively pollinated by flies, whereas Arcangeli reported beetles as the main pollinators (Engler 1920). In 1889, Delpino emphasised the idea that flies are the main pollinators of *Dracunculus vulgaris* and that the beetles only follow the flies to prey on them. Subsequent investigations revealed that both Diptera as well as Coleoptera can act as pollinators in *Dracunculus vulgaris* (Engler 1920). However, the impact of predators on pollinators and pollination in deceit flowers still remains to be investigated, at least in *Amorphophallus*.

Summary and outlook

The aim of this review was to compile, review and discuss the state of the art of insect visitors and pollinators in the genus *Amorphophallus*. In summary, insect visitors or pollinators are reported for a total of 22 *Amorphophallus* species, which is less than 10% of the species diversity of the genus (ca. 230 spp.). Moreover, approximately a third of the reported observations were made on behalf of a single *Amorphophallus* inflorescence in the wild (Table 1), and the actual success of pollination, the fruit set, has been reported or documented in only four cases (Singh and Gadgil 1995; Beath 1996; Jung 2006; Chai and Wong 2019).

A most interesting observation is that stingless bees have been repeatedly observed in different *Amorphophallus* species, in India, Thailand and Sumatra. This may indicate that their role has to be considered more closely in future studies, particularly in conjunction with the observations made regarding fungal layers at the base of the spathe (Ruprecht et al. 2021).

It becomes evident through the presented data that the knowledge about pollinators in the genus *Amorphophallus* remains limited. The motives of the visiting insects are often not obvious, i.e., if they are in search of a mating or a breeding place, possibly also attracted by the plant's food resources or if they are predators in search of prey? Or simply in search of a shelter? However, if no clear motives are discernible, this may as well signify the unspecific attraction of all copro-necrophagous insects or the attraction of unspecialised Coleoptera and Diptera alike. For example, Moretto et al. (2019) identified members of the beetle genus *Sphaeridium* as pollinators of *Amorphophallus*. These beetles are ubiquitous in tropical Africa and they are attracted

by decomposing organic material of all kinds, such as excrement, carrion, mushrooms, fruits, vegetables.

The only tentative conclusion that can be drawn from the compiled data is that beetles are most likely the main pollinator group in *Amorphophallus*, and that although various Diptera are attracted by many *Amorphophallus* species, they seem to contribute less to actual pollination. However, more detailed observations based on larger samplings are required to draw more specific conclusions.

In conclusion, the plant-pollinator interaction seems to follow a generalist pattern in most of the *Amorphophallus* species investigated, attracting copro-necrophagous Coleoptera and Diptera alike. Similarly, Gibernau et al. (2010) found an "imperfect discrimination" of quantitative floral traits between fly and beetle-pollinated aroids.

However, attracting a multitude of insects suggests a generalist pollination strategy that is at the same time highly efficient insofar as insects can be attracted anywhere as copro-necrophagous insects are ubiquitous. It might therefore be speculated that relying on this functional group of insects as pollinators, which is available everywhere on earth, might have contributed to the evolutionary success of the genus *Amorphophallus*, which is the largest palaeotropical aroid genus and the third largest genus of the Araceae altogether (Boyce and Croat (2018 onwards).

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