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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.

Pollinisation d'*Amorphophallus barthlottii* et *A. abyssinicus* (Araceae) par des bousiers (Insecta : Coleoptera : Scarabaeoidea)

Résumé. – Après avoir rappelé les mécanismes de pollinisation des *Amorphophallus* et les différentes espèces de Scarabaeoidea, en particulier les Scarabaeidae, visitant les inflorescences d'Araceae, les observations réalisées sur *Amorphophallus* (*Afrophallus*) *barthlottii* Ittenb. & Lobin et sur *Amorphophallus* (*Afrophallus*) *abyssinicus subsp. akeassii* Ittenbach en Côte d'Ivoire sont décrites. Les coléoptères récoltés dans les inflorescences sont des Scarabaeidae Onthophagini (Genres *Caccobius*, *Cleptocaccobius*, *Furconthophagus*, *Hyalonthophagus* et *Onthophagus*), des Aphodiidae et des Hydrophilidae (genre *Sphaeridium*). Les pollinisations d'*A. barthlottii* et d'*A. abyssinicus* sont décrites et discutées dans un contexte écologique et phylogénétique.
Mots clefs. – 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.
DMNS	Denver Museum of Nature & Science, Denver, Colorado, U.S.A.
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 adaptions 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, Lyctidae, Brenthidae, 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

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 & DÖTTERL, 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 *Leucocelis* 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 (VAN DER 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 paeoniifolius* (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. nigripennis* 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).

Hybosoridae (necrophagous): *Phaeochrous amplus* Arrow, 1909, pollinates *Amorphophallus johnsonii* N. E. Brown in Ghana (BEATH, 1996), a species emitting a sewage smell, composed mainly of sulphuric compounds (KITE & HETTERSCHEID, 2017: 128). *P. camerunensis* Arrow, 1909, pollinates *A angolensis ssp. maculatus* N. E. Brown in Gabon (BOGNER, 1976; HETTERSCHEID & ITTENBACH, 1996). *Phaeochrous dissimilis* Arrow, 1909, *P. emarginatus* Castelnau, 1840, and *P. intermedius* Pic, 1928, were found on *Amorphophallus paeoniifolius* (Dennst.) Nicolson in Thailand (GRIMM, 2009; SITES, 2017); *P. emarginatus* on *A. titanum* and *A. paeoniifolius* in Sumatra (GIORDANO, 1999).

Aphodiidae (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 trilobatum* (L.) Schott in India (CLEGHORN, 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 (MONTEITH, 1973) and *Sisyphus sp*. on *Sauromatum* in India (DAKWALE & BHATNAGAR, 1982). *Furconthophagus furcatus* (Fabricius, 1781) and *Caccobius schreberi* (Linné, 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 argyropygus* 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 subterraneous 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 saproxylophagy) 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.

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 hygophilous and mesophilic forests (CAMBEFORT, 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* Ill. 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 (CAMBEFORT, 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.

