Pollination of *Amorphophallus barthlottii* and
*A. abyssinicus subsp. akeassii* (Araceae) by dung beetles
(Insecta: Coleoptera: Scarabaeoidea)

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**Abstract.** – After summarizing the current knowledge on pollination mechanisms in the genus *Amorphophallus* (Araceae) and the scarab beetles (Scarabaeoidea) visiting inflorescences of Araceae, we present new observations from Côte d’Ivoire on pollinators of *Amorphophallus* (subg. *Afrophallus* Hett. & Claudel) *barthlottii* Ittenb. & Lobin and *Amorphophallus* (Afrophallus) *abyssinicus subsp. akeassii* Ittenbach. The beetles we recovered from inflorescences of these species belong to Scarabaeidae: Onthophagini (*genera Caccobius, Cleptocaccobius, Furconthophagus, Hyalonthophagus* and *Onthophagus*), Aphodiidae, Hydrophilidae (genus *Sphaeridium*), and Staphylinidae. Species lists of the pollinators are provided and discussed in ecological and phylogenetic context.

**Key words.** – Africa, Côte d’Ivoire, Taï National Park, Comoé National Park, pollination, Plantae, Araceae, Coleoptera, Scarabaeoidea, Scarabaeidae, Onthophagini, Aphodiidae, Hydrophilidae, Staphylinidae.

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**Mots clés.** – Afrique, Côte d’Ivoire, Parc National de Taï, Parc National de la Comoé, pollinisation, Plantae, Araceae, Coleoptera, Scarabaeoidea, Scarabaeidae, Onthophagini, Aphodiidae, Hydrophilidae, Staphylinidae.

**Abbreviations**

- ANHRT African Natural History Research Trust, Leominster, U.K.
- BMNH The Natural History Museum, London, U.K.
- BC Bertrand Cosson.
- FTK Frank-Thorsten Krell.
- MA Marios Aristophanous.
- PM Philippe Moretto.
Introduction

Pollination mechanisms in *Amorphophallus*

The genus *Amorphophallus* Blume ex Decne (Araceae) comprises more than 200 species (CLAUDEL et al., 2017) and is distributed along the tropical belt from Africa to south-east Asia, Australia, and Polynesia. The majority of species are found in the Indo-Malayan region (MAYO et al., 1997; BOYCE & CROAT, 2011). The African species form a morphologically and genetically distinct group, the subgenus *Afrophallus* Hett. & Claudel (SEDAYU et al., 2010; CLAUDEL et al., 2017).

*Amorphophallus* species are herbaceous geophytes that usually produce only a single leaf and a unique inflorescence during or just prior to the rainy season. Numerous studies revealed the diversity of this genus, particularly in morphology and chemistry of the inflorescence reflecting adaptations to pollination processes (HETTERSCHEID & ITTENBACH, 1996). On the other hand, the knowledge of the pollinating insects remains anecdotal and is limited to about twenty *Amorphophallus* species (GIBERNAU, 2003, 2011, 2016).

Inflorescence and blooming patterns in *Amorphophallus* are typical for the subfamily Aroideae. A spathe is wrapping around a spadix that carries the tiny unisexual flowers, with the female flowers near the bottom and the male ones above. The spathe of *Amorphophallus* forms a floral chamber around the lower half of the spadix with the tiny flowers (Fig. 1). The upper appendix of the spadix usually sticks out of the floral chamber and releases strong and often nauseating odours at the beginning of the flowering period (MEEUSE & RASKIN, 1988; KITE et al., 1998, KITE & HETTERSCHEID, 2017), generally at night, promoted by the ability to produce heat. The flowers are protogynous with the female flowers being receptive on the first day of flowering and the male flowers releasing pollen on the second day when the female flowers are no longer receptive, hence avoiding self-pollination.

Morphology and physiology of the inflorescence provide a characteristic mechanism to attract pollinators by olfactory deception. The odour emitted by the spadix simulates that of a food source or a reproductive substratum for coprophagous or necrophagous beetles and other insects, which are, once attracted, held captive in the floral chamber during the whole flowering period (URRU et al. 2011; SCHIESTL & DOTTERL., 2012).

A well known example of a spectacular, meat-coloured inflorescence is that of *A. titanum* (Becc.) Becc. ex Arcang, which produces a fetid odour that attracts necrophagous beetles such as the silphid *Diamesus osculans* Vigors, 1825, and its predators such as the staphylinid *Creophilus villipennis* Kraatz, 1859 (VAN DER PIJL, 1937), as well as a hybosorid, *Phaeochrous emarginatus* Castelnau, 1840, and predatory Histeridae (GIORDANO, 1999: 16).

The spadix can remain attractive during the day, attracting other, not necrophagous, often melitophagous beetle families, such as Dynastidae, Rutelidae, Nitidulidae, Bostrichidae, Lycitidae, Brentidae, and Staphylinidae. Other orders like Diptera, Hymenoptera, and even Blattodea can also be attracted (GIORDANO, 1999; PUNEKAR & KUMARAN, 2010). Some of these visitors take advantage of the trophic resources but are not considered pollinators as they are rarely present in the floral chamber during the flowering period.

The structural diversity of the inflorescences partly reflects their adaption to the various types of pollinators. A detailed knowledge of taxonomy, biology, ethology, and ecology of the pollinator species helps to understand the adaptive value of the morphology of the inflorescence.

Selection processes are influenced by phenology, composition of odours emitted by the spadix (KITE et al., 1998, 2017), the different types of trophic recompensation offered by the plant (BRODERBAUER et al., 2013; CHARTIER et al., 2013), the morphological structures of the
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inflorescence retaining the pollinators, and even by the type of exine of the pollen grains (GRAYUM, 1986) as to which sticks best to the pollinator.

The inflorescence of Amorphophallus uses a trapping mechanism of the “Arisarum” type with a more or less strong constriction of the spathe and slippery surfaces inside the spathe where the insects are retained.

In a mutualistic system, pollinators may be offered trophic compensation such as exudates, appendices, sterile flowers, or pollen. They may be offered a place for mating (CHATURVEDI, 2017: fig. B; SITES, 2017), and/or for depositing their eggs (SCHIESTL & DOTTERL, 2012). In cases of pollination by deception, the pollinators receive nothing (PUNEKAR & KUMARAN, 2010), as we find with our Amorphophallus species.

Scarabaeoidea known as pollinators of Araceae

In the literature about pollination of Araceae (e.g., GIBERNAU, 2011; PUNEKAR & KUMARAN, 2010; SCHIESTL & DOTTERL, 2012), species of Scarabaeoidea are not always correctly identified, not identified to species, or just taken from previous sources. The reference to “Scarabaeidae” often relates to a whole group of families (or subfamilies) with diverse trophic and ecological preferences and habits, rendering such reports difficult to interpret. In these cases, we need to trace information at its source and rectify errors of identification and classification.

Under these circumstances, it seems useful to summarize on a global scale the species or genera of the different Scarabaeoidea families involved in the pollination of Araceae, particularly of Amorphophallus:

Cetoniidae (mainly anthophiles and/or frugivores): Anoplochilus MacLeay and Leucoceles Burmeister, amongst other beetles, on Zantedeschia spp. in South Africa (SINGH et al., 1996); Cetonia aurata Linné, 1761, Oxythyrea funesta Poda, 1761, and Gnorimus nobilis (Linné, 1758) on Zantedeschia aethiopica (L.) Spreng. in France, outside the natural range of the plant (PM, pers.obs.); Tropinota hirta (Poda, 1761) as occasional visitor of Biarum dispar (Schott) Talavera in Spain (RUIZ, 2009).

Melolonthidae (phytophagous): Apogonia destructor Bos, 1890, on Amorphophallus muelleri Bl. (sub: A. oncophyllus Prain) in Borneo, probably as an occasional visitor (VANDER PIJL, 1937); a probable Apogonia species on Amorphophallus bulbifer (Roxb.) Blume in India (PUNEKAR & KUMARAN, 2010: figs. 3 C-F, not Hybosoridae), also likely an occasional visitor.

Dynastidae (anthophilous and/or frugivorous, amongst other trophic regimes): in a remarkable, well documented analysis, MOORE & JAMESON (2013) present an overview of all species of four Cyclocephalini genera (Cyclocephala, Erioscelis, Aspidolea, and Arriguttia) that are involved in the pollination of thirteen genera of Araceae in the neotropical region. Referring to this paper, we will refrain from recapitulating the references on Neotropical Araceae here.