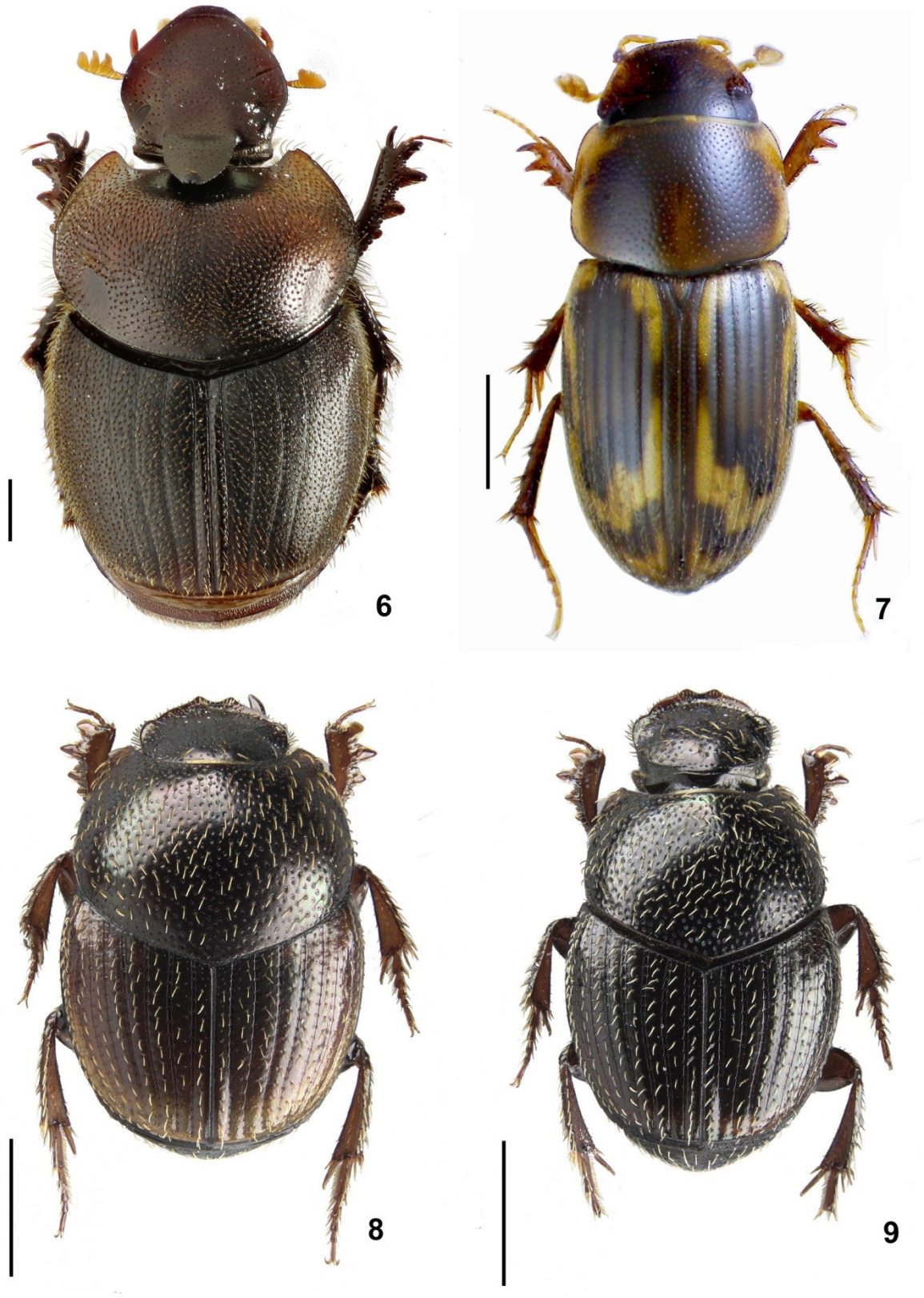
Mechanisms of capture and pollination

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



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.

Digitonthophagus fimator Génier, 2017: 2 ♀♀.

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

Mesontoplatys dorsalis (Klug, 1855): 1 spm.
Aphodobius zumpti (Balthasar, 1937): 1 spm.
Pseudopharaphodius phalacronothoides (Balthasar, 1960): 2 spm.
Trichaphodius amplitarsis (Bordat, 1989): 1 ♀.
Trichaphodius copulatus (Schmidt, 1916) (Fig. 7): 1 spm.
Trichaphodius flavus (Endrődi, 1955): 2 ♀♀.
Trichaphodius maldesi (Bordat, 1989): 7 ♂♂, 4 ♀♀.

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. fimator*, 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. barthlotii*, 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 Aphodiini 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 bartlottii*: 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.

BIBLIOGRAPHY

BACKER C. A., 1913. – Het Slanglenblad. *De Tropische Natuur,* 2: 165–168, 177–179.

BEATH D. N., 1996. – Pollination of *Amorphophallus johnsonii* (Araceae) by carrion beetles (*Phaeochrous amplus*) in a Ghanaian rain forest. *Journal of Tropical Ecology,* 12: 409–418.

BOGNER J., 1976. – *Amorphophallus maculatum*. *Der Palmengarten,* 3: 83–86.

BOYCE P. C. & CROAT T. B., 2011. – *The Überlist of Araceae: totals for published and estimated number of species in aroid genera*. Available at http://www.aroid.org/genera/160330uberlist.pdf, last accessed on 5 April 2017.

BRODERBAUER D., DIAZ A. & WEBER A., 2012. – Reconstructing the origin and elaboration of insect-trapping inflorescence in the Araceae. *American Journal of Botany,* 99 (10): 1666–1679.

CAMBEFORT Y., 1984. – Étude écologique des coléoptères Scarabaeidae de Côte d'Ivoire. *Travaux des Chercheurs de la Station de Lamto* (RCI), 3: VIII, 294, 13 pp.

CHARTIER M., GIBERNAU M. & RENNER S. S., 2013. – The evolution of pollinator-plant interaction types in the Araceae. *Evolution,* 68: 1533–1543.