The Asian genus Peltonotus, also in the tribe Cyclocephalini (JAMESON & WADA, 2004, 2009; JAMESON & DRUMONT, 2013), is closely dependent on Araceae. Peltonotus nasutus Arrow, 1910, was found on Amorphophallus paenifolius (Dennst.) Nicolson in Thailand (GRIMM, 2009; SITES, 2017); P. malayensis Arrow, 1910, on Epipremnum falcifolium Engl. in Brunei (JAMESON & WADA, 2004); and an unidentified Peltonotus species (photo identification of the genus: D. Keith) on A. napalensis (Wall.) Bogner & Mayo (CHATURVEDI, 2017, figs B-E, not Parastasia) in India.
Rutelidae (phytophagous and/or floricolous): Parastasia bimaculata Guérin, 1843 was found on Homalomena propinqua (Kumano & Yamaoka, 2016); Parastasia gestroi Ohaus, 1900, and P. nigrifennis Sharp, 1881, on several Homalomena species (HOE et al., 2016) in Borneo; and Anomala spp. (identifications after photos by D. Keith) on Amorphophallus commutatus (Schott) Engl. var. commutatus and A. paeoniifolius (Dennst.) Nicolson in India (PUNEKAR & KUMARAN, 2010: figs. 3K & 4P), probably opportunistic visitors. An Adoretus sp. (identification to be confirmed) was found in numbers on Amorphophallus paeoniifolius in India (SINGH & GADGIL, 1995).


Aphodidae (coprophagous or saprophagous): A number of species of Aphodius s. l. and Oxyomus are known to pollinate Arum and Biarum in Europe and the Middle East (KNOLL, 1926; KULLENBERG, 1953; RUIZ, 2009; PM, pers. obs.), but it appears that they are at best secondary pollinators. They occur in low numbers (RUIZ, 2009) compared to Diptera, which outnumber the beetles by far.

Scarabaeidae or proper dung beetles, being generally coprophagous or necrophagous, are relatively rarely cited as pollinators of Araceae in the dung beetle literature (HALFFTER & MATTHEWS, 1966, NICHOLS et al., 2008, KRYGER, 2009). It is the botanical literature about Araceae that provides us with more information.

Onthophagus (s. l.) tarandus Fabricius, 1792 and Caccobius (s. l.) diminutivus Walk., 1858, pollinate Typhonium trifoliatum (L.) Schott in India (CLEHORN, 1914: 421-424 & pl. 32, cited by ARROW (1931: 143 & 180) who identified the specimens years after Cleghorn’s observation). Onthophagus (s. l.) pugnax Harold, 1868, and Onthophagus (s. l.) sydneyensis Blackburn, 1903, were found on Typhonium brownii Schott in Australia (MONTIEITH, 1973) and Sisyphus sp. on Sauromatum in India (DAKWALE & BHATNAGAR, 1982). Furconthophagus furcatus (Fabricius, 1781) and Caccobius schereberi (Linne, 1767) were found in the spathes of Arum nigrum Schott in Montenegro (KNOLL, 1926) and Palaeonthophagus ovatus (Linné, 1767) on Arum maculatum in Spain (RUIZ, 2009). Palaeonthophagus ovatus (Linné, 1767) and Onthophagus (s. l.) sellatus Klug, 1845, pollinated Arum dioscoridis Sibth. & Sm. in Lebanon (KULLENBERG, 1953). In Europe and the Middle East, Onthophagini are only secondary pollinators of Araceae.

The following species were recorded from Amorphophallus: Onthophagus sp. on Amorphophallus commutatus var. anmodensis Sivad & Jaleel; Onthophagus sp. and Heliocopris sp. on A. commutatus (Schott) Engl and A. paeoniifolius (Dennst.) Nicolson (PUNEKAR & KUMARAN, 2010: 332, 334,-figs. 4B & 4N) in India; and Paraphanaeomorphus argyropogus Gillet, 1927, Indachorius koshunensis Balthasar, 1941, Gibbonthophagus proletarius Harold, 1875, Onthophagus sauteri Gillet, 1924, Gibbonthophagus taurinus White, 1844, Onthophagus sp., and Paragymnopleurus sp. on A. henryi N. E. Br. in Taiwan (JUNG, 2006: 22; CHEN, 2002).

The genus Heliocopris, cited by PUNEKAR & KUMARAN (2010), and the genus Paragymnopleurus, cited once by JUNG (2006), both large beetles, might not be considered regular pollinators if not confirmed by concordant observations. Heliocopris, while certainly identified correctly being the largest dung beetles in India (30-60 mm), are massive and strong.
beetles that would easily destroy rather than pollinate *Amorphophallus* inflorescences in their attempt to escape.

Amongst the Scarabaeoidea, three families are commonly, but not exclusively cited as pollinators of *Amorphophallus*: Dynastidae of the floricolous genus *Peltonotus* in India and South East Asia; necrophagous Hybosoridae of the genus *Phaeochrous* in South East Asia and Africa; and copro-necrophagous Scarabaeidae of the tribe Onthophagini in India and South East Asia.

While Scarabaeidae (*s. str.*) are generally coprophagous and often specialized in certain types of dung, certain species and even whole genera are adapted to using other trophic resources and are necrophagous, feeding on vertebrate carrion, or even on freshly dead, chinone-secreting diplopodes (Schmitt *et al.*, 2004), are mycetophagous, frugivorous, saprophagous, or saproxylophagous. Some are adapted to anthills, abandoned termite mounds, or vertebrate burrows, and a few are phoretic on mammals.

We distinguish four main functional groups or guilds of dung beetles: telecoprids (rollers), which roll a portion of dung away from the source in order to avoid competition; paracoprids (tunnelers), which dig a nest under the dung source where they deposit portions of dung for their larvae and, finally endocoprids (dwellers), which live and develop directly in the dung dropping. Certain species are kleptoparasites using the dung portions secured by larger dung beetle species. Some dung beetles are diurnal, others nocturnal. The vision of the night-flyers seems to be adapted for orientation in the middle of the night, even in thick undergrowth (McIntyre & Caveney, 1998; Warrant, 2016).

Dung beetles use an ephemeral and insular resource of different sizes, that is randomly distributed on the ground. They locate their food by olfaction. In the tropics, competition for this resource is fierce and generally follows the simple rule "first come first served". Nocturnal species, for example, become active early in the night, generally during the short dusk (Krell-Westerwalbesloh *et al.*, 2004), when they start flying in search for faecal odour. The duration of this prospection is rather short. For the rest of the night, and as soon as the resource is reached, the beetles exploit the food source or secure dung for their offspring. Day or night, latecomers often loose out and leave empty handed (PM, FTK, pers. obs.).

Like most other Scarabaeidae, the Onthophagini fly randomly to prospect for and follow the odour trails emerging from excrement, carrion, etc., which they feed on or use for supplying their subterranean nests. Once arrived at the source of the odour, they can land directly on it, but more often land at some distance and reach the resource by walking.

It is among the Onthophagini that we observe the greatest variety of diets (all those mentioned above, excluding saproxylophy) and lifestyles, and thus the ability to perceive the presumably greatest variety of volatile compounds. In Africa, the tribe Onthophagini contains about 1100 species in 30 genera, including the mega-genus *Onthophagus*, which alone accounts for 800 species. Their evolutionary success is due to their ability to rapidly occupy a maximum of niches and to access limited resources through a variety of behaviours. The size of Onthophagini (2.3-12 mm) makes it possible for them to be captured by *Amorphophallus* inflorescences. The flowering period of African *Amorphophallus* at the beginning of the main rainy season coincides with the beginning of the activity period of many Onthophagini species, which generally stay active throughout the rainy season and beyond.
Field observations

Amorphophallus (Afrophallus) barthlottii Ittenbach & Lobin

One inflorescence of *A. barthlottii* was observed (BC) on 3 April 2017 at the forest edge on the side of the track (Fig. 11) leading to the Centre de Recherche en Écologie, Parc National de Taï, Côte d’Ivoire (5°49’59.8’’N, 07°20’32.0’’W). Searches in the area and elsewhere in the forest did not reveal any other inflorescence of this species. Our observation, albeit limited to a single specimen, provided the first data on pollinators of *A. barthlottii*, one of the smallest African species of the genus. Described just over twenty years ago (ITTENBACH & LOBIN, 1997), the species appears to be endemic in the dense tropical forests of Côte d’Ivoire and Liberia. Its foliation and fructification are still unknown since the species has not been found since the original description (W. HETTERSCHEID, pers. comm.)

In the leaf litter, the single inflorescence was not very visible. The spathe began opening in the afternoon, but the smell was probably not emitted before dusk around 18:30 hrs. The beetles all arrived within one hour after dusk. Their repeated movements on the female area of the spadix and the presence of pollen on their bodies suggest that they participate effectively in pollination. The smell gradually decreased until the next evening, when the pollen was released. In spite of our frequent visits, no other beetle was observed afterwards, indicating a very short window of attractiveness of the plant for these insects. All specimens were collected on the first evening around 20:00 hrs and were preserved in 70% alcohol.