CHATURVEDI S. K., 2017. – Pollinators and visitors of *Amorphophallus napalensis* (Wall) Bogner & Mayo (Araceae) in Nagaland state, north-east India. *Pleione,* 11 (2): 336–340.

CHEN K.-M., 2002. – *An introduction to Scarabaeinae of the world. Description of 700 species worldwide including information about distribution. Information about the known 85 species of Taiwan*. Owl-press. 303.

CLAUDEL C., BUERKI S., CHATROU L. W., ANTONELLI A., ALVAREZ N. & HETTERSCHEID W. L. A. 2017. – Large-scale phylogeny of *Amorphophallus* (Araceae) derived from nuclear and plastid sequences reveals new subgeneric delineation. *Botanical Journal of the Linnean Society,* 184: 32–45.

CLEGHORN M. L., 1915. – A note on the floral mechanism of *Typhonium trilobatum*. *Journal & Proceedings of the Asiatic Society of Bengal. New Series,* 10[1914]: 421–424, pl. 32.

EMLEN D. J., 1997. – Alternative reproductive tactics and male-dimorphism in the horned beetle *Onthophagus acuminatus*. *Behavioral Ecology and Sociobiology,* 41: 335–341.

GIBERNAU M., 2003. – Pollinators and visitors of aroid inflorescences. *Aroideana,* 26: 66–83.

GIBERNAU M., 2011. – Pollinators and visitors of aroid inflorescences: an addendum. *Aroideana,* 34: 70–83.

GIBERNAU M., 2016. – Pollinators and visitors of aroid inflorescences III - Phylogenetic & chemical insights. *Aroideana,* 39: 4–22.

GRAYUM M. H., 1986. – Correlations between pollination biology and pollen morphology in the Araceae, with some implications for angiosperm evolution. *Pollen and Spores: Form and Function*. I. K. Ferguson & S. Blackmore. London, Elsevier: 313–327.

GRIMM R., 2009. – *Peltonotus nasutus* Arrow, 1910 und *Phaeochrous*-Arten als Bestäuber von *Amorphophallus paeoniifolius* (Araceae) in Thailand (Coleoptera: Scarabaeidae). *Entomologische Zeitschrift,* 119 (4): 167–168.

HALFFTER G. & MATTHEWS G., 1966. – The natural history of dung beetles of the subfamily Scarabaeinae. *Folia Entomologica Mexicana,* 12–14: 1–312.

HETTERSCHEID W. L. A. & ITTENBACH S., 1996. – Everything you always wanted to know about *Amorphophallus*, but were afraid to stick your nose into. *Aroideana,* 19: 7–131.

HOE Y. C., GIBERNAU M., MAIA A. C. D. & WONG S. Y., 2016. – Flowering mechanisms, pollination strategies and floral scent analyses of syntopically co-flowering *Homalomena* spp. (Araceae) on Borneo. *Plant Biology,* 18: 563–576.

ITTENBACH S., 2003. – Revision der afrikanischen Arten der Gattung *Amorphophallus* (Araceae). *Englera*, 25: 1–263.

ITTENBACH S. & LOBIN W., 1997. – Notes on the genus *Amorphophallus (Araceae)* – 6. Six new species and two new subspecies from Africa. *Willdenowia,* 27: 147–160.

JAMESON M. L. & DRUMONT A., 2013. – Aroid scarabs in the genus *Peltonotus* Burmeister (Coleoptera, Scarabaeidae, Dynastinae): key to species and new distributional data. *ZooKeys,* 320: 63–95.

JAMESON M. L. & WADA K., 2004. – Revision of the genus *Peltonotus* Burmeister (Coleoptera: Scarabaeidae: Dynastinae) from Southeastern Asia. *Zootaxa,* 502: 1–66.

JAMESON M. L. & WADA K., 2009. – Five new species of *Peltonotus* Burmeister (Scarabaeidae: Dynastinae: Cyclocephalini) from Southeast Asia. *Insecta Mundi,* 102: 1–16.

JUNG M.-J., 2006. –*The Pollination Biology of* Amorphophallus henryi *N. E. Br.* Master thesis. Graduate Institute of Life Sciences. National Cheng-Kung University, Tainan, Taiwan. 94 pp.

KITE G. C. & HETTERSCHEID W. L. A. 2017. – Phylogenetic trends in the evolution of inflorescence odours in *Amorphophallus*. *Phytochemistry,* 142: 126–142.