Description of the observed inflorescence (ANHRT)

Our specimen of *A. barthlottii* (Figs. 1-2) flowered after the first rains during the main rainy season. The single inflorescence measures 20 cm. The 10 cm long spadix sits on a short, 10 cm long peduncle (Fig. 2) The tuber is 4 cm thick and 6 cm in diameter and bears a crown of roots in its upper part (Fig. 1). The spadix shows a typical zonation with the fertile part in the first quarter, the female flowers at the bottom and the male flowers at the top (Fig. 3). The pollen is smooth (psilate) (ITTENBACH & LOBIN, 1997). As in all *Amorphophallus*, the flowers are lacking petals and do not produce nectar. *A. barthlottii* has neither sterile flowers nor staminodes. The terminal three quarters of the spadix is formed by a curved appendix with largely protrudes the spathe (Fig. 4). Its surface is papillose.

The base of the spathe encloses all the flowers by forming a floral chamber. On the inside the limb spathe is dark purple with a hint of transparency letting the exterior white colour shine through as fine white stripes. Between the floral chamber and the limb, we find a slight constriction which is short and purely white, forming a triangular, slightly erected collar. The inside of the spathe is irregularly wrinkled and has a slippery surface with glandular hairs producing a yellow resin (Fig. 5).

The odour of this species has not been analysed, but the inflorescence clearly emits an unpleasant smell (evoking rotten meat). With the contrasting internal purple and external white colour and the odour emission, the inflorescence of this species might easily appear to be a decomposing carcass.
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Figs. 1-5. – *Amorphophallus barthlottii* from Taï N.P. 1-2. – Entire specimen and inflorescence; 3-4. – The spadix inside the spathe; 5. – Inside of the spathe showing glandular hairs.
Beetles collected (BMNH)

Family Scarabaeidae

Onthophagus liberianus Lansberge, 1883 (Fig. 6): 2♂♂, 6♀♀.

This tunneling, nocturnal, copro-necrophagous beetle measures between 7 and 10 mm and is widely distributed in hygrophilous and mesophilic forests (CAMEFORT, 1984) from Sierra Leone to Bénin.

Family Hydrophilidae

Sphaeridium sp.: 7 specimens.

The species of this genus measure between 5 and 6 mm. They are widely distributed in tropical Africa and attracted by all sorts of moist, decomposing organic material (excrement, carrion, mushrooms, fruits and other vegetable matter, etc.). Smaller Hydrophilidae (2-3 mm) were already known as potential pollinators of Araceae: Cycreon sp. on some Homalomena (HOE et al., 2016), Cercyon sp. and Cryptopleurum sp. on Arum nigrum (KNOLL, 1926), Cercyon haemorrhoidalis F. on Dracunculus vulgaris var. creticus (SCHMUCKER, 1930) and Cercyon pygmaeus III. on Dracunculus vulgaris (MEEUSE & HATCH, 1960).

Lacking other observations, we may assume that Onthophagus liberianus and Sphaeridium sp. are the specific pollinators of A. barthlottii, attracted by the malodours emanating from the plant. O. liberianus is the main nocturnal copro-necrophagous scarabaeid species in the Parc National de Taï (CAMEFORT, 1984; PM, pers. obs.). Other local copro-necrophagous nocturnal Onthophagus species, e.g., Onthophagus foulliouxi Cambefort, 1971, or Onthophagus rufopygus Frey, 1957, are much rarer.

Mechanisms of capture and pollination

The spathe opens late afternoon and releases an odour attracting Onthophagus liberianus and Sphaeridium sp. The odour persists at least throughout the night but probably not much beyond. In dark litter of the nocturnal undergrowth, the contrast between the pale blade of the spathe and the dark center might be a visible target for insects searching for decaying material or excrement by flying in a zigzag pattern at low height. Water droplets caused by nocturnal condensation render the inner edge of the limb slippery (Fig. 4). The slight constriction of the spathe leaves a gap between spathe and spadix that accommodates insects of the size of the attracted species (5-10 mm). Beetles attracted by the odour fall into the floral chamber from where they are unable to escape. With no food around, the beetles repeatedly try to climb the slippery walls of the spathe, fall back down, and so on. It is during these round-trips in the floral chamber that they can deposit on the receptive stigmata the pollen previously picked up in another inflorescence.

Despite the presence of males and females, the floral chamber does not provide the conditions for mating and reproduction, since neither a substratum for digging nor any food source is available (EMLEN, 1997). Ultimately, they can escape only after the release of pollen that triggers the spathe's wilting.

Amorphophallus (Afrophallus) abyssinicus subsp. akeassii Ittenbach

One inflorescence of A. abyssinicus was observed and collected in the Parc National de la Comoé, in the savanna parkland of the Lola plaine (8°45.1’N, 3°49.0’W), on 13 May 1997, at 22:00 hrs (FTK). All insects from the spathe chamber and the few approaching the plant or
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Figs. 6-9. – Dung beetles. 6. – *Onthophagus liberianus* Lansberge ♂; 7. – *Trichaphodius copulatus* (Schmidt); 8. – *Cleptocaccobius dorbignyi* Cambefort ♂; 9. – *Cleptocaccobius uniseries* (d’Orbigny) ♂. Scale: 1 mm.
trying to enter the chamber at the time were collected. The smaller beetles (Cleptocaccobius, Aphodiidae, etc.) were in the spathe chamber of the inflorescence. Plant and beetles are preserved at DMNS.

**Description of the inflorescence**

*A. abyssinicus* is widely distributed in Africa and arranged into three subspecies (ITTENBACH, 2003). The nominal subspecies occurs from Togo to Ethiopia and Malawi, the subspecies *unyikae* from Congo to Zimbabwe, and the western subspecies *akeassii* (Fig. 10) is found from Côte d’Ivoire to Nigeria. The latter is easily distinguished from the other two by its female flowers possessing a distinct style (ITTENBACH & LOBIN, 1997; ITTENBACH, 2003).

This species is even smaller than *A. barthlotti*. The spadix in our specimen is 8 cm long. The peduncle is not preserved, but measures generally 3-31 cm in this species (ITTENBACH, 2003). The inflorescence of our specimen was close to the ground indicating a very short peduncle. The spathe measures about 10.5 cm in length and was of a purple colour. In our specimen the spathe is constricted where the male flowers end, leaving only about 3 mm space all around the spadix for pollinators to enter the flower chamber. The conical appendix is 4 cm long and max. 1.2 cm in diameter. The interior of the spathe is longitudinally ribbed and without any hairs. The subspecies flowers from December to May (ITTENBACH, 2003). KITE & HETTERScheid (2017: 127) classify the odour of the flower as “cow dung” (The reference in KITE & HETTERScheid (2017) to two different scent types, namely rotting meat and cow dung, is due to a mix-up of some flowering plants in cultivation actually proving to be *A. mossambicensis* instead of *A. abyssinicus*, with a rotting meat smell in the former, whereas all verified *A. abyssinicus* have a distinct cow dung smell. W. Hetterscheid, pers. comm., 2018).

**Beetles collected (DMNS)**

Family Scarabaeidae

*Chalconotus suturalis* (Janssens, 1938): 1 ♂.

This large opportunistic nocturnal species, common in Côte d’Ivoire, tried in vain to enter the spathe chamber.


These nocturnal coprophagous dung beetles walked towards the plant.

*Sisyphus goryi* Harold, 1859: 2 spm.

*Caccobius* (s. l.) *auberti* d’Orbigny, 1902: 1 ♂.

*Caccobius* (s. l.) *ivorensis* Cambefort, 1984: 1 ♂.

*Cleptocaccobius convexifrons* (Raffray, 1877): 1 ♀.

*Cleptocaccobius dorbignyi* Cambefort, 1984 (Fig. 8): 2 ♂♂, 2 ♀♀.

*Cleptocaccobius uniseries* (d’Orbigny, 1905) (Fig. 9): 55 ♂♂, 59 ♀♀.

*Hyalonthophagus nigroviolaceus* (d’Orbigny, 1902): 1 ♀.

*Furconthophagus flaviclava* (d’Orbigny, 1902): 2 ♂♂, 2 ♀♀.

*Onthophagus* (s. l.) *lutaticollis* d’Orbigny, 1907: 1 ♂, 1 ♀.

*Onthophagus* (s. l.) *tersipennis* d’Orbigny, 1902: 1 ♂.

These 10 diurnal paracoprid species have been collected inside the spathe. They are widely distributed in western Africa, and half of them are cleptoparasites: *C. convexifrons*, *C. dorbignyi*, *C. uniseries*, *H. nigroviolaceus* and *O. tersipennis*. All ten species are typically coprophagous.