KITE G. C., HETTERSCHEID W. L. A., LEWIS M. J., BOYCE P. C., OLLERTON J., COCKLIN E., DIAZ A. & SIMMONDS M. S J., 1998. – Inflorescence odours and pollinators of *Arum* and *Amorphophallus* (Araceae), *in*: OWENS S. J. & RUDALL P. J. (Eds.), *Reproductive Biology*. Royal Botanical Gardens, Kew, pp. 295–315.

KNECHT M., 1983. – Aracées de Côte d'Ivoire - Contribution à l'étude biosystématique des représentants d'Aracées de la Côte d'Ivoire. *Phanerogamarum Monographiae,* 17. Cramer, Vaduz, 290 pp.

KNOLL F., 1926. – Die *Arum*-Blütenstände und ihre Besucher, pp. 379–482 *in*: Insekten und Blumen. Experimentelle Arbeiten zur Vertiefung unserer Kenntnisse über die Wechselbeziehungen zwischen Planzen und Tieren. *Abhandlungen der Zoologisch-Botanischen Gesellschaft in Wien,* 12: 1–616, pls.

KRELL F.-T., KRELL-WESTERWALBESLOH S., WEISS I., EGGLETON P. & LINSENMAIR K. E. 2003. – Spatial separation of Afrotropical dung beetle guilds: a trade-off between competitive superiority and energetic constraints (Coleoptera: Scarabaeidae). *Ecography,* 26: 210–222.

KRELL F.-T. & SCHMITT T., in press. – The fecal volatilome– a compilation of the odorous components of vertebrate feces. *Denver Museum of Nature & Science Reports*.

KRELL F.-T., SCHMITT T. & HERZNER G., 2006. – The attractive odors of dung. *The Third, Highly Irregular, Scarab Workshop. An International Scarab Workshop held at*

The Piccadilly University Hotel Fresno, CA, May 3-4, 2006. Program and Abstracts: (8).

KRELL-WESTERWALBESLOH S., KRELL F.-T. & LINSENMAIR K. E., 2004. – Diel separation of Afrotropical dung beetle guilds – avoiding competition and neglecting resources. *Journal of Natural History,* 38: 2225–2249.

KRYGER U., 2009. – Conservation of dung beetles, *in* : SCHOLTZ C., DAVIS A. J. & KRYGER U. Evolutionary Biology and Conservation of dung Beetles. Pensoft, Sofia-Moscow. 387–480.

KULLENBERG B., 1953. – Observationer över *Arum*-pollinerare i Libanons kustområde. *Svensk Botanisk Tidskrift,* 47 (1): 24–29.

MAYO S. J., BOGNER J. & BOYCE P. C., 1997. – *The genera of Araceae*. Royal Botanic Gardens, Kew. xi, 370 pp.

MCINTYRE P. & CAVENEY S., 1998. – Superposition optics and the time of flight in onitine dung beetles. *Journal of Comparative Physiology A,* 183: 45–60.

MEEUSE B. J. D. & HATCH M. H., 1960. – Beetle pollination in *Dracunculus* and *Sauromatum* (Araceae). *Coleopterists' Bulletin*, 14: 70–74.

MEEUSE B. J. D. & RASKIN I., 1988. – Sexual reproduction in the arum lily family, with emphasis on thermogenicity. *Sexual Plant Reproduction,* 1: 3–15.

MONTEITH G. B., 1973. – Entomological notes: Dung beetles as pollinators of an arum lily. *The News Bulletin of the Entomological Society of Queensland,* 97: 13.

MOORE M. R. & JAMESON M. L. 2013. – Floral associations of cyclocephaline scarab beetles. *Journal of Insect Science,* 13(100): 1–43.

NICHOLS E., SPECTOR S., LOUZADA J., LARSEN T., AMEZQUITA S., FAVILA M. E. & THE SCARABAEINAE RESEARCH NETWORK, 2008. – Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biological Conservation,* 141: 1461–1474.

PUNEKAR S. A. & KUMARAN K. P. N., 2010. – Pollen morphology and pollination ecology of *Amorphophallus* species from North Western Ghats and Konkan region of India. *Flora,* 205: 326–336.

RUIZ J. L., 2009. – Contribución al conocimiento de los insectos polinizadores potenciales y visitantes de Aracaee en los Pirineos (Huesca y Lérida) y el Macizo Cazorla-Segura (Jaén, España) (Insecta). *Boletín Sociedad Entomológica Aragonesa,* 45: 415–418.