*Cleptocaccobius uniseries*, which represents 77 % of all collected Scarabaeidae and Aphodiidae, appears to be the main pollinator species of *A. abyssinicus* in this case.
Family Aphodiidae

Mesonotoplatus dorsalis (Klug, 1855): 1 spm.
Aphodobius zumpti (Balthasar, 1937): 1 spm.
Trichaphodius copulatus (Schmidt, 1916) (Fig. 7): 1 spm.

These 7 endocoprid species were collected inside the spathe. They are presumed diurnal and/or crepuscular and are true coprophagous, which are regularly attracted to human baited traps, but also to light traps at dusk.

Except C. suturalis and D. fimat or, which were fortuitous visitors, all collected Scarabaeidae and Aphodiidae are small: 2.3 to 6.1 mm, and C. uniseries 2.4 to 3.8 mm only.

Family Hydrophilidae

Sphaeridium sp.: 1 spm.

Family Staphylinidae: 3 spm.

Mechanisms of capture and pollination

Since the majority of captured beetles are diurnal, we assume that the odour emission began during the day, possibly even in the morning. As noted above, due to their small size (2.3 to 6.1 mm) the captured beetles are capable of entering the floral chamber through the spathe constriction. The dark colour of limb and spadix contrasts with the savanna soil. The erected limb could act as a flight interception trap for small insects flying at low height. It is reasonable to assume that small coprophagous, attracted by the smell, hit the limb and fall directly into the base of the spathe, actively moving downward into the floral chamber. Two factors can explain the large number of scarabaeoids (ca. 150) captured in the floral chamber: the density of dung beetles is higher in the savanna than in the forest (Krell et al., 2003), and odours are dispersed over longer distances in open habitats. Cleptocaccobius was the dominant pollinator group found in the floral chamber. At the site in the savanna parkland, cleptoparasites of telecoprids, to which Cleptocaccobius belong, make up 12% to over 40% of the dung beetle assemblages (Krell et al. 2003; Krell-Westerwalbesloh et al. 2004). We note that this is the first record of Aphodiidae as pollinators of Araceae in Africa, of which 19 specimens were found in our A. abyssinicus.

The odour produced by the inflorescence of A. abyssinicus contains 2,7-dimethyl-1,7-octadiene, 3,7-dimethyl-2-octene, 3,7-dimethyl-1-octene, 2-methyl-1-butanol, 2-butanone, and β-selinene, as well as unidentified sesquiterpenes and sesquiterpenoids (Kite & Hetterscheid, 2017). All but one of the identified substances (3,7-dimethyl-1-octene) have been found in faeces of one to seven species of vertebrates (Krell & Schmitt, in press). 2-Butanone is known to be a crucial component of the odorous bouquet attractive to dung beetles (Krell et al., 2006; Wurmitzer et al., 2016).
Fig. 10: Another specimen of *Amorphophallus abyssinicus* ssp. *akeassii* Ittenbach from Parc National de la Comoé, Côte d’Ivoire, near the Comoé National Park Research Station, 8°46′N, 3°47′W, 21.IV.2012.

Fig. 11. – Taï National Park: the side of the track where the *A. barthlottii* was found.
Discussion

Nocturnal beetle species are associated with *A. barthlottii*, which flowers at night, and diurnal species are associated with *A. abyssinicus*, which likely begins flowering during the day. While the odour composition of *A. barthlottii* remains unknown, the attraction of a copro-necrophagous species of Onthophagini might indicate a similar or related bouquet to that of *A. abyssinicus*. Heat production, albeit likely, has not been studied and remains an assumption for both species.

The morphology of the pollen grain exine is psilate (smooth) in *A. barthlottii* and verrucate in *A. abyssinicus* subsp. *akeassii* (ITTENBACH, 2003). In the subgenus *Afrophallus*, most species have psilate pollen, which is believed to be adapted to pollination by beetles whereas verrucate pollen are assumed to be associated with pollination by Diptera (GRAYUM, 1986; VAN DER HAM *et al.*, 2005; SANNIER *et al.*, 2009). Not so in our case of *A. abyssinicus* subsp. *akeassii*.

*Amorphophallus* seems to be mainly pollinated by beetles. Each species has its own adaptations to the particular kind of pollinating beetles. In Africa, based on data from four *Amorphophallus* species, namely *A. abyssinicus* subsp. *akeassii*, *A. angolensis* subsp. *maculatus*, *A. barthlottii*, and *A. johnsonii*, the pollinators are Onthophagini (Scarabaeidae) or *Phaeochrous* (Hybosoridae). In both *A. barthlottii* and *A. abyssinicus* we find the trapping mechanism of the "*Arisaema*" type with a constricted spathe that has a wrinkled, slippery internal surface. This surface bears papillae covered in cuticular waxes which prevent insects from escaping, supported, in *A. barthlottii*, by glandular hairs producing a yellow resin. As in other *Amorphophallus* species (see above), here we have a pollination mechanism of deception. Sterile flowers or staminodes, which are often used as food for melitophagous beetles, are absent in African species and are apparently unnecessary as the inflorescences are so well adapted to their pollinators, in our cases to coprophagous beetles.

In other species, we also find beetles, but not always copro-necrophagous species. The Asian species of the section *Raphiophallus*, for example, seem to be pollinated by melitophagous/palynophagous Nitidulidae. Those species do possess inflorescences with sterile flowers and staminodes as a reward for the pollinators, have a long peduncle, and are of light colour (PUNEKAR & KUMARAN, 2010; SIVADASAN & SABU, 1989). They do not need to resemble a piece of carrion on the soil surface.

Recent phylogenetic studies or Araceae (SCHIESTL & DÖTTERL, 2012; SCHIESTL & JOHNSON, 2013) show a correlation between the production of skatole, indole, and cresol by the flower and the pollination by coprophagous or necrophagous Scarabaeoidea. Skatole, indole, and cresol are indeed amongst the most common odorous compounds in a variety of faeces (KRELL & SCHMITT, in press) and are proven to attract or at least contribute to the attraction of dung beetles (WURMITZER *et al.*, 2016; FTK, pers.obs.). Our *Amorphophallus* species exploit the adaptation of dung beetles to being attracted to dung odours, which is explained by the Exploitation of Perceptual Biases Model (SCHAEFER & RUXTON, 2009; SCHIESTL & DÖTTERL, 2012). This model postulates "that receivers have pre-existing sensory and/or cognitive biases for particular traits and that selection therefore favours any sender that evolves a trait matching these biases“ (SCHAEFER & RUXTON, 2009). Entomologists exploit these biases by using dung-baited traps to harvest dung beetles. The deception performed by Araceae is without serious consequences for the pollinators since they are released once the flower is fertilized and can fly away to find some food or to fertilize another inflorescence.
Conclusion

We present the first observation of Scarabaeidae (Onthophagini) and Aphodiidae as pollinators of *Amorphophallus* in tropical Africa. Given the diversity of Onthophagini and Aphodiiini on this continent, we expect more similar observations in the future.

In the two species studied, *A. barthlottii* et *A. abyssinicus subsp. akeassii*, we found pollination by deception with adaptation to copro-necro-cantharophily.

Given the diversity of *Amorphophallus*, it would be interesting reconstructing the phylogeny by integrating morphological characters, the composition of odours of the inflorescence, and the type of pollinators, to better understand the evolution of the pollination mechanisms within the genus. Therefore, it is important to continue exploring the pollinator species of *Amorphophallus*, ensure the precise identification of those species and gain knowledge about their behaviour and ecology.

From a conservation standpoint, observations such as ours on the pollinators of *Amorphophallus barthlottii* and *A. abyssinicus subsp. akeassii* are particularly relevant as they indicate that the pollination, hence the survival of those plants depends on the presence of large mammals as they provide the food for the pollinators.

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Photo credits. *Amorphophallus abyssinicus ssp. akeassii*: Stefan POREMBSKI; *Amorphophallus barthlottii*: 1-5 and 11 Marios ARISTOPHANOUS (ANHRT); *Onthophagus liberianus*: Keita MATSUMOTO (BMNH); *Cleptocaccobius dorbignyi, C. uniseries* and *Trichaphodius copulatus*: François GÉNIER.
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**Note.** One author, FTK, does not support the across-the-board upgrading of all *Aphodius* subgenera to genera given that no comprehensive phylogenetic analysis of *Aphodius* (s.l.) has ever been published that would suggest such upgrading. FTK also does not support the upgrading of Scarabaeidae subfamilies, such as Aphodiinae, to family status. Ranking is inherently subjective, and different models can be followed, as it is done by the lead author of this paper.

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