SANNIER J., BAKER W. J., ANSTETT M.-C. & NADOT S., 2009. – A comparative analysis of pollinator type and pollen ornamentation in the Araceae and the Arecaceae, two unrelated families of the monocots. *BMC Research Notes* 2009, 2: 145.

SCHAEFER H. M. & RUXTON, G. D., 2010. – Deception in plants: mimicry or perceptual exploitation? *Trends in Ecology and Evolution,* 24 (12): 676–685.

SCHIESTL F. P. & DÖTTERL S., 2012. – The evolution of floral scent and olfactory preferences in pollinators: coevolution or pre-existing bias? *Evolution,* 66: 2042–2055.

SCHIESTL F. P. & JOHNSON S. D., 2013. – Pollinator-mediated evolution of floral signals. *Trends in Ecology & Evolution,* 28 (5): 307–315.

SCHMITT T., KRELL F.-T. & LINSENMAIR K. E., 2004. – Quinone mixture as attractant for necrophagous dung beetles specialized on dead millipedes. *Journal of Chemical Ecology,* 30 (4): 731–740.

SCHMUCKER T., 1930. – Blüten-biologische und –morphologische Beobachtungen. *Planta*, 9: 718–747.

SEDAYU A., EURLINGS M. C. M., GRAVENDEEL B. & HETTERSCHEID W. L. A., 2010. – Morphological character evolution of *Amorphophallus* (Araceae) based on a combined phylogenetic analysis of trnL, rbcL and LEAFY second intron sequences. *Botanical Studies,* 51:473–490.

SINGH S. N. & GADGIL M., 1995. – Ecology of *Amorphophallus* species in Uttara Kannada District of the Karnataka State, India: implications for conservation. *Aroideana,* 18: 32–36.

SINGH Y., VANWYK A. E. & BAIJNATH H., 1996. – Floral biology of *Zantedeschia aethiopica* (L) Spreng (Araceae). *South African Journal of Botany,* 62 (3):146–150.

SITES R. W., 2017. – The Aroid Scarab *Peltonotus nasutus* (Coleoptera: Scarabaeidae) in Thailand and its association with *Amorphophallus paeoniifolius* (Araceae). *Natural History Bulletin of the Siam Society,* 62 (1): 107–109.

SIVADASAN M. & SABU T., 1989. – Beetle-pollination, cantharophily, in *Amorphophallus hohenackeri* (Araceae). *Aroideana,* 12: 32–37.

URRU I., STENSMYR M. C. & HANSSON B. S., 2011. – Pollination by brood-site deception. *Phytochemistry,* 72: 1655–1666.

VAN DER HAM R. W. J. M., HETTERSCHEID W. L. A. & VAN HEUVEN B. J., 1998. – Notes on the genus *Amorphophallus* (Araceae) – 8 Pollen morphology of *Amorphophallus* and *Pseudodracontium*. *Review of Palaeobotany and Palynology,* 103: 95–142.

VAN DER HAM R. W. J. M., HETTERSCHEID W. L. A. & VAN HEUVEN B. J., 2005. – Notes on the genus *Amorphophallus* (Araceae) – 13. Evolution of pollen ornamentation and ultrastructure in *Amorphophallus* and *Pseudodracontium*. *Grana*, 44: 252–265.

VAN DER PIJL L., 1937. – Biological and physiological observations on the inflorescence of *Amorphophallus*. *Recueil des Travaux Botaniques Néerlandais,* 34: 157–167.

WARRANT E. J., 2016. – Superior visual performance in nocturnal insects: Neural principles and bio-inspired technologies, *in*: MARTÍN-PALMA R. J., LAKHTAKIA A. & KNEZ M. (eds.): Bioinspiration, Biomimetics, and Bioreplication. *Proceedings of SPIE*, 9797: 979703 (14 pp.). doi: 10.1117/12.2218336.

WERYSZKO-CHMIELEWSKA E. & STPICZYNSKA M., 1995. – Osmophores of *Amorphophallus rivieri* Durieu (Araceae). *Acta Societatis Botanicorum Poloniae,* 64: 121–129.

WURMITZER C., BLÜTHGEN N., KRELL F.-T., MALDONADO B., OCAMPO F., MÜLLER J. K. & SCHMITT T., 2017. – Attraction of dung beetles to herbivore dung and synthetic compounds in a comparative field study. *Chemoecology,* 27: 75–84.

YADAV S. R., 1998. – Adaptive significance of phenology and spadix architecture in Araceae of Western Ghats of India. *Acta Botanica Yunnanica Suppl*., 10: 31–40